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Edited by Douglas A. Kelt, Enrique P. Lessa,
Jorge Salazar-Bravo, and James L. Patton

THE QUINTESSENTIAL NATURALIST: HONORING THE LIFE AND LEGACY OF OLIVER P. PEARSON

To Paynie and Anita,
for their friendship, scholarship, and continuing inspiration

THE QUINTESSENTIAL NATURALIST: HONORING THE LIFE AND LEGACY OF OLIVER P. PEARSON

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CONTENTS

PART 2.

PREFACE

Over a 5 decade career, Oliver Payne Pearson -- Paynie to many -- became a defining force in the development of mammalian biology. Likely best known for his work on the role of predation on vole demography and population cycles, and for his piercing contributions to the biology of South American mammals, his earlier studies on reproductive and physiological ecology are highly regarded as well. As a package, his is one of rigor, passion, and unbridled enthusiasm. As a result, Oliver Pearson influenced the careers of innumerable young mammal biologists; in many cases, he took pains to remain anonymous, preferring to foster science without drawing attention to himself.

Oliver Pearson died in March of 2003. Only a few months later, the editors of this volume were gathered in the parking lot of Hub City Brewery in Lubbock, Texas (venerable site of the Picnic for the American Society of Mammalogists meeting). We rapidly agreed on the need for a memorial to honor a man we all held in such high prestige. We promptly drafted a rough list of invitees, and begin soliciting contributions. Not all that we invited were able to contribute, and not all that contributed were able to follow through to a final paper, but the overwhelming response was one of enthusiastic support. Indeed, the project "snowballed", quickly gaining steam and growing to unexpected proportions. We received sage advice from some senior colleagues: Mike Mares offered kind words of support (something like "you have no idea what you're getting into, do you?!") and we are here to confirm that Mike has the wisdom borne of a history with numerous such multi-authored volumes. We're still standing, however, and we hope that the resulting tome will stand as a suitable tribute to a remarkable man and a remarkable career.

We owe thanks to the many authors who provided contributions and responded (more or less promptly) to our requests for editorial revisions. At least as much, we owe thanks and deep appreciation to the numerous reviewers who critiqued and commented on these manuscripts. Every editor knows that the final product is critically dependent on the quality of reviews, and this is no exception. Our jobs were greatly facilitated by the high caliber of our panel of anonymous reviewers.

We also thank the staff and editorial board at UC Press. Carla Cicero handled the volume for the Press, and her rapid and efficient editing was and is sincerely appreciated. Chuck Crumly and Michelle Echinique helped to guide us on the path to submission and publication – their input was perhaps more important than they realized.

This volume was formatted and copy-edited in Adobe InSight CS2; Sara Krause helped with formatting the volume, and Shane Waddell provided critical insights to software that was new to us all. He bears more than trivial responsibility for the fact that this project ever made it from boiler plate to reality.

Panorama of the Caccachara Valley (ca. 16,000′ elev., Dept. Puna, Peru), where Oliver and Anita Pearson stayed during his early studies on the reproductive biology of mountain vizcacha (*Lagidium viscacia*). Photo taken by Oliver Pearson, courtesy of Anita Pearson.

OLIVER P. PEARSON: SCIENTIST, STATESMAN, GENTLEMAN

Douglas A. Kelt, Enrique P. Lessa, Jorge Salazar-Bravo, and James L. Patton

Oliver Payne Pearson was born on 21 October 1915, in Philadelphia, Pennsylvania, to Olive Payne Corning Pearson and Forrest Garfield Pearson. He was the third surviving son (a first son had died in infancy), and his mother, despairing of not having a daughter, gave him her name, slightly modified (5 years later she finally did have a daugher). Oliver P. Pearson passed away 4 March 2003, leaving the world poorer in his absence. In his 87 years he became a decisive force promoting our understanding of mammalian biology, with notable advances in physiological and reproductive ecology, predator-prey interactions, taxonomy, zoogeography, and perhaps most notably to some, the general biology of small mammals in temperate and Andean South America.

Oliver Pearson, "Paynie" to many that knew him, graduated from Swarthmore College in 1937. He attended Harvard University for both his M.S. (1939) and Ph.D. (1947), and was then hired by UC Berkeley as an Instructor in Zoology (1947-48), entering the ranks of the tenured series the following year. He was an Assistant Professor of Zoology (Department of Zoology) and Assistant Curator of Mammals (Museum of Vertebrate Zoology, MVZ) from 1949 to 1955, gaining tenure and advancing to Associate Professor of Zoology and Associate Curator of Mammals in the MVZ in 1955. In 1957 he resigned his tenured position, maintaining status at UC Berkeley as a Lecturer in Zoology and as a Research Associate at the Museum. This allowed him to focus his attentions on his studies of voles and predation (see below), and to spend a year as a Visiting Professor of Ecology at the University of Buenos Aires (1964-65). When Alden Miller, Director of MVZ, died in 1965, Paynie returned to the tenure series, this time as full Professor of Zoology (which he retained until his real and very active retirement in 1971), and as Acting Director of MVZ (1966-67) and then Director (1967-71). Additionally, Pearson served as Vice Chairman of the Zoology Department in 1953-54, and then as Acting Chairman in 1968. He was never highly fond of these administrative roles, as they detracted from the time he had to dedicate to fieldwork and writing.

In 1944 he married Anita Kelley, who was to be his companion in all his subsequent travels. When awarded an honorary doctoral degree ("Doctor Honoris Causa") from

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Pp. 1-26 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

the University of La Plata, Pearson famously stated "Yo soy un simple atrapador de ratones, y nada hubiese sido posible sin Anita" ("I am a simple mouse-trapper, and nothing would have been possible without Anita") (UC Berkeley News, 7 March 2003). They had 4 children, Carol Ann (1947), Peter Kelley (1949), Sandia Coming (1956), and Alison Payne (1958), and toted them along on subsequent field trips.

Oliver Pearson was an early convert to science; he set his first trapline at age 8 or 10, capturing a short-tailed shrew (*Blarina brevicauda*; see Pearson, 1982). As a Research Assistant in the Philadelphia Academy of Natural Sciences, Paynie participated in 2 trips to Panama with his undergraduate mentor, Robert K. Enders. They published on the taxonomy of small mammals from these trips (Enders and Pearson, 1939, 1940; Pearson 1939) while pursuing numerous studies on the reproductive physiology of North American mustelids, canids, and other groups (e.g., Pearson and Enders, 1943a, 1943b, 1944a, 1944b; Enders and Pearson, 1943a, 1943b; Pearson 1944 ; Pearson and Bassett 1944; Enders et al. 1946; Pearson and Bassett, 1946). At Harvard, collaboration with his fellow student, Peter Morrison, led to a paper in *Science*, on "The metabolism of a very small mammal" (Morrison and Pearson, 1946). A subsequent paper on this topic (Pearson, 1947) was later recognized as a "Citation classic" in Current Contents (Current Contents (Agriculture, Biology, & Environmental Science) 35:16 (27 August 1984)). The field trips to Panama may have whetted Pearson's appetite for the Neotropics, as he pursued subsequent fieldwork in Peru (1939-40, 1946, 1952, 1955, 1967, 1972), Colombia (1950), and Argentina (1955, 1964-65, then annually 1978-1999). Work in the Peruvian Andes was productive and fertile ground for an energetic young field biologist. Essentially uncharted terrain, the mammals of this region were known only moderately well taxonomically, but poorly at best in ecologic terms. Pearson's long-standing interest in tuco-tuco's (*Ctenomys*) began with a description of the species known from Peru (Sanborn and Pearson, 1947), followed 13 years later by a short monograph on Peruvian tuco's (Pearson 1959[1960]); his long-standing interest in this group was memorialized with the naming of *Ctenomys pearsoni* (Lessa and Langguth, 1983; see Tomasco and Lessa, This volume). Additionally, 1 species of *Andalgalomys* (*A. pearsoni* (Myers, 1977)) and 1 genus (*Pearsonomys* Patterson, 1992) have been named in recognition of Oliver Pearson.

Meanwhile, Pearson pursued groundbreaking work on the ecology and reproductive biology of viscachas (*Lagidium viscacia*; Pearson, 1948, 1949); at the time this was only the second extensive study on any hystricomorph rodent, and for this study the Pearson's camped at 16,000 ft in the Caccachara Valley (Fig. 1, 2, 3). Pearson later (1951) synthesized his observations on highland mammals. Upon returning from his first Andean trip in 1940, he "found it impossible to identify many specimens of *Phyllotis*"; he "soon formed the opinion that the real number of species was much less than indicated by the existing nomenclature" and that "a revision of the genus therefore seemed desirable." He embarked on this daunting task, and in 1958 he published the definitive treatment of the genus (Pearson, 1958:quotations from p. 394). Pearson also wrote a paper in 1975 on "an outbreak of mice" that set the bar for rigor in natural history observation; all subsequent studies of rodent outbreaks ("ratadas") have followed Pearson's lead in this regard. Thus, in the span of just a couple of decades, Pearson reported on natural history, population ecology, physiology, reproductive biology, biogeography, and systematics. Few are the contemporary biologists with such breadth!

Although this volume emphasizes mammals, it is worth noting that Oliver Pearson

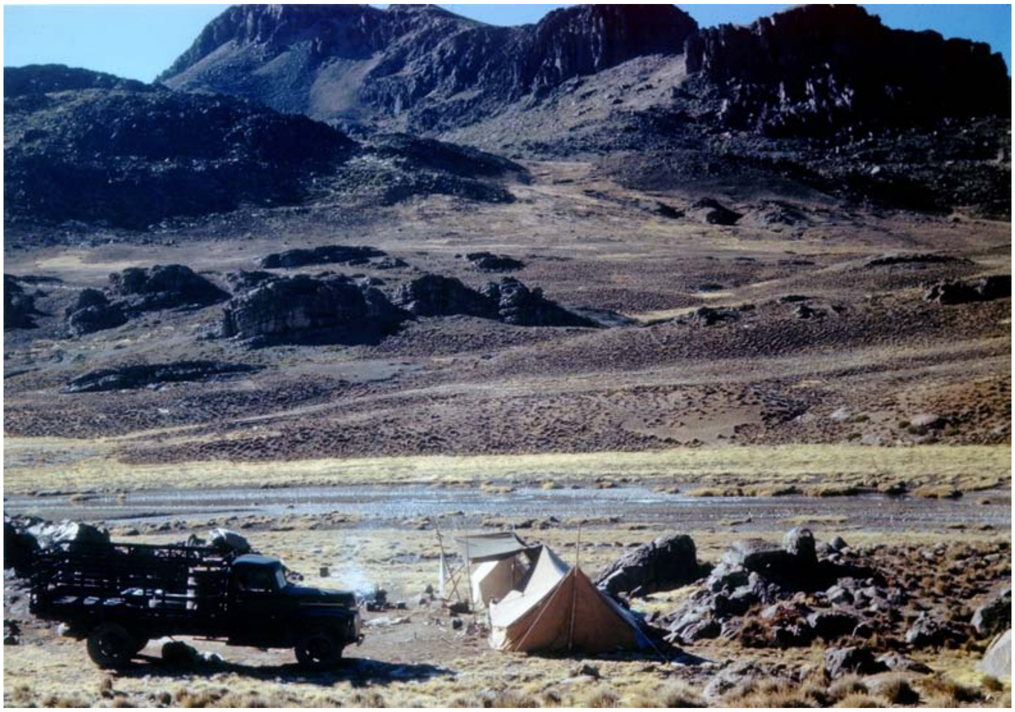

Figure 1. Campsite in Caccachara Valley, Dept. Puna, Peru. 1946. Photo courtesy of Anita Pearson.

Figure 2. Oliver Pearson holding a home-made livetrap. Caccachara Valley, Peru, 1946.

Figure 3. Anita Pearson in the Peruvian Andes, 1946.

also published seminal papers on frogs, lizards, and birds during this period. This included papers on hummingbird ecology and metabolism (5 papers), flight speeds in Allen's hummingbird (Pearson, 1960a), torpidity in small birds (Pearson, 1960b), tinamou (*Nothoprocta*) natural history and reproduction ([A. K.] Pearson and [O. P.] Pearson, 1955), and spacing behavior in sparrows (*Zonotrichia*; Pearson 1979). He also reported on lizard ecology (Pearson, 1954) and thermoregulation (Pearson, 1977, Pearson and Bradford, 1976), and he included reptiles and amphibians in his well-known Andean altitudinal gradient (Pearson and Ralph, 1978).

When Paynie and Anita turned their attention to southern Argentina, they channeled their energies to what was then a very poorly known fauna. Although Osgood (1943) and Mann (1978) had provided thorough treatments of Chilean mammals, the ecology and natural history of mammals of Patagonia and the Valdivian temperate rainforest region were known more from anecdotes than science; this was soon to change, in large part through the efforts of the Pearsons, although their attention here was rapidly followed by others, both in Chile and Argentina. The Pearsons obtained an apartment in Bariloche, which they used as a base for biennial trips to study the small mammals both in Valdivian temperate rainforest and Patagonian steppe. Following the Peruvian "ratada" they observed in the 1970s, they were receptive to the importance of major food pulses on wild small mammal populations, and they quickly turned their attention to the local bamboo, *Chusquea culeo*, documenting both the growth and population biology of this species (Pearson et al., 1994) while waiting for the next flowering. The waiting proved to be a standing topic of humor for Paynie (see comments in Mastozoología Neotropical 10:195-205), but the mass flowering finally occurred in 2000 (Pearson, 2002), and the remarkable impacts on small mammals are documented in this volume (Sage et al., This volume). During the lengthy wait for the bamboo, Paynie and Anita made tremendous strides towards understanding all facets of this fauna, from basic field identification (Pearson, 1995) and natural history (Pearson, 1983, 1984) to ecology (Pearson and Pearson, 1982), reproductive and foraging ecology (Pearson, 1988, 1992; Pearson and Pearson, 1989), demography and population biology (Pearson et al., 1987), community and biogeographic ecology (Pearson and Pearson, 1982; Pearson, 1994), systematics (Pearson, 1984; Pearson and Smith, 1999), and historical ecology (Pearson, 1987; Pearson and Christie 1993; Pearson and Pearson, 1993). In short, they did what they do so well – a fair amount of everything!

During intervening periods in California, Pearson pursued his well-known studies on the effects of predators on small mammal communities, especially California voles (*Microtus californicus*; Pearson, 1964, 1966, 1971), reinvigorating this field with his empirical and conclusive evidence for the role of predators in population cycles. Two of these (Pearson 1966, 1971) have been extensively cited in the literature (Fig. 4). He also spearheaded one of the most comprehensive studies on bat reproductive ecology (Pearson et al., 1952); this paper has been cited at least 125 times (according to ISI; Table 1).

Oliver Pearson was a gifted communicator. Robert Baker (Fonseca et al. his volume) comments on the clarity of Pearson's oral presentations, noting that he was "fascinated with his class and style in presentations of papers" and that "he had such control over the English language and word order that many of his sentences were poetic." The same was true of his written prose, which combined piercing knowledge of the animals he studied with clarity and focus, liberally infused with his well known sense of humor.

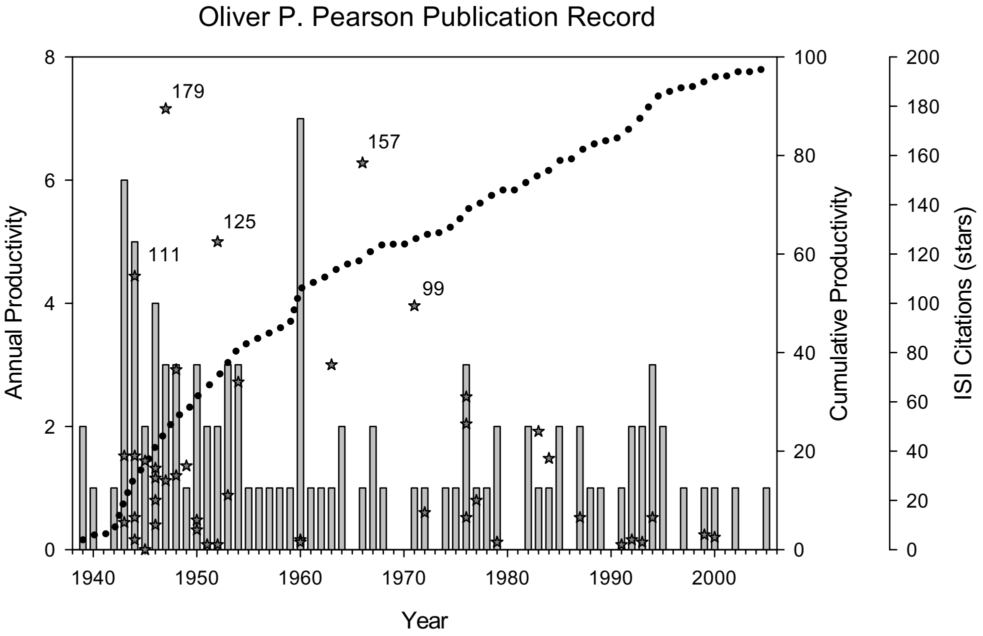

Figure 4. Publication record for Oliver P. Pearson. Following pulses in the 1940s and in 1960, he maintained a consistent output throughout his life, as indicated by the monotonically increasing cumulative productivity curve. Citations, as taken from the ISI database (Thompson Scientific; http://scientific.thomson.com), are indicated with stars.

Pearson's passion for empirical studies on Neotropical small mammals, and his willingness to help students and colleagues whenever possible, left a powerful legacy. He was not interested in trivial science, and he always strived for productive and useful research. When one of us (DAK) sent him a draft manuscript documenting chromosomal variation in *Eligmodontia* and confirming the separation of *E. morgani* and *E. puerulus* (Kelt et al., 1991), his primary comment was a question – although the underlying science was useful and interesting, how could a field biologist distinguish these genetic entities with a live animal in hand?

Finally, Oliver Pearson was not only a scientist; he also was an accomplished artist. After one of his early trips to Panama he prepared a woodcut showing a field biologist conducting nocturnal censuses with a headlamp (Fig. 5). Many years later he and Anita were surprised at the dearth of scenic postcards from the Patagonian region, and Oliver proceeded to convert some of his scenic photographs to cards that he sold to merchants in Bariloche.

Oliver Pearson was an honorary member of the American Society of Mammalogists (1979), the Cooper Ornithological Society (1979), the Sociedad Argentina para el estudio de los Mamíferos (1983), and the Comité Argentino de Conservación de la Naturaleza. He was elected as a Fellow of the California Academy of Sciences in 1964. He served as a trustee for ASM from 1969 through 1984, helping to solidify the financial underpinnings of that society. He held a similar role on the Investment Committee for

Figure 5. Block print of an intrepid field biologist hunting kinkajous (*Potos flavus*). This print was hand-carved by Oliver Pearson in ca. 1942.

the Cooper Ornithological Society from 1972 to 1987. He also was an elected Director for the ASM over 17 years between 1952 and 1990, for the COS in 1969-71, and for the San Francisco Zoological Society in 1959-60. He also served as a Councillor for the Save the Redwoods League. He served as Vice President for ASM from 1969 to 1972. Reflecting his years of dedication to the ASM, he received the Hartley H. T. Jackson Award "for long and outstanding service to ASM" in 1984. And, as noted above, Pearson was awarded an honorary doctoral degree from the University of La Plata in 2000, as much for his contributions to the knowledge of the fauna of Argentina as for his seminal role in the development of ecological and mammalogical science in that country. The following year, he was honored at the First Biennial Meeting of the Ecological Societies of Argentina and Chile (Bariloche, 2001); as Adrian Monjeau put it (pers. comm. 2006), this was "a public recognition as one of the 'fathers' of Ecology in Argentina."

Table 1. Publications by Oliver Pearson with > 50 citations in the ISI database (Thompson Scientific; http://scientific.thomson.com), arranged in chronological order.

Article		No. Citations (ISI)
Pearson, O. P.		
1944	Reproduction in the shrew (*Blarina brevicauda* Say). American Journal of Anatomy 75:39-93.	111
Pearson, O. P.		
1947	The rate of metabolism of some small mammals. Ecology 28:127-145.	179
Pearson, O. P.		
1948	Metabolism of small mammals, with remarks on the lower limit of mammalian size. Science 108:44.	73
Pearson, O. P., M. R. Koford, and A. K. Pearson		
1952	Reproduction of the lump-nosed bat (*Corynorhinus rafinesquei*) in California. Journal of Mammalogy 33:273-320.	125
Pearson, O. P.		
1954	Habits of the lizard *Liolaemus multiformis multiformis* at high altitudes in southern Peru. Copeia 2:111-116.	68
Pearson, O. P.		
1963	History of two local outbreaks of feral house mice. Ecology 44:540-548.	75
Pearson, O. P.		
1966	The prey of carnivores during one cycle of mouse abundance. Journal of Animal Ecology 35:217-233.	157
Pearson, O. P.		
1971	Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). Journal of Mammalogy 52:41-49.	99
Pearson, O. P., and D. F. Bradford		
1976	Thermoregulation of lizards and toads at high altitudes in Peru. Copeia 1976:155-170	62
Pearson, O. P., and J. L. Patton		
1976	Relationships among South American phyllotine rodents based on chromosome analysis. Journal of Mammalogy 57:339-350	51

Oliver Pearson reviewing papers at his office in the Museum of Vertebrate Zoology, 1979.

Concluding comments. Oliver Pearson was the field biologist's field biologist. He combined a keen intellect with a probing curiosity. He also knew how to "think like a mouse" as the following vignette illustrates. Pearson once co-taught a brief course on small mammal ecology at the Universidad Austral (Valdivia, Chile). One participant of this course (Ricardo Martínez) provided the following recollection:

> *"We [students] set 400 live traps . . . to get some mice for preparing study skins. Back at camp, I was lucky to find that Dr. Pearson was just leaving to have a walk, thus I asked him if I was welcomed and the gentleman of course told me that was OK. We talked about everything and he asked me if we had set the traps. He explained that during summer it was rather difficult to get some mice, but just in case he was thinking of setting some. Suddenly, he stopped at some quila [bamboo] near the trail and he took from his parka pocket a small Museum Special trap and got some oats from the other pocket, and rather embarrassed he spit on the oats and showed me how to prepare the bait, and he set the trap between the canes. We continued walking and then he stopped and began to search with his hands on the grass along the trail, he showed me my first mouse "runway"; he set the trap, and we continued walking. He set eight Museum Special traps. Early the next day we [students] checked our 400 Sherman traps to retrieve just one chucao [a bird]. Feeling pretty battered we went back to camp just to found that Dr. Pearson got FIVE mice: 2* A. olivaceus, *1* A. longipilis *and 2* O. longicaudatus*...(63% catch success)."*

Cartoon by Alison Pearson, depicting her father's tireless pursuit of small mammals, bamboo, and the interactions among them.

To catch mice, one needs to think like mice, and in this regard, Pearson had few peers. He was driven by a passion to decipher how they lived, how they died, and what they did in the intervening times. He eagerly shared his knowledge with all takers, and his influence on colleagues and students alike was both enduring and endearing.

Shortly after returning from Argentina in November 2000, Paynie suffered an embolism in his lower leg. A vein graft was not successful, and when given the option of another attempt vs. amputation, Paynie opted for the latter. This likely was influenced by the fact that the bamboo in southern Argentina was flowering (see Sage et al., This volume), and he desperately wanted to see this. Not long thereafter, Dick Sage offered to collect animals in the Austral fall of 2001; Paynie thanked Dick, but said "WE are going!" As Dick reported to us, "So we went, he, Anita, his daugher Ali and her friend, and myself. It was a great expedition!" (it was during this trip that Pearson was formally recognized at the joint meeting of the Argentine and Chilean Ecological Societies). Although Paynie could not navigate the woods well, the abundance of small mammals in response to the immense pulse of food (bamboo seeds) was phenomenal (see Sage et al., This volume). Dick Sage reported (pers. comm. to DAK) that "we were camped amidst the clumps of (now-dead) bamboo, and the mice were plainly visible at night in the clumps of canes over our tents. I had mice dropping down onto my tent during three of the four nights we were camped there." This irruption comprised one snapshot in a cycle that likely will not be repeated for many decades. Paynie's drive and dedication to observing and documenting this phenomenon was well captured in his daughter's depiction (see the cartoon above) of Paynie -- our friend, colleague, and mentor -- maintaining his diligent watch from somewhere in the heavens.

Oliver Pearson passed away in March of 2003. In respect for his life's work and interests, his ashes were spread in 3 areas that were special to him. Some of these were in the region of the Berkeley Hills where he had studied small mammals and predator-prey interactions, and some around his home in Orinda. Finally, Dick Sage carried some to Bariloche, where he and Miguel Cristie laid them to rest amongst regions of Patagonia where he and Anita had labored so fruitfully. As recorded by Dick Sage and Miguel Christie (2003),

> *". . . durante un remanso en medio de una fuerte tormenta propia del solsticio de invierno, tuvimos el honor es esparcir sus cenizas entre los lugares que él mas amaba. Inmendiatamente de concluida la sencilla ceremonia se levantó un fuerte viento y una procession de unos 30 cóndores sobrevoló el lugar. ¡Fue emocionante! Tras nuestra despedida, los grandes Señores de los Cielos Patagónicos honraban a otro grande con un merecido saludo de bienvenida, como diciendo: 'Nuestra casa es tu casa' . . . y lo será por siempre."*

To this we can only add our own grateful appreciation for many years of friendship, mentoring, and support.

ACKNOWLEDGMENTS

We wish to thank Anita Pearson for providing the photographs used in this chapter. Additionally, one of us (DAK) thanks her for spending an afternoon discussing Paynie, his career, their life, and filling in gaps useful for this chapter. We also thank Dick Sage for his insights and for comments that helped to improve this contribution.

LITERATURE CITED

Enders, R. K., and O. P. Pearson
1939 Three new rodent subspecies of *Scotinomys* from Chirique, Panama. Notulae Naturae of the Academy of Natural Sciences of Philadelphia 34:1-4.

Enders, R. K., and O. P. Pearson
1940 A new subspecies of *Reithrodontomys mexicanus* from Panama with remarks on *R. mexicanus cherrii*. Notulae Naturae of the Academy of Natural Sciences of Philadelphia 60:1-2.

Enders, R. K., and O. P. Pearson
1943a The blastocyst of the fisher. Anatomical Record 85:285-287.

1943b Shortening gestation by inducing early implantation with increased light in the marten. American Fur Breeder, January:18-19.

Enders, R. K., O. P. Pearson, and A. K. Pearson
1946 Certain aspects of reproduction in the fur seal. Anatomical Record 94:213-227.

Fonseca, R. M., S. R. Hoofer, C. A. Porter, C. A. Cline, D. A. Parish, F. G. Hoffmann, and R. J. Baker (This volume)
Morphological and Molecular Variation within Little Big-eared Bats of the Genus *Micronycteris* (Phyllostomidae: Micronycterinae) from San Lorenzo, Ecuador / Variación Morfológica y Molecular en el Género *Micronycteris* (Phyllostomidae: Micronycterinae) de San Lorenzo, Ecuador. Pp. 721-746 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

Kelt, D. A., R. E. Palma, M. H. Gallardo, and J. Cook
1991 Chromosomal multiformity in *Eligmodontia* (Muridae, Sigmodontinae), and verification of the status of *E. morgani*. Zeitschrift für Säugetierkunde 56:352-358.

Lessa, E. P., and A. Langguth
1983 *Ctenomys pearsoni*, n. sp. (Rodentia, Octodontidae), del Uruguay. Resultados Comunicados Jornadas Ciencias Naturales, Montevideo, Uruguay 3:86-88.

Mann, G. F.
1978 Los pequeños mamíferos de Chile: marsupiales, quirópterors, edentados y roedores. Guyana (Zoología) 40:1-342.

Morrison, P. R., and O. P. Pearson
1946 The metabolism of a very small mammal. Science 104:287-289.

Myers, P.
1977 A new phyllotine rodent (genus *Graomys*) from Paraguay. Occasional Papers of the Museum of Zoology, University of Michigan 676:1-7.

Osgood, W. H.
1943 The mammals of Chile. Field Museum of Natural History, Zoological Series 30:1-268.

Patterson, B. D.
1992 A new genus and species of long-clawed mouse (Rodentia: Muridae) from temperate rainforests of Chile. Zoological Journal of the Linnean Society 106:127-145.

Pearson, A. K., and O. P. Pearson
1955 Natural history and breeding behavior of the tinamou, *Nothoprocta ornata*. Auk 72:113-127.

Pearson, A. K., O. P. Pearson, and I. A. Gomez

1994 Biology of the bamboo *Chusquea culeou* (Poacea: Bambusoideae) in southern Argentina. Vegetatio 111:93-126.

Pearson, O. P.

1939 Three new small mammals from eastern Panama. Notulae Naturae of the Academy of Natural Sciences of Philadelphia 6:1-5.

1944 Reproduction in the shrew (*Blarina brevicauda* Say). American Journal of Anatomy 75:39-93.

1947 The rate of metabolism of some small mammals. Ecology 28:127-145.

1948 Life history of mountain viscachas in Peru. Journal of Mammalogy 29:345-374.

1949 Reproduction of a South American rodent, the mountain viscacha. The American Journal of Anatomy 84:143-173.

1951 Mammals in the highlands of southern Peru. Bulletin of the Museum of Comparative Zoology 106(3):117-174.

1954 Habits of the lizard *Liolaemus multiformis multiformis* at high altitudes in southern Peru. Copeia 2:111-116.

1958 A taxonomic revision of the rodent genus *Phyllotis*. University of California Publications in Zoology 56:391-477.

1959 [1960]
Biology of the subterranean rodents, *Ctenomys*, in Peru. Memorias del Museo de Historia Natural 'Javier Prado' 9:1-56.

1960a Speed of the Allen hummingbird while diving. Condor 62:403.

1960b Torpidity in birds. Bulletin of the Museum of Comparative Zoology 124:93-103.

1964 Carnivore-mouse predation: An example of its intensity and bioenergetics. Journal of Mammalogy 45:177-188.

1966 The prey of carnivores during one cycle of mouse abundance. Journal of Animal Ecology 35:217-233.

1971 Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). Journal of Mammalogy 52:41-49.

1975 An outbreak of mice in the coastal desert of Peru. Mammalia 39:375-386

1977 The effect of substrate and of skin color on thermoregulation of a lizard. Comparative Biochemistry and Physiology 58:363-358

1979 Spacing and orientation among feeding golden-crowned sparrows. Condor 81:278-285

1982 Round Table – Research Priorities in South America. P. 537 in Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). The Pymatuning Symposia in Ecology, Special Publication Series, 6. Pymatuning Laboratory of Ecology, University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

1983 Characteristics of a mammalian fauna from forests in Patagonia, Southern Argentina. Journal of Mammalogy 64:476-492.

1984 Taxonomy and natural history of some fossorial rodents of Patagonia, southern Argentina. Journal of Zoology 202:225-237.

1987 Mice and the postglacial history of the Traful Valley of Argentina. Journal of Mammalogy 68:469-478.

1988 Biology and feeding dynamics of a South American herbivorous rodent, Reithrodon. Studies on Neotropical Fauna and Environment 23:25-39.

1992 Reproduction in a South American mouse, *Abrothrix longipilis*. Anatomical Record 234:73-88.

1994 The impact of an eruption of Volcan Hadson on small mammals in Argentine Patagonia. Mastozoologia Neotropical 1:103-112.

1995 Annotated keys for identifying small mammals living in or near Nahuel Huapi National Park or Lanin National Park, southern Argentina. Mastozoologia Neotropical 2:99-148.

2002 A perplexing outbreak of mice in Patagonia, Argentina. Studies on Neotropical Fauna and Environment 37:187-200.

Pearson, O. P., and C. F. Bassett

1944 Size of the vulva in the fox and its relation to fertility. Anatomical Record 89:455-459.

1946 Certain aspects of reproduction in a herd of silver foxes. American Naturalist 53:45-67.

Pearson, O. P., and D. F. Bradford

1976 Thermoregulation of lizards and toads at high altitudes in Peru. Copeia 1976:155-170

Pearson, O. P., and M. I. Christie

1993 Rodent guano (amberat) from caves in Argentina. Studies on Neotropical Fauna and Environment 28:105-111.

Pearson, O. P., and R. K. Enders

1943a Your mating of foxes should be timed with great care. Black Fox Magazine, December:20-21, 34.

1943b Ovulation, maturation and fertilization in the fox. Anatomical Record 85:69-83.

1944a Duration of pregnancy in certain mustelids. Journal of Experimental Zoology 95:21-35.

1944b Pearson, O. P., and R. K. Enders. Duration of pregnancy in marten, mink, and related species. American Fur Breeder, July: 24, 26, 28, August: 26, 28, 30, 42.

Pearson, O. P., M. R. Koford, and A. K. Pearson

1952 Reproduction of the lump-nosed bat (*Corynorhinus rafinesquei*) in California. Journal of Mammalogy 33:273-320.

Pearson, O., S. Martin, and J. Bellati

1987 Demography and reproduction of the silky desert mouse (*Eligmodontia*) in Argentina. Fieldiana: Zoology, new series 39:433-446.

Pearson, O. P. and A. K. Pearson

1982 Ecology and biogeography of the southern rainforests of Argentina. Pp. 129-142 Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). The Pymatuning Symposia in Ecology, Special Publication Series, 6. Pymatuning Laboratory of Ecology, University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

1989 Reproduction of bats in Southern Argentina. Pp. 549-566 in Advances in Neotropical Mammalogy (Redford, K. H, and J. F. Eisenberg, eds.). Sandhill Crane Press, Gainesville, Florida, USA.

1993 La fauna de mamiferos pequeños de Cueva Traful I, Argentina: pasado y presente. Praehistoria 1:211-214 (PREP-CONICET, Buenos Aires, Argentina).

Pearson, O. P., and C. P. Ralph
1978 The diversity and abundance of vertebrates along an altitudinal gradient in Peru. Memoria del Museo de Historia Natural "Javier Prado" 18:1-97.

Pearson, O. P., and M. F. Smith
1999 Genetic similarity between *Akodon olivaceus* and *Akodon xanthorhinus* (Rodentia: Muridae) in Argenitina. Journal of Zoology 247:43-52.

Sage, R. D., and M. I. Christie
2003 "Mi casa es tu casa": un homenaje a Oliver P. Pearsoni. Mastozoología Neotropical 10:196-199.

Sage, R. D., O. P. Pearson, J. Sanguinetti, and A. K. Pearson (This volume)
Ratada 2001: A rodent outbreak following the flowering of bamboo (*Chusquea culeou*) in southern Argentina / Ratada 2001: Una irrupción de roedores siguiendo al florecimiento de bambú (*Chusquea culeou*) en el sur de la Argentina. Pp. 177-224 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

Sanborn, C. C., and O. P. Pearson
1947 The tuco-tucos of Peru (Genus *Ctenomys*). Proceedings of the Biological Society of Washington 60:135-138.

Tomasco, I. H., and E. P. Lessa (This volume)
Phylogeography of the Tuco-tuco *Ctenomys pearsoni*: mtDNA Variation and its Implication for Chromosomal Differentiation / Filogeografia del Tuco-tuco *Ctenomys pearsoni*: Variación en el mtADN y sus Implicaciones para la Diferenciación Cromosómica. Pp. 859-882 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

APPENDIX 1. BIBLIOGRAPHY FOR OLIVER P. PEARSON.

This listing, compiled by the editors with assistance from Anita K. Pearson and the staff of MVZ, includes all publications htat were authored or co-authored by Paynie. These begin with results from his first Neotropical field trips. Collaboration with his mentor, Robert Enders, is apparent, as is an applied focus on breeding ecology and physiology of furberaing mammals. This rapidly yields to his better-known studies on vertebrate physiology, South American mammals, and a rare integration of systematics, ecology, biogeography, and natural history.

1939

Pearson, O. P. Three new small mammals from eastern Panama. Notulae Naturae of the Academy of Natural Sciences of Philadelphia 6:1-5.

Enders, R. K., and O. P. Pearson. Three new rodent subspecies of *Scotinomys* from Chirique, Panama. Notulae Naturae of the Academy of Natural Sciences of Philadelphia 34:1-4.

1940

Enders, R. K., and O. P. Pearson. A new subspecies of *Reithrodontomys mexicanus* from Panama with remarks on *R. mexicanus cherrii*. Notulae Naturae of the Academy of Natural Sciences of Philadelphia 60:1-2.

1942

Pearson, O. P. On the cause and nature of a poisonous action produced by the bite of a shrew (*Blarina brevicauda*). Journal of Mammalogy 23:159-166.

1943

Pearson, O. P., and R. K. Enders. Ovulation, maturation and fertilization in the fox. Anatomical Record 85:69-83.

Pearson, O. P. The status of the vicuna in southern Peru, 1940. Journal of Mammalogy 24:97.

Enders, R. K., and O. P. Pearson. The blastocyst of the fisher. Anatomical Record 85:285-287.

Enders, R. K., and O. P. Pearson. Shortening gestation by inducing early implantation with increased light in the marten. American Fur Breeder, January:18-19.

Pearson, O. P., and R. K. Enders. Your mating of foxes should be timed with great care. Black Fox Magazine, December:20-21, 34.

1944

Pearson, O. P., and R. K. Enders. Duration of pregnancy in marten, mink, and related species. American Fur Breeder, July: 24, 26, 28, August: 26, 28, 30, 42.

Bassett, C. F., F. Wilke, and O. P. Pearson. The effect of mating time on productivity in foxes. Black Fox Magazine, January: 12-13, 27, 29.

Pearson, O. P., and R. K. Enders. Duration of pregnancy in certain mustelids. Journal of Experimental Zoology 95:21-35.

Pearson, O. P. Reproduction in the shrew (*Blarina brevicauda* Say). American Journal of Anatomy 75:39-93.

Pearson, O. P., and C. F. Bassett. Size of the vulva in the fox and its relation to fertility. Anatomical Record 89:455-459.

Bassett, C. F., F. Wilke, and O. P. Pearson. Relative productivity under different systems of mink mating. The Fur Journal 10:10-12.

Bassett, C. F., O. P. Pearson, and F. Wilke. The effect of artificially increased length of day on molt, growth, and priming of silver fox pelts. Journal of Experimental Zoology 96:77-83.

1945

Pearson, O. P. Longevity of the short-tailed shrew. American Midland Naturalist 34:531-546.

1946

Pearson, O. P., and C. F. Bassett. Certain aspects of reproduction in a herd of silver foxes. American Naturalist 53:45-67.

Enders, R. K., O. P. Pearson, and A. K. Pearson. Certain aspects of reproduction in the fur seal. Anatomical Record 94:213-227.

Pearson, O. P. Scent glands of the short-tailed shrew. Anatomical Record 94:615-629.

Morrison, P. R., and O. P. Pearson. The metabolism of a very small mammal. Science 104:287-289.

1947

Pearson, O. P. The rate of metabolism of some small mammals. Ecology 28:127-145.

Pearson, O. P., and A. K. Pearson. Owl predation in Pennsylvania, with notes on the small mammals of Delaware County. Journal of Mammalogy 28:137-147.

Sanborn, C. C., and O. P. Pearson. The tuco-tucos of Peru (Genus *Ctenomys*). Proceedings of the Biological Society of Washington 60:135-138.

1948

Pearson, O. P. Metabolism and bioenergetics. Scientific Monthly 66:131-134.

Pearson, O. P. Metabolism of small mammals, with remarks on the lower limit of mammalian size. Science 108:44.

Pearson, O. P. Life history of mountain viscachas in Peru. Journal of Mammalogy 29:345-374.

1949

Pearson, O. P. Reproduction of a South American rodent, the mountain viscacha. The American Journal of Anatomy 84:143-173.

1950

Pearson, O. P. The submaxillary glands of shrews. Anatomical Record 107:161-169.

Pearson, O. P. The metabolism of hummingbirds. Condor 52:145-152.

Pearson, O. P. Keeping shrews in captivity. Journal of Mammalogy 31:351-352.

1951

Pearson, O. P. Mammals in the highland of southern Peru. Bulletin of the Museum of Comparative Zoology 106(3):117-174.

Pearson, O. P. Additions to the fauna of Santa Cruz Island, California, with description of a new subspecies of *Reithrodontomys megalotis*. Journal of Mammalogy 32:366-368.

1952

Pearson, O. P., M. R. Koford, and A. K. Pearson. Reproduction of the lump-nosed bat (*Corynorhinus rafinesquei*) in California. Journal of Mammalogy 33:273-320.

Pearson, O. P. Notes on a pregnant sea otter. Journal of Mammalogy 33:387.

1953

Pearson, O. P. Metabolism of hummingbirds. Scientific American 188:69-42.

Pearson, O. P. Use of caves by hummingbirds and other species at high altitudes in Peru. Condor 55:17-20.

Pearson, O. P., and P. Baldwin. Reproduction and age structure of a mongoose population in Hawaii. Journal of Mammalogy 34:436-447.

1954

Pearson, O. P. Habits of the lizard *Liolaemus multiformis multiformis* at high altitudes in southern Peru. Copeia 2:111-116.

Pearson, O. P. Shrews. Scientific American 191(2):66-70.

Pearson, O. P. The daily energy requirements of a wild Anna hummingbird. Condor 56:317-322.

Pearson, A. K., and O. P. Pearson. Natural history and breeding behavior of the tinamou, *Nothoprocta ornata.* Auk 72:113-127.

1956

Pearson, O. P. A toxic substance from the salivary glands of a mammal (short-tailed shrew). Venoms 44:55-58.

1957

Pearson, O. P. Additions to the mammalian fauna of Peru and notes on some other Peruvian mammals. Breviora 73:1-7.

1958

Pearson, O. P. A taxonomic revision of the rodent genus *Phyllotis*. University of California Publications in Zoology 56:391-477.

Pearson, O. P. Certain aspects of the biology of mouse runways. Science 128:1148-1148.

1959

Pearson, O. P. A traffic survey of *Microtus-Reithrodontomys* runways. Journal of Mammalogy 40:169-180.

1960

Pearson, O. P. Habits of harvest mice revealed by automatic photographic recorders. Journal of Mammalogy 41:58-74.

Pearson, O. P. The oxygen consumption and bioenergetics of harvest mice. Physiological Zoology 33:152-160.

Pearson, O. P. Biology of the subterranean rodents, *Ctenomys*, in Peru. Memorias del Museo de Historia Natural 'Javier Prado' 9:1-56.

Pearson, O. P. Speed of the Allen hummingbird while diving. Condor 62:403.

Pearson, O. P. A mechanical model for the study of population dynamics. Ecology 41:494-508.

Pearson, O. P. Habits of *Microtus californicus* revealed by automatic photographic recorders. Ecological Monographs 30:231-249.

Pearson, O. P. Torpidity in birds. Bulletin of the Museum of Comparative Zoology 124:93-103.

1961

Pearson, O. P. Flight speeds of some small birds. Condor 63:506-507.

1962

Pearson, O. P. Survival value of vibrissae. Journal of Mammalogy 43:105-106.

1963

Pearson, O. P. History of two local outbreaks of feral house mice. Ecology 44:540-548.

1964

Pearson, O. P. Carnivore-mouse predation: An example of its intensity and bioenergetics. Journal of Mammalogy 45:177-188.

Pearson, O. P. Metabolism and heat loss during flight in pidgeons. Condor 66:182-185.

1966

Pearson, O. P. The prey of carnivores during one cycle of mouse abundance. Journal of Animal Ecology 35:217-233.

1967

Pearson, O. P. La estructura por edades y la dinamica reproductive en una poblacion de ratones de campo, *Akodon azarae*. Physis 27:53-58.

Pearson, O. P. Review: Comparative biology of reproduction in mammals. Journal of Mammalogy 48:335.

1968

Pearson, O., N. Binszstein, L. Boiry, C. Busch, M. Di Pace, G. Gallopin, P. Penchaszadeh, and M. Piantanida. Estructura social, distribucion espacial y composicion por edades, de una poblacion de tuco-tucos (*Ctenomys talarum*). Investigaciones Zoologicas Chilenas 13:47-80.

1971

Pearson, O. P. Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). Journal of Mammalogy 52:41-49.

1972

Pearson, O. P. New information on ranges and relationships within the rodent genus *Phyllotis* in Peru and Ecuador. Journal of Mammalogy 53:677-686

1974

Pearson, O. P. Ecology and behavior. Chairman's introduction: Symposium of the Zoological Society of London 34:109-111

1975

Pearson, O. P. An outbreak of mice in the coastal desert of Peru. Mammalia 39:375-386

1976

Pearson, O. P. and D. F. Bradford. Thermoregulation of lizards and toads at high altitudes in Peru. Copeia 1976:155-170

Pearson, O. P. and J. L. Patton. Relationships among South American phyllotine rodents based on chromosome analysis. Journal of Mammalogy 57:339-350

Pearson, O. P. and A. K. Pearson. A stereological analysis of the ultrastructure of the lungs of wild mice living at low and high altitude. Journal of Morphology 250:359-368

1977

Pearson, O. P. The effect of substrate and of skin color on thermoregulation of a lizard. Comparative Biochemistry and Physiology 58:363-358

1978

Pearson, O. P., and C. P. Ralph. The diversity and abundance of vertebrates along an altitudinal gradient in Peru. Memoria del Museo de Historia Natural "Javier Prado" 18:1-97.

1979

Pearson, A. K. and O. P. Pearson. Granular pneumocytes and altitude: a stereological evaluation. Cell and Tissue Research 201:137-144

Pearson, O. P. Spacing and orientation among feeding golden-crowned sparrows. Condor 81:278-285

1982

Pearson, O. P. Distribución de pequeños mamíferos en el Altiplano y los desiertos del Perú. Pp. 263-284 in Salinas, P. (ed.), Zoología Neotropical: Actas de VIII Congreso Latinoamericano de Zoología, Mérida, Venezuela.

Pearson, O. P. and A. K. Pearson. Ecology and biogeography of the southern rainforests of Argentina. Pp. 129-142 in: The Pymatuning Symposia in Ecology, Vol. 6: Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Special Publication Series, Pymatuning Laboratory of Ecology, University of Pittsburgh, Linesville, Pennsylvania.

1983

Pearson, O. P. Characteristics of a mammalian fauna from forests in Patagonia, Southern Argentina. Journal of Mammalogy 64:476-492.

1984

Pearson, O. P. Taxonomy and natural history of some fossorial rodents of Patagonia, southern Argentina. Journal of Zoology 202:225-237.

1985

Pearson, O. P. Predation. Pp. 535-566 in Biology of New World *Microtus* (Tamarin, R. H., ed.). Special Publication, American Society of Mammalogists 8.

Pearson, O. P. and M. I. Christie. Los tuco-tucos (genero *Ctenomys*) de los parques nacionales Lanin y Nahuel Huapi, Argentina. Historia Natural 5:337-344

1987

Pearson, O. P. Mice and the postglacial history of the Traful Valley of Argentina. Journal of Mammalogy 68:469-478.

Pearson, O., S. Martin, and J. Bellati. Demography and reproduction of the silky desert mouse (*Eligmodontia*) in Argentina. Fieldiana: Zoology, new series 39:433-446.

1988

Pearson, O. P. Biology and feeding dynamics of a South American herbivorous rodent, *Reithrodon*. Studies on Neotropical Fauna and Environment 23:25-39.

1989

Pearson, O. P. and A. K. Pearson. Reproduction of bats in Southern Argentina. Advances in Neotropical Mammalogy, pp. 549-566.

1991

Pearson, O. P. and M. I. Christie. Sympatric species of *Euneomys* (Rodentia, Cricetidae). Studies on Neotropical Fauna and Environment 26:121-127.

1992

Pearson, O. P. Reproduction in a South American mouse, *Abrothrix longipilis.* Anatomical Record 234:73-88.

Pearson, O. and H. A. Lagiglia. "Fuerte de San Rafael": una localidad tipo ilusoria. Revista del Museo de Historia Natural de San Rafael (Mendoza) 12:35-43.

1993

Pearson, O. P. and M. I. Christie. Rodent guano (amberat) from caves in Argentina. Studies on Neotropical Fauna and Environment 28:105-111.

Pearson, O. P., and A. K. Pearson. La fauna de mamiferos pequeños de Cueva Traful I, Argentina: pasado y presente. Praehistoria 1:211-214 (PREP-CONICET, Buenos Aires, Argentina).

1994

Pearson, A. K., O. P. Pearson, and I. A. Gomez. Biology of the bamboo *Chusquea culeou* (Poacea: Bambusoideae) in southern Argentina. Vegetatio 111:93-126.

Pearson, O. P. and G. J. Kenagy. Reproduction. In Seventy-five years of Mammalogy (1919-1994). Special Publication No. 11, the American Society of Mammalogists (Birney, E.C., and J.R. Choate, eds.), pp. 271-287.

Pearson, O. P. The impact of an eruption of Volcan Hadson on small mammals in Argentine Patagonia. Mastozoologia Neotropical 1(2):103-112.

1995

Pearson, O. P. Annotated keys for identifying small mammals living in or near Nahuel Huapi National Park or Lanin National Park, southern Argentina. Mastozoologia Neotropical 2:99-148.

Pearson, O. P. In memoriam: Wilbur Brooks Quay, 1927-1994. Auk 112:489-491.

1997

Pearson, O. P. Monticulos “Mima”. Revista Patagonia Silvestre/Snap No. 4, 2 p.

1999

Pearson, O. P., and M. F. Smith. Genetic similarity between *Akodon olivaceus and Akodon xanthorhinus* (Rodentia: Muridae) in Argenitina. Journal of Zoology 247:43-52.

2000

Kenagy, G. J. and O. P. Pearson. Life with fur and without: experimental field energetics and survival of naked meadow voles. Oecologia 122:220-224.

2002

Pearson, O. P. A perplexing outbreak of mice in Patagonia, Argentina. Studies on Neotropical Fauna and Environment 37:187-200.

2005

Chan, Y. L., E. A. Lacey, O. P. Pearson, and E. A. Hadly. Ancient DNA reveals Holocene loss of genetic diversity in a South American rodent. Biology Letters 1:423-426.

2006

Pearson, A. K., O. P. Pearson, and P. L. Ralph. Growth and activity patterns in a backyard population of the banana slug, *Aridimax columbianus*. The Veliger 48:143-150.

This volume

Sage, R. D., O. P. Pearson, J. Sanguinetti, and A. K. Pearson. Ratada 2001: A Rodent Outbreak Following the Flowering of Bamboo (*Chusquea culeou*) in Southern Argentina / Ratada 2001: Una Irrupción de Roedores Siguiendo al Florecimiento de Bambú (*Chusquea culeou*) en el Sur de la Argentina. Pp. 177-224 in The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson (Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton, eds.). University of California Publications in Zoology 134:1-981.

PART 1: ECOLOGY, BIOGEOGRAPHY, NATURAL HISTORY

Oliver Pearson began his career studying mammalian reproduction and physiology. This rapidly diversified to include multiple facets of mammalian life history and ecology, reflecting his catholic interests and endless curiosity. The Ecology, Biogeography, Natural History section of this volume presents contributions from much of this intellectual range. As a whole, these contributions reflect the wide range of Pearson's interests, conceptually, taxonomically, and geographically.

Pearson's seminal contributions to the biology of voles (*Microtus*) are reflected in papers by 2 leading figures in this arena, one on the factors leading to extra-large males during peaks in demographic cycles (Lidicker) and another assessing the relative importance of predators, food supply, and interspecific competition on population growth (Batzli et al.). McNab provides a far-ranging review of the evolution of energetics in both birds and mammals, whereas Antinuchi et al. focus on the energy budget of a single species (a tuco-tuco, one of Pearson's favorite beasts). Bozinovic and colleagues address seasonal and annual variation in urine concentration by several rodent species in northern Chile, demonstrating that these species are able to adjust their concentrating abilities according to environmental needs. Yunger et al. report on how biotic interactions (predation and competition) influence spatial behavior of small mammals from the same region as Bozinovic's animals, providing a complementary perspective on this fauna. Solari provides the first dietary assessment for a poorly-known Peruvian highland rodent assemblage, and Spotorno et al. reassess the domestication of a key Andean species, the guinea pig. Pearson had a lengthy interest in biogeographic patterns, and both Tarifa et al. and Cofré et al. provide insights to the distribution of mammals, in *Polylepis* woodlands and in Mediterranean and Temperate Chile, respectively. In a fitting complement to Pearson and Ralph's Andean transect (Pearson and Ralph 1978), Tarifa et al. also consider amphibians and reptiles in their study in addition to mammals. Cofre et al. apply a GIS approach to understanding the factors influencing the distribution of Chilean mammals; at a larger spatial scale, Tognelli evaluates the potential of existing protected areas in South America for the preservation of the mammal fauna. Timm and McClearn report on a remarkable bat fauna in Costa Rica, putting their observations in both historical and ecological context, and commenting on the implications of their observations for bat conservation. Finally, Sage et al. provide the definitive treatment of the 2001 rodent outbreak in southern Argentina, which Paynie and Anita (both co-authors on this paper) waited for so patiently; we believe the product is reflective of the efforts.

GROWTH RATES OF MALE CALIFORNIA VOLES DURING A PEAK DENSITY YEAR: THE CHITTY EFFECT REVISITED

TASAS DE CRECIMIENTO EN MACHOS DEL METORITO DE CALIFORNIA DURANTE UN AÑO DE DENSIDADES MAXIMAS: UNA REVISIÓN DEL EFECTO CHITTY

William Z. Lidicker, Jr.

Dedicated to the memory of my friend and colleague Oliver P. Pearson, who made major contributions to small mammal ecology and reproductive physiology, including seminal research on California voles.

ABSTRACT

Temporal changes in body mass can serve as sensitive indicators of demographic processes. In arvicoline rodents undergoing multi-annual cycles, body mass tends to increase significantly during phases of rapid growth to peak numbers (Chitty Effect). Because of this association, considerable research effort has been directed toward understanding this phenomenon in the expectation that it will lead to elucidation of the cyclic mechanisms. Individual body growth rates were examined in a population of California voles (*Microtus californicus*) over an 11 month period when the density grew to about 1000/ha and then abruptly declined. Eighty-nine male voles were caught in at least 2 trapping periods (intervals of 7 or more days) generating 138 individual growth rate estimates. Voles were classified as "Chitty males" if they were known to have reached the extra-large size of 60 g (33.5% of 266 males). The percent of Chitty males peaked in February through April although density peaked in June/July. As expected, the regression of body growth rates (g/day) against initial weight was negative, but Chitty males had a steeper slope and higher growth asymptote (intercept) than did non-Chitty males. However, these differences are accounted for by strong seasonal and minor micro-habitat influences on growth rates. Overall, Chitty males averaged rates of 0.21g/day and non-Chitty males 0.22 g/day. These results are analyzed in the context of 6 hypotheses that have been proposed to account for the Chitty Effect. It is concluded that significant influences leading to extra-large sizes include adequate food supply, a long period that is favorable for growth, relatively high starting densities (a consequence of good survival over the preceding non-breeding period), low predation pressure, and in some individuals allocation of resources to growth

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Pp. 29-48 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

instead of reproduction. This multi-factor explanation includes many of the elements thought to characterize the cyclic mechanism itself.

Key words: *Microtus californicus*, body growth rate, demography, body mass, extra-large males, multiannual cycles, multifactor explanation

RESUMEN

Los cambios temporales en la masa corporal sirven como indicadores sensibles de los procesos demográficos. En los roedores arvicolinos que sufren ciclos multianuales, la masa corporal tiende a aumentar significativamente durante las fases de crecimiento rápido hacia picos poblacionales (el denominado Efecto de Chitty). Debido a esta asociación, se han realizado esfuerzos considerables para entender este fenómeno con la expectativa de que llevarán a la elucidación de los mecanismos de ciclado. Se examinaron las tasas individuales de crecimiento de la masa corporal en una población de metoritos de California (*Microtus californicus*) a lo largo de 11 meses de estudio, durante los cuales la densidad creció hasta unos 1000/ha y luego declinó abruptamente. Ochenta y nueve ratones machos fueron capturados en al menos dos períodos de trampeo (intervalos de 7 días o más) generando 138 estimaciones de tasas de crecimiento individual. Los machos que alcanzaron el tamaño extra-grande de 60 g fueron denominados "machos Chitty" (33.5% de 266 machos). El porcentaje de machos Chitty llegó a su máximo entre febrero y abril aunque la densidad fue máxima en junio/julio. Como era de esperarse, la regresión de tasas de crecimiento de la masa corporal (g/día) contra el peso inicial fue negativa, pero los machos Chitty tuvieron una pendiente más pronunciada y un tamaño asintótico mayor (intercepto) que los machos restantes. Sin embargo, esas diferencias son explicadas por fuertes influencias estacionales y menores efectos de microhabitat sobre las tasas de crecimiento. En promedio, los machos Chitty tuvieron tasas de 0.21 g/día y los restantes de 0.22 g/día. Los resultados de estos estudios son discutidos en el contexto de 6 hipótesis que han sido propuestas para dar cuenta del Efecto de Chitty. Se concluye que los factores que contribuyen significativamente al desarrollo de tamaños extra-grandes incluyen una oferta de alimentos adecuada, un período largo favorable para el crecimiento, densidades iniciales relativamente elevadas (consecuencia de una buena supervivencia durante el período no reproductivo precedente), baja presión de depredación, y en algunos individuos la asignación de recursos al crecimiento, en lugar de a la reproducción. Esta explicación multifactorial incluye muchos de los elementos que se consideran característicos del propio mecanismo cíclico.

Palabras claves: *Microtus californicus*, tasa de crecimiento corporal, demografía, peso corporal, machos de tamaño extra-grande, ciclos multi-anuales, explicaciones multifactoriales

INTRODUCTION

Changes in body mass as population numbers change can reveal important insights into age structure, condition or health, reproductive activities, and possibly other features of organisms such as sex, genetic makeup, or recent experiences. For example, California voles (*Microtus californicus*) that manage to survive a long summer dry season under high-density conditions in central California are not able to gain body mass for 2 to 6 months after favorable food and water conditions return (Lidicker 1973, 1976, 1988). Information on how individuals grow or diminish in mass under various circumstances can therefore lead to enhanced understanding of demographic mechanisms (Norrdahl 1995; Bryja et al. 2002).

Many species of arvicoline rodents exhibit multi-annual cycles in population density, and it has often been observed that mean body mass increases as populations grow to peak numbers. This is generally called the Chitty Effect (Boonstra and Krebs 1979; Lidicker and Ostfeld 1991). It has been particularly well established for males, although females have been less studied in this regard because of weight changes associated with pregnancy and lactation (but see Lidicker and Ostfeld 1991). A Chitty Effect also has been described for *Peromyscus leucopus*, a non-arvicoline (Wolff 1993). Dennis Chitty can be credited with bringing this phenomenon to our attention by claiming that it was so fundamental to vole cycling that it held the key to our understanding of the mechanism of multi-annual cycles (Krebs 1978; Taitt and Krebs 1985; Chitty 1987). He further postulated that cyclic changes in vole body mass were the result of a genetic polymorphism in which there were 2 morphs, a fast growing one capable of reaching especially large body size and a slow growing counterpart that lacked this growth potential (Chitty 1967; Boonstra and Krebs 1979; Krebs 1978; Stenseth 1978 ; Hansson 1991, 1995). Moreover, natural selection favored the former during periods of rapid population growth, larger size having an adaptive advantage during crowded conditions. In contrast, the small-bodied morph, which also had a higher reproductive potential, was favored during low and declining density phases of the cycle.

It is a fact that individual growth rates of voles and lemmings vary greatly individually, seasonally, and over the course of a cycle. Some of this variation could have a genetic basis, or it could be based on nutritional or social status, and there might even be maternal influences involved. The genetic polymorphism hypothesis has not found much empirical support over the years, and in fact Boonstra and Boag (1987) have reported that at least for *Microtus pennsylvanicus*, body growth rates have zero heritability. Similar results have been found for *M. townsendii* (Anderson 1975). On the other hand, Hansson (1988, 1995) presented evidence from laboratory-reared *Microtus agrestis* and *Clethrionomys glareolus* that body mass was polymorphic, possibly dimorphic. He suggested, as did Chitty, that large-sized voles generally were selected against except during prolonged periods favorable for rapid population growth. Hansson and Jaarola (1989) further hypothesized that large individuals were at a selective advantage under high density conditions because their relatively large intestines increased digestive efficiency at a time when food quality and possibly quantity were declining. Nevertheless, the lack of consistent support for the Chitty hypothesis has led to other suggestions being proposed to explain the Chitty Effect.

Large size during peak populations could be the result of especially favorable food supplies at these times (Gustafsson and Batzli 1985; Lidicker and Ostfeld 1991; Norrdahl and Korpimäki 2002). Another suggestion is that extra-large individuals are produced when the breeding season is especially long, allowing more time for individuals to grow. Consistent with this idea is the observation that rapid population growth is often enhanced by reproduction or at least good survival rates in the preceding normally non-breeding period (winter in temperate to arctic climates and summer in Mediterranean climates). In strongly seasonal environments, vole populations generally occur in distinct cohorts, including recruits born early in the breeding season, those born late in the season, and over-wintering adults (Gliwicz et al. 1968; Brown 1973; Gliwicz 1990; Gliwicz and Jancewicz 2001). These cohorts may respond differently to the same environmental circumstances, generating distinct morphs but without a genetic basis. Further, it has been postulated that extra-large males represent individuals that allocate energy to growth rather than reproduction because they are socially subordinate or live in microhabitats with a paucity of adult females (Lidicker and Ostfeld 1991; Hansson 1992; Oli 1999). Finally, it has been proposed that predators preferentially select large voles, and hence such individuals can occur in significant numbers only when predator pressure is low (Norrdahl and Korpimäki 2002).

These various non-genetic hypotheses are not mutually exclusive. Nevertheless the different proposed mechanisms generate somewhat different predictions regarding how individual voles will change in mass over the course of a density cycle, and particularly how the pattern of growth is manifested over a population's growth to peak numbers (Table 1). In this report, I examine in detail the patterns of body growth in a population of California voles growing to very high numbers (Cockburn and Lidicker 1983; Ostfeld et al. 1985 ; Lidicker and Ostfeld 1991). Earlier growth data from nearby populations compiled by C. Krebs (Krebs and DeLong 1965; Krebs 1966) are also utilized. By comparing these results with the various predictions outlined, it is hoped that additional understanding of the mechanisms underlying the Chitty Effect will be forthcoming.

MATERIALS AND METHODS

The data analyzed here were obtained from a population of California voles at the Russell Reservation, Contra Costa County, California. This is a property of the University of California Berkeley, and is located about 20 km east of San Francisco Bay in the coastal ranges (Bowen 1982; Cockburn and Lidicker 1983; Lidicker 1989). Voles were monitored with varying intensity from 1975 to 2002, and exhibit multi-annual fluctuations at this site. The year 1979/1980 witnessed a period of rapid population growth (Fig. 1) with numbers reaching 1000 voles per hectare in June 1980 (Cockburn and Lidicker 1983; Lidicker 1985; Lidicker and Ostfeld 1991). The population crashed during the ensuing summer and early autumn. Voles were monitored on 4 small grids (50 to 75 m apart and totaling about 0.25 ha.) placed across a California annual grassland largely dominated by introduced species (Bowen 1982; Cockburn and Lidicker 1983; Lidicker 1989); the inclusive study area was about 8 ha. Each grid represented a somewhat different microhabitat. Grid 1 was dominated by the native perennial grass *Elymus triticoides*, while Grid 2 was a mixture of *Elymus* and annual grasses and forbs, and was the most mesic of the grids; Grid 3 was dominated by the introduced forbs *Conium maculatum* and *Raphanus sativus*, with grasses occurring only on the periphery; Grid 4 was composed entirely of annual grasses and forbs and had the lowest stature of the 4 grids (Cockburn and Lidicker 1983). Grids 1 and 2 were high quality microhabitats relative to Grids 3 and 4 based on average densities of voles, reproductive output, average length of residency, persistence (mean per cent of voles captured during a given trap session that are captured in a subsequent trap session),

Table 1. Hypotheses for explaining the Chitty Effect and some predictions generated by them, especially with respect to populations in the rapid growth phase of cyclic change.

Hypothesis	Predictions
Genetic polymorphism	Two genetically based morphs present, each morphotype having quite different growth rates and asymptotes. The proportion of the 2 types would be cyclic phase dependent, with extra-large genotypes increasing rapidly with population growth.
Growth rate and body size correlated with food supplies	Food resources better during peak years than in others. Individuals in the same microhabitat will show similar growth trajectories, with fastest and most prolonged growth occurring in times of growth to peak numbers.
Long breeding seasons correlated with extra-large individuals	Peak years will coincide with especially long breeding seasons and extra-large individuals will occur only toward the end of those periods.
Seasonal cohorts have different growth behaviors	During phases of population growth, seasonal cohorts of voles will show different growth responses. Extra-large individuals will be produced by a cohort favored during rapid population growth.
Differential resource allocation	Some voles, especially males, will allocate energy to body growth rather than reproduction, and thus bimodal growth behavior will characterize phases of rapid population growth.
Differential predation	Selective predation on large voles prevents extra-large individuals from accumulating except when predator pressure is low. There will therefore be an inverse relationship between the impact of predators and prevalence of extra-large voles.

and number of resident adult females (Ostfeld et al. 1985; Lidicker and Ostfeld 1991).

The 4 grids were trapped from November 1977 to March 1981 at approximately monthly intervals. Trap sessions were 2 or 3 days. Each grid consisted of 25 trap stations spaced 5 m apart in a 5x5 array. A single Longworth live trap baited with rolled oats was set at each grid point, provisioned with cotton nesting material, and covered with a pulpwood board for shade and additional insulation. Body weight, reproductive condition, and point of capture were recorded each time a vole was caught. At first capture, all voles were individually marked by toe-clipping.

California voles in this region can reach sexual maturity at about 25 (females) to 28 g (males). Occasionally, females become pregnant at a pre-weaning weight of only 15 g. In the population studied here, modal body weight for males was consistently in the 51 to 60 g range during peak and pre-peak years, and 31 to 50 g at other times. Only twice did the mode exceed 60 g; in March 1980 when the population was in a

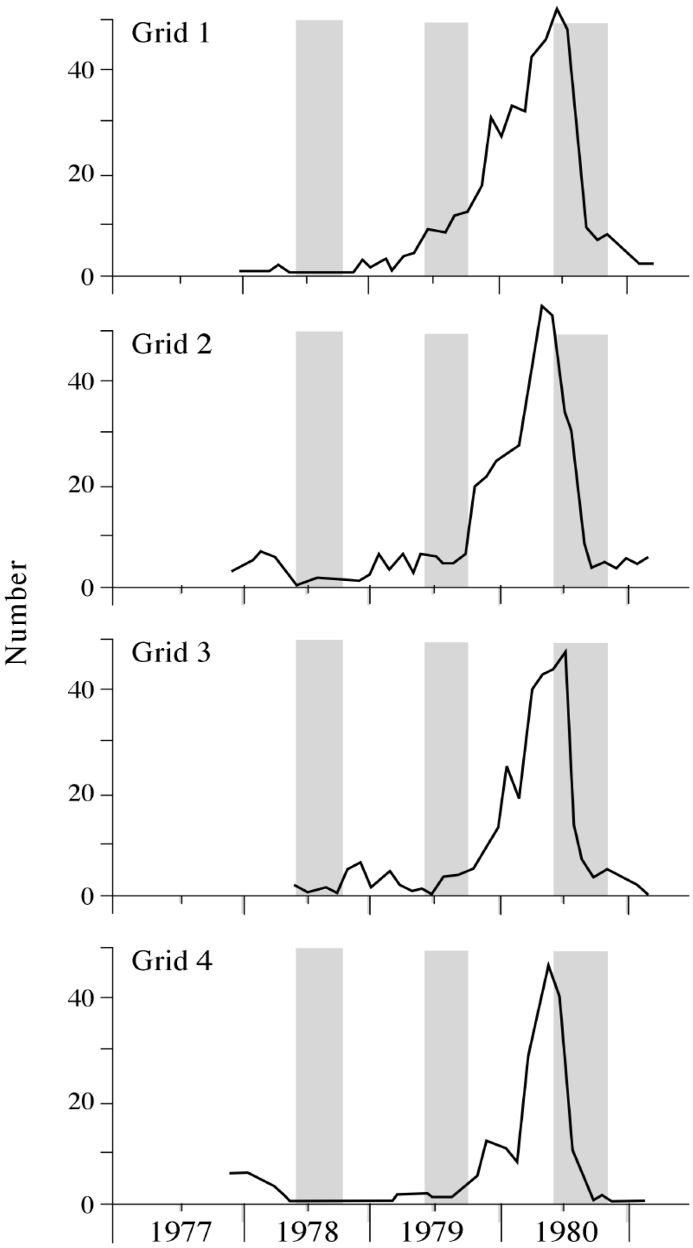

Figure 1. Density fluctuations on the 4 grids from late 1977 to early 1981. Density is expressed as the minimum numbers known to be alive, and the shaded areas represent the summer, non-breeding period. The similarity in demographic pattern among the grids indicates that this pattern characterized the entire 8 ha study area. This figure is reprinted from Ostfeld et al. 1985 (fig. 1).

rapid growth phase and in November 1978 when the population was just beginning its recovery from a crash following a peak in 1976 (Lidicker and Ostfeld 1991). Based on these considerations, I classified males that were known to reach a weight of 60 g or more as extra-large or "Chitty males." Other adult males were considered modal or "non-Chitty males." Of course the latter category would have included an unknown number of males that might have reached 60 g if they had not died first or failed to be trapped at that size. The maximum weights recorded in this population were 81 g for a male and 80.9 g for a pregnant female (Lidicker and Ostfeld 1991).

Data were analyzed using linear regression (unweighted least squares) and analysis of variance (ANOVA; fixed effects model). In some cases means were compared using Student's t-test. A p-value of 0.05 was used to judge statistical significance.

RESULTS

Growth Rates as a Function of Initial Weight

Although arvicoline rodents can show indeterminate growth trajectories, at least over the time period of their maximum age under natural conditions of 12 to 13 months (Morrison et al. 1977; Zullinger et al. 1984), it is anticipated that growth rates will be negatively correlated with body size. In Fig. 2, individual growth rates are plotted against initial body weights for the 138 growth measurements derived from males

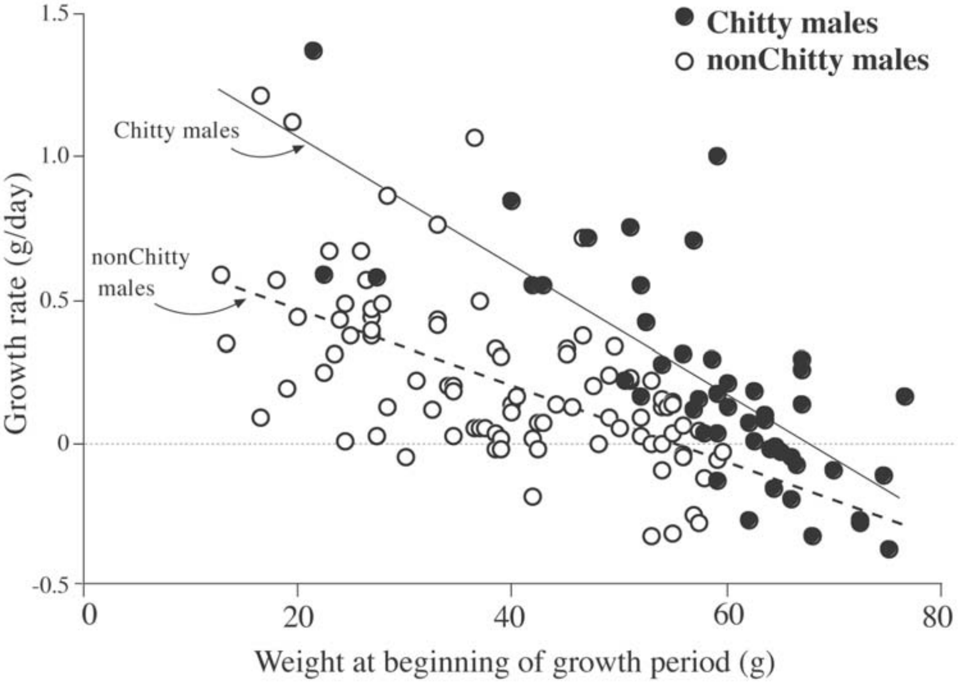

Figure 2. Individual growth rates (g/day) as a function of body weight (g) at the beginning of the growth interval. Chitty and non-Chitty males are regressed separately; $N = 138$.

recaptured at least once after an interval of 7 or more days. The regression is strongly negative as predicted. When Chitty and non-Chitty males are plotted separately, both the regression slopes and intercepts are statistically significantly different (for slopes: $F = 7.04$, $d.f. = 1, 134$; $p = 0.009$, and for intercepts: $F = 30.63$; $d.f. = 3, 135$; $p < 0.0001$). At any given body size, Chitty males grow at a faster rate than non-Chitty males, and achieve zero growth (asymptote) at a higher mass.

Influences of Cyclic Phase and Season

Incidence of Chitty Males: As previously reported (Lidicker and Ostfeld 1991; fig. 7), Chitty males were present in this population at all cyclic phases except for the one and a half year interval following peak densities. However, these extra-large males were rare until the population began its spurt to peak numbers in August 1979, and then disappeared again 1 month after the peak was achieved (July 1980). Fig. 3 shows the per cent of resident Chitty males among all adult resident males in the population during the growth and early decline phases ($N = 266$). The percentage exceeded 50% in March and April of 1980, and was still 11.5% in July of that year. The per cent of Chitty males in the entire sample was 33.5%.

Individual Growth Rates: Measurements were obtained for the entire 11 months of the study, but sample sizes were 8 or more starting in December. The percentage of Chitty males in the samples was 26% or more from October through May (Fig. 3). A total of 89 males were captured during this period in 2 or more trapping periods (minimum inter-session interval was 7 days). These recaptures generated 138 individual growth rate measurements, 34.1% of which were for Chitty males (those known to have reached

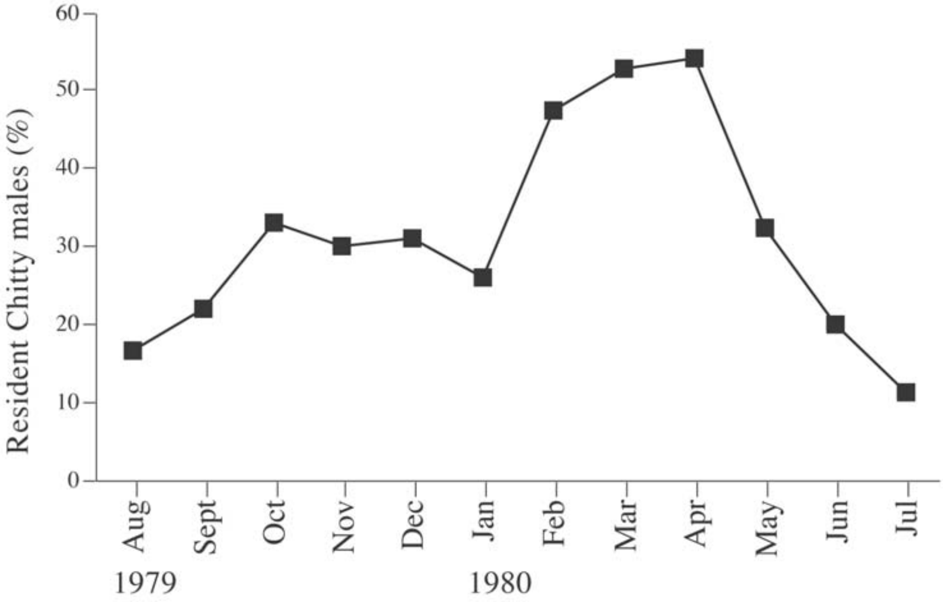

Figure 3. Resident Chitty males ($N = 89$) as a percentage of all adult males resident arranged by month ($N = 266$).

at least 60 g body mass). Fig. 4 plots these growth rates (g/day) for the Chitty and non-Chitty males separately, and for all the males together. A minor peak in October for Chitty males followed the beginning of the rainy season in that year. Growth rates peaked in February for all 3 groups at more than 0.6g/day. Rates were also high in December, but declined in January probably because this is the coldest and wettest time of the year. Growth rates then declined from March through June although this was a period of continuing rapid population growth that culminated in a peak of about 1000 voles per hectare (Fig. 1; Cockburn and Lidicker 1983).

The data were re-analyzed omitting 21 growth measurements that were based on recapture intervals exceeding 35 days. The rationale for this is that in such short-lived creatures sustained rapid growth may be difficult over such long periods. Rates based on these longer intervals are thus likely to be significantly lower than those measured over shorter time spans. In fact, the average growth rate for those 21 longer intervals (55 to 147 days) averaged only half as much as that for the entire sample of 138. This reduced data set, however, generated the same seasonal pattern of average growth rates. Two minor differences were that Chitty males in the peak growth month of February averaged 0.71g/day instead of 0.60, and non-Chitty males in October showed rates just over zero instead of negative.

An important result is that Chitty and non-Chitty males showed the same pattern of seasonal change in growth rates, and showed no consistent differences in magnitude from each other. For the entire 11 month period, individual growth rates for Chitty males averaged 0.21 g/day (*N* = 47), and non-Chitty males averaged 0.22 g/day (*N* = 91).

Because growth rates are influenced by body size (Fig. 2), it is possible that this

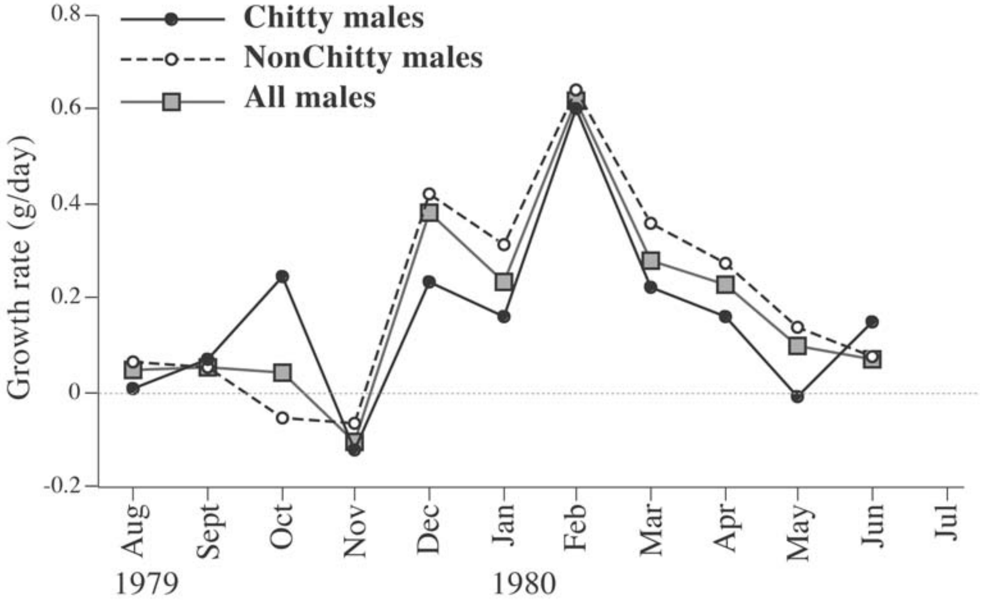

Figure 4. Average individual growth rates for males (g/day) as a function of month. Chitty (*N* = 47) and non-Chitty males (*N* = 91) plotted separately as well as all males combined (*N* = 138).

seasonal pattern may be influenced by differing age structures across the seasons. To test for this effect, body weights were regressed against growth rates for each of the 4 major seasons (see Fig. 5) separately. The slopes of these 4 seasonal regressions do not differ statistically ($F = 2.29$, *d.f.* = 3, 130, $p = 0.082$), but the intercepts do ($F = 23.18$, *d.f.* = 3, 133, $p = <0.001$). From these regressions, I calculated the expected body growth rate for a hypothetical 40 g. male in each season. The results are shown in Table 2, and indicate that the seasonal pattern shown in Fig. 4 remains intact.

Influence of Micro-habitat

The 4 small grids used in this study were chosen so as to sample different micro-habitats across the annual grassland community at the study site. Moreover, as pointed out, these 4 grids can be ranked with respect to their suitability or quality for supporting California vole populations. Based on multiple criteria, the grids can be ranked as follows: 1 > 2 >> 4 > 3.

Figure 5 shows how average individual body growth rates for males change on the grids across the time period of August 1979 to June 1980. Data are grouped into 4 time periods ranging from 37 to 93 days duration, the intervals being derived from the overall pattern of seasonal changes in growth rates as shown in Fig. 4. Consistent with that pattern, the fastest growth rates occurred in the December to March 2 interval. The mean for this period is statistically significantly different from the other 3 periods (pairwise *t*-test: $p = <0.001$, < 0.01, $<< 0.001$ for autumn, early spring, late spring respectively). Among the other 3 time periods, only autumn and early spring differ statistically significantly ($p = 0.043$). All grids follow the same seasonal trends, except

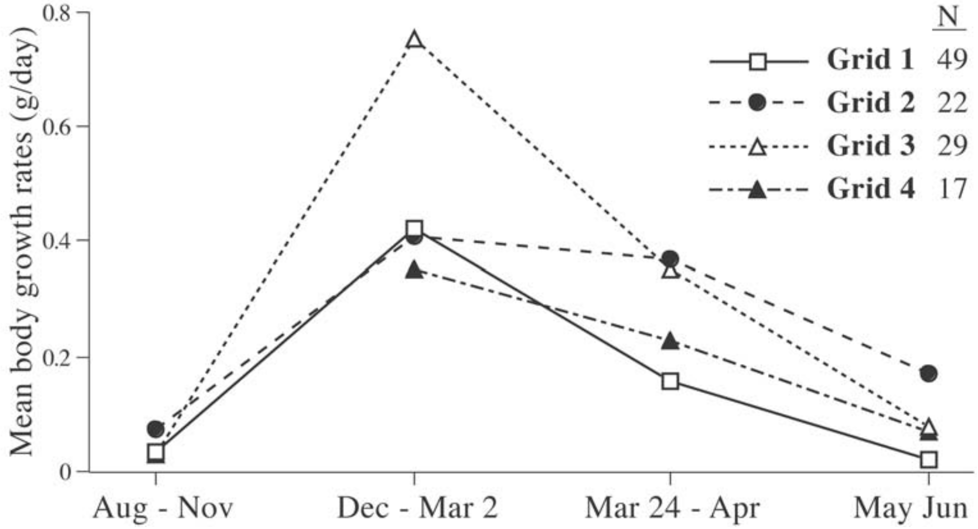

Figure 5. Mean body growth rates (g/day) as a function of micro-habitats (Grids 1-4) for males. Data are arranged into 4 seasonal periods ranging from 37 to 93 days in length. Only growth rates based on time intervals greater than 6 and less than 36 days are included ($N = 117$). Mean individual growth rates per day +/- 2 SE's for the 4 seasonal periods are Aug-Nov: 0.028 +/- 0.075; Dec-Mar 2: 0.449 +/- 0.115; Mar 24-Apr: 0.221 +/- 0.114; May-June: 0.090 +/- 0.055.

Table 2. Calculated body growth rates for a hypothetical 40 g male for the 4 seasons (see Fig. 5) and 4 grids (Fig. 5). The regressions for the 4 seasons do not differ in slope but do have different intercepts (see text). Regressions for the 4 grids do not differ in slope or intercept (see text). Growth rates are in g/day, and *N* = sample sizes.

Seasons	*N*	Growth Rates
August – November	19	0.16
December – March 2	42	0.50
March 24 – April	26	0.34
May - June	51	0.10
Grids		
1	49	0.31
2	22	0.24
3	29	0.36
4	17	0.28

that grid no. 2 declines less abruptly from early March to June than do the other 3. The most obvious deviation is shown by grid no. 3 which shows a strongly inflated growth rate at 0.75g/day in the favorable winter period. Grid no. 3 is the one ranked lowest on overall quality, but paradoxically contained the highest percentage of Chitty males. The largest proportion of extra-large females was found on Grid no. 4 (Cockburn and Lidicker 1983), also a relatively low quality micro-habitat.

Overall, the 4 grids do not differ statistically in their average growth rates (*F* = 0.33, *d.f.* = 3, 134, *p* = 0.80). Moreover, the regressions of initial weight on growth rate for the 4 grids separately, do not differ statistically in either slope (*F* = 1.47, *d.f.* = 3, 130, *p* = 0.23) or intercept (*F* = 0.70, *d.f.* = 3, 133, *p* = 0.55). ANOVA (1 way) also reveals no differences among the grids in individual growth rates (*F* = 0.33, *d.f.* = 137, *p* = 0.80). When the trimmed sample of 117 growth rates are tested, the results are similar (slope: *F* = 0.92, *d.f.* = 3, 109, *p* = 0.43; intercept: *F* = 0.77, *d.f.* = 3, 112, *p* = 0.51, ANOVA: *F* = 0.21, *d.f.* = 116, *p* = 0.89). As these grids are not different in these tests, it is not surprising that calculations of growth rates for a hypothetical 40 g male are also similar (Table 2) for all the grids, although Grid 3 still shows the highest rate (Fig. 5).

DISCUSSION

Do the data presented here offer new insights into the meaning and mechanism of the Chitty Effect? Comparison with the 6 hypotheses outlined in Table 1 is revealing in this regard.

Genetic Polymorphism: The results illustrated in Fig. 2 suggest that there may be 2 types of males in this population since Chitty and non-Chitty males have statistically different regression slopes for individual growth rates and growth asymptotes. Moreover, this is manifest over the full range of body weights. However, as shown in Fig. 3, the highest proportion of Chitty males was present in February to April (1980), which was the period of most rapid body growth and continuing into the immediately following time interval (Fig. 4). Hence the faster growth of Chitty males may be attributable to the largest number of them being present during the period most favorable for growth.

The polymorphic hypothesis further suggests that the proportion of extra-large individuals should increase steadily as population density increases. Instead the numbers and percentage of these males declines precipitously during the rapid growth of the population from May into July (Fig. 3). This decline was partly the result of an influx of many juvenile recruits, but there was also a failure to add many new Chitty males to the population during this period. Moreover, the large percentage of heavy individuals in November 1978 (Lidicker and Ostfeld 1991) is inconsistent with this hypothesis. In this instance, growth to large size occurred at a low density and at the moment when the recovery phase of the population was just beginning. Similarly, in the autumn of 1979, following a dry season with unusually high survival rates (Cockburn and Lidicker 1983, fig. 3), there was a minor increase in Chitty male abundance immediately following the start of the rainy season (Fig. 3). It is relevant also that the Chitty and non-Chitty males followed the same seasonal pattern in body growth (Fig. 4), and did not differ in average growth performance. Finally, Lidicker and Ostfeld (1991) noted that individuals apparently excluded from the primary breeding micro-habitats were likely to be the ones achieving extra-large status. This was based on the fact that most of the Chitty males occurring after March were living on Grid 3, and secondarily Grid 4, which were the 2 grids with the lowest numbers of adult females and otherwise deemed least favorable for voles. It was concluded therefore that Chitty males were not the individuals most favored by natural selection during periods of rapid population growth as postulated by this hypothesis. Rather, they are social outcasts, putting their energy into growth and surviving long enough to grow very large.

It is relevant to point out as well that several authors have shown a disconnect between the occurrence of extra-large individuals and multi-annual cycles (Krebs 1966; Lidicker and Ostfeld 1991, Agrell et al. 1992; Hansson 1995). These reports suggest that all of the ingredients for a Chitty Effect are present in non-cyclic as well as cyclic populations. Agrell et al. (1992) reported data covering 21 years. There were no multi-annual cycles and no clear Chitty Effect. Yet, significant between-year differences were found in body weight, survival, and recruitment, all of which were positively correlated.

Krebs (1966) studied 8 populations of California voles in the vicinity of Berkeley, California, from 1962 to 1964. These were monitored for varying lengths of time, the longest being 21 months. I compiled his data on the occurrence of extra-large males in 5 of these populations (the unmanipulated ones) arranged by cyclic phase (Table 3). I equated his weight categories of 62 g. and larger with Chitty males; his males of 60 and 61 g. were lumped with those weighing 58 and 59 g. Therefore, there were likely a few more Chitty males in his populations based on the 60 g. criterion than reported in Table 3. In assigning trapping dates to cyclic phase, I considered densities less than 100 per ac. (247 /ha) as "low density", those from 100 to 200 per ac. (494/ha) as pre-peak or declining depending on the direction of density trends, and populations at more

Table 3. Occurrences of extra-large males (> or = to 62 g) in 5 unmanipulated populations of *Microtus californicus* from the Berkeley, California, vicinity, arranged by cyclic phase (see text for details). Data from Krebs (1966; table 14).

Cyclic phase	Numbers of months	Total males	Extra-large males	% extra-large males
Pre-peak	7	517	106	20.5
Peak	7	822	63	7.9
Decline	3	127	5	3.9
Low numbers	32	714	64	9.0

than 200 per ac. as representing peaks. As in my study (Fig. 3; Lidicker and Ostfeld 1991), Krebs recorded Chitty males in all demographic phases, but they were most numerous in pre-peak populations. Contrary to the genetic polymorphism hypothesis, peak populations had considerably lower proportions. Krebs also sometimes observed as I did an increase in Chitty males immediately following the onset of autumnal rains (Fig. 4), even at low densities.

Food Resources: We were not able to measure food supplies directly. This hypothesis, however, suggests that, if food resources are of prevailing importance, all individuals of equivalent size will show similar growth trajectories in a given microhabitat, and that this should continue almost to the attainment of peak numbers. Individuals were, however, highly variable in their growth patterns, and showed steadily declining growth rates from March through June (Figs. 4, 5). Moreover, there was good vegetation growth during the wet seasons of 1977, 1978, and 1979 when only low densities were achieved. Obviously, adequate food is a necessary prerequisite to body weight gains, but clearly the pattern of weight changes is much more complex than can be explained by this factor alone. It is probably significant also that the highest percentage of extra-large individuals (males and females) was on Grid 3 which by other criteria was considered the poorest quality micro-habitat sampled. Further arguing against food as the primary causal mechanism for the Chitty Effect is the fact that population growth continued well into July on Grid 4, which was also a low-ranking micro-habitat in overall quality. Krebs and DeLong (1965) gave supplemental food to a population of voles for 11 months, and showed that abundant food resources could not produce an abundance of extra-large individuals or prevent a population crash in the dry season. This population did, however, sustain high body growth rates for several months longer than in the control population. Non-cyclic populations may show a closer correspondence between body growth rates and food resources (Lidicker and Ostfeld 1991; Agrell et al. 1992; Hansson 1995).

Long Breeding Season: The breeding season commenced with the autumn rains in October and continued into July on Grid 4 (Cockburn and Lidicker 1983). This 9 month period is indeed long for this area. Occasionally, the rainy season begins as early as September, but often breeding ends by mid-May or early June. In some years, the rains begin later than October, and in some years breeding is delayed as late as February in spite of good growth of vegetation much earlier (Lidicker 1988). In the spring of 1976 this population was headed for a major peak in numbers, but growth was truncated in February when significant rainfall ended (Cockburn and Lidicker 1983). Thus a 9 month breeding season, while not unprecedented, is near the upper limit for this area.

Another factor that undoubtedly was critical for developing the peak numbers in June/July of 1980 was the fact that the population survivorship over the summer of 1979 was unusually good (Cockburn and Lidicker 1983). When population growth resumed the population density was about 20 voles per hectare, much higher than in non-peak years. Numbers were also 20/ha in October 1975 preceding the peak of 1976 (Bowen 1982; Cockburn and Lidicker 1983). I suspect that the combination of high starting density and a long breeding season made it possible for many voles to live for a relatively long time and grow unusually large.

Seasonal Cohorts: This hypothesis posits that seasonal cohorts will respond differentially depending on whether or not they are present during periods favoring rapid body growth. Extra-large individuals will be produced only in those cohorts that can respond to favorable conditions. For this analysis, the individuals providing growth rate data were sorted into 3 cohorts: 1) individuals surviving the summer non-breeding periods (N = 23 measurements); 2) those born early in the breeding season, i.e., December through February (yielding 58 growth rates); and 3) individuals recruiting late in the breeding season, i.e., March through June (N = 57 growth rates). Their average growth rates were statistically different (1-way ANOVA, $F = 6.68$, *d.f.* = 137, $p = 0.0017$), Cohort 2 showing the fastest rates. When these cohorts are compared by regression of growth rates on initial body weights, the regression slopes and intercepts are all statistically different ($F = 4.24$, *d.f.* = 2, 132, $p = 0.016$, $F = 18.07$, *d.f.* = 2, 134, $p = < 0.0001$, respectively). Again, it is Cohort 2 that demonstrates the fastest growth and heaviest asymptote. Contrary to this hypothesis, however, Chitty males were found in all 3 cohorts in substantial proportions (Cohort 1 = 9 (39.1%); Cohort 2 = 28 (48.3%); Cohort 3 = 10 (17.5%)). Individually, only Cohort 3 differs significantly ($p < 0.05$) from random expectations of Chitty male proportions.

This cohort analysis, which ignores the distinction between Chitty and non-Chitty males, further demonstrates the strong seasonal pattern in growth rates as shown in Figs. 4 and 5. It further supports the conclusion that the Chitty versus non-Chitty differences shown in Fig. 2 reflect these seasonal patterns and does not suggest that 2 genetically-based morphs are present in this population. Krebs (1966) also documented maximum body growth rates in the December through March season in 5 (unmanipulated) populations of this species.

Differential Resource Allocation: This hypothesis explains extra-large individuals as occurring when resources are shunted to body growth rather than reproduction (Lidicker and Ostfeld 1991; Hansson 1992; Oli 1999). As such, it offers no explanation for why individuals adopt different allocation strategies. As discussed under the genetic polymorphism hypothesis, Lidicker and Ostfeld (1991) presented the case that Chitty males in this population included many individuals excluded from reproduction, living in marginal micro-habitats, and consequently using their energy resources to grow large.

The resource allocation hypothesis would also imply that at some point in ontogeny, males would adopt either the growth or reproduction strategy, perhaps in so doing generate a bimodal distribution of growth rates from that point on. A plausible time for this "decision" to be made is when males reach their normal non-Chitty adult modal weight, which is in the 40 to 60 g range. There are 65 growth rates in the sample for males at a body weight of 40.0 to 59.9 g. Twenty of these (30.8%) are known to have become Chitty males. If we examine the frequency distribution of growth rates in this sample (Table 4), we find it is unimodal. A total of 34 individuals (52.3%) fall into the range of -0.09 to 0.19 g/day. Chitty males are distributed widely across growth rate categories, although all but 1 of those rates exceeding 0.4 g/day ($N = 10$) are from known Chitty males. These data therefore provide only weak support for a bifurcation of growth rates among adult males. Norrdahl and Korpimäki (2002) considered this hypothesis for *Microtus agrestis, M. rossiaemeridionalis,* and *Clethrionomys glareolus* in western Finland, and found no support for it.

Selective Predation: This hypothesis predicts that the Chitty Effect will only be manifest when predation pressure is low. This is because predators are presumed to differentially

Table 4. Frequency distribution of body growth rates for adult males in the 40.0 to 59.9 g weight range ($N = 65$). Numbers of known Chitty-males are given in parentheses for each growth and initial weight category.

Body growth rates (g/day) greater than:	Body weight category		
	40.0-49.9 g	50.0-59.9 g	Combined
-0.3	-	2 (0)	2 (0)
-0.2	-	2 (0)	2 (0)
-0.1	1 (0)	3 (1)	4 (1)
0.0	6 (0)	14 (2)	20 (2)
0.1	5 (0)	9 (4)	14 (4)
0.2	2 (0)	6 (3)	8 (3)
0.3	4 (0)	1 (1)	5 (1)
0.4	-	1 (1)	1 (1)
0.5	2 (2)	1 (1)	3 (3)
0.6	-	-	0
0.7	2 (1)	2 (2)	4 (3)
0.8	1 (1)	-	1 (1)
0.9	-	-	0
1.0	-	1 (1)	1 (1)
Totals	23	42	65
Total Chitty-males	4	16	20
Percent Chitty-males in wt. group	17.7	38.1	30.8

select the largest individuals which perhaps are also the most vulnerable (Hansson 1995; Norrdahl and Korpimäki 2002). Norrdahl and Korpimäki (2002) suggest that this predation impact is most important during cyclic declines. Hansson (1995) suggested that the lack of a clear Chitty Effect in non-cyclic populations is caused both by strong selection against large individuals by predators and an overall higher mortality rate that greatly reduces the opportunity for individuals to grow to large size.

In the case of *Microtus californicus,* Pearson (1964, 1966, 1971, 1985) has amply demonstrated the major impact that mammalian predators can have on population numbers. Moreover, in cyclic populations, this impact is felt mainly in the decline phase (Pearson 1985; Lidicker 1988). At Russell Reservation, mammalian predators (primarily coyotes, *Canis latrans*, and raccoons, *Procyon lotor*) were monitored monthly for 33 months by regular collection of scats (Lidicker 1988, fig. 5). Except for a minor increase in the summer of 1979 when voles were unusually abundant throughout the dry period, predation pressure remained low until June 1980. It then rose rapidly to a peak in September, declining thereafter but continuing at a substantial level until January 1981. This pattern corresponds to the massive mortalities of voles in the decline phase (an anti-regulating influence). The decline phase is also the time when extra-large individuals have been observed consistently to be completely absent. The Russell data are thus consistent with the conclusion that the selective predation hypothesis may be a contributing component of the Chitty Effect mechanism.

We can conclude from this survey of hypotheses that evidence does not support the genetic polymorphism hypothesis as being involved in California vole demography. An adequate food supply is clearly a prerequisite for rapid body growth, but the seasonal pattern of food production and decline, while permissive, does not explain all aspects of the pattern of occurrence of extra-large individuals. It does support the growth to large size that occurs among healthy individuals when good food conditions return at the beginning of the rainy season. A long breeding season appears to be a second critical component in producing large numbers of heavy individuals. More accurately, what seems to be involved is a long period of time favorable to individual growth or at least maintenance of body weight. Following the summer of 1979 when survival was unusually good and body weights did not decline as much as usual, many individuals grew rapidly to large size as soon as the rainy season began and food and water supplies improved dramatically (Fig. 4). The combination of a long breeding season and moderately high numbers initially (2 orders of magnitude greater than what densities often are in the autumn period) is undoubtedly what made it possible for the super high peak that was reached in June/July of 1980. Growth data analyzed by seasonal cohorts did reveal important differences among these groups. However, this finding added no new insights to explaining the Chitty Effect beyond those based on seasonal and breeding season influences. There is some support for the idea that extra-large males result when some individuals allocate resources to growth rather than reproduction. This phenomenon is most evident late in the breeding season when densities in the best micro-habitats are high. It does not explain the appearance of Chitty males early in the breeding season and at low densities. Since predators, especially mammalian, often have delayed response to rapidly increasing vole numbers, their impact occurs primarily during the decline and early low phases. The relatively low predation pressure that therefore tends to prevail during growth and peak cyclic phases may be an important permissive factor in the development of a Chitty Effect.

We can predict that a strong Chitty Effect can be expected when there is an unusually long period of conditions favorable to vole survival. These will be associated with years in which survival over the non-breeding season is especially good, when the breeding season is prolonged, and when low predation pressure allows excellent survival rates. Thus, much as the explanation for multi-annual cycles is multi-factorial (Lidicker 1988, 1991, 2002), so too is the pattern of body mass changes over a cycle, one manifestation of which is the Chitty Effect. Ironically, Dennis Chitty's intuition that an understanding of the Chitty Effect would be closely connected to an understanding of multi-annual cycles now seems correct.

LITERATURE CITED

Agrell, J., S. Erlinge, J. Nelson, and M. Sandell
1992 Body weight and population dynamics: cyclic demography in a noncyclic population of the field vole (*Microtus agrestis*). Canadian Journal of Zoology 70:494-501.

Anderson, J. L.
1975 Phenotypic correlations among relatives and variability in reproductive performance in populations of the vole *Microtus townsendii.* Ph.D. Dissertation, University of British Columbia, Vancouver.

Boonstra, R., and P. T. Boag
1987 A test of the Chitty hypothesis: inheritance of life-history traits in meadow voles *Microtus pennsylvanicus*. Evolution 41:929-947.

Boonstra, R., and C. J. Krebs
1979 Viability of large- and small-sized adults in fluctuating vole populations. Ecology 60:567-573.

Bowen, B. S.
1982 Temporal dynamics of microgeographic structure of genetic variation in *Microtus californicus.* Journal of Mammalogy 63:625-638.

Brown, E. B. III
1973 Changes in patterns of seasonal growth of *Microtus pennsylvanicus.* Ecology 54:1103-1110.

Bryja, J., E. Tkadlec, J. Nesvadbová, and M. Heroldová
2002 Phase-dependent growth of body mass in spring populations of the common vole. 8th International Rodens & Spatium Conference, Louvain-la-Neuve, Belgium, Abstract No. 12.

Chitty, D.
1967 The natural selection of self-regulatory behaviour in animal populations. Proceedings of the Ecological Society of Australia 2:51-78.

1987 Social and local environments of the vole *Microtus townsendii*. Canadian Journal of Zoology 65:2555-2566.

Cockburn, A., and W. Z. Lidicker, Jr.
1983 Microhabitat heterogeneity and population ecology of an herbivorous rodent, *Microtus californicus* Oecologia. 59:167-177.

Gliwicz, J.
1990 The first born, their dispersal, and vole cycles. Oecologia 83:519-522.

Gliwicz, J., R. Andrzejewski, G. Bujalska, and K. Petrusewicz
1968 Productivity investigations of an island population of *Clethrionomys glareolus* (Schreber, 1780). I. Dynamics of cohorts. Acta Theriologica 13:401-413.

Gliwicz, J., and E. Jancewicz
2001 Aging and cohort dynamics in *Sorex* shrews. Acta Theriologica 46:225-234.

Gustafsson, T. O., and G. O. Batzli
1985 Effects of diet and origin on growth and reproduction of *Clethrionomys glareolus.* Annales Zoologici Fennici 22:273-276.

Hansson, L.
1988 Parent-offspring correlations for growth and reproduction in the vole *Clethrionomys glareolus* in relation to the Chitty hypothesis. Zeitschrift für Säugetierkunde 53:7-10.

1991 Regional and individual variation in body growth in winter of bank voles *Clethrionomys glareolus.* Acta Theriologica 36:357-362.

1992 Fitness and life history correlates of weight variations in small mammals. Oikos 64:479-484.

1995 Size dimorphism in microtine populations: characteristics of growth and selection against large-sized individuals. Journal of Mammalogy 76:867-872.

Hansson, L., and M. Jaarola
1989 Body size related to cyclicity in microtines: dominance behaviour or digestive efficiency? Oikos 55:356-364.

Krebs, C. J.
1966 Demographic changes in fluctuating populations of *Microtus californicus*. Ecological Monographs 36:239-273.

1978 A review of the Chitty hypothesis of population regulation. Canadian Journal of Zoology 56:2463-2480.

Krebs, C. J., and K. T. DeLong

1965 A *Microtus* population with supplemental food. Journal of Mammalogy 46:566-573.

Lidicker, W. Z., Jr.

1973 Regulation of numbers in an island population of the California vole, a problem in community dynamics. Ecological Monographs 43:271-302.

1976 Experimental manipulation of the timing of reproduction in the California vole. Researches on Population Ecology 18:14-27.

1985 Population structuring as a factor in understanding microtine cycles. Acta Zoologica Fennica 173:23-27.

1988 Solving the enigma of microtine "cycles." Journal of Mammalogy 69:225-235.

1989 Impacts of non-domesticated vertebrates on California grasslands. Pp. 135-150 in Grassland Structure and Function: California Annual Grassland (Huenneke, L. F., and H. Mooney, eds.). Kluwer Academic Publishers, Dordrecht, The Netherlands.

1991 In defense of a multifactor perspective in population ecology. Journal of Mammalogy 72:631-635.

2002 From dispersal to landscapes: progress in the understanding of population dynamics. Acta Theriologica 47, Suppl. 1:23-37.

Lidicker, W. Z., Jr., and R. S. Ostfeld

1991 Extra-large body size in California voles: causes and fitness consequences. Oikos 61:108-121.

Morrison, P., R. Dieterich, and D. Preston

1977 Body growth in sixteen rodent species and subspecies maintained in laboratory colonies. Physiological Zoology 50:294-310.

Norrdahl, K.

1995 Population cycles in northern small mammals. Biological Reviews 70:621-637.

Norrdahl, K., and E. Korpimäki

2002 Changes in individual quality during a 3-year population cycle of voles. Oecologia 130:239-249.

Oli, M. K.

1999 The Chitty Effect: a consequence of dynamic energy allocation in a fluctuating environment. Theoretical Population Biology 56:293-300.

Ostfeld, R. S., W. Z. Lidicker, Jr., and E. J. Heske
1985 The relationship between habitat heterogeneity, space use, and demography in a population of California voles. Oikos 45:433-442.

Pearson, O. P.
1964 Carnivore-mouse predation: an example of its intensity and bioenergetics. Journal of Mammalogy 45:177-188.

1966 The prey of carnivores during one cycle of mouse abundance. Journal of Animal Ecology 35:217-233.

1971 Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). Journal of Mammalogy 52:41-49.

1985 Predation. Pp. 535-566 in Biology of New World *Microtus* (Tamarin, R. H., ed.). Special Publication, American Society of Mammalogists 8.

Stenseth, N. C.
1978 Demographic strategies in fluctuating populations of small mammals. Oecologia 33:149-172.

Taitt, M. J., and C. J. Krebs
1985 Population dynamics and cycles. Pp. 567-620 in Biology of New World *Microtus* (Tamarin, R. H., ed.). Special Publication 8, American Society of Mammalogists.

Wolff, J. O.
1993 Does the "Chitty Effect" occur in *Peromyscus*? Journal of Mammalogy 74:846-851.

Zullinger, E. M., R. E. Ricklefs, K. H. Redford, and G. M. Mace
1984 Fitting sigmoidal equations to mammalian growth curves. Journal of Mammalogy 65:607-636.

THE RELATIVE IMPORTANCE OF PREDATION, FOOD, AND INTERSPECIFIC COMPETITION FOR GROWTH OF PRAIRIE VOLE (*MICROTUS OCHROGASTER*) POPULATIONS

LA IMPORTANCIA RELATIVA DE PREDACIÓN, ALIMENTACIÓN, Y COMPETENCIA INTERESPECÍFICA EN EL CRECIMIENTO POBLACIONAL DEL METORITO DE LA PRADERA (*MICROTUS OCHROGASTER*)

George O. Batzli, Steven J. Harper, and Yu-teh K. Lin

ABSTRACT

Oliver Pearson's observations on the intensity of predation on California voles led to a reemphasis on the importance of predation as an explanation for the population dynamics of small mammals. Recent experimental and theoretical work has supported this view for the role of predators during population declines and as a cause of population cycling, but quantitative estimates of the importance of predation as populations increase remain rare. In this paper we present a new analysis of experimental data that examines the relative effects of 3 factors -- predation, food supply, and interspecific competition -- on the population growth of voles. Our objective is to test the proposition that predation is an important factor that reduces population growth of small mammals during population increases as well as declines, an idea that we call Pearson's hypothesis.

By manipulating access by predators, food supply, and presence of a competing species (the meadow vole, *M. ochrogaster*), we were able to quantify their relative impact on growth of prairie vole populations during the growing season. Using analysis of variance and linear modeling, we found that all 3 factors had substantial effects on population growth, but that predation had 2-3 times greater impact than did food supply and competition. An interaction between predation and competition occurred because predators appeared to respond to the greater overall density of voles that occurred when competitors were present, which reinforced the importance of predation. A relatively good supply of natural food in the habitat used for our experiment and an additional interaction (a reduced effect of food supply in the presence of competitors) likely resulted in a lower estimate of the importance of food than expected. Nevertheless, we conclude that our results in general supported Pearson's hypothesis.

Key words: Food supply, interspecific competition, *Microtus ochrogaster*, prairie voles, predation, population growth

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Pp. 49-66 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

RESUMEN

Las observaciones de Oliver Pearson sobre la intensidad de la depredación sobre el metorito de California (*Microtus californicus*) llevaron a un nuevo énfasis en la importancia de la depredación como una explicación de la dinámica poblacional de pequeños mamíferos. Esta visión del papel de los depredadores durante los descensos de los tamaños poblacionales ha sido apoyada por el trabajo experimental y teórico reciente, pero son raras las estimaciones de la importancia de la depredación cuando la población experimenta un crecimiento. En este trabajo, presentamos un nuevo análisis de los datos experimentales que examinan los efectos relativos de 3 factores—depredación, oferta de alimentos, y competencia interespecífica—en el crecimiento poblacional de meteoros. Nuestro objetivo es poner a prueba la idea de que la depredación es un factor importante que reduce el crecimiento poblacional de los pequeños mamíferos tanto durante las fases de crecimiento como de declive, una idea que denominamos la hipótesis de Pearson.

Manipulando el acceso por parte de depredadores, la oferta de alimentos, y la presencia de una especie competidora (el metorito de la pradera, *M. ochrogaster*), nos fue posible cuantificar su impacto relativo sobre el crecimiento de las poblaciones del meteoro de California durante la estación de crecimiento. Usando análisis de varianza y modelos lineales, encontramos que los 3 factores tenían efectos sustanciales sobre el crecimiento poblacional, pero que la depredación tenía efectos 2-3 veces mayores que la oferta de alimentos y la competencia. Ocurre una interacción entre depredación y competencia porque los depredadores parecieron responder a la mayor densidad relativa de meteoros que ocurrió cuando los competidores estaban presentes, lo cual reforzó la importancia de la depredación. Una oferta de alimentos relativamente buena en el habitat utilizado para nuestro experimento y una interacción adicional (efecto reducido de la oferta de alimentos en presencia de competidores) posiblemente resultaron en una subestimación de la importancia del alimento respecto a lo esperado. No obstante, concluímos que nuestros resultados apoyan en general la hipótesis de Pearson.

Palabras claves: Provisión de comidas, competencia interespecífica, *Microtus ochrogaster*, meteoros de pradera, predación, crecimiento demográfico

INTRODUCTION

Shortly after Elton (1924) began to study periodic fluctuations of small mammals, Lotka (1925) and Volterra (1926) concluded that, in theory, predator-prey interactions could cause population cycles. The predator-prey hypothesis fell out of favor, however, and a reawakening did not begin until Oliver Pearson reported his observations on the intensity of predation on California voles (*Microtus californicus*) in a series of papers (Pearson, 1964, 1966, 1971). Pearson argued that predation is an essential component of multi-annual cycles in populations of arvicoline (microtine) rodents. In a later review (Pearson, 1985), he concluded that, although other factors must help predators stop a vigorously growing vole population, predators depress vole densities to extremely low levels, which delays recovery so that several years elapse between peak densities. He also pointed out that voles appear easily caught by predators so that predators probably have other important demographic effects in addition to their role in population cycling.

Subsequent results from experiments and output from mechanistic models generally supported Pearson's original insights (Desy and Batzli, 1989; Korpimäki and Norrdahl, 1998; Batzli et al., 1999; Klemola et al., 2000; Hanski et al., 2001; Korpimäki et al., 2002, 2005). Predation appeared sufficient to cause population cycles, but only if some other factor helped to slow population growth of voles as they neared peak densities. The relative importance of factors that affect the rate of population increase remains largely unknown, however, because quantitative estimates of the influence of different factors on population growth have been rare. Such estimates require field experiments with a replicated, factorial design because only such experiments can detect factor interactions, which can complicate the assessment of relative importance.

Although many single-factor experiments using voles have been conducted, few experiments have simultaneously manipulated both food and predation in the field. One that manipulated cover, access by predators, and available food implicated predation as the cause of a spring decline in Townsend's voles (*Microtus townsendii*) in British Columbia, but the experiment was neither factorial nor replicated (Taitt and Krebs, 1983). A later experiment manipulated predation and availability of high quality food in a replicated, factorial design and found that protection from predators and provision of supplementary food had equal and additive effects on population growth of prairie voles (*M. ochrogaster*) during the growing season in Illinois (Desy and Batzli, 1989). A third experiment, using field voles (*M. agrestis*) in Finland, excluded predators and provided supplemental food (Huitu et al., 2003) and found a factor interaction; populations with supplemental food maintained higher densities than those without supplemental food, but only when protected from predation. Supplemental food was not provided during the growing season, however. Finally, in the early 1990s we conducted a replicated, factorial experiment to test a multi-factorial hypothesis regarding the direct, indirect, and interactive effects of predation, food, and interspecific competition on population growth of prairie voles (Batzli et al., 1999). Results from a preliminary analysis indicated that supplemental food increased population growth of voles and that predation and competition decreased population growth. An interaction also occurred; predation had a greater effect when competitors were present.

In this paper we reanalyze data from the study by Batzli et al. (1999) to develop quantitative estimates of the relative importance of each factor on population growth. Our purpose is to test a general hypothesis that predation substantially reduces the rate of population growth of voles during increases in density as well as during declines. Because Oliver Pearson emphasized the overall importance of predation on arvicoline populations, not just their role in population cycles, we call this Pearson's hypothesis. We also test the corollary that factor interactions do not obscure this effect.

EXPERIMENTAL DESIGN AND METHODS

We conducted our research in 2 ha of old pasture at the University of Illinois Ecological Research Area, which is 5 km NE of Urbana, Illinois. Half of the site has been continuously maintained in grassland by removal of invading trees and non-native shrubs, but the other half was released to succession in 1970 and required removal of woody vegetation during the summer of 1990. During our experiment vegetation remained dominated by bluegrass (*Poa pratensis*), fescue (*Festuca elatior*), and brome grass (*Bromus inermis*) throughout the study site, although spatial variation occurred. A variety of other, less important species occurred throughout the study site, with goldenrod (*Solidago altissima*), red clover (*Trifolium pratensis*), wild carrot (*Daucus carota*), wild parsnip (*Pastinaca sativa*), and wild blackberry (*Rubus alleghenensis*) being particularly widespread.

We built 16 enclosures (33 X 39 m or 0.13- ha) and conducted a 2 X 2 X 2 factorial experiment (with and without supplemental food, with and without access by predators, and with and without interspecific competitors) with 2 replicates during each of 3 growing seasons (1991-1993). Half of the pens had high sides (1-m high panels of galvanized roofing buried 0.5 m below ground) and were covered with netting to prevent

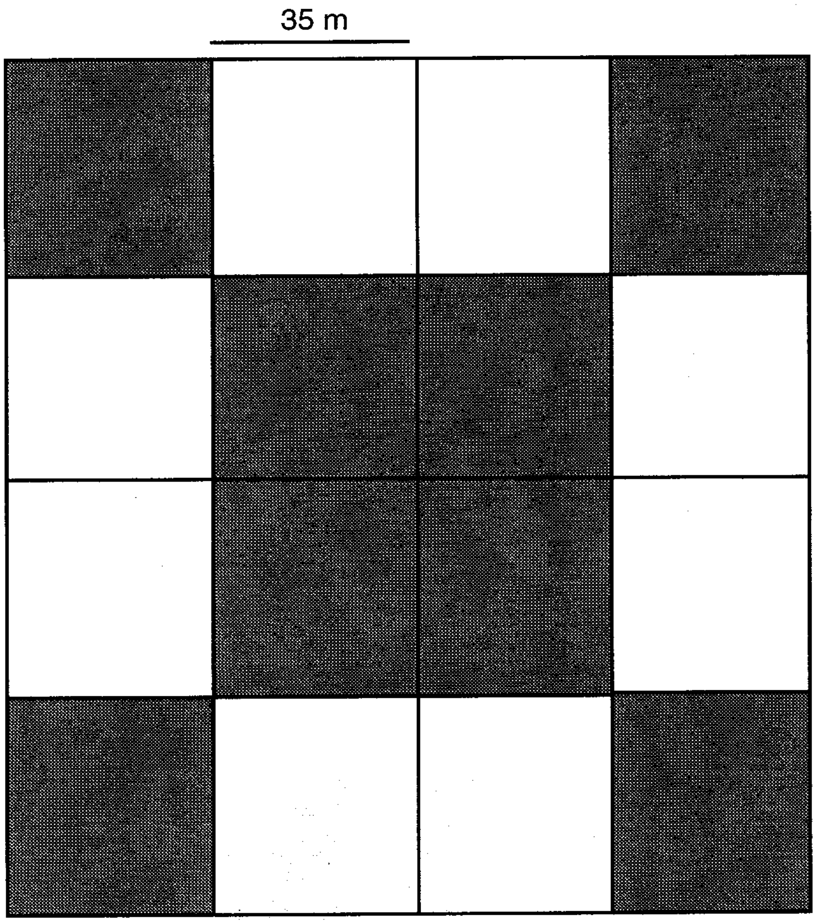

Figure 1. Spatial arrangement of 16 enclosures for 2 replicates of 8 treatments. The top set of 8 enclosures (block 1) were on higher ground (upslope) than bottom set of 8 (block 2). Each enclosure was 33 X 39 m. Predator-proof enclosures (shaded) remained in place for all 3 years, but combinations of food and competition treatments assigned randomly each year.

entrance by predators. The other half had low panels (0.3 m high) every 5 m and no netting so that predators could enter but voles still could not leave (trapping outside the pens never caught marked voles and no voles moved between pens). The 16 pens were arranged in a 4 X 4 square with the predator-proof pens along the diagonals (Fig. 1), an arrangement that ensured that predators had equal access to the pens they could enter. The pens that contained supplemental food or the competing species (meadow voles, *M. pennslyvanicus*) could be randomly assigned each year, but access by predators was not changed for logistical reasons.

All pens were staked in a 7 X 8 grid at 5-m intervals, and at each station a single Longworth trap was placed in a cage to protect them from interference from raccoons (Getz and Batzli, 1974). Feeding stations, consisting of a 300-ml jar containing rabbit chow (a high quality diet for voles; Batzli, 1985) and protected from disturbance by rabbits and deer by wire mesh, were established near every other trapping station in pens that received supplemental food. We checked feeding stations twice each week, refilled them as needed, and broadcast a handful of additional chow near each station at that time.

Populations of prairie voles were established in the pens in late May each year by introducing 4 pair of unrelated young adults that were born in an animal colony to voles collected earlier in nearby grassland. We monitored abundance of voles in each pen by live trapping for 3 nights and 2 days every 2 weeks from June to November (24 weeks each year). Voles were removed from all pens at the end of each growing season to allow recovery of the vegetation during winter and spring. Traps were closed from 1000 to 1600 hrs when temperature peaked during mid-summer to prevent heat-related deaths in traps. We marked each animal with a numbered monel ear tag. At every capture we noted the number, species, sex, reproductive condition, body weight (measured with a spring balance), general condition, and location for each animal. All animals, except those caught twice in dispersal sinks (described below), were released at their point of capture.

We introduced the same number of the target species (prairie voles) and the competing species (meadow voles) into the 8 pens with interspecific competition. We wanted to control the meadow vole populations so that their density did not vary widely among replicates, and we also wanted to vary the intensity of competition. Therefore, we cropped populations of meadow voles during each trapping session by removal of new recruits in an effort to maintain different target densities of adults with a 1:1 sex ratio each year -- 10 per pen in 1991, 20 per pen in 1992, and 40 per pen in 1993.

To reduce effects of fencing on population growth (Krebs et al., 1969; Ostfeld, 1994), dispersal sinks were created in 2 diagonal corners of each pen by removing vegetation along a 1-m wide strip so that the trapping stations in these corners were isolated from the rest of the pen. Traps in dispersal sinks remained open for 6 nights every week. The first time prairie voles were caught within a sink they were returned to the center of the pen; if caught again in a sink, they were considered dispersers and removed from the population. At the end of each growing season, all animals were removed from the pens by first live trapping for one week then snap trapping for 2 weeks. From these data we could estimate the effectiveness of our live trapping regime. After 3 nights of live trapping, approximately 90% of the voles known to reside within a pen had been captured, so we treated our measurements of abundance as enumerations (Boonstra, 1985).

Eight pens that contained the treatment combinations for one replicate had been built for an earlier experiment (Desy and Batzli 1989) and lay on the upper reaches of a gentle slope (Fig. 1). Newly built pens, which held the 8 treatments of the second replicate, were connected to the old pens but lower on the slope in an area that contained scattered trees (up to 15 cm dbh) and shrubs until they were removed in the summer of 1990. At the start of our experiment in 1991, vegetation in the new pens appeared to have more dicots and fewer monocots.

To document differences in vegetative composition in each pen, we clipped all plants in 16 randomly placed quadrats (20 X 50 cm) at ground level during late June and in late September of each year. All samples were air dried and sorted by species, condition (live or dead), and part of plant (shoot or head for monocots and forbs; stem, leaves, or head for woody dicots). Samples were then dried at 60°C to a constant weight. Because data for individual species varied widely among pens, we summed species and parts of plants into several composite variables: total live monocots, total live dicots, total live preferred food plants (determined by stomach content analysis, Haken and Batzli 1996), and total biomass (live plus dead as an indication of available cover). We used two 4-way ANOVAs when examining the relationships of treatments to the several measures of vegetation because there were no replicates of treatments within blocks for a given year. The main factors in both ANOVAs consisted of the 3 treatments (predation, food, and competition) and either block (with years as replicates) or year (with blocks as replicates). Results for data from June and September did not differ markedly, so we report only data from September, when preferred foods were much less abundant.

Because the summer of 1991 had a serious drought (see Results), unmanipulated control populations (+ predator, - food, - competitors) showed little growth, and abundance of voles differed dramatically from those in 1992 and 1993. We therefore standardized population abundance by calculating the difference of a given population (each unique combination of supplemental feeding, protection from predators, and presence of competitors) from the overall mean value for their replicate (block) each year. This standardization allowed analysis of results with 6 replicates of 8 treatments (2 blocks for each of 3 years, each block with $N = 8$ and mean values of 0) without the confounding effects of differences in population growth because of temporal patterns of weather or spatial (block) patterns in vegetation.

We examined the standardized data in several ways to quantify the relative strength of main factors and their interactions. Analyses of abundance of voles in response to manipulations were first conducted using fixed-factor ANOVA. Repeated measures analyses of abundance during the course of the season showed no substantial difference from analyses of final densities, so only the latter 3-way ANOVA is reported. Because the number of competitors (meadow voles) varied among years, we also used a general linear models approach (Ott, 1988) with the presence of meadow voles treated as a continuous variable and with supplemental food and predation treated as categorical variables. First, we constructed a complete model with all factors and all possible interactions. Then we compared Akaike scores (Akaike, 1973), corrected for relatively small sample size, to choose reduced models with the best combinations of explanatory power and number of parameters. We present only the 10 best models and the full model with Akaike criteria in tables as recommended by Anderson et al. (2000). All data were transformed as needed to meet assumptions of parametric tests.

To measure the use of pens by terrestrial predators during 1992-93 we maintained sand-tracking stations inside of each pen and adjacent to low panels that allowed access by predators. Each station was 0.75 X 0.75 m and filled with 2.5 cm of fine sand. Tracks found in the sand were identified according to Murie (1974), counted (number of animals), and the sand re-smoothed each morning. If the sand was not too wet (shortly after rainfall), mammalian predators left identifiable tracks, but snakes did not, even when we put them on the tracking station. Some pens had 15 gates and some had 14 gates, and the numbers of days that we could read the tracks varied among months. Therefore, we calculated number of mammalian predators (cats, foxes, and weasels) entering each pen per gate per day for each month (June-October). We used Pearson's correlation coefficient to examine the relationship between the frequency of tracks and the average number of voles in each pen that month (N = 8 pens X 5 months X 2 years = 80).

RESULTS

Weather

Summer weather patterns differed considerably during the 3 years of this experiment (Illinois State Water Survey Weather Data for Urbana, Illinois). In 1991 vegetation grew rapidly in late spring owing to unusually warm, wet weather (+3.8°C, +13.6 cm above 30-year averages for mean temperature and total precipitation in May, respectively), but a summer drought then occurred (+2.6°C, -8.7 cm in June; +0.6°C, -4.8 cm in July; and +1.3°C, -4.4 cm in August). During May through August of 1992 and 1993, average temperatures were close to or below normal (-0.9 to - 2.2°C and -0.6 to +0.9°C in 1991 and 1992, respectively) and total precipitation was above normal (+13.3 cm and +23.4 cm for 1991 and 1992, respectively).

Vegetation

Using log-transformed data, the first 4-way ANOVA (with years as replicates) indicated that only block (position on slope) had a substantial effect on preferred food plants, monocots, and dicots ($p < 0.003$ in all cases), except for a smaller effect of competition on monocots ($p = 0.02$), and that no interactions occurred. No substantial effects of any kind occurred for total biomass ($p > 0.25$ for all effects). The second 4-way ANOVA (with blocks as replicates and using log-transformed data) indicated relatively strong effects of year on preferred food plants ($p = 0.04$) and for live dicots ($p = 0.03$), but no other strong effects ($p > 0.18$ in all cases) for either. Neither year nor any other factor strongly influenced live monocots or total biomass ($p > 0.13$ in all cases).

To examine the pattern and strength of effects we summarized data for September vegetation by block and year (Fig. 2). Preferred food plants were much more abundant downslope and were particularly abundant downslope in 1992 (Fig. 2A; 2-way ANOVA on log-transformed data, $p < 0.003$ for main factors and $p = 0.05$ for interaction). Live monocots were much more abundant upslope and more abundant in 1992, but the difference associated with location decreased in 1993 (Fig. 2B; $p \leq 0.005$ for main factors, $p = 0.05$ for interaction). Live dicots were much more abundant downslope, much less abundant in 1992, and showed a much smaller effect of location in 1992 (Fig. 2C; $p < 0.004$ for main factors, $p = 0.02$ for interaction). Total biomass (cover) did not

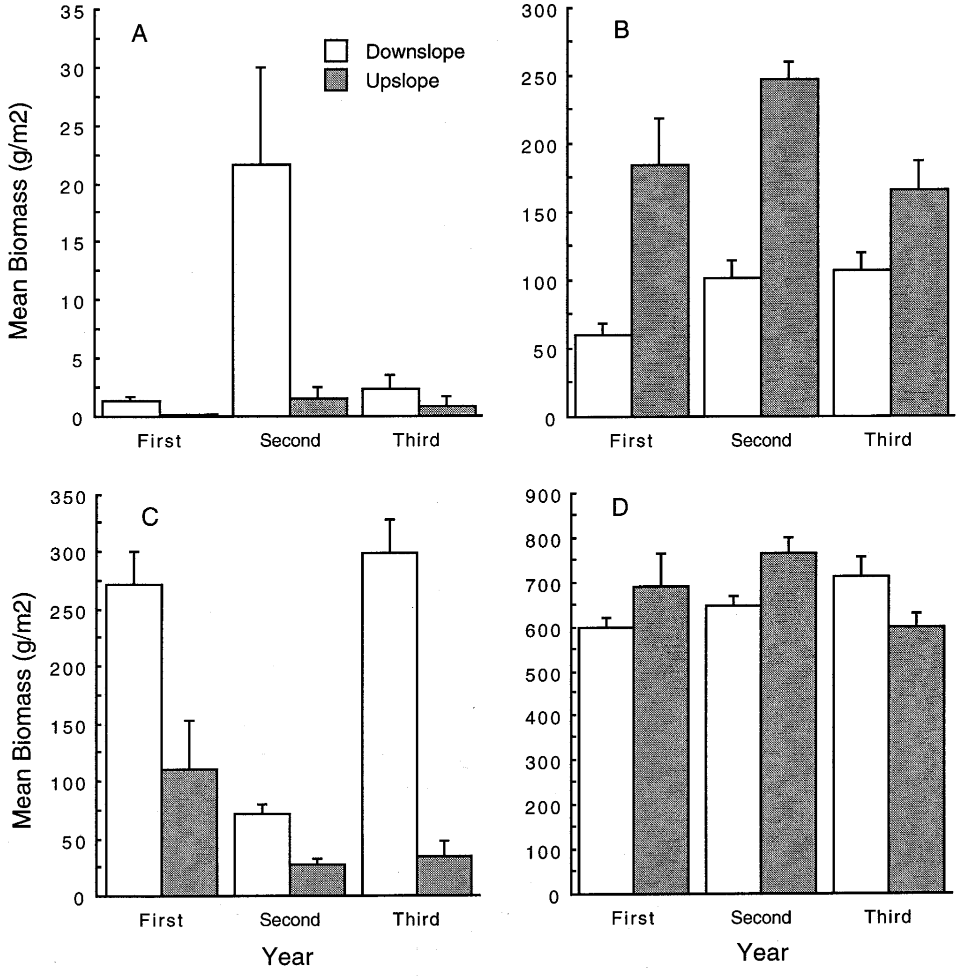

Figure 2. Mean biomass (dry weight per m2) of live food plants (A), live monocots (B), live dicots (C), and total live and dead plant material (D) in two blocks (upslope and downslope) over 3 years. Vertical lines indicate ± 1 SE, *N* = 8 in all cases.

differ among years or with position on the slope, but was greater upslope in 1991 and 1992 and greater downslope in 1993 (Fig. 2D; $p > 0.15$ for main factors, $p = 0.001$ for interaction).

Vole Populations

Control populations of prairie voles (+ predation, - food, - competition) showed little or no growth during 24 weeks of the growing season in 1991, whereas densities in 1992 and 1993 increased 3- to 5-fold (Fig. 3, $N = 2$ each year). Similarly, across all treatments ($N = 16$ each year) the number of voles doubled in 1991 but increased 5- to 6-fold in the latter 2 years (mean number per pen ± 1 SE in final trapping, 22.8 ± 4.2 for 1991, 59.1 ± 8.5 for 1992, 55.6 ± 7.5 for 1993). Differences between 1991 and both 1992 and 1993

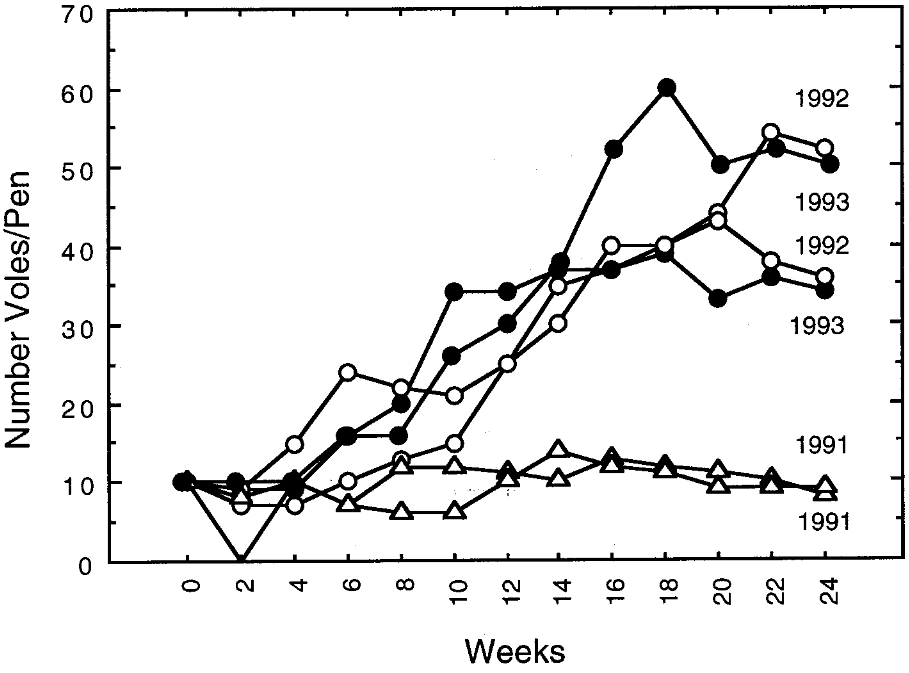

Figure 3. Population growth of prairie voles in 2 replicates of unmanipulated controls (+ predation, - food, and - competition) during the growing season for each year of experiment. One population needed to be restarted in 1991.

were highly significant (for log-transformed data, $t = 4.44$, $p = 0.0001$ and $t = 3.23$, $p = 0.003$, respectively), but the difference between 1992 and 1993 was not ($t = 0.303$, $p = 0.764$).

Because of the strong effect of block (upslope or downslope replicate) on vegetation, we also tested for differences in final density of voles between blocks within each year. Although there was little difference between blocks in 1991 when mean number per pen remained relatively low (22.8 ± 6.4 for downslope and 28.8 ± 5.6 for upslope, $N = 8$ in both cases), differences between blocks for 1992 and 1993 were substantial and similar (71.2 ± 15.9 for downslope, 46.9 ± 4.0 for upslope in 1992; 66.6 ± 12.2 for downslope, 44.6 ± 7.7 for upslope; $N = 8$ in all cases). Combined data for 1992 and 1993 indicated an overall difference between blocks for mean number of voles per pen (68.9 ± 9.7 for downslope and 45.8 ± 4.2 for upslope, $N = 16$ in both cases; $t = 1.993$, $p = 0.055$, for log-transformed data).

Results of 3-way fixed-factor ANOVA for standardized densities with predation, food, and competition as the main factors (including competition as a categorical variable and ignoring differences in abundance of meadow voles among treatments) indicated that food had positive effects, but predation and competition had negative effects on final densities of prairie voles (Fig. 4, Table 1). No factor interactions were significant. As can be calculated from the sum of squares in Table 1, the combined factors explained 36.2% of the variance. Predation accounted for over twice as much variance (18.7%) as either food (8.7%) or competition (8.7%). Curiously, food and

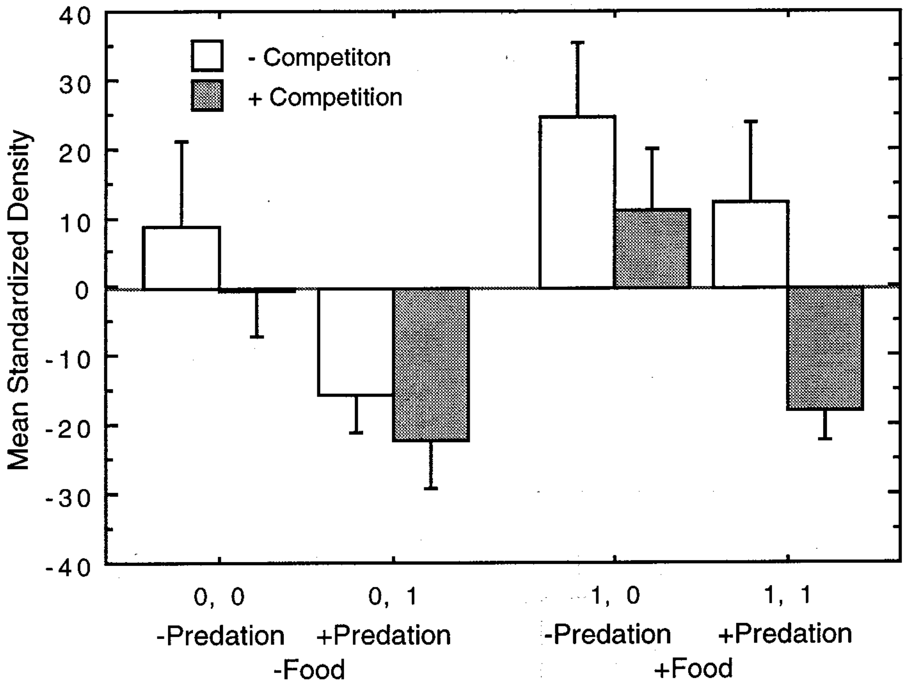

Figure 4. Mean standardized densities (difference between voles per pen for treatment and block mean) of prairie voles under 8 combinations of treatments (+ or - access by predators, + or - supplemental food, and + or - presence of interspecific competitors). Vertical lines indicate ± 1 SE, N = 6 in all cases.

Table 1. Results of a 3-way fixed-factor ANOVA of standardized densities of prairie voles (difference between each treatment and block means). All treatment combinations included (*N* = 48).

Factor	*d.f*	Sum of Squares	*F*	*p*
Predation	1	5742	12.37	0.001
Food	1	2685	5.78	0.021
Competition	1	2685	5.78	0.021
Pred X Food	1	16	0.03	0.857
Pred X Comp	1	144	0.31	0.581
Food X Comp	1	581	1.25	0.270
Pred X Food X Comp	1	276	0.59	0.446
Residual	40	18568		
Total	47	30697		

Table 2. Akaike criteria for linear models of prairie vole abundance using all treatment combinations (*N* = 48). Standardized density (difference between each treatment and block mean) was used as the dependent variable, and predation (p), food (f), number of competitors (mp), and their interactions (x) were used as independent variables. K = number of parameters in model, AIC_c = Akaike information criterion, ΔAIC = difference between AIC_c and minimum AIC_c, and ω = probability that is the best model.

Model	K	AIC_c	ΔAIC	ω
p, f, mp	4	296.463	0.000	0.370
p, f, mp, pxmp	5	298.695	2.232	0.121
p, f, mp, fxmp	5	298.783	2.320	0.116
p, f, mp, pxfxmp	5	298.869	2.406	0.111
p, f, mp, pxf	5	298.954	2.491	0.106
p, mp	3	300.946	4.483	0.039
p, f, mp, pxmp, fxmp	6	301.146	4.683	0.036
p, f	3	301.251	4.788	0.034
p, f, mp, pxmp, pxfxmp	6	301.313	4.850	0.033
p, f, mp, fxmp, pxfxmp	6	301.373	4.910	0.032
full model	8	306.712	10.249	0.002

competition had the same overall treatment means, which explains their identical strength, even though they differed among replicates.

In spite of the initial analysis, a careful look at the mean values for the overall data on abundance presented in Fig. 4 suggested 2 possible 2-way interactions. First, the difference between the mean standardized abundance of prairie voles for treatments with and without predators was greater when competitors were present than when they were not (ignoring the food treatment); 25.3 with competitors (-20.2 ± 4.0 and +5.2 ± 5.6 with and without predators, respectively; $t = 3.69$, *d.f.* = 22, $p = 0.001$) and 18.4 without competitors (-1.7 ± 7.4 and +16.7 ± 8.1 with and without predators, respectively; $t = 1.68$, *d.f.* = 22, $p = 0.11$). Also, the difference between treatments with and without food was greater when competitors were not present than when they were (ignoring the predation treatment); 21.9 without competitors (+18.4 ± 7.7 and -3.5 ± 7.3 with and without food, respectively ($t = 2.17$, *d.f.* = 22, $p = 0.04$) and 8.0 with competitors (-3.5 ± 6.5 and -11.5 ± 5.6 with and without food, respectively; $t = 0.86$, *d.f.* = 22, $p = 0.40$).

Because ANOVA uses categorical variables, it did not include the differences in the abundance of competitors (meadow voles) during different years, differences that we purposely maintained (mean number of meadow voles for weeks 10-24, 6.6 ± 1.9 for 1991, 23.6 ± 3.0 for 1992, 41.5 ± 3.3 for 1993, $N = 8$ in all cases; $p < 0.02$ for all comparisons with log-transformed or untransformed data). We therefore developed linear regression models in which competition (the number of meadow voles) was included as a continuous variable while treatments for predation and supplemental

Table 3. Results of a 3-way fixed-factor ANOVA of standardized densities of prairie voles (difference between each treatment and block mean) using only treatment combinations that included competition by meadow voles (N = 24). Year served as a surrogate for different levels of competition.

Factor	*d.f.*	Sum of Squares	*F*	*p*
Predation	1	3851	18.76	0.001
Food	1	384	1.87	0.196
Year	2	1516	3.69	0.056
Pred X Food	1	81	0.39	0.542
Pred X Year	2	1425	3.47	0.065
Food X Year	2	2	0.00	0.996
Pred X Food X Year	2	363	0.88	0.439
Residual	12	2463		
Total	23	10085		

Table 4. Akaike criteria for linear models of prairie vole abundance using only treatments that included competition by meadow voles (N = 24). Difference between each treatment and block mean used as the dependent variable, and predation (p), food (f), numbers of competitors (mp), and their interactions (x) used as independent variables. K = number of parameters in model, AIC_c = Akaike information criterion, ΔAIC = difference between AIC_c and minimum AIC_c, and ω = probability that this is the best model.

Model	K	AIC_c	ΔAIC	ω
p, mp	3	137.932	0.000	0.243
p	2	138.000	0.068	0.235
p, f, mp	4	138.583	0.651	0.175
p, f	3	139.103	1.171	0.135
f, pxf, pxmp, fxmp, pxmpxf	6	140.802	2.870	0.058
pxf, pxmp, pxmpxf	4	140.938	3.006	0.054
f, pxf, pxmp, pxfxmp	5	141.691	3.759	0.037
pxmp	2	142.079	4.147	0.031
pxmp, pxfxmp	3	142.629	4.697	0.023
pxf, pxmp	3	144.464	6.532	0.009
full model	8	148.786	10.854	0.001

food were represented by dummy variables. The best model, selected by Akaike criteria, used just predation, food, and competitors without interactions (Table 2), a result consistent with 3-way ANOVA. The best model accounted for a proportion of the variance in abundance of prairie voles (adj. $R^2 = 0.333$) that was similar to results from the 3-way ANOVA (0.362). Standardized coefficients again indicated that predation had a substantially greater effect on abundance of voles than did food or competition (-0.489, +0.310, and -0.323, respectively). The next 4 models were less likely to be correct individually, but the sum of the probabilities for models 2-5 being correct (Table 2) exceeded that of the best model. Each of the possible interactions was included in one of those models, and the same interactions as those suggested by examining the overall data were included in model 2 (predation X competition) in model 3 (food X competition).

A shortcoming of analyzing all the data with general linear models, however, was that the experimental design became unbalanced because treatments with no competition were over-represented (half the values for density of meadow voles were 0). To examine the possibility that interactions among the factors might be stronger in a balanced data set, we also conducted analyses using only treatments that included competition (3 replicates of 8 treatments, $N = 24$). Results from a 3-way ANOVA (Table 3) that used predation, food, and year (a surrogate for 3 levels of competition) as major factors indicated a negative effect of predation ($p = 0.001$), a negative effect of competition ($p = 0.056$), and a predation X competition interaction ($p = 0.065$). As calculated from the sum of squares, these factors accounted for about twice as much of the variance in abundance of prairie voles (67.3%) as the 2 previous analyses (33.3% and 36.2%), again with predation (38.2%) accounting for over twice that of competition (15.0%) or their interaction (14.1%). Supplemental food accounted for only 3.8% of the variance in this analysis.

A general linear models approach that included only treatments with competitors identified 4 models with probabilities of being correct that ranged from 13.5% to 24.3% (Table 4). These 4 best models all included only main factors and no interactions; one included predation and competition (adj. $R^2 = 0.395$), one included predation only (adj. $R^2 = 0.354$), one included predation, food, and competition (adj. $R^2 = 0.439$), and one included predation and food (adj. $R^2 = 0.365$). Standardized coefficients indicated that predation always had 2-3 times the effect of any other factor (-0.720 for predation and -0.276 for competition in model 1; -0.618 for predation in model 2; -0.792 for predation, +0.224 for food, and -0.301 for competition in model 3; -0.618 for predation and +0.195 for food in model 4).

Visitation by Predators

Cats were by far the most common mammalian predator (93% of all tracks), and the frequency of their tracks showed a strong positive correlation with the total density of voles in a pen ($r = 0.581$, $d.f. = 78$, $p < 0.0001$). Adding in tracks of foxes and weasels did little to change the correlation ($r = 0.567$, $d.f. = 78$, $p < 0.0001$). The correlations dropped when only prairie vole density was considered ($r = 0.493$ for cats only and $r = 0.485$ for all predators).

DISCUSSION

In general our results support Pearson's hypothesis that predation strongly reduces the growth rate of vole populations whether they are increasing or decreasing. Although predation, available food, and competition all had substantial effects on the abundance of prairie voles, multiple analyses generally indicated that predation accounted for at least twice as much of the observed variation in population growth as did the other factors. Furthermore, the 3 main factors largely operated in an additive manner with relatively weak indications of factor interactions.

The strongest evidence for factor interaction involved a greater effect of predation when competitors were present, as indicated by comparison of differences among means in the overall data (Fig. 4), by the general linear models analysis of all data (Table 2), and by ANOVA using only treatments with competition (Table 3). Net per capita recruitment (the difference between per capita recruitment and per capita mortality) is density-dependent for prairie voles (Lin and Batzli 2001), which accounts for the reduction of population growth at the end of the growing season (Fig. 2.) and suggests that mortality from predators may increase as density of voles increases. Density of voles generally was greater in pens with competitors (prairie voles + meadow voles) than in pens without competitors (prairie voles only), as shown by mean monthly densities (45.5 ± 3.4 with competitors and 36.2 ± 3.6 without competitors, $t = 1.88$, *d.f.* = 78, $p = 0.065$), and activity of mammalian predators in pens increased with increasing density of voles. Thus, the interaction between predation and competition apparently occurred because of enhanced activity of predators in pens with increased overall density of voles. If anything, this interaction increases the support of Pearson's hypothesis offered by our results.

A second factor interaction may have occurred between food and competition; the impact of food supply on abundance of prairie voles decreased in the presence of competitors. This finding was supported by comparison of differences among means for the overall data (Fig. 4), the reduction in the importance of food in the ANOVA for data with competition (Table 3) compared to the results for all data (Table 1), and by the general linear models analysis of all data (Table 2). This interaction would lead to an underestimate of the importance of food in limiting population growth of prairie voles.

One might argue that our experiment underestimated the importance of available food because a relatively good food supply existed in old pasture habitat even without supplementation. No doubt the relative importance of food would increase if an experiment such as ours were conducted in a habitat with food supplies closer to the minimal needed to support prairie voles, such as found in restored tall grass prairie (Cole and Batzli 1979). While poorer in food supply, such habitat might also provide greater cover, thereby reducing the impact of predation. Thus, the relative importance of factors for population growth likely depends on the habitat in which experiments are conducted.

Habitat changes may also influence the results of experiments completed at the same location at different times. Thus, we found the effect of predation on prairie voles to be about twice that of food supply, whereas Desy and Batzli (1989), who conducted their study using similar methods and at the same site as the upslope block of this experiment, concluded that the effects of supplemental food and protection from predation were about equal. Results from their 2-way ANOVA on vole densities after 24 weeks did indicate a somewhat stronger effect of predation (29.0% of variance accounted for by food vs. 37.3% by predation), but the difference was far less than found in our experiment. These quantitatively different results could be explained by variation in the natural food supply on our study site. Recall that the downslope block had greater availability of preferred foods in September (Fig. 2), so the response of voles to supplemental food could have been reduced in this block. Our data showed the opposite trend, however. Final absolute density of prairie voles increased by an average of 11.2 (32%) upslope when supplemented by food (45.7 ± 5.1 with food and 34.5 ± 5.0 without food, $t = 1.56$, $d.f. = 22$, $p = 0.13$) and by an average of 18.7 (42%) when supplemented by food downslope (62.9 ± 12.9 with food and 44.2 ± 9.6 without food, $t = 1.17$, $d.f. = 22$, $p = 0.26$).

Finally, the greater relative impact of predators in our results may have simply reflected a greater density of predators. Unfortunately, we have no data on densities of predators during our study, although we do know that a wide variety of mammalian, avian, and reptilian predators occurred at our study site (Lin and Batzli, 1995). Whatever the cause of differences in the results of the 2 studies, they generally agreed that predation substantially reduces the rate of population growth of prairie voles even as densities increase during the growing season.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Akaike, H.
1973 Information theory as an extension of the maximum likelihood principle. Pp. 267-281 in Second International Symposium on Information Theory (Petrov, B. N., and F. Csaki, eds.). Akademiai Kiado, Budapest, Hungary.

Anderson, D. R., K. P. Burnham, and W. L. Thompson
2000 Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64:912-923.

Batzli, G. O.
1985 Nutrition. Pp. 779-811 in Biology of New World *Microtus* (Tamarin, R., ed.). American Society of Mammalogists Special Publication 8.

Batzli, G. O., S. J. Harper, Y. K. Lin, and E. A. Desy
1999 Experimental analyses of population dynamics: scaling up to the landscape. Pp. 107-127 in Landscape Ecology of Small Mammals (Barrett, G. W., and J. D. Peles, eds.). Springer-Verlag, New York, New York, USA.

Boonstra, R.
1985 Demography of *Microtus pennsylvanicus* in southern Ontario: enumeration versus Jolly-Seber estimation compared. Canadian Journal of Zoology 55:1166-1175.

Cole, F. R., and G. O. Batzli
1979 Nutrition and population dynamics of the prairie vole, *Microtus ochrogaster*, in central Illinois. Journal of Animal Ecology 48:455-470.

Desy, E. A., and G. O. Batzli
1989 Effects of food and predation on density of prairie voles: a field experiment. Ecology 70:411-421.

Elton, C. S.
1924 Periodic fluctuations in the numbers of animals: their causes and effects. British Journal of Experimental Biology 2:119-163.

Getz, L. L., and G. O. Batzli
1974 A device for preventing disturbance of small mammal live traps. Journal of Mammalogy 55:447-448.

Haken, A. E., and G. O. Batzli
1996 Effects of food availability and competition on diets of prairie voles. Journal of Mammalogy 77:315-324.

Hanski, I., H. Henttonen, E. Korpimäki, L. Oksanen, and P. Turchin
2001 Small rodent dynamics and predation. Ecology 82:1501-1520.

Huitu, O., M. Koivula, E. Korpimäki, T. Klemola, and K. Norrdahl
2003 Winter food supply limits growth of northern vole populations in the absence of predation. Ecology 84:2108-2118.

Klemola, T., M. Koivula, E. Korpimäki, and K. Norrdahl
2000 Experimental tests of predation and food hypotheses for population cycles of voles. Proceedings of the Royal Society of London Series B 267:351-356.

Korpimäki, E., and K. Norrdahl
1998 Experimental reduction of predators reverses the crash phase of small-rodent cycles. Ecology 79:2448-2455.

Korpimäki, E., K. Norrdahl, T. Klemola, T. Pettersen, and N. C. Stenseth
2002 Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. Proceedings of the Royal Society of London Series B 269:991-997.

Korpimäki, E., L. Oksanen, T. Oksanen, T. Klemola, K. Norrdahl, and P. B. Banks
2005 Vole cycles and predation in temperate and boreal zones of Europe. Journal of Animal Ecology 74: 1150-1159.

Krebs, C. J., B. L. Keller, and R. H. Tamarin
1969 *Microtus* population biology: demographic changes in fluctuation populations *Microtus ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecology 50:587-607.

Lin, Y. K., and G. O. Batzli
1995 Predation on voles: an experimental approach. Journal of Mammalogy 76:1003-1012.

2001 The influence of habitat quality on dispersal, demography, and dynamics of voles. Ecological Monographs 71:245-275.

Lotka, A. J.
1925 Elements of Physical Biology. Williams & Wilkins, Baltimore, Maryland, USA. 463 pp.

Murie, O. J.
1974 Animal Tracks (2nd ed.). Houghton Mifflin Co., Boston, Massachusetts, USA. 374 pp.

Ostfeld, R. S.
1994 The fence effect reconsidered. Oikos 70:340-348.

Ott, L.
1988 An Introduction to Statistical Methods and Data Analysis (3rd ed.). PWS-KENT Publishing, Boston, Massachusetts, USA. 835 pp.

Pearson, O. P.
1964 Carnivore-mouse predation: an example of its intensity and bioenergetics. Journal of Mammalogy 45:177-188.

1966 The prey of carnivores during one cycle of mouse abundance. Journal of Animal Ecology 35:217-233.

1971 Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). Journal of Mammalogy 52:41-49.

1985 Predation. Pp. 535-566 in Biology of New World *Microtus* (Tamarin, R., ed.). Special Publication 8, The American Society of Mammalogists.

Taitt, M. J., and C. J. Krebs
1983 Predation, cover, and food manipulations during a spring decline *of Microtus townsendii*. Journal of Animal Ecology 50:837-848.

Volterra, V.
1926 Fluctuations in the abundance of a species considered mathematically. Nature 118:558-600.

THE EVOLUTION OF ENERGETICS IN BIRDS AND MAMMALS

LA EVOLUCIÓN DE LA ENERGÉTICA EN AVES Y MAMÍFEROS

Brian K. McNab[1]

ABSTRACT

Energetics effectively integrates diverse aspects of the natural history of an organism with conditions in the environment. This integration is most evident in endotherms as a result of their high cost of maintenance and the limited quantities and qualities of resources in most environments. Endotherms that show the greatest ecological and behavioral diversity have the greatest diversity in energetics. Basal energy expenditures in endotherms are correlated principally with body mass, but also with body composition and its relation to activity level, food habits, climate and its surrogates latitude and altitude, as well as life with restrictive habits or in restrictive environments. These factors in combination usually account for over 95% of the variation in basal rates of metabolism in birds and mammals. One of the most restrictive environments are oceanic islands, where many endemic birds and some endemic bats have low energy expenditures compared to their continental relatives. An extreme reaction to life on oceanic islands is the evolution in some birds of a flightless condition with its associated reduction in energy expenditure. Variation in field energy expenditures,

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[1] I am honored to contribute to a volume dedicated to the memory of Paynie Pearson. I started my graduate work at the University of California at Berkeley in 1955 to work with Paynie, having just graduated from Oregon State College (now University) and having worked that summer with Frank Pitelka on lemmings at Point Barrow, Alaska. Paynie was in Argentina in the fall and returned to Berkeley before Christmas. In early January he had a gathering at his house for his graduate students and for me as his presumptive student. After feeding us, he notified us that we needed to find other chairmen because he was resigning his university position! After considering every possible alternative, including a kind offer from Seth Benson, the mammalogist—who queried whether I was a "thermocouple man"-- I left and went to the University of Wisconsin, at Madison, to work with Paynie's friend, Peter Morrison. Paynie set an example of how the energetics and ecology of birds and mammals could be meaningfully combined, thereby giving analytical insights into the factors responsible for the organic diversity found in nature.

Pp. 67-110 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

independent of body mass correlates with mass-independent variation in basal rate both in birds and mammals, which suggests that field expenditures also correlate with the factors that appear to influence basal rates. The attempt to account for the variation in energetics with phylogenetic analyses fails because phylogeny cannot be separated from the ecological and behavioral characteristics of species. Oliver Pearson, the dedicatee of this volume, was pivotal in the early application of energetics to the natural history of birds and mammals.

Key words: Basal metabolic rate, field energy expenditure; island endemics; marsupials.

RESUMEN

La energética integra efectivamente diversos aspectos de la historia natural de las relaciones de un organismo y las condiciones ambientales. Esta integración es más evidente en los endotermos, como resultado de su alto costo de manutención y las limitadas cantidades y calidades de recursos en la mayor parte de los ambientes. Los endotermos que muestran la mayor diversidad ecológica y etológica tienen la mayor diversidad energética. Los gastos basales de energía en los endotermos están correlacionados principalmente con la masa corporal, pero también con la composición del cuerpo y su relación con el nivel de actividad, los hábitos alimenticios, el clima y sus sucedáneos la latitud y la longitud, así como con la vida de hábitos restringidos o en ambientes restrictivos. La combinación de estos factores normalmente explica más del 95% de la variación en tasas de metabolismo basal en aves y mamíferos. Uno de los ambientes más restrictivos son las islas oceánicas, donde muchas aves y algunos murciélagos endémicos tienen bajos gastos de energía comparados con sus parientes continentales. Una reacción extrema a la vida en islas oceánicas es la pérdida evolutiva, en ciertas aves, de la capacidad de vuelo. Independiente de la masa corporal, la variación en los gastos de energía en el campo se correlaciona con cambios en la tasa metabólica basal independientes de la masa corporal, lo cual sugiere que estos también se correlacionan con aquellos factores que parecen influir las tasas basales. Los intentos de dar cuenta de la variación en la energética con análisis filogenéticos fallan porque la filogenia no se puede separar de las características ecológicas y comportamentales de las especies. Oliver Pearson, a quien se dedica este volumen, tuvo un papel pionero y crucial en la aplicación de la energética a la historia natural de aves y mamíferos.

Palabras claves: Tasa metabólica basal, gasto energético en el campo, especies endémicas de islas, marsupiales.

Integration of the anatomical, physiological, behavioral, and environmental characteristics of birds and mammals has been difficult, often because the analytical approach to each aspect of existence developed its own methodology and terminology. This difficulty can be reduced through the use of a common metric, such as energy expenditure. Energetics is an especially appropriate tool to integrate various aspects of a species' biology because all aspects require an expenditure of energy for their development, use, and maintenance. Furthermore, these expenditures are influenced by the physical characteristics of the environments in which species live, by the abundance and properties of the resources used, and by the presence of conspecifics, competition, and predation in the environment, so the use of energetics potentially integrates an organism's performance with the environment in which it lives.

This approach to natural history can be spottily traced back at least to the work of Carl Bergmann, who in 1848—11 years before Darwin's *On the Origin of Species*—published a treatise on the relationship among the energetics of birds and mammals, their body size, and distribution. A few articles on the energetics of wild mammals were written in the mid-1940's by Oliver P. Pearson, the dedicatee of this festschrift, and Peter R. Morrison, both of whom had been undergraduates at Swarthmore College, where they encountered Lawrence Irving and Per Scholander on the faculty, and later were graduate students at Harvard.[2]

A coherent beginning to the study of the interaction between avian and mammalian physiology and ecology was given in 1950, 102 years after Bergmann, by Scholander, Irving, and colleagues in 3 papers published on the energy expenditure of arctic and tropical species. We have progressed sufficiently in the ensuing 55 years that some system-wide patterns in the energy expenditure of birds and mammals have been described, but as we shall see, these patterns are complex, reflecting the diversity in endotherms and in their responses to the environments in which they live.

Science always attempts to find overriding principles that transcend the particulars of specific observations. This approach, of course, reached its zenith in physics, but the extent to which such generalizations are possible in the infinitely more complex systems of biology, especially at the level of organismal and community ecology, is contentious. The search for generalizations in organismal biology at times appears to be an act of desperation. Its principal difficulty is the very large number of degrees of freedom in biological, and especially ecological, systems. As the degrees of freedom increase, the possibility of giving a simple analysis, as represented by an equation, decreases, except as the generalization describes a trend devoid of specifics. Indeed, this desire for analytical simplicity and generality is why so much effort has been given to attempts to derive a theoretical basis for the scaling of rate of metabolism in organisms (see later). Rate of metabolism, of course, is but one aspect of biology.[3] I am not arguing that no generalizations are possible (as we shall see), but they usually are restricted to one aspect of organic existence. Indeed, the most interesting

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[2] Pearson (1947) and Morrison (1948) together measured the rate of metabolism of some 14 species of mammals, but amusingly could not agree on how to analyze and present the data, so each published their own versions of the data, Pearson (according to Morrison) "…considering the more mammalogical aspects…," and Morrison (according to Pearson) "…a more specialized [physiological] analysis of much of the data." This difference in viewpoint continued throughout their careers. With my switch from Berkeley to Madison, I became an ecologist marginally surviving in a physiology laboratory.

[3] Some time in the 1980's I met Paynie at the mammal meetings and he asked me what I was working on. I replied that I had been measuring the metabolism of some group of mammals. He noted that I had already done that and wasn't I going to do anything else? This question neatly contrasted 2 radically different approaches to science. Paynie's research career was wide-ranging and only occasionally examined the same questions, whereas my view is that one can rarely clarify a complex phenomenon without an extended and diverse approach to the same topic. Each approach has its own merits.

generalizations concerning organismal performance are as likely to be found in the residual variation around general trends, as in the trends themselves, and they usually involve many restrictive clauses. It is in the dissection of residual variation around general trends that we increase our understanding of organismal performance and thereby our models of performance become more realistic. This is the approach used here.

THE HIGH COST OF ENDOTHERMY

By restricting this discussion to the energetics of birds and mammals, it concerns vertebrates that have the highest rates of metabolism. High rates occur in part because these vertebrates maintain body temperature independent of variations in ambient temperature by balancing the heat lost to the environment with heat generated through metabolism; this homeostatic system is endothermy. Endothermic temperature regulation can be exceedingly expensive, most notably when ambient temperatures are low, heat loss is great, and heat production is high, which is the case during temperate and polar winters. But even the minimal cost of endothermy, the basal rate of metabolism, which occurs in a range of mild ambient temperatures called the zone of thermoneutrality, when the endotherm is post-absorptive and inactive (McNab, 1997), is 8-10 times the rate of metabolism of equally-sized ectotherms at the same body temperature.

Since energy expenditure cannot exceed energy income over extended periods, the high energy expenditures of endotherms increase the likelihood that the expenditures will be subject to selection because they must be fulfilled by collection from the environment of resources that may be limited in quantity or quality. Concern for this aspect of energy expenditure ultimately diverts the discussion from physiology to ecology. The use of daily torpor, seasonal torpor, and migration by endotherms in highly seasonal environments is evidence of a limitation in resource availability. Furthermore, limits to the geographical distribution of birds and mammals often are byproducts of a limit to energy expenditure (Root, 1988; McNab, 2002a). I here examine the factors that influence the energy expenditure of endotherms and how it is adjusted to conditions in the environment, and then attempt to put these data into an evolutionary context.

Energy expenditure takes many forms. Ultimately, field expenditures are those that are most relevant to the life of organisms because they reflect an organism's requirements and the conditions encountered in the environment. Until recently, however, field expenditures were difficult to measure, or even to estimate, so much attention was given to the expenditures of organisms under controlled conditions in the laboratory. This approach has been highly productive, especially in establishing a "standard" rate of metabolism, but it will not generally substitute for field measurements. Nevertheless, an examination of the factors responsible for the appreciable variation in the standard rate will give insight into the energy expenditure of endotherms. Standard energetics in endotherms refers principally to the basal rate of metabolism.

FACTORS THAT INFLUENCE THE BASAL RATE OF METABOLISM IN ENDOTHERMS

A variety of factors influence the basal rate of endotherms. These include body mass, body composition, food habits, climate, and life with restrictive habits or in restrictive environments, factors that emphasize the ecological (i.e., the economic) basis of endothermy.

Body Mass. Body mass is the single most important factor influencing the basal energy expenditure of mammals and birds (Kleiber, 1932; Aschoff and Pohl, 1970). For example, of 320 species of mammals (McNab, 1988a), body mass directly accounts for 50.3% of the variation in basal rate when total basal rate is plotted against body mass. However, when both basal rate and body mass are logged, $\log_{10}$ body mass now accounts for 95.6% of the variation in $\log_{10}$ basal rate. Such a pattern between standard rate of metabolism and body mass is universal in that it applies to all animals (Hemmingsen, 1960). Basal rate therefore is usually described as a power function in which it is proportional to body mass raised to a power, b, which is the fitted slope of the log-log curve. This power usually varies from ca. 0.60 to 0.80. Because the power of mass is < 1.00, mass-specific rates of metabolism are proportional to $m^b/m^{1.00} = m^{b-1.00}$: i.e., they are proportional to between $m^{-0.40}$ and $m^{-0.20}$ (McNab, 1988a).

Much has been made as to whether a universal power of mass exists for energy expenditure and if so, the two favored powers are 0.67 (Heusner, 1991; White and Seymour, 2003) and 0.75 (MacMahon, 1973; West et al., 1997, 1999; Banavar et al., 1999, 2002). The analyses of West et al. have been criticized both from the viewpoint of their underlying mathematics and applicabilities (Kozłowski and Konarzewski, 2004), whereas the analysis of White and Seymour suffers from the use of 'phylogenetic contrasts' (see *Difficulties* below).

Several problems exist with the concept that one unique power applies to all organisms. For example, the fitted power for a set of data almost never is 0.67 or 0.75, and its actual value depends on how data are organized (Hayssen and Lacy, 1985; McNab 1988a). Furthermore, the fitted power depends on whether factors other than body mass are brought into the analysis (McNab and Ellis, 2006). The presence or absence of these factors potentially produces the correlations of b seen with taxonomic group because factors like food habits and climate are themselves correlated with body mass. In fact, nearly all discussions of the universality of a power are restricted to analyses that use body mass as the only variable, thereby ignoring the existence of residual variation in basal rate, which often is appreciable.

A radically different theoretical approach to the scaling of rate of metabolism was derived from the concept of a "cascade" of interacting and potentially limiting biochemical steps. Each limiting step was characterized by its own mass-power relation and modified by a coefficient that reflects the level at which the limitation occurs, these steps summing to produce a range of scaling powers (Darveau et al., 2002, Hochachka et al., 2003). This approach potentially accounts for the difference in the scaling of maximal and basal rates of metabolism, which cannot be accounted for by advocacy for one, and only one, limitation to metabolism. The cascade approach potentially permits the taxonomically and ecologically correlated variation in b to be accounted for by variations in body composition, mitochondrial density, protein turnover, cardiac output, etc. (i.e., by variations in energy demand and supply).

The principal limitation of the cascade approach is that the scaling of whole-animal metabolism is derived from biochemical-step scaling, and thereby ignores the cause for scaling *per se* (West et al., 2003). Hochachka et al. (2003) argued that if the basal rate were scaled in an isometric manner, large mammals would have no capacity to increase scope for activity because of a limit to maximal metabolism. Thus, they implied that the scaling of basal metabolism with a power < 1.0 was a means of assuring an adequate aerobic scope at a large mass, an explanation that verges on having a teleological basis. Banavar et al. (2003) have also criticized the cascade approach for mathematical inconsistencies.

The available data on basal rate from mammals are much more complete than those from birds: although there are half as many species of mammals as birds, more than twice as many mammals have been measured as birds. The great deficit of data in birds is that tropical species have been nearly ignored: of some 2200 Neotropical passerines belonging to 29 families, only 7 endemic species belonging to 5 families have had their basal rates measured! So, any generalizations about avian energetics are suspect. As a result of the greater fraction of the taxonomic and ecological diversity of mammals being measured, a more complete analysis can be given for the basal rates of mammals than for birds. As noted, the power function of mammalian body mass alone accounts for 95.6% of the variation in total basal rate, or 77.7% of the variation in mass-specific basal rate, when mammals are collectively considered (McNab, 1988a). The variation in basal rate, however, is not equally distributed among mammalian orders in that data set: body mass accounted for 83.4% of the variation in total basal rate in 26 carnivorans, 88.0% in 37 bats, 93.2% in 128 rodents, and 96.1% in 13 artiodactyls. An important proportion of the variation is obviously unaccounted for by body mass. A similar situation exists in birds.

The energy expenditure of endotherms at the smallest masses raises the question whether a lower limit to body size exists for continuous endothermy. Oliver Pearson was concerned with rates of metabolism in the smallest birds and mammals, namely shrews (Morrison and Pearson, 1946; Pearson, 1948a), shrews, bats, and mice (Pearson, 1947), and hummingbirds (Pearson, 1950, 1954). He argued that the lower limit of continuous endothermy was set near 2.5 g because at smaller masses the increase in mass-specific rate of metabolism would be so great that a "… mammal smaller than this would be unable to gather enough food to support its infinitely rapid metabolism…" (Pearson, 1948a).[4] But a question can be raised whether mass-specific rates are the best basis for analysis (McNab, 1999).

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[4] Pearson, eschewing the "fancy" equipment approach of his friend Peter Morrison (1951), took some pride, even glee, in advocating, if not using, the simplest possible means of measuring rates of metabolism. This will explain why most of Payne's published measurements now appear to be too high. I still have Paynie's sketch from the early 1960's of such an apparatus, the chamber of which consisted of a glass desiccator top that was sealed by vasoline to a metal plate. The chamber was hooked through the chamber floor by tubing to an orange juice can full of O_2, inverted into a tomato soup can full of water. The orange juice can was attached to a horizontal rod that at one end had a pointed tip that was placed against a ruler and was counter-balanced by a mass at the other end of the rod. Ruler markings were calibrated to represent changes in the oxygen volume in the orange juice can. The resulting measurements from this slow-response system would have been integrative, not minimal or "standard." I never used this suggestion.

Many eutherians, most notably soricine shrews and arvicoline rodents, ensure continuous endothermy as masses decrease from 50 to 3 g by progressively increasing their basal rates of metabolism, compared to a general mammalian standard (McNab, 1983, 1991, 1992; Calder, 1984). They then appear to conform to another, higher standard curve, the so-called "boundary curve" for endothermy (McNab, 1983). This adjustment ensures that the cost of continuous endothermy in small species is very high. A lower limit to body size in endotherms can be reduced to 1.8 to 2.0 g, however, by relaxing the commitment to continuous endothermy (i.e., by the use of torpor) as has been seen in some crocidurine shrews, insectivorous bats, and hummingbirds.

Body Composition. Several lines of evidence indicate that basal rate correlates with body composition. For example, the basal rate of metabolism in rails, corrected for body mass, decreases with pectoral muscle mass, the culmination of this trend being that flightless rails have lower basal rates of metabolism and much smaller pectoral muscle masses than their flighted relatives (McNab, 1994a, 2001a; McNab and Ellis, 2006). Similarly, some large, inactive arboreal mammals, such as tree-sloths, are characterized by low basal rates (McNab, 1978a) and small muscle masses (Grand, 1978). The low basal rate found in the arboreal felid *Leopardus wiedii*, the margay, may also reflect a small muscle mass (McNab, 2000b). Birds of prey that soar extensively in the pursuit of prey have smaller pectoral muscle masses (Hartman, 1961) and tend to have lower basal rates than those that use powered flight (data from Wasser [1986]). Insectivorous birds and bats that forage with intermittent flight have basal rates that are 75% of species that forage continuously (Bonaccorso and McNab, 2003), which also may reflect differences in body composition.

More generally, Kersten and Piersma (1987) concluded that variation in the basal rate of knots (*Calidris canutus*) reflected variations in "metabolic machinery"; Konarzewski and Diamond (1995) associated a change in basal rate of white mice with changes in "active" tissues; and Bech and Østnes (1999) showed that variation in the resting rate of metabolism in nestling cormorants (*Phalacrocorax aristoteles*) correlated with changes in the size of the gut and liver. Variation in the mass of heart and kidneys accounted for approximately 50% of the variation in basal rate of 22 species of birds (Daan et al., 1990).

The use of body composition to account for the variation in basal rate depends on the rates of metabolism that characterize various tissues and organs when endotherms are expending energy at the basal rate. For example, fat tissues are generally thought to have low rates of metabolism (Wallgren, 1954; but see Kekwick 1965), which led Hayward (1965) to suggest that the low basal rates found in desert *Peromyscus maniculatus* reflected the greater deposition of body fat in captivity compared to that deposited in individuals collected in mesic environments. However, this explanation did not account for the low basal rates in 2 xeric-distributed species, *P. crinitus* and *Heterocephalus glaber* (McNab, 1968); this study suggested that moderate amounts (up to 20%) of body fat may be within "standard" conditions. Nevertheless, a given body mass does not always have the same impact on rate of metabolism because differences in the composition of cells and tissues, such as the number of mitochondria (Else and Hulbert, 1985, 1987; Hulbert and Else, 1989), may differentially effect rate of metabolism. This is one reason why mass alone does not completely account for all variation in basal rate.

Food Habits. The basal rate of metabolism in mammals and birds has been repeatedly described as a function of food habits. Terrestrial mammals that weigh more than 100 g and feed on vertebrates, nuts, or grass have high basal rates (compared to a general mammalian standard), whereas those that feed on ant/termites or other invertebrates have low basal rates (McNab, 1984, 1986a). Fruit- and leaf-eaters tend to have intermediate basal rates, the level of which depends on whether the species are arboreal or terrestrial (see *Body Composition* above). At masses less than 100 g, most mammals, as noted, have high basal rates (McNab, 1983), unless they use torpor.

These conclusions are often derived from the comparison of unrelated species, a procedure that has been justifiably criticized (Harvey et al., 1991) because some of the differences in rate of metabolism among these species undoubtedly reflect differences associated with characteristics other than the foods consumed. A direct way around this problem is to examine energetics within an ecologically and trophically diverse genus or family. For example, the chisel-toothed kangaroo-rat (*Dipodomys microps*) has a high basal rate (Breyen et al., 1973) and feeds extensively on the leaves of desert shrubs, after discarding hypersaline tissues (Kenagy, 1972). Other members of this desert-dwelling genus, most of which have low basal rates (see *Climate* below), preferentially consume seeds. In the family Phyllostomidae, the leaf-nosed bats of Central and South America, species are known to specialize on a variety of foods; those that have a mixed diet of nectar and insects have the highest basal rates, corrected for body mass, followed by those that eat *Piper/Vismia/Solanum* fruits, nectar & fruits, *Ficus* fruits, vertebrate & insects, omnivores, insect-eaters, avian blood, and finally mammalian blood (McNab, 2003b). Within this family, basal rate of metabolism clearly correlates with food habits, and this correlation occurs within genera and subfamilies, as well as between the food-habit correlated subfamilies.

Within the Order Carnivora, basal rates of metabolism in 62 species, belonging to 11 families, correlate with food habits (McNab, 2005c). Species that were committed to eating vertebrates had basal rates that were about 43% greater than those that consumed few vertebrates, most notably frugivores, folivores, or insectivores. For example, one of the most insectivorous carnivorans, the fennec (*Vulpes zerda*), has a basal rate that is 68% of the value expected from mass (Noll-Banholzer, 1979), the folivorous red panda (*Ailurus fulgens*) has a basal rate equal to 43% (McNab, 1988b), and the frugivorous binturong (*Arctictis binturong*) a basal rate of only 28% (McNab, 1995).

The effect of food habits on basal rate in birds is less well-known because a much smaller fraction of bird diversity has been measured, but a pattern similar to that found in mammals appears to be present (McNab, 1988c). Species that weigh more than 100 g tend to have high basal rates (now using a general avian standard) if they feed on grass, seeds and nuts, or vertebrates (but see *Body Composition* above), whereas species that feed principally on fruits, leaves, or invertebrates tend to have low basal rates. At masses less than 100 g, species generally have high basal rates, unless they feed preferentially on fruit or flying insects, and especially if they use torpor.

Relatively few extensive studies have been made of avian families that have a diversity of food habits, which makes the effect of food habits on metabolism uncomplicated by other factors difficult to evaluate. Two families capable of consideration are the Rallidae (McNab and Ellis, 2006) and Paradiseaidae (McNab, 2003c, 2005a). Herbivorous rails have basal rates that average 35% greater than those with other food habits. The food habits of paradisaeids range from strict frugivory through mixed diets of fruits and insects to extensive insectivory with some fruits.

Fruit-eating specialists have basal rates that average 79% of species that consume > 10% of food intake as insects. Toucans (Ramphastidae), all of which are frugivorous, also have low basal rates, as do a barbet (Capitonidae) and a hornbill (Bucerotidae) (McNab, 2001b), as well as other frugivores, including 2 manakins (Pipridae) (Vleck and Vleck, 1979, Bartholomew et al., 1983), and a trumpeter (Psophiidae) (pers. observ.). Some of the larger toucans appear to have slightly higher basal rates in apparent association with a propensity for predatory behavior.

The complex relations of basal rate with food habits are unlikely to have simple, easily verified, explanations. For example, small insectivorous eutherians, most notably soricine shrews, have very high basal rates, whereas insect-eating specialists that weigh > 200 g, such as hedgehogs, tamanduas, armadillos, pangolins, and the aardvark (*Orycteropus afer*), have basal rates that average 69% of the values expected from mass (Fig. 1). Insect-eating specialists that enter torpor, especially at masses < 20 g (e.g., crocidurine shrews) have lower basal rates. In contrast, carnivores at masses > 200 g have basal rates that average 149% of expected values, or 2.2 times those of insect specialists (Fig. 1).

Why these differences when these species all eat a high protein diet? Of course many factors may contribute, but 2 appear to be most important. 1) The bodies of

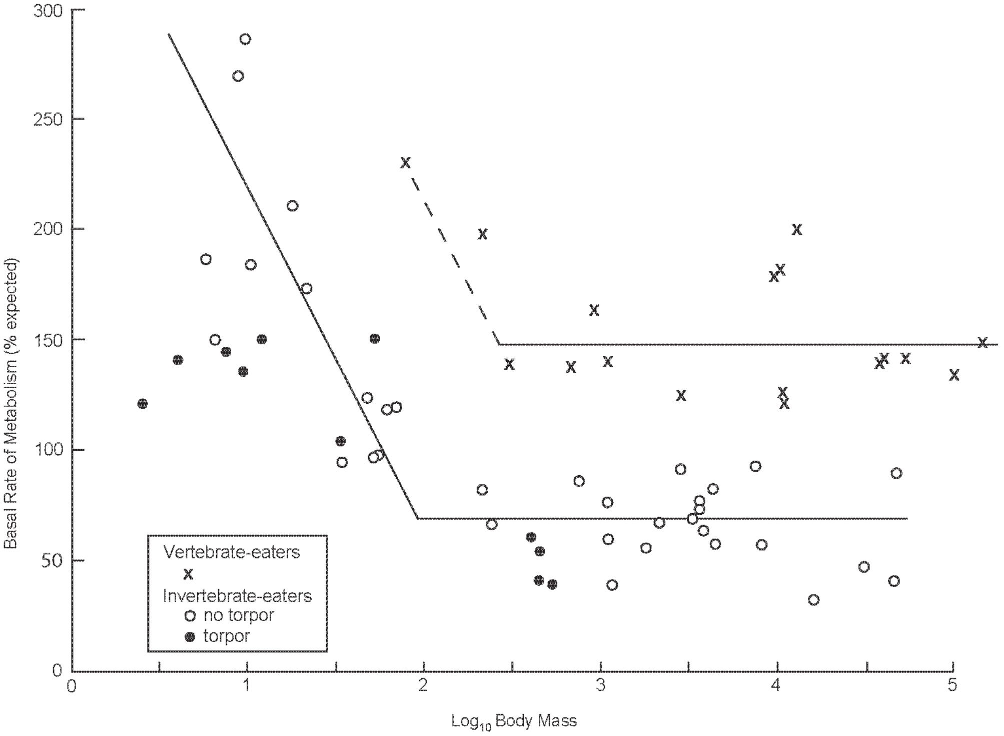


Figure 1. The basal rate of metabolism of insectivorous and carnivorous eutherian mammals, expressed as a percentage of the value expected from mass as a function of $\log_{10}$ body mass. Data were obtained from Genoud (1988) and McNab (1988a, 1991, 2000b).

vertebrates represent large, highly concentrated food items, whereas insects principally consist of chitinous exoskeletons that are indigestible, which greatly diminishes the nutritive value of insects as food. This might not be a problem for small predators, such as shrews, which have a small intake and can select individual prey items. But up to 50% of the volume intake of large ant/termite-eaters is soil, sand, and nest carton (McNab, 1984), further reducing the proportion of volume intake that is digestible. 2) Insects may be a much more undependable food resource than vertebrates, especially for species that feed on flying insects, even in the tropics, where insectivorous bats that feed beyond a forest canopy have a greater amplitude in their seasonal fat cycle than species that feed below the canopy or off surfaces (McNab, 1976; Bonaccorso and McNab, 2003).

A similar situation exists in birds: small species that glean insects from surfaces tend to have higher basal rates than those that feed in flight, a difference that may reflect the reliability of the food supply (Bonaccorso and McNab, 2003). In some cases, such as the birds-of-paradise, the addition of insects to a fruit diet adds protein to a protein-poor fruit diet, which may account for the increase in basal rate, especially given that the insects consumed are gleaned off surfaces. The addition of insects to a diet, however, need not always have the same impact on metabolism because of contextual differences in diets. Noteworthy is the observation that birds-of-paradise with the highest insect intakes (>25%) have higher basal rates than committed frugivores, but lower basal rates than species in which insect intake is only 10-25% (McNab, 2005a). This implies that adding insects to a fruit diet is a positive step (by adding protein?), but a dependency on insects for an appreciable proportion of the diet may entail a handicap (reliability of insect availability?). A higher protein intake may also account for the higher basal rates of frugivorous phyllostomids, such as *Carollia* and *Sturnira*, that feed on *Vismia*, as compared to those that feed on *Ficus* fruits (e.g., *Artibeus*): *Vismia* fruits have higher protein contents than *Ficus* fruits (Gustavo Londoño, pers. comm.). Clearly, the rate of metabolism of consumers may be very complexly tied to their food supplies.

These explanations, which will be refined as data are added, are fundamentally different from the vague attribution of residual variation in basal rate to phylogeny in that food-habit dependencies are potentially capable of being tested. The attribution of the residual variation in basal rate to phylogeny, however, is at best an association without a functional basis.

Climate. The first direct attempt to examine whether a correlation exists between the basal rate of endotherms and the climate in which they live was by Scholander et al. (1950a, 1950b, 1950c). They (1950c, p. 265) concluded narrowly that the basal rate of terrestrial mammals is "…phylogenetically nonadaptive to external temperature conditions…," while ignoring data collected on marine mammals and terrestrial birds. A reexamination of these data, however, suggests a higher basal rate in arctic than in tropical species, although the determination of the cause for this difference is complicated by the great taxonomic and ecological differences between the arctic and tropical species studied.

Many subsequent studies showed that the basal rate of endotherms correlates with climate. The first to do so demonstrated that desert-mountain subspecies of widespread North American species of *Peromyscus* have lower basal rates than their mesic subspecies, and species of this genus restricted to desert valleys have even lower basal rates (McNab and Morrison, 1963), a pattern seen again by Mueller and Diamond (2001). MacMillen and Lee (1970) found that Australian desert mice belonging to the genus *Notomys* had low basal rates and Shkolnik and Schmidt-Nielsen (1976) showed that desert hedgehogs have lower basal rates, corrected for body mass, than species living in mesic environments. Low basal rates in desert rodents have also been found by Haim and Borut (1986), Haim (1987a, 1987b), and Haim and Izaki (1993), as was seen in the desert fennec. Furthermore, although most heteromyid rodents dwell in arid to desert environments, feed on seeds, and have standard to low basal rates, species belonging to the genus *Heteromys* feed on seeds, live in tropical rainforests in Central and northern South America, and have high basal rates (McNab, 1979a; Hinds and MacMillen, 1985). Lovegrove (2000) demonstrated that the correlation of basal rate in mammals with geographic distribution principally reflected low basal rates in desert regions.

Whether basal rate in mammals correlates with latitude in response to a climatic gradient is complicated by the variation in food habits and other character states with respect to latitude. For example, soricine shrews (insectivores), lagomorphs (browsers), and arvicoline rodents (grazers, browsers), all of which have high basal rates, are principally found in north-temperate and north-polar regions, although the few arvicolines that live in warmer latitudes have lower basal rates (McNab, 1992). However, the arvicoline *Clethrionomys glareolus* avoids this correlation by the selective use of higher altitudes at lower latitudes, thereby encountering ambient temperatures that are independent of latitude (Aalto et al., 1993). In contrast, many tropical mammals with low basal rates have food habits, such as fruit- and ant/termite-eating, that are limited to the subtropics or tropics. The influences of food habits and climate on basal rate therefore may be difficult to separate.

As an extreme example of the complex nature of character state determinations, polar marine mammals, especially seals and dolphins, have much higher basal rates (Hansen et al., 1995; Ochoa-Acuña, 1999) than tropical manatees (Gallivan and Best, 1980). That difference is very difficult to interpret because of the radical differences between these groups in many characters, including great differences in diet and water temperature. Tropical seals and dolphins need to be measured; they will undoubtedly have much higher basal rates than manatees, although they may not be as high as polar species. The unfortunate extinction of the 7.5 m, 4,000 kg Steller's sea-cow, *Hydrodramalus stelleri*, the last in a series of North-Pacific, cold-water dugongs (Domning, 1978), precluded us from obtaining some intriguing information on the comparative influences of body mass, food habits, climate, and possibly phylogeny, assuming that an effect of phylogeny on energy expenditure can be distinguished from that of food habits and climate.

A limited amount of information is available on the influence of climate on the basal rate of birds, undoubtedly because so few species have been studied as a function of geography, the shortage of data being most notable in tropical passerines. In one of the earliest studies, Hudson and Kinzey (1966) demonstrated that house sparrows (*Passer domesticus*) living in a seasonally hot, humid environment (Houston, Texas) had a lower basal rate of metabolism than temperate populations from Ann Arbor (Michigan), Boulder (Colorado), and Syracuse (New York). This difference appeared within the 153 years of the first introduction of this European species into North America.

Basal rates in birds have been shown to increase with latitude, both in terrestrial

(Weathers, 1979; Hails, 1983) and marine species (Ellis, 1985). Wasser (1986) showed that warm-climate falconiforms have lower basal rates than temperate species, although that correlation is complicated by the influence of prey-searching strategy and body composition (see *Body Composition*). The low basal rate in a desert-dwelling population of the stonechat (*Saxicola torquata*) from Kenya, compared to that from a temperate Austrian population, appeared to have a genetic basis (Klaasen, 1995), a conclusion that has been extended to include populations of the same species from Ireland and Kazakhstan (Wikelski et al., 2003). The highest basal rates were found in the migratory populations of the stonechat from Kazakhstan and Austria, the lowest from the sedentary population in Kenya, and an intermediate basal rate in a sedentary population from Ireland. So, some combination of activity level (body composition?) and climate appears to affect basal rate in this species. A low basal rate also has been found in a desert babbler (Anava et al., 2001). Among pigeons (Columbidae), temperate, seed-eating species had higher basal rates than desert, seed-eating species (McNab, 2000a). Given that food habits and the propensity for migration are not independent of latitude, the causes for the correlation of basal rate with latitude undoubtedly are complex. This conclusion is reinforced by the correlation of the basal rate of herons with plumage color, nest placement, and solar radiation in subtropical Florida (Ellis, 1980).

Various explanations for the correlation of basal rate with climate have included the kinds of foods used and their seasonal availability, the cost of temperature regulation, and the availability of water, either directly or through the foods used. Few studies have attempted to determine directly the causes for these correlations, except as the variation of basal rate might be correlated with climatic parameters. An early attempt (McNab and Morrison, 1963) demonstrated that a "summated desert adaptation," which was defined as the summed percentage reduction from general mammalian standards in thermal conductance and basal rate in *Peromyscus*, was correlated positively with a "desert index," the ratio of the mean July temperature to mean annual rainfall. Recently, Mueller and Diamond (2001) showed that basal rate in *Peromyscus* was positively correlated with the net primary production in the environment, which of course would be inversely correlated with the desert index. Similarly, larks belonging to the avian family Laudidae showed a positive correlation of log basal rate with log body mass and log "aridity index," which is proportional to rainfall and inversely related to a thermal factor (Tieleman et al., 2003). This index is directly related to primary production. A reexamination of the data on larks, however, indicates a slightly greater correlation of log basal rate with the combination of log body mass and negatively with the maximal environmental temperature. These studies collectively demonstrated that the basal rates of some endotherms, corrected for body mass, are directly correlated with primary production in the environments in which they live.

Restrictive Habits and Environments. Some mammals and birds have habits, or live in environments, that are associated with a restricted resource base. As we have seen, a desert environment is a restrictive environment, restricted because of the dependence of primary production on rainfall, as well as by the direct impact of water availability on endotherms. The effects imposed by a species' habits or environment may be difficult to distinguish.

One of the first studies of a restrictive habit, after life in a desert enviroment, was of the adaptation to a fossorial life, wherein some mammals are so specialized for a subterranean environment that they rarely emerge above ground. These groups include moles (Talpidae) in the northern hemisphere, golden-moles (Chrysochloridae) in Africa, marsupial moles (Notorycteridae) in Australia, and many groups of rodents, namely pocket-gophers (Geomyidae) in North America, tuco-tucos (Ctenomyidae) in South America, mole-rats (Bathyergidae) in Africa, zokors (*Myospalax*) in eastern Asia, and blind mole-rats (Spalacidae) in the Middle East.

Some of the earliest ecological work on fossorial rodents was by Hill et al. (1957) on *Heterocephalus* in Kenya, Pearson (1959) on *Ctenomys* in Perú, Kennerly (1964) on *Geomys* in Texas, and Pearson et al. (1968) on *Ctenomys* in Argentina. Fossorial rodents and golden-moles, at least, tend to be characterized by low basal rates, which have been interpreted to be a response to the subterranean microclimate (McNab, 1966, 1979b; Nevo and Shkolnik, 1974; Lovegrove, 1986a), gas exchange in a low oxygen, high carbon dioxide environment (Arieli et al., 1977; Arieli, 1979), high cost of burrowing (Vleck, 1979; Lovegrove, 1986b), a restricted resource base (Jarvis, 1978; Lovegrove, 1987), or as a mixed response (Contreras and McNab, 1990; Nevo, 1999).

Another habit that appears to be associated with a low basal rate in mammals is the commitment by some larger mammals to an arboreal life. The clearest examples are found in folivores, most notably tree-sloths (McNab, 1978a) and the bamboo-eating red panda (McNab, 1988b), but also in arboreal viverrids, which principally consume fruits and insects (McNab, 1995). Unfortunately, so few arboreal mammals that weigh > 500 g have been studied that a general analysis of their energetics cannot be made. Many smaller arboreal mammals, especially seed- or nut-eating squirrels (Bolls and Perfect, 1972; Golightly and Ohmart, 1978; Pauls, 1981) and the red tree-vole (*Arborimus pomo*) (McNab, 1992), have high basal rates.

What are especially needed are extensive measurements of primate energetics in relation to diet and to arboreal or terrestrial habits. At small masses, tropical primates, including tarsiers, galagos, and lorisids, have low basal rates, possibly in relation to their feeding habits, which variously include insects and fruit. What about larger primates? Do arboreal cebids and cercopithids have lower basal rates than terrestrial cercopithids? No systematic examination of this question has been made. Müller et al. (1983) demonstrated that the folivorous, arboreal *Colobus guereza* had a lower basal rate than the omnivorous, arboreal *Cercopithecus mitis*, although both had rates above the general mammalian standard. The few data available from howler monkeys (*Alouatta palliata*) indicated a typical mammalian basal rate (Milton et al., 1979), but they were unfortunately measured during the daytime and thus these rates may not have been basal. However, howlers have field expenditures that are only 60% of that expected generally from eutherians (Nagy, 1994), which implies a low basal rate (see field expenditures below), although they simply may have had low activity levels.

The observation that the strictly carnivorous margay (*Leopardus wiedii*), a tropical felid that is extensively arboreal, is one of the few felids to have a low basal rate (McNab, 2000b) lends support to the distinctive nature of an arboreal habit in intermediate to large mammals. (Does the other tropical, arboreal felid, the clouded leopard [*Neofelis nebulosa*], also have a low basal rate?) That is, some arboreal mammals that feed on vertebrates, leaves, or fruit have low basal rates, and the depression of basal rate increases with body mass and the proportion of time spent in trees (McNab, 1995). The basis for a low basal rate in arboreal mammals, which may in some cases reflect the quality of foods used, more generally may represent a reduction in muscle mass associated with a reduced level of activity (see *Body Composition* above).

Oceanic islands, like continental deserts, appear to be a restrictive environment. Many birds and bats endemic to oceanic islands reduce energy expenditure in a variety of ways (McNab 1994b, 2001a, 2002b, 2003a; McNab and Bonaccorso 2001). These include: 1) a reduction in body mass, 2) a reduction in activity level, 3) a reduction in homeostatic costs, as demonstrated by a reduction in basal rate, and 4) the evolution of a flightless condition in many birds, most repeatedly in the families Anatidae and Rallidae. Small-island tramp pigeons, such as *Ducula pacifica* and *D. pistrinaria*, which are strong fliers, have by far the lowest basal rates of all pigeons measured (McNab, 2000a). An extinct goat (*Myotragus balearicus*) endemic to the Balearic Islands in the Mediterranean had reduced brain and sense organs (Köhler and Moyà-Solà, 2003), as well as a reduced capacity for jumping and running (Köhler and Moyà-Solà, 2001). Further evidence of a reduction in energy expenditure on islands is illustrated by the tendency of large ectotherms, such as lizards, tortoises, and terrestrial crocodiles, to replace endothermic vertebrates on oceanic islands.

Why a reduction in energy expenditure occurs on oceanic islands, however, is not completely clear. An early explanation, at least for the evolution of flightless birds and the reduction in activity (i.e., increased approachability), was the absence of mammalian predators. The difficulty with this explanation is its incompleteness: the absence of mammalian (actually eutherian) predators may *permit* the evolution of flightlessness and a reduction in activity, but it does not *cause* the evolution of these character states (McNab 1994b, 2001a, 2002b; McNab and Ellis 2006). After all, most birds endemic to oceanic islands retain the capacity for flight in the absence of eutherian predators. Indeed, it would be difficult to imagine the evolution of a flightless swallow or swift without the most radical change in their *Gestalt*, although an extinct New Zealand owlet-nightjar (*Aegotheles novaezealandiae*) had small wings and might have been a marginal flier (Olson et al., 1987; Worthy and Holdaway, 2002). Owlet-nightjars, however, may be to some extent ground feeders (Pizzey, 1987; Holyoak, 1999), which would facilitate the evolution of a flightless condition. Furthermore, the absence of eutherian predators does not contribute to the reduction in body mass or the reduction in homeostatic costs.

At least 2 possible explanations for the reduction in energy expenditure come to mind. One is that small islands are characterized by low levels of primary production (small area, and in some cases poor soils) and unstable conditions produced by cyclones, El Niño/La Niña events, and volcanic activity. The reduced energy expenditure of island endemics would permit larger populations, which may facilitate a long-term persistence, as long as environmental events are not too extreme (McNab, 1994a, 1994b, 2000b, 2001a). A similar analysis was independently suggested by Köhler and Moyà-Solà (2001, 2003).

A related explanation for the low energy expenditures of island endemics is associated with the greatly reduced species richness on small oceanic islands. On continents, where primary production is greater and the climate more predictable, selection for an increased rate of reproduction to compensate for a reduced life span in the face of stringent competitive circumstances and the presence of eutherian predators, conditions that are absent from oceanic islands, may be facilitated by selection for high-energy expenditures (McNab, 1980). Little incentive thus exists for island endemics to maintain the high energy expenditures and high rates of reproduction presumably characteristic of their mainland immigrant antecedents. Island endemics indeed generally have large populations (Crowell, 1962), long lifespans, and low rates of reproduction (Cody, 1966; Mueller and Diamond, 2001).

THE ABILITY TO ACCOUNT FOR THE VARIATION IN STANDARD ENERGETICS

The basal rate of metabolism in endotherms clearly correlates with many factors, which raises the question of the extent to which they collectively account for variation in the basal rate of endotherms. Such analyses indicate the factors that should be examined to determine the means by which they influence the energy expenditures of birds and mammals. Recent work on various birds and mammals indicated that from 90.8 to 99.4% of the variation in basal rate is accounted for (Table 1).

The ability to account for the variation in basal rate generally increases with the number of factors included in the analysis, except when a group is ecologically constricted. Then almost all of the variation in basal rate is accounted for by mass alone, as in cats (Felidae, 96.0%), toucans (Ramphastidae, 98.4%), ant/termite-eaters (Myrmecophagidae, 98.6%), and marsupials (98.8%). Mass alone was less successful accounting for basal rate in the Arvicolinae (88.5%), presumably because some factor other than mass was associated with basal rate. Part of the problem in analyzing data from arvicolines is that the power of body mass appears to change from 0.292 at masses less than about 52 g to 0.774 at larger masses (McNab, 1992). When basal rates in arvicolines are compared to those expected from the mean arvicoline curve, cold-climate species have basal rates that are 19% higher than those of warm-climate species. Among warm-climate species, 96.9% of the variation in basal rate was accounted for by the combination of mass and a "size" category, i.e., smaller or larger than 52 g. This illustrates the complexities involved in determining basal rate.

In ecologically diverse taxa, basal rate of metabolism was more variable, much of which was associated with factors other than body mass. For example, 4 factors, namely body mass, food habits, altitudinal distribution, and presence on islands or mainlands accounted for 99.4% of the variation in the total basal rate of 30 species of phyllostomid bats, whereas mass alone accounted only for 78.7% of the variation in basal rate (McNab, 2003b). Fully 20.7% (i.e., 97.2% of the residual variation) was accounted for by the 3 other factors, which can be used to guide an analysis of how food habits, altitudinal distribution, and presence on islands or continents influence basal rate in phyllostomid bats.

This approach can be extended to more inclusive taxa than families, or to groups defined by habits. Thus, among 30 species of the rodent suborder Hystricognatha, which belonged to 10 families, 96.1 to 96.9% of the variation in basal rate is accounted for, depending on which of 3 factors are included in the analysis (Arends and McNab, 2001). Among these Neotropical rodents, mass alone accounts for 94.5% of the variation in total basal rate, whereas 96.1% of the variation is accounted for by body mass and food habits (folivory or other food habits), and 96.9% by a combination of body mass and substrate (aquatic, terrestrial, or arboreal). Food habits and substrate, however, cannot be combined in the same analysis because they are mutually dependent: terrestrial species tend to be grazers or frugivores and arboreal species folivores. The addition and subtraction of factors in an analysis is also seen in the Rallidae, where a tradeoff occurs between distribution and flight ability, and between distribution and foods consumed (McNab and Ellis, 2006).

Basal rate in the order Carnivora varies with body mass, diet, substrate, habitat, and latitude. When these 5 factors are taken into consideration, 98.7% of the variation in the basal rate of 62 species was accounted for (McNab, 2005c). However, larger

Table 1. Recent attempts to account for the variation in the basal rate of endotherms.

Group	Species	r^2	Factors	Source
Myrmecophagidae	4	0.986	mass	McNab pers. observ.
Ramphastidae	7	0.984	mass	McNab 2001b
Dasypodidae	9	0.989	mass, food	McNab pers. observ.
Felidae	11	0.960	mass	McNab 2000b
Alaudidae	12	0.908	mass, aridity	Tieleman et al. 2003
	12	0.952	mass, Tmax	pers. obs.
Paradisaeidae	13	0.990	mass, food, altitude	McNab 2003c
Rallidae	15	0.928	mass, distribution	McNab & Ellis 2006
	15	0.961	mass, flighted/ flightless, food habits	" "
Pteropodidae	21	0.980	mass, temp. reg., island/continent	McNab & Bonaccorso 2001
Arvicolidae	24	0.885	mass	McNab 1992
	14	0.969	mass, "size", mass-size interaction	" "
Anatidae	27	0.936	mass, island/ continent	McNab 2003a
Columbidae	27	0.943	mass, climate, distribution	McNab 2000a
Phyllostomidae	30	0.994	mass, food, altitude, island/continent	McNab 2003b
Hystricomorpha	30	0.961	mass, food	Arends & McNab 2001
	30	0.969	mass, substrate	
Insectivorous birds (25) and bats (21)	46	0.972	mass, "order", foraging mode, torpor	Bonaccorso & McNab 2003
Carnivora	62	0.987	mass, food, substrate, habitat, latitude	McNab 2005c
Marsupialia	70	0.992	mass, altitude, substrate	McNab 2005b

arboreal carnivorans (*Nandinia*, *Paradoxurus*, *Ailurus*, *Arctictis*), which feed on fruit, leaves, or insects, tend to have lower basal rates relative to expectations than smaller carnivorans (*Bassariscus*, *Potos*, *Eira*) with the same habits. This observation emphasizes the interactions among these various factors and mass in arboreal species.

An analysis of 25 species of birds and 21 species of bats, grouped together by their insectivorous habits, indicated that the combination of 4 factors, body mass, "order" affiliation, foraging mode (continuous or discontinuous), and the use or not of torpor, accounted for 97.2% of the variation in basal rate of metabolism in the 46 species (Bonaccorso and McNab, 2003). One factor, "order," is a dummy variable in that no obvious character clearly defines the "orders" Chiroptera, Passeriformes, and "non-passerines," but reflects the undefined differences found between birds and mammals and between non-passerines and passerines that influence basal rate.

Clearly, extensive factor interactions are present in the determination of phenotypic character states: food habits are not independent of body mass, climate, substrate, and distribution; body mass is associated with latitude and with presence on islands; climate varies with latitude and altitude; and in some cases taxon codes for unspecified influences on metabolism. These interactions invalidate any analytical scheme that does not take them into explicit consideration, which is the case with phylogenetic contrasts (see *Difficulties* below).

THE CORRELATION OF FIELD EXPENDITURES WITH STANDARD ENERGETICS

Some of the earliest attempts to define the field energy expenditures of endotherms were made by Oliver Pearson both at the individual (1954, 1960) and populational (1948b, 1964a) levels. They were based on constructing a time budget of activities, multiplying the time of each activity by its measured or assumed energy equivalency, and summing the products. Following Pearson, I (1963) used a time budget to estimate the energy budget of a wild mouse, and later (1978a) that of tree-sloths. To facilitate estimating field energy expenditures of birds, Pearson (1950, 1964b) made some of the first measurements of the cost of flight in birds, e.g., by oxygen consumption while hummingbirds hovered in a chamber and by plugging the cloaca of pigeons and measuring changes in body mass during a period of free flight. Now field energy expenditures are routinely measured by the doubly-labeled water technique. Energy budgets estimated with that technique are often greater than those obtained from time-budget estimates (e.g., compare Nagy and Montgomery [1980] on *Bradypus* with McNab [1978a]), probably from underestimating either the times or costs of activities in a time-budget.

The reason to be concerned with field energy expenditures, of course, is that they are the expenditures that impact survival and reproduction. Basal rate of metabolism, however, has been widely used as a standard index of energy expenditure because of its convenience of measurement and its diversity beyond that associated with body mass. Its value would increase if it also could be used as an index of field energy budgets (e.g., if species with high basal rates have high field expenditures). Several studies have indicated such a positive correlation in mammals (Nagy, 1987, 1994; Koteja, 1991; Ricklefs et al., 1996; Speakman, 1997, 2000; McNab, 2002a) and birds (Bryant and Tatner, 1991), although the correlation in birds is marginal (Koteja, 1991) or has been contested (Ricklefs et al., 1996). The reason why some confusion exists whether this correlation occurs in birds is that many species that have had field expenditures *measured* have had basal rates *estimated* from body mass, but as we have seen, basal rates cannot be accurately predicted by body mass alone. Therefore, the failure to find a correlation of field expenditures with basal rates in birds, independent of the effect of body mass, is likely artifactitious.

Field expenditures usually are 3-4 times the basal rate in birds and mammals (Chappell, 1980; Drent and Daan, 1980; Koteja, 1991; Ricklefs et al., 1996; Speakman, 1997, 2000), which means that basal rate constitutes 25 to 33% of total expenditures, although it may make an even larger contribution in inactive species (e.g., ca. 60% in the tree-sloth *Bradypus*). Therefore, a correlation between field and basal expenditures is to be expected. Some species appear to have a larger ratio of field to basal expenditures, either because of a high cost of foraging, especially during the breeding season, or because of lower basal rates, as is the case in marsupials. The ratio of sustained maximal and field rates of metabolism to basal rate, however, is usually limited to ca. 7:1 (Peterson et al., 1990; Bryant and Tatner, 1991; Weiner, 1992; Hammond and Diamond, 1997).

A careful comparison of the field expenditures of the blue tit (*Parus caeruleus*) in Corsica with those in a marginal habitat in mainland France (Thomas et al., 2001) indicated that the "metabolic effort," measured as the ratio field/basal rate, increased from 2-4 on Corsica to 6-9 in France. This increase occurred because the mainland, unlike the Corsican, tits foraged earlier than the optimal date for the appearance of caterpillar larvae, an important food item of reproducing tits. As a result, the cost of raising young in the mainland population, compared to that in Corsica, increased 2.5 times, the ratio field/basal rate increased 2.0 times, and as an apparent penalty, the proportion of females that bred in more than one year fell from 53 to 25%. As the authors concluded (p. 2599): "The consequent mismatching between nestling demand and prey abundance forces parents [in the mainland population] to increase foraging effort beyond their sustainable limit, resulting in a tradeoff between immediate metabolic effort and persistence in the breeding population."

Because most of the variation in basal rate is accounted for by a series of internal and environmental factors, a correlation of field expenditures with basal rate implies that some of the variation in field expenditures must correlate with the same factors. This correlation, of course, can be modified by the differential use of activity in the field. Nevertheless, field expenditures are high in marine birds and low in desert birds; carnivorous, insectivorous, and nectarivorous birds have higher field expenditures than omnivores and granivores; and carnivorous mammals have higher field expenditures than similarly-sized mammals with other food habits (Nagy et al., 1999). Speakman (2000) argued that the field expenditures of small mammals correlated with ambient temperature and latitude, but not with diet, although his data summary had few tropical species and none had such distinctive food habits as ant/termite-eating and frugivory, although tree-sloths were included. Seabird field expenditures correlated with life style and latitude (Ellis and Gabrielsen, 2001). High arctic shorebirds have higher field expenditures than temperate shorebirds (Peirsma et al., 2003).

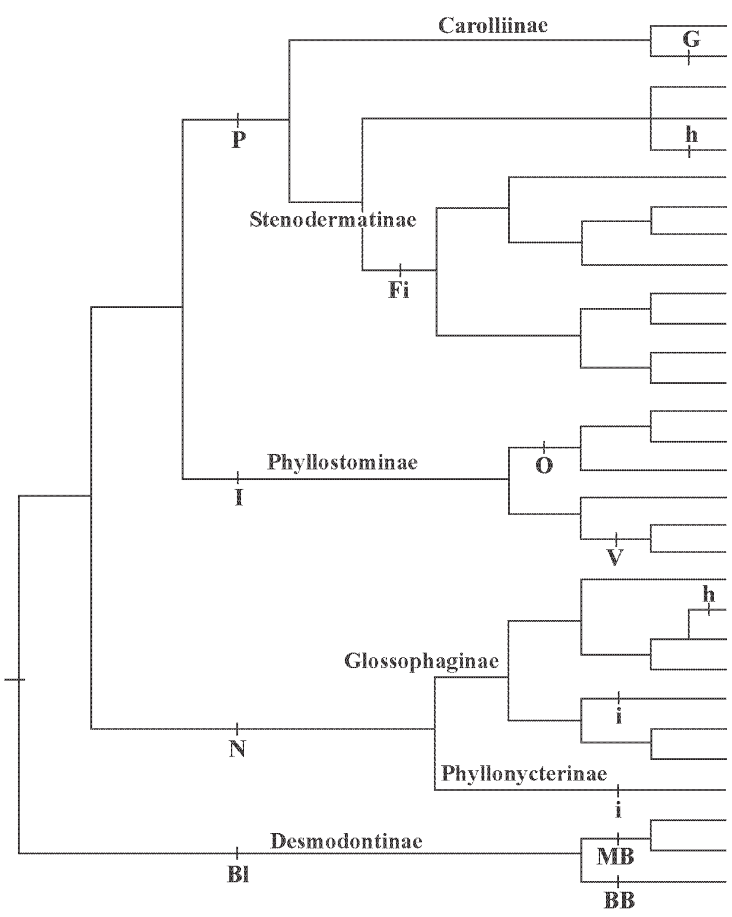
Fundamental to the observation that field expenditures are usually correlated with basal rates is the question whether the correlation stems from intrinsic or extrinsic factors (for an extensive discussion of this dichotomy, see Speakman [2000]). Field expenditures are obviously influenced by environmental factors, such as temperature, food availability, and the presence of other individuals and species. It is usually assumed that they are also influenced by internal factors, such as limits to shared biochemical pathways (e.g., Hochachka et al., 2003), the differential hypertrophy of organ systems (Konarzewski and Diamond, 1995; Selman et al., 2001), and by the observation that basal rates make a noteworthy contribution to field expenditures. The view that the evolution of a high maximal rate of metabolism (i.e., a high aerobic scope) facilitates the acquisition of a high standard rate of metabolism and endothermy (Bennett and Ruben, 1979; Taigen, 1983; Hammond and Diamond, 1997) implies that maximal rates and probably field rates are internally linked with basal rates (but see Krosniunas and Gerstner, 2003). In an examination of the resting and field expenditures of field voles (*Microtus arvalis*), Speakman et al. (2003), however, argued that habitat quality, defined by the date at which 50% of the females had mated and by the biweekly survival rate, influenced resting and field expenditures independently (i.e., more by extrinsic than intrinsic factors).

THE EVOLUTION OF ENERGETICS

The analysis given above indicates that much of the variation in endothermic energetics, both under standard conditions and in the field, is related to a finite number of internal and external factors, which permits the energy expenditure of endotherms to be examined in relation to their evolutionary history. Unfortunately, the spotty availability of data on energetics and the limited availability of quality phylogenies, especially now when molecular-based phylogenies are radically revising our understanding of the evolution of many taxa, restrict these analyses. Some groups with data on energetics are not examined here because either a small proportion of the species or diversity were studied (e.g., Columbidae, Muridae), or little ecological and physiological diversity is present (e.g., Arvicolinae, Dasypodidae, Myrmecophagidae). Four groups will be examined, the Phyllostomidae, Rallidae, Alaudidae, and Paradisaeidae, which were chosen because recent phylogenies and sufficient data on basal rate of metabolism in a diversity of species were available.

Phyllostomidae. The basal rates of 30 species of phyllostomid bats were affected by body mass, food habits, altitude, and presence on islands or continents (McNab 2003b). Phyllostomids have high basal rates, corrected for body mass, if they 1) feed on nectar, vertebrates, or the fruits of *Piper, Vismia,* or *Solanum*; 2) live at high altitudes; or 3) live on continents. They have lower basal rates if they 1) feed on Guttiferae, *Ficus*, insects, or blood; 2) live at low altitudes; or 3) are endemic to islands. An examination of a cladogram of measured phyllostomids (Fig. 2) indicates that a high basal rate evolved at least 4 times, namely at P, V, O (dietary categories), and h (high altitudes). A reduction in basal rate appears to have occurred at least 4 times, at G, Fi, Bl (dietary categories), and i (island endemism). This family obviously has been highly flexible in its response to the opportunities available in Neotropical environments (see the contrast with *Megadermatidae and Nycteridae* below).

Rallidae. Measurements on 15 species of rails indicate that basal rate, corrected for body mass, correlates with the presence or absence of a capacity for flight, presence on islands or continents, size of the pectoral muscle mass, and type of food consumed (McNab and Ellis, 2006). The high basal rates associated with a herbivorous diet evolved at



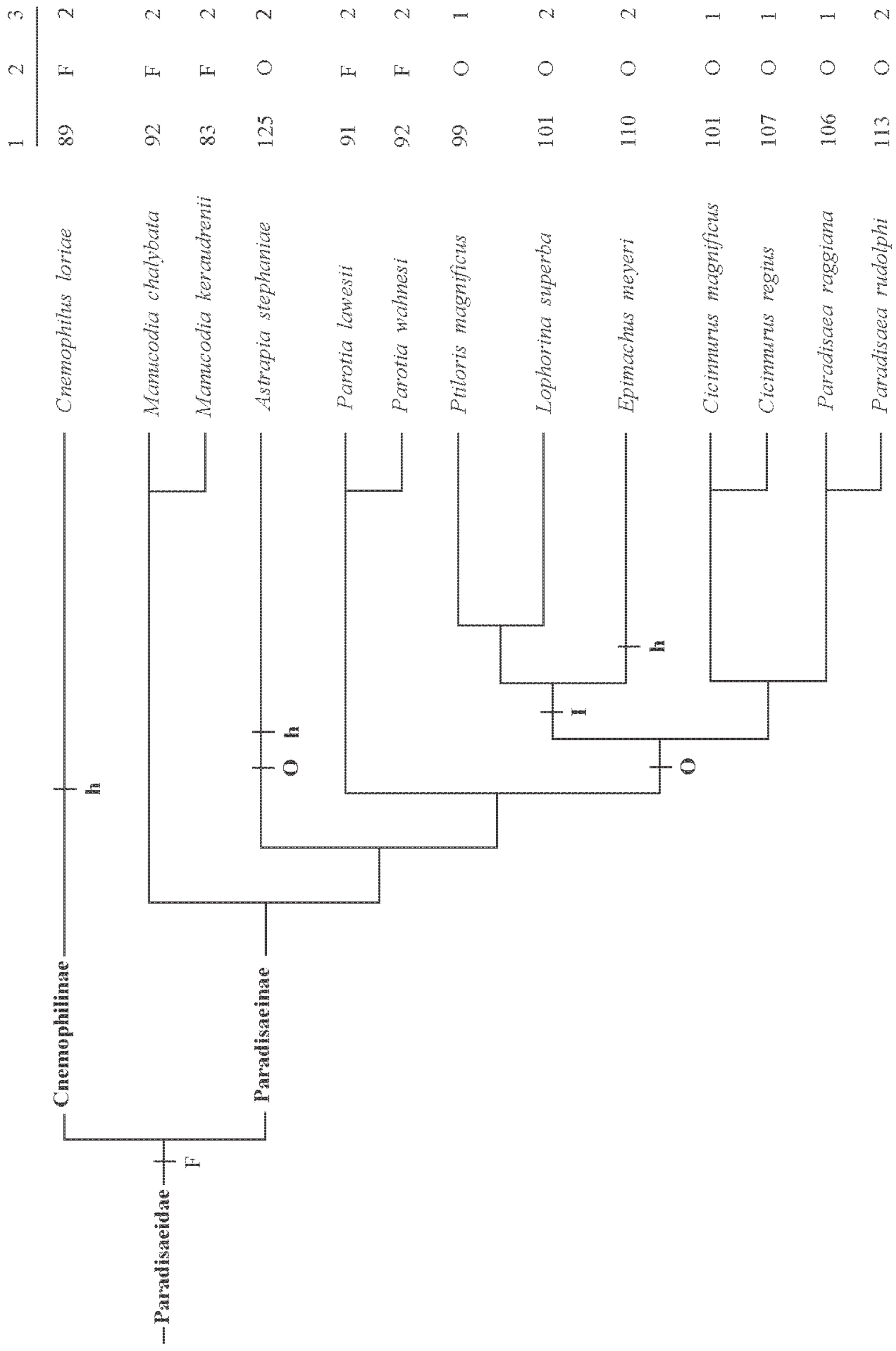
	1	2	3
Carollia perspicillata	116	F	P
Rhinophylla pumilio	87	F	G
Sturnira lilium	120	F	P
Sturnira tildae	127	F	P
Sturnira erythromos	151	F	P
Artibeus concolor	108	F	Fi
Artibeus fimbriatus	116	F	Fi
Artibeus lituratus	121	F	Fi
Artibeus jamaicensis	106	F	Fi
Uroderma bilobatum	99	F	Fi
Platyrrhinus lineatus	93	F	Fi
Chiroderma doriae	101	F	Fi
Vampressa pusilla	105	F	Fi
Phyllostomus elongatus	85	I	O
Phyllostomus discolor	79	I	O
Phyllostomus hastatus	87	I	O
Macrotus californicus	68	I	I
Tonatia bidens	103	I	I/V
Chrotopterus auritus	115	V	V/I
Leptonycteris curasoae	116	N	N/F
Anoura latidens	155	N	N/F
Anoura caudifer	134	N	N/I
Choeroniscus godmani	102	N	N/F
Monophyllus redmani	63	N	N/F
Glossophaga soricina	120	N	F/N
Glossophaga longirostris	112	N	F/N
Erophylla bombifrons	66	N	F/N
Desmodus rotundus	67	Bl	MB
Diaemus youngi	74	Bl	MB
Diphylla ecaudata	88	Bl	BB

Figure 2 (preceding page). The evolution of basal rate of metabolism in leaf-nosed bats (Phyllostomidae). Column 1, basal rate (% of the value expected from mass in phyllostomids). Column 2, general food habits: Bl, blood of endotherms; F, fruit; I, insects; N, nectar; V, vertebrates. Column 3, subdivided food habits: BB, bird blood; Fi, Ficus; G, Guttiferae; I, insects; MB, mammalian blood; N, nectar; O, omnivorous; P, Piper/Vismia/Solanum; V, vertebrates. Shifts into the highlands are indicated by h and to an island distribution by i. Modified from McNab (2003b).

least twice (once for *Porphyrio* and once for the *Gallinula-Fulica* group). Because all flightless species have low basal rates, live on islands, and have small pectoral muscle masses, whereas all continental residents have the opposite characteristics, these 3 character states cannot be included in the analysis at the same time because they code for associated information. The only exceptions are that some "continental" species, namely *Porphyrio porphyrio* and *Gallirallus philippensis*, have dispersed to islands, where they retain the capacity for flight, have large pectoral muscles, and have high basal rates. (The basal rate of an Australian population of *G. philippensis* is similar to that of a New Zealand population.) The evolution of a flightless condition in the studied species occurred on islands independently in all 6 cases. The evolution of this island syndrome requires the absence of eutherian predators, but it has occurred on land masses with marsupial predators, namely on Australia, Tasmania, and New Guinea, and on many islands with avian predators (McNab and Ellis, 2006).

Alaudidae. Tieleman et al. (2003) presented data on the basal rates of 12 species of larks and a cladogram that includes 11 of these species (Fig. 3). Basal rates in these species increased with body mass and an aridity index, and decreased with the maximal temperature in the environment, although because temperature is incorporated into the index, these 2 factors cannot be combined in the same analysis. The pleisomorphic environmental conditions for larks appears, from the limited sample, to have been xeric with high ambient temperatures (Fig. 3). Larks appear to have moved into mesic (M), intermediate-temperature (I) environments 3 times and into mesic, low-temperature (L) environments once, with the appropriate modification of basal rate of metabolism.

Paradisaeidae. The basal rates of 13 species of birds-of-paradise are affected by body mass, food habits, and altitudinal limits to distribution (McNab, 2003c, 2005a). Paradisaeids have higher basal rates, corrected for body mass, if 1) insects comprise more than 10% of their diet and 2) they are found at altitudes > 1000 m in New Guinea. Most species with low basal rates feed nearly exclusively on fruit and are limited in distribution to altitudes < 1000 m. The evolution of high basal rates occurred at least twice in these species with an increased intake of insects and thrice with movement into the highlands of New Guinea (Fig. 4). The influence of food habits on basal rate may take precedence over that of altitude, which would explain the low basal rate in the frugivore *Cnemophilus loriae*, which lives at altitudes > 1500 m. No evidence of any influence on basal rate by plumage dimorphism or reproductive strategy was found in spite of the diversity in these aspects of bird-of-paradise biology. Yet, the diversity in reproductive strategy might affect field expenditures through its impact on activity, especially in males participating in lek displays.


1
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3
89 F 2
92 F 2
83 F 2
125 O 2
91 F 2
92 F 2
99 O 1
101 O 2
110 O 2
101 O 1
107 O 1
106 O 1
113 O 2
Cnemophilus loriae
Manucodia chalybata
Manucodia keraudrenii
Astrapia stephaniae
Parotia lawesii
Parotia wahnesi
Ptiloris magnificus
Lophorina superba
Epimachus meyeri
Cicinnurus magnificus
Cicinnurus regius
Paradisaea raggiana
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Figure 3 (precdeding page). The evolution of basal rate of metabolism in larks (Alaudidae). Column 1, basal rate (% of the value expected from mass in larks). Column 2, aridity index (annual rainfall/1000 x ([Tmax + Tmin][Tmax - Tmin]). Column 3, maximal environmental temperature. Tolerance of high ambient temperatures indicated by H, intermediate temperatures by I, and low temperatures by L. Modified from Tieleman et al. (2003).

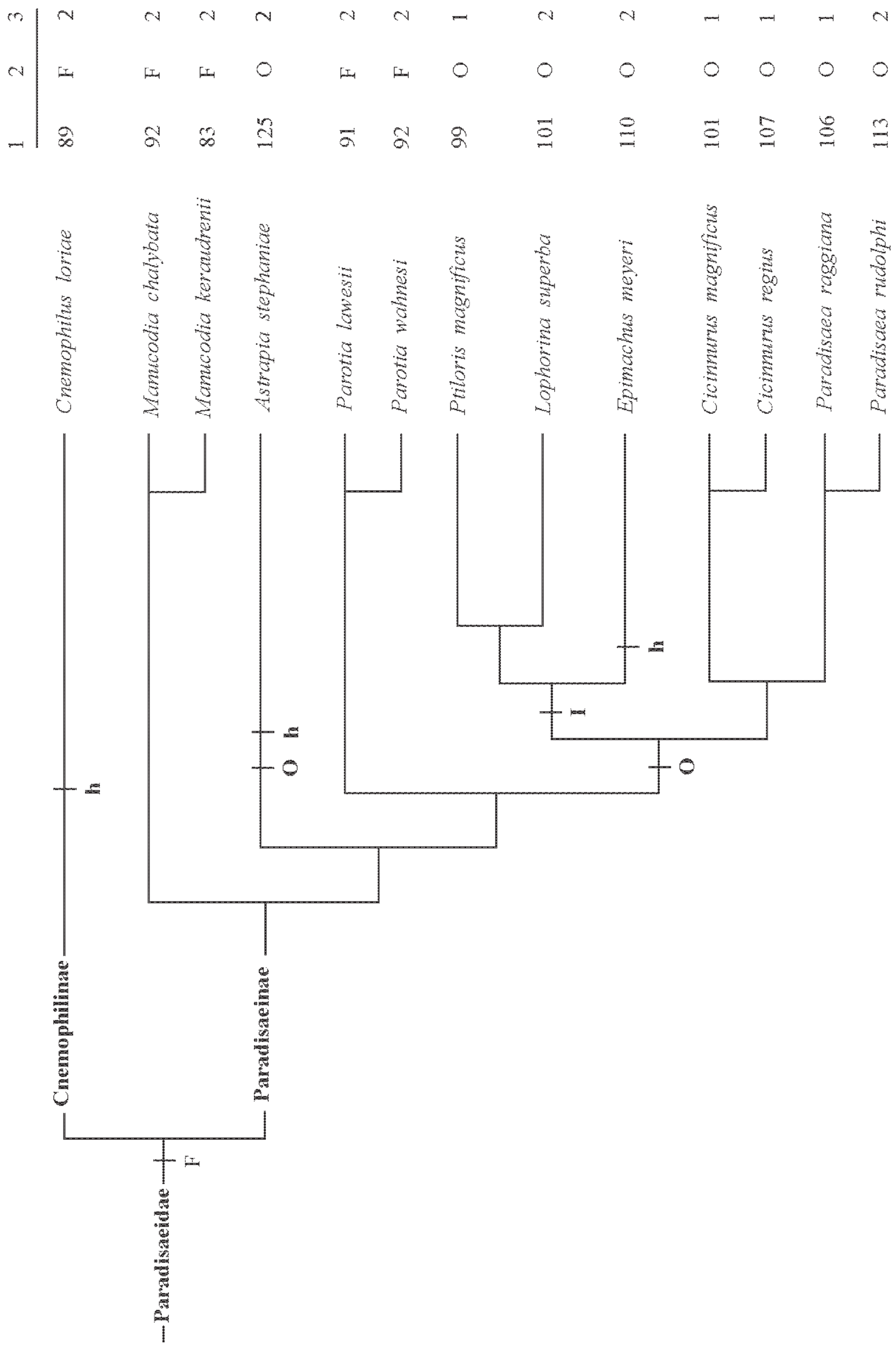
DIFFICULTIES IN THE ANALYSIS OF THE EVOLUTION OF CHARACTER STATES

As is to be expected from the complexity of the interactions among character states and their causative factors, the disentanglement of these relationships is difficult. For example, the attempt to account for the difference in energy expenditure between arctic seals and tropical manatees involves so many differences in character states that one cannot easily ascribe it simply to a difference in food habits or water temperature, contributory through these factors may be. This difficulty led to an attempt to "correct" the analysis of character states for phylogenetic history (Harvey and Pagel, 1991; Garland et al., 1992). It essentially assumes as a null hypothesis that most of the similarities among related species are due to the inheritance of character states from a common ancestor unless proven otherwise.

The difficulty with a technique like "independent contrasts" is that it appropriates nearly all of the residual variation in a character to phylogeny by giving it preference, thereby leaving little to correlate with other factors. This procedure has been applied to energetics (Elgar and Harvey, 1987; Harvey and Elgar, 1987; Harvey et al., 1991; Cruz-Neto et al., 2001), but has been criticized (McNab, 1987, 2003b; Derrickson, 1989; Westoby et al., 1995) for its simplicity of viewpoint and for ignoring factor interactions.

Most relatives of a species have a similar body mass, have similar food habits, live in a similar climate, and have similar behaviors, and *therefore* have similar rates of metabolism. That is not unexpected, but to ascribe these similarities to phylogeny is meaningless, because it essentially dismisses the correlation of character states with phylogeny and ignores the direction of character states. Thus, why do carnivorous eutherians consistently have high basal rates, irrespective of whether they are phyllostomids, megadermatids, canids, herpestids, mustelids, viverrids, felids, phocids, or delphinids? Or, why do avian frugivores, including columbids, coliids, trogonids, bucerotids, capitonids, ramphastids, and piprids, consistently have low basal rates? These consistencies are well beyond a phylogenetic interpretation and are unlikely simply to be accidents. One would better ascribe the similarities in basal rate of relatives to their similarities in mass, climate, food habits, or behavior. In the analysis of character states, "phylogeny" represents a "collective" for all factors other than body mass that influence basal rate, which raises the question whether anything remains after the effects of all other correlates of basal rate, such as climate and food habits, are extracted. In a sense, then, "phylogeny" represents the residual of functionally based factors that have not been yet identified.

What is most interesting in this context is that some groups seem to be radical innovators, whereas others are conservative. Arvicoline rodents are similar in climatic distribution, food habits, and absence of torpor: they differ principally in body size. They uniformly have, corrected for body mass, high basal rates of metabolism, the



	1	2	3
Cnemophilus loriae	89	F	2
Manucodia chalybata	92	F	2
Manucodia keraudrenii	83	F	2
Astrapia stephaniae	125	O	2
Parotia lawesii	91	F	2
Parotia wahnesi	92	F	2
Ptiloris magnificus	99	O	1
Lophorina superba	101	O	2
Epimachus meyeri	110	O	2
Cicinnurus magnificus	101	O	1
Cicinnurus regius	107	O	1
Paradisaea raggiana	106	O	1
Paradisaea rudolphi	113	O	2

Figure 4 (preceding page). The evolution of basal rate of metabolism in birds-of-paradise (Paradiseaidae). Column 1, basal rate (% of the value expected from mass in birds-of-paradise). Column 2, food habits (F, fruit; O, omnivory). Column 3, altitudinal distribution (1, < 1000 m; 2, > 1000 m). Modified from McNab (2005a).

highest values principally found in small species that live in cold climates (McNab, 1992). In contrast, phyllostomid bats are radical innovators in terms of diet and body size and *as a result* have highly diversified basal rates.

Why this difference among clades? Does it reflect differences in internal flexibility or environmental opportunity? Whatever the answer to this question (see next section), the means of analyzing the evolution of character states needs techniques that will take all complications that occur among determinative factors into consideration. An effective technique is the analysis of covariance, which permits factor interactions to be explored, thereby avoiding a simplistic lumping of character states. Phylogeny depicts the historical evolution of a group, but is not its determinative agent. The existence of particular character states in a species may prolong the time required for the evolution of new character states, but this affect is transitory under conditions that select for different states. *Phylogeny is not destiny.*

EVOLUTIONARY DIFFERENCES AMONG PHYLETIC GROUPS

A potentially interesting approach would be to compare evolutionary groups that represent a dichotomy in diversification, such as the difference between marsupials and eutherians or between phyllostomid and megadermatid or nycterid bats, to pick 2 readily available examples.

Eutheria vs Metatheria. Marsupials usually are described as having lower basal rates of metabolism, when corrected for body mass, than eutherians (Martin 1902, McNab 1978b), a conclusion that is statistically justifiable, but simplistic. Marsupials do not have the lowest basal rates (McNab, 1986b; Lillegraven et al., 1987). Of 70 measured marsupials (McNab, 2005b), no species had a basal rate less than 50% of the value expected from mammals generally, but of 272 eutherians (McNab, 1988a), 10 (3.7%) species had such low rates.

What is most distinctive about marsupials is that no species has a basal rate appreciably greater than expected from the all-mammal curve (i.e., their distribution in basal rates is truncated at the higher end; Fig. 5). Only 6 of 70 marsupials (8.5%) had basal rates that were 105-110% those expected from mammals generally, the highest basal rates reported. In contrast, of 272 eutherians 112 (41.2%) had basal rates between 100 and 150%, 26 (9.6%) between 150 and 200%, 11 (4.0%) between 200 and 300%, and 3 (1.1%) aquatic species had basal rates that exceeded 300%. That is, 55.9% of the measured eutherians had basal rate is equal to, or greater than, the basal rates expected from the general mammalian curve. The reason why marsupials collectively have lower basal rates than eutherians is that no marsupials have basal rates high enough to raise the collective mean to that found in eutherians, whereas the majority of measured eutherians have basal rates greater than the general mammalian curve. This difference is clearly demonstrated in terrestrial carnivores, where eutherians

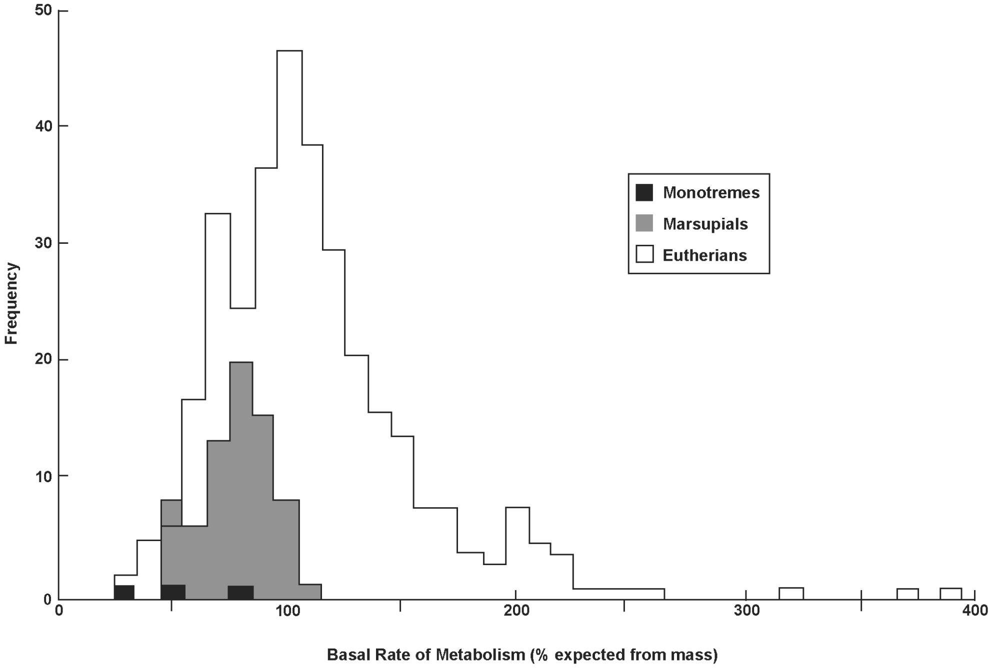


Figure. 5. Frequency distribution of basal rates of metabolism in monotreme, marsupial, and eutherian mammals, expressed as a percent of the values expected from the general mammal equation (McNab, 1988a). Data derived from McNab (1988a and 2005b).

have basal rates between 116 and 231% of the values expected from mass, whereas marsupials have basal rates between 82 and 96% (i.e., no overlap in basal rate exists between these 2 groups of carnivores). A similar difference is seen between macropods and ungulates.

Why does this difference exist? A simplistic explanation would suggest that it is a difference that reflects phylogeny—which tells us nothing. A more meaningful suggestion would be that *some feature or features of eutherians facilitate(s) the evolution of high basal rates under certain circumstances, and that feature(s) is (are) not present in marsupials*. In that sense, the high basal rates in eutherians indeed are a byproduct of phylogenetic history, although that admission does not expose the reason(s) for their presence. The difficulty, of course, is to identify this feature, or features.

As a preliminary suggestion, I argued that the feature is the presence of the trophoblast in eutherians, which is the part of the placenta that protects fetuses against immunological rejection (McNab, 1986b; Lillegraven et al., 1987), while permitting high levels of gaseous, nutritional, and waste exchange between a gravid female and her developing fetuses. High rates of exchange permit high growth rates in her developing offspring. If in a competitive bind, if the resources are available in the environment, and if these resources can be easily processed, the rate of metabolism of eutherians increases, thereby maximizing the growth rate of the fetuses and the female's reproductive output. High basal rates in eutherians also appear to facilitate high post-partum growth rates (McNab, 1980), whereas eutherians with low basal rates have reduced rates of lactation (Glazier, 1985), reduced growth rates (McNab, 1980; Rasmussen and Izard, 1988), and smaller litter sizes (Genoud, 1988) compared to those with high basal rates. Selection in house mice for an increased appetite (and presumably a high rate of metabolism) resulted in an increased reproductive rate produced by an increased ovulation rate and litter size (Brien et al., 1984). Harvey et al. (1991) denied these correlations based on phylogeny, which again reflects an inability to distinguish phylogeny from (reproductive) character states.

The eutherians most noted for their propensity to have large cyclic population fluctuations, which requires high rates of reproduction, are species with high basal rates (e.g., arvicoline rodents [especially lemmings] and hares; McNab, 1980). From this view, the presence of low basal rates in many eutherians represents the absence of sufficient resources in the environment, the inability to process these resources at rates sufficient to support high rates of metabolism, or the absence of competition sufficient to require a response by eutherians, in spite of having a form of reproduction that would permit high rates of reproduction.

Increasing reproductive output in marsupials is not facilitated by increasing rate of metabolism during pregnancy because gas and nutrient exchanges between the gravid mother and fetuses are limited by the presence of a shell membrane that protects the fetuses from immunological rejection (Lillegraven, 1976; Lillegraven et al., 1987), but restricts the exchange between the mother and her fetuses. That is why high basal rates do not appear even in marsupials that have food habits, such as carnivory and grazing, in which eutherians consistently have high basal rates. The difference in reproductive output between eutherians and marsupials can be seen in a comparison of 2 herbivores of equal size, the hare *Oryctolagus cuniculus* and the quokka *Setonix brachyurus* (Tyndale-Biscoe, 1973): the hare can produce 35 kittens weighing 1700 g in 240 days, lactation lasting about 20 days, whereas the quokka in the same period produces one joey weighing 500 g, lactation lasting 190 days. The basal rate of *Oryctolagus* is 107% of the value expected from mammals generally (Benedict, 1938), whereas that of *Setonix* is 87% (Kinnear and Shield, 1975).

Some problems potentially exist with this idea: if the handicap of marsupials is the difficulty transferring gases, nutrients, and wastes between the fetuses and a gravid parent, why don't marsupials simply increase their rate of metabolism after birth to facilitate high rates of milk production and of post-natal growth? The answer may be that at birth marsupials are still in an embryonic stage and they may have a limited capacity to process milk because of the slow development of their digestive, respiratory, and excretory systems (Parker, 1977), which may explain why the one joey produced requires 190 days of lactation.

The difference in basal rates of metabolism between marsupials and eutherians must be definable in the character states between marsupials and eutherians, and not simply passed off as a vague difference *due to* phylogeny. No substantive, alternate explanation for this difference has been suggested. The prevalence in marsupials of basal rates of metabolism that are 60-80% of those expected from mammals suggests that the higher basal rates of eutherians is not due to the cost of endothermy (except possibly at the smallest masses and in the coldest environments) because marsupials are just as good thermoregulators as eutherians.

The absence of high basal rates in marsupials, the real difference with eutherians, and its implications for reproductive rate may account for the ecological diversity of marsupials in eutherian-poor (except for bats and mice) Australia/Tasmania/New

Guinea and for their persistence in niches in the eutherian-rich Neotropics (McNab, 1986b, 2005b) that require eutherians to have depressed rates of metabolism and reproduction. The extinction of the thylacine (*Thylacinus cynocephalus*), Tasmanian devil (*Sarcophilus harrisii*), and eastern quoll (*Dasyurus viverrinus*) on mainland Australia correlated with the transport by humans, some 3,500 years ago (Corbett, 1995), to Australia of the dingo (*Canis lupus* [*dingo*]). These marsupial carnivores, however, survived in Tasmania in the absence of dingos. That is, marsupials do not survive in the presence of eutherians when both have habits that in eutherians are associated with high basal rates and high rates of reproduction. Furthermore, marsupials show a reduced diversity in cold climates, both at high latitudes and high altitudes, where they, unlike eutherians, show no tendency to increase basal rate (McNab, 2005b).

Phyllostomidae vs Megadermatidae and Nycteridae. Another approach to the analysis of character states is to compare groups that have responded differently to what appears to have been similar opportunities. An example is found in tropical bats. One lineage, the Phyllostomidae in the Neotropics, evolved many food habits and a marked diversity in body mass and basal rate of metabolism (McNab, 2003b). In contrast, the Megadermatidae and Nycteridae in the Paleotropics have only diversified in body mass in association with the differential consumption of insects and vertebrates (Fenton et al., 1990, 1993; Freeman, 2000). The largest studied carnivores in the Megadermatidae (*Macroderma gigas*) and the Phyllostomidae (*Chrotopterus auritus*) have converged on a large mass (ca. 100 g), a high basal rate, and precise endothermy (Leitner and Nelson, 1967; McNab, 1969). (The larger Neotropical *Vampyrum spectrum*, which is unstudied, will undoubtedly be similar.) Is the limited differentiation in the Megadermatidae and Nycteridae a reflection of a difference with the Phyllostomidae in internal (genetic?) flexibility, or does the difference reflect conditions in the Neotropical and the Paleotropical environments? The latter explanation may hold because the Paleotropics have the diverse chiropteran family Pteropodidae, which feeds on nectar and fruit; their presence may have prevented the megadermatids and nycterids from exploiting these resources. In contrast, the pteropodid-free Neotropics may have permitted phyllostomids to exploit the food habits used by the pteropodids, as well as to expand into carnivory and sanguinivory.

CONCLUSIONS

The energy expenditure of endotherms is complexly tied to their body mass, behavior, and ecology, as modified by environmental conditions. Endotherms generally maximize energy expenditure in thermally and competitively demanding environments as long as sufficiently high quality food resources can be accessed. Maximizing energy expenditure permits eutherian mammals to survive harsh environmental conditions and to withstand competition by maximizing reproductive output. If, however, resources are limited, especially in an unpredictable manner, or if they are of poor quality, eutherians reduce energy expenditure and reproductive output and survive by an increase in individual longevity. This strategy is carried to an extreme by bats and birds on oceanic islands free of eutherian predators. Marsupials do not appear to have the same capacity to convert high levels of resource availability into high rates of reproductive output, possibly because of their form of reproduction. A consequence of this limitation is that marsupials coexist with similar eutherians only when both use resources that require eutherians to have low rates of metabolism. The energetics of birds is not as well known as that of mammals, but birds appear to be more similar to eutherians than to marsupials in that high basal rates may be correlated with an increased capacity for reproduction: the use of egg laying may permit birds to evade the limitations that appear to be associated with the marsupial form of reproduction.

The study of energetics permits a diversity of biological and environmental characteristics to be integrated, thereby giving a comparatively holistic approach to natural history, ecology, and evolution. Oliver Pearson was one of the first persons to see the integrative value in the study of the energetics of free-living vertebrates, which was a significant contribution to the intellectual development of natural history and evolutionary biology.

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LITERATURE CITED

Aalto, M., A. Górecki, R. Meczeva, H. Wallgren, and J. Weiner
1993 Metabolic rates of the bank voles (*Clethrionomys glareolus*) in Europe along a latitudinal gradient from Lapland to Bulgaria. Annales Zoologici Fennici 30:233-238.

Anava, A., M. Kam, A Shkolnik, and A. A. Degan
2001 Heat production and body temperature of Arabian babblers (*Turdoides squamiceps*): a bird from hot desert habitats. Journal of Arid Environments 48: 59-67.

Arends, A., and B. K. McNab
2001 The comparative energetics of 'caviomorph' rodents. Comparative Biochemistry and Physiology 130A:105-122.

Arieli, R.
1979 The atmospheric environment of the fossorial rodent (*Spalax ehrenbergi*): Effects of season, soil texture, rain, temperature and activity. Comparative Biochemistry and Physiology 63A:569-575.

Arieli, R., A. Ar, and A. Shkolnik
1977 Metabolic responses of a fossorial rodent (*Spalax ehrenbergi*) to simulated burrow conditions. Physiological Zoology 50:61-75.

Aschoff, J., and H. Pohl
1970 Rhythmic variations in energy metabolism. Federal Proceedings 29:1541-1552.

Banavar, J. R., J. Damath, A. Maritan, and A. Rinaldo
2002 Supply-demand balance and metabolic scaling. Proceedings of the National Academy of Science (USA) 99:10506-10509.

2003 Allometric cascades. Nature 421: 713-714.

Banavar, J. R., A. Maritan, and A. Rinaldo
1999 Size and form in efficient transportation networks. Nature 399:130-132.

Bartholomew, G. A., C. M. Vleck, and T. L. Bucher
1983 Energy metabolism and nocturnal hypothermia in two tropical passerine frugivores, *Manacus vitellinus* and *Pipra mentalis*. Physiological Zoology 56:370-379.

Bech, C., and J. E. Østnes
1999 Influence of body composition on the metabolic rate of nestling European shags (*Phalacrocorax aristotelis*). Journal of Comparative Physiology B 169:263-270.

Benedict, F. G.
1938 Vital energetics: a study in comparative basal metabolism. Publ. 503. Carnegie Inst. Washington, Washington, D.C., USA.

Bennett, A. F., and J. A. Ruben
1979 Endothermy and activity in vertebrates. Science 206:649-654.

Bergmann, C.
1848 Ueber die Verhältnisse der Wärmeökonomie der Tiere zu ihrere Grösse. Gottinger Studien 3:595-708.

Bolls, N. J., and J. R. Perfect
1972 Summer resting metabolic rate of the gray squirrel. Physiological Zoology 45:54-59.

Bonaccorso, F. J., and B. K. McNab
2003 Standard energetics in leaf-nosed bats (Hipposideridae): its relationship to intermittent and protracted foraging tactics in batsand birds. Journal of Comparative Physiology B 173:43-53.

Breyen, L. J., W. G. Bradley, and M. K. Yousef
1973 Physiological and ecological studies on the chisel-toothed kangroo rat *Dipodomys microps*. Comparative Biochemistry and Physiology 44A:543-555.

Brien, F. B., G. L. Sharp, W. G. Hill, and A. Robertson
1984 Effects of selection on growth, body composition and food intake in mice. II. Correlated responses in reproduction. Genetical Research, Cambridge 44: 73-85.

Bryant, D. M., and P. Tatner
1991 Intraspecific variation in avian energy expenditure: correlates and constraints. Ibis 133:236-245.

Calder, W. A., III.
1984 Size, Function, and Life History. Harvard University Press, Cambridge, Massachusetts, USA. 431 pp.

Chappell, M. A.
1980 Thermal energetics and thermoregulatory costs of small arctic mammals. Journal of Mammalogy 61:278-291.

Cody, M. L.
1966 A general theory of clutch size. Evolution 20:174-184.

Contreras, L. C., and B. K. McNab
1990 Thermoregulation and energetics in subterranean mammals. Pp. 231-250 in Evolution in Subterranean Mammals at the Organismal and Molecular Levels (Nevo, E., and O.A. Reig, eds.). Alan R. Liss, Inc., New York, New York, USA.

Corbett, L. K.
1995 The Dingo in Australia and Asia. Comstock/Cornell, Ithaca, New York, USA. 200 pp.

Crowell, K. L.
1962 Reduced interspecific competition among the birds of Bermuda. Ecology 43:75-88.

Cruz-Neto, A. P., T. Garland, and A. S. Abe
2001 Diet, phylogeny, and basal metabolic rate in phyllostomid bats. Zoology 104:49-58.

Daan, S., D. Masman, and A. Groenewold
1990 Avian basal metabolic rates: their association with body composition and energy expenditure in nature. American Journal of Physiology 259: R333-R340.

Darveau, C.-A., R. K. Saurez, R. D. Andrews, and P. W. Hochachka
2002 Allometric cascade as a unifying principle of body mass effects on metabolism. Nature 417:166-170.

Derrickson, E. M.

1989 The comparative method of Elgar and Harvey: silent ammunition for McNab. Functional Ecology 3:123-126.

Domning, D. P.

1978 Sirenian evolution in the North Pacific Ocean. University of California Publications in Geological Sciences 118:1-176.

Drent, R. H., and S. Daan

1980 The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225-252.

Elgar, M. A., and P. H. Harvey

1987 Basal metabolic rates in mammals: Allometry, phylogeny and ecology. Functional Ecology 1:25-36.

Ellis, H. I.

1980 Metabolism and solar radiation in dark and white herons in hot climates. Physiological Zoology 53:358-372.

1985 Energetics of free-ranging sea birds. Pp. 203-234 in Seabird Energetics (Whittow, G. C., and H. Rahn, eds.). Plenum, New York, New York, USA.

Ellis, H. I., and G. W. Gabrielsen

2001 Energetics of free-ranging seabirds. Pp. 359-407 in Biology of Marine Birds (Schreiber, E. A., and J. Burger, eds.). CRC Press, Boca Raton, Florida, USA.

Else, P. L., and A. J. Hulbert

1985 An allometric comparison of the mitochondria of mammalian and reptilian tissues: the implications for the evolution of endothermy. Journal of Comparative Physiology B 156:3-11.

1987 Evolution of mammalian endothermic metabolism: "leaky" membranes as a source of heat. American Journal of Physiology 253: R1-R7.

Fenton, H. B., I. L. Rautenbach, D. Chipese, M. B. Cumming, M. K. Musgrave, J. S. Taylor, and T. Volpers

1993 Variation in foraging behaviour, habitat use, and diet of large slit-faced bats (*Nycteris grandis*). Zeitschrift für Säugetierkunde 58:65-74.

Fenton, H. B., C. M. Swanepoel, R. M. Brigham, J. Cebek, and M. B. C. Hickey

1990 Foraging behavior and prey selection by large slit-faced bats (*Nycteris grandis*; Chiroptera: Nycteridae). Biotropica 22:2-8.

Freeman, P. W.

2000 Macroevolution in Microchiroptera: recoupling morphology and ecology with phylogeny. Evolutionary Ecology Research 2:317-335.

Gallivan, G. J., and R. C. Best

1980 Metabolism and respiration of the Amazonian manatee (*Trichechus inunguis*). Physiological Zoology 53:245-253.

Garland, T., P. H. Harvey, and A. R. Ives

1992 Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology 41:18-32.

Genoud, M.

1988 Energetic strategies of shrews: Ecological constraints and evolutionary implications. Mammal Review 18:173-193.

Glazier, D. S.

1985 Relationship between metabolic rate and energy expenditure for lactation in *Peromyscus*. Comparative Biochemistry and Physiology 80A:587-590.

Golightly, R. T., and R. D. Ohmart

1978 Heterothermy in free-ranging Abert's squirrels (*Sciurus aberti*). Ecology 59:897-909.

Grand, T.

1978 Adaptations of tissue and limb segments to facilitate moving and feeding in arboreal folivores. Pp. 231-241 in The Ecology of Arboreal Folivores (Montgomery, G. G., ed.). Smithsonian Institution Press, Washington, D.C., USA.

Hails, C. J.

1983 The metabolic rate of tropical birds. Condor 85:61-65.

Haim, A.

1987a Thermoregulation and metabolism of Wagner's gerbil (*Gerbillus dasyurus*): a rock-dwelling rodent adapted to arid and mesic environments. Journal of Thermal Biology 12:45-48.

1987b Metabolism and thermoregulation in rodents: are these adaptations to habitat and food quality? South African Journal of Science 83:639-642.

Haim, A., and A. Borut

1986 Reduced heat production in the bushy-tailed gerbil *Skeetamys calurus* (Rodentia) as an adaptation to arid environments. Mammalia 50:27-33.

Haim, A., and I. Izhaki

1993 The ecological significance of metabolic rate and nonshivering thermogenesis in rodents. Journal of Thermal Biology 18:71-81.

Hammond, K. A., and J. Diamond
1997 Maximal sustained energy budgets in humans and animals. Nature 386: 457-462.

Hansen, S., D. M. Lavigne, and S. Innes
1995 Energy metabolism and thermoregulation in juvenile harbor seals (*Phoca vitulina*) in air. Physiological Zoology 68:290-315.

Hartman, F. A.
1961 Locomotor mechanisms of birds. Smithsonian Miscellaneous Collections 143:1-91.

Harvey, P. H., and M. A. Elgar
1987 In defense of the comparative method. Functional Ecology 1:160-161.

Harvey, P. H., and M. D. Pagel
1991 The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford, UK. 239 pp.

Harvey, P. H., M. D. Pagel, and J. A. Rees
1991 Mammalian metabolism and life histories. American Naturalist 137:556-566.

Hayssen, V., and R. C. Lacy
1985 Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. Comparative Biochemistry and Physiology 81A: 741-754.

Hayward, J. S.
1965 Metabolic rate and its temperature-adaptive significance in six geographic races of *Peromyscus*. Canadian Journal of Zoology 43:309-323.

Hemmingsen, A. M.
1960 Energy metabolism as related to body size and respiratory surfaces, and its evolution. Reports of the Steno Memorial Hospital and the Nordisk Insulinlaboratorium 9:1-110.

Heusner, A. A.
1991 Size and power in mammals. Journal of Experimental Biology 160:25-54.

Hill, W. C. O., A. Porter, R. T. Bloom, J. Seago, and M. D. Southwick
1957 Field and laboratory studies on the naked mole rat, *Heterocephalus glaber.* Proceedings of the Zoological Society of London 128:455-514.

Hinds, D. S., and R. E. MacMillen
1985 Scaling of energy metabolism and evaporative water loss in heteromyid rodents. Physiological Zoology 58:282-298.

Hochachka, P. W., C.-A. Darveau, R. D. Andrews, and R. K. Suarez
2003 Allometric cascade: a model for resolving body mass effects on metabolism. Comparative Biochemistry and Physiology 134A: 675-691.

Holyoak, D. T.
1999 Family Aegothelidae (Owlet-Nightjars). Pp. 252-265. in Handbook of the Birds of the World. Vol. 5 (del Hoyo, J., A. Elliott, and J. Sargatal, eds.). Lynx Edicions, Barcelona, Spain.

Hudson, J. W., and S. L. Kinzey
1966 Temperature regulation and metabolic rhythms in populations of the house sparrow, *Passer domesticus*. Comparative Biochemistry and Physiology 17:203-217.

Hulbert, A. J., and P. L. Else
1989 Evolution of mammalian endothermic metabolism: mitochondrial activity and cell composition. American Journal of Physiology 256:R63-R69.

Jarvis, J. U. M.
1978 Energetics of survival in *Heterocephalus glaber* (Ruppell), the naked mole-rat (Rodentia: Bathyergidae). Bulletin of Carnegie Museum of Natural History 6:81-87.

Kekwick, A.
1965 Adiposity. Pp. 617-624 in Handbook of Physiology, Section 5 (Florkin, M., and E. H. Stotz, eds.). American Physiological Society, Washington, D.C., USA.

Kenagy, G. J.
1972 Saltbush leaves: excision of hypersaline tissue by a kangaroo rat. Science 178:1094-1096.

Kennerly, T. E.
1964 Microenvironmental conditions of the pocket gopher burrow. Texas Journal of Science 16:395-441.

Kersten, M., and T. Piersma
1987 High levels of energy expenditure in shorebirds: metabolic adaptations to an expensive way of life. Ardea 75:175-187.

Kinnear, A. and J. W. Shield
1975 Metabolism and temperature regulation in marsupials. Comparative Biochemistry and Physiology 52A: 235-246.

Klaasen, M.
1995 Moult and basal metabolic cost in males of two subspecies of Stonechats: the European *Saxicola torquata rubicula* and East African *S. t. axillaris.* Oecologia (Berlin) 104:424-432.

Kleiber, M.
1932 Body size and metabolic rate. Hilgardia 6:315-353.

Köhler, M., and S. Moyà-Solà
2001 Phalangial adaptations in the fossil insular goat *Myotragus*. Journal of Vertebrate Paleontology 21:621-624.

2003 Reduction of brain and sense organs in the fossil insular bovid *Myotragus.* Brain, Behavior and Evolution 63: 125-140.

Konarzewski, M., and J. Diamond
1995 Evolution of basal metabolic rate and organ masses in laboratory mice. Evolution 49:1239-1248.

Koteja, P.
1991 On the relation between basal and field metabolic rates in birds and mammals. Functional Ecology 5:56-64.

Kozłowski, J., and M. Konarzewski
2004 Is West, Brown and Enquist's model of allometric scaling mathematically correct and biological relevant? Functional Ecology 18:283-289.

Krosniunas, E. H., and G. E. Gerstner
2003 A model of vertebrate resting metabolic rate: balancing energetics and O_2 transport in system design. Respiratory Physiology and Neurobiology 134:93-113.

Leitner, P., and J. E. Nelson
1967 Body temperature, oxygen consumption and heart rate in the Australian false vampire bat, *Macroderma gigas*. Comparative Biochemistry and Physiology 21:65-74.

Lillegraven, J. A.
1976 Biological considerations of the marsupial-placental dichotomy. Evolution 29:707-722.

Lillegraven, J. A., S. D. Thompson, B. K. McNab, and J. L. Patton
1987 The origin of eutherian mammals. Biological Journal of the Linnean Society 32:281-336.

Lovegrove, B. G.
1986a Thermoregulation of the subterranean rodent genus *Bathyergus* (Bathyergidae). South African Journal of Zoology 21:283-288.

1986b The metabolism of social subterranean rodents: adaptation to aridity. Oecologia (Berlin) 69:551-555.

1987 Thermoregulation in the subterranean rodent *Georychus capensis* (Rodentia: Bathyergidae). Physiological Zoology 60:174-180.

2000 The zoogeography of mammalian basal metabolic rates. American Naturalist 156:201-219.

MacMillen, R. E., and A. K. Lee
1970 Energy metabolism and pulmocutaneous water loss of Australian hopping mice. Comparative Biochemistry and Physiology 35:355-369.

MacMahon, T.
1973 Size and shape in biology. Science 179:1201-1204.

Martin, C. J.
1902 Thermal adjustment and respiratory exchange in monotremes and marsupials -- a study in the development of homeothermism. Philosophical Transactions of the Royal Society of London B, Biological Sciences 195:1-37.

McNab, B. K.
1963 A model of the energy budget of a wild mouse. Ecology 44:521-532.

1966 The metabolism of fossorial rodents: a study of convergence. Ecology 47:712-733.

1968 The influence of fat deposits on the basal rate of metabolism in desert homoiotherms. Comparative Biochemistry and Physiology 26:337-343.

1969 The economics of temperature regulation in Neotropical bats. Comparative Biochemistry and Physiology 31:227-268.

1976 Seasonal fat reserves of bats in two tropical environments. Ecology 57:332-338.

1978a Energetics of arboreal folivores: Physiological problems and ecological consequences of feeding on an ubiquitous food supply. Pp. 153-162 in The Ecology of Arboreal Folivores (Montgomery, G. G., ed.). Smithsonian Institution Press, Washington, D.C., USA.

1978b The compartive energetics of marsupials. Journal of Comparative Physiology 125:113-128.

1979a Climatic adaptation in the energetics of heteromyid rodents. Comparative Biochemistry and Physiology 62A:813-820.

1979b The influence of body size on the energetics and distribution of fossorial and burrowing mammals. Ecology 60:1010-1021.

1980 Food habits, energetics, and the population biology of mammals. American Naturalist 116:106-124.

1983 Energetics, body size, and the limits to endothermy. Journal of Zoology (London) 199:1-29.

1984 Physiological convergence amongst ant-eating and termite-eating mammals. Journal of Zoology (London) 203:485-510.

1986a The influence of food habits on the energetics of eutherian mammals. Ecological Monographs 56:1-19.

1986b Food habits, energetics, and the reproduction of marsupials. Journal of Zoology (London) 208:595-614.

1987 Basal rate and phylogeny. Functional Ecology 1:159-160.

1988a Complications inherent in scaling basal rate of metabolism in mammals. Quarterly Review of Biology 63:25-54.

1988b Energy conservation in a tree-kangaroo (*Dendrolagus matschiei*) andthe red panda (*Ailurus fulgens*). Physiological Zoology 61:280-292.

1988c Food habits and the basal rate of metabolism in birds. Oecologia 77:343-349.

1991 The energy expenditure of shrews. Pp: 35-45 in The Biology of the Soricidae (Findley, J. S., and T. L. Yates, eds.). Museum of Southwestern Biology, University New Mexico, Albuquerque, New Mexico, USA.

1992 The comparative energetics of rigid endothermy: The Arvicolidae. Journal of Zoology (London) 227:585-606.

1994a Energy conservation and the evolution of flightlessness in birds. American Naturalist 144:628-642.

1994b Resource use and the survival of land and freshwater vertebrates on oceanic islands. American Naturalist 144:643-660.

1995 Energy expenditure and conservation in frugivorous and mixed-dietcarnivorans. Journal of Mammalogy 76:206-222.

1997 On the utility of uniformity in the definition of basal rate of metabolism. Physiological Zoology 70:718-720.

1999 On the comparative ecological and evolutionary significance of total and mass-specific rates of metabolism. Physiological and Biochemical Zoology 72:642-644.

2000a The influence of body mass, climate, and distribution on the energetics of South Pacific pigeons. Comparative Biochemistry and Physiology 127A:309-329.

2000b The standard energetics of mammalian carnivores: Felidae and Hyaenidae. Canadian Journal of Zoology 78:2227-2239.

2001a Functional adaptations to island life in the West Indies. Pp. 55-62 in Biogeography of the West Indies. Patterns and Perspectives (Woods, C. A., and F. E. Sergile, eds.). CRC Press, Boca Raton, Florida., USA

2001b Energetics of toucans, a barbet, and a hornbill: implications for avian folivory. Auk 118:916-933.

2002a The Physiological Ecology of Vertebrates: A View from Energetics. Comstock/Cornell University Press, Ithaca, New York, USA. 576 pp.

2002b Minimizing energy expenditure facilitates vertebrate persistence on oceanic islands. Ecology Letters 5:693-704.

2003a The energetics of New Zealand's ducks. Comparative Biochemistry and Physiology 135A:229-247.

2003b Standard energetics of phyllostomid bats: the inadequacies of phylogenetic-contrast analyses. Comparative Biochemistry and Physiology 135A:357-368.

2003c Ecology shapes bird bioenergetics. Nature 426:620-621.

2005a Food habits and the evolution of energetics of birds-of-paradise (Paradiseidae). Journal of Comparative Physiology B 175:117-132.

2005b Uniformity in the BMR of marsupials: its causes and consequences. Revista Chilena de Historia Natural 78:183-198.

2005c Ecological factors influence energetics in the Order Carnivora. Acta Zoologica Sinica 51:535-545.

McNab, B. K., and F. J. Bonaccorso
2001 The metabolism of New Guinean pteropodid bats. Journal of Comparative Physiology B 171:201-214.

McNab, B. K., and H. I. Ellis

2006 Flightless rails endemic to oceanic islands have lower energy expenditures and clutch sizes than flighted rails on islands and continents. Comparative Biochemistry and Physiology 145A:295-311.

McNab, B. K., and P. R. Morrison

1963 Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. Ecological Monographs 33:63-82.

Milton, K., T. M. Casey, and K. K. Casey

1979 The basal metabolism of mantled howler monkeys (*Alouatta palliata*). Journal of Mammalogy 60:373-376.

Morrison, P. R.

1948 Oxygen consumption in several mammals under basal conditions. Journal of Cellular and Comparative Physiology 31:281-292.

1951 An automatic manometric respirometer. Review of Scientific Instruments 22:264-267.

Morrison, P. R., and O. P. Pearson

1946 The metabolism of a very small mammal. Science 104:287-289.

Mueller, P., and J. Diamond

2001 Metabolic rate and environmental productivity: well-provisioned animals evolved to run and idle fast. Proceedings of the National Academy of Science (USA) 98:12550-12554.

Müller, E. F., J. M. Z. Kamau, and G. M. O. Maloiy

1983 A comparative study of basal metabolism and thermoregulation in a folivorous (*Colobus guereza*) and an omnivorous (*Cercopithecus mitis*) primate species. Comparative Biochemistry and Physiology 79A:319-322.

Nagy, K. A.

1987 Field metabolic rate and food requirement scaling in mammals and birds. Ecological Monographs 57:111-128.

1994 Field bioenergetics of mammals: what determines field metabolic rates? Australian Journal of Zoology 42:43-53.

Nagy, K. A., I. A. Girard, and T. K. Brown

1999 Energetics of free-ranging mammals, reptiles, and birds. Annual Review of Nutrition 19:247-277.

Nagy, K. A., and G. G. Montgomery

1980 Field metabolic rate, water flux, and food consumption in three-toed sloths (*Bradypus variegatus*). Journal of Mammalogy 61:465-472.

Nevo, E.
1999 Mosaic Evolution of Subterranean Mammals. Oxford University Press, Oxford, UK. 413 pp.

Nevo, E., and A. Shkolnik
1974 Adaptive metabolic variation of chromosome forms in mole rats, *Spalax*. Experientia 30:724-726.

Noll-Banholzer, U. G.
1979 Body temperature, oxygen consumption, evaporative water loss and heart rate in the fennec. Comparative Biochemistry and Physiology 62A:585-592.

Ochoa-Acuña, H.
1999 Energetics of Northern Phocid Seals: The Influence of Seasonality on Food Intake and Energy Expenditure. Ph.D. dissertation, University of Florida, Gainesville, 107 pp.

Olson, S. L., J. C. Balouet, and C. J. Fisher
1987 The owlet-nightjar of New Caledonia, *Aegotheles savesi*, with comments on the systematics of the Aegothelidae. Gerfaut 37:341-352.

Parker, P.
1977 An ecological comparison of marsupial and placental patterns of reproduction. Pp. 273-286 in The Biology of Marsupials (Stonehouse, B., and D. Gilmore, eds.). University Park Press, Baltimore., Maryland, USA

Pauls, R. W.
1981 Energetics of the red squirrel: a laboratory study of the effects of temperature, seasonal acclimation, use of the nest and exercise. Journal of Thermal Biology 6:79-86.

Pearson, O. P.
1947 The rate of metabolism of some small mammals. Ecology 28:127-145.

1948a Metabolism of small mammals, with remarks on the lower limitof mammalian size. Science 108:44-46.

1948b Metabolism and bioenergetics. Science Monthly 66:131-134.

1950 The metabolism of hummingbirds. Condor 52:145-152.

1954 The daily energy requirements of a wild Anna hummingbird. Condor 56:317-322.

1959 Biology of the subterranean rodents, *Ctenomys*, in Perú. Memorias del Museo de Historia Natural Javier Prado. 9:1-56.

1960 The oxygen consumption and bioenergetics of harvest mice. Physiological Zoology 33:152-160.

1964a Carnivore-mouse predation: an example of its intensity and bioenergetics. Journal of Mammalogy 45:177-188.

1964b Metabolism and heat loss during flight in pigeons. Condor 66:182-185.

Pearson, O. P., N. Binztein, L. Boiry, C. Busch, M. DiPace, G. Gallopin, P. Penchaszadeh, and M. Piantanida
1968 Estructura social, distribucion especial y composicion por edades de una populacion de tuco-tucos (*Ctenomys talarum*). Investigaciones Zoologicas Chilenas 13:47-80.

Peterson, C. C., K .A. Nagy, and J. Diamond
1990 Sustained metabolic scope. Proceedings of the National Academy of Science (USA) 87:2324-2328.

Piersma, T., Å. Lindström, R. H. Drent, I. Tulp, J. Jukema, R. I. G. Morrison, J. Reneerkens, H. Schekkerman, and G. H. Visser
2003 High daily energy expenditure of incubating shorebirds on High Arctic tundra: a circumpolar study. Functional Ecology 17:356-362.

Pizzey, G.
1980 A Field Guide to the Birds of Australia. Collins, Sydney, Australia. 460 pp.

Rasmussen, D. T., and M. K. Izard
1988 Scaling of growth and life history traits relative to body size, brain size, and metabolic rate in lorises and galagos (Lorisidae, Primates). American Journal of Physical Anthropology 75:357-367.

Ricklefs, R. E., M. Konarzewski, and S. Daan
1996 The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. American Naturalist 147:1047-1071.

Root, T.
1988 Energy constraints on avian distributions and abundances. Ecology 69:330-339.

Scholander, P. F., V. Walters, R. Hock, and L. Irving
1950a Body insulation of some arctic and tropical mammals and birds. Biological Bulletin 99:225-236.

Scholander, P. F., R. Hock, V. Walters, F. Johnson, and L. Irving
1950b Heat regulation in some arctic and tropical mammals and birds. Biological Bulletin 99:237-258.

Scholander, P. F., R. Hock, V. Walters, and L. Irving
1950c Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biological Bulletin 99:259-271.

Selman, C. T. K. Korhonen, L. Búnger, W. G. Hill, and J. R. Speakman
2001 Thermoregulatory responses of two mouse *Mus musculus* strains selectively bred for high and low food intake. Journal of Comparative Physiology B 171:661-668.

Shkolnik, A., and K. Schmidt-Nielsen
1976 Temperature regulation in hedgehogs from temperate and desertenvironments. Physiological Zoology 49:56-64.

Speakman, J. R.
1997 Factors influencing the daily energy expenditure of small mammals. Proceedings of the Nutrition Society 56:1119-1136.

2000 The cost of living: field metabolic rates of small mammals. Advances in Ecological Research 30:177-297.

Speakman, J. R., T. Ergon, R. Cavanagh, K. Reid, D. M. Scantlebury, and Z. Lambin
2003 Resting and daily energy expenditures of free-living field voles are positively correlated but reflect extrinsic rather than intrinsic effects. Proceedings of the National Academy of Science (USA) 100:14057-14062.

Taigen, T. L.
1983 Activity metabolism of anuran amphibians: implications for the origin of endothermy. American Naturalist 121:94-109.

Tieleman, B. I., J. B. Williams, and P. Bloomer
2003 Adaptation of metabolism and evaporative water loss along an aridity gradient. Proceedings of the Royal Society of London B 270:207-214.

Thomas, D. W., J. Blondel, P. Perret, M. M. Lambrechts, and J. R. Speakman
2001 Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. Science 291:2598-2600.

Tyndale-Biscoe, H.
1973 Life of Mammals. American Elsevier Publishers Co., New York, New York, USA. 340 pp.

Vleck, C. M., and D. Vleck
1979 Metabolic rate in five tropical bird species. Condor 81:89-91.

Vleck, D.
1979 The energy cost of burrowing by the pocket gopher *Thomomys bottae*. Physiological Zoology 52:122-136.

Wallgren, H.
1954 Energy metabolism of two species of the genus *Emberiza* as correlated with distribution and migration. Acta Zoologica Fennici 84:1-110.

Wasser, J. S.
1986 The relationship of energetics of falconiform birds to body mass and climate. Condor 88:57-62.

Weathers, W. W.
1979 Climatic adaptation in avian standard metabolic rate. Oecologia 42:81-89.

Weiner, J.
1992 Physiological limits to sustainable energy budgets in birds and mammals: ecological limitations. Trends in Ecology and Evolution 7:384-388.

West, G. B., J. H. Brown, and B. J. Enquist
1997 A general model for the origin of allometric scaling laws in biology. Science 276:122-126.

1999 The fourth dimension of life: Fractal geometry and allometric scaling of organisms. Science 284:1677-1679.

West, G. B., V. M. Savage, J. Gillooly, B. J. Enquist, W. H. Woodruff, and J. H. Brown
2003 Why does metabolic rate scale with body size? Nature 421:713.

Westoby, M., M. R. Leishman, and J. M. Lord
1995 On misinterpreting the ‘phylogenetic correction.’ Journal of Ecology 83:531-534.

White, C. R., and R. S. Seymour
2003 Mammalian basal metabolic rate is proportional to body mass$^{2/3}$. Proceedings of the National Academy of Science (USA) 100:4046-4049.

Wikelski, M., L. Spinney, W. Schelsky, A. Scheuerlein, and E. Gwinner
2003 Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. Proceedings of the Royal Society of London B 270:2383-2388.

Worthy, T. H., and R. N. Holdaway
2002 The Lost World of the Moa: Prehistoric Life of New Zealand. Indiana University Press, Bloomington, Indiana, USA.

ENERGY BUDGET IN SUBTERRANEAN RODENTS: INSIGHTS FROM THE TUCO-TUCO *CTENOMYS TALARUM* (RODENTIA: CTENOMYIDAE)

EL PRESUPUESTO ENERGÉTICO EN ROEDORES SUBTERRÁNEOS A LA LUZ DE ESTUDIOS EN EL TUCO-TUCO *CTENOMYS TALARUM* (RODENTIA: CTENOMYIDAE)

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Paula P. Perissinotti, and Cristina Busch

DEDICATION

This paper is dedicated to the memory of Oliver P. Pearson, a great mammalogist and a man whose authority was based on decency, modesty, and outstanding integrity. As a Ford Foundation exchange Professor at the Universidad de Buenos Aires (Argentina) he played a supportive and encouraging role in the first studies on the ecology of tuco-tucos and provided essential stimuli for our later active involvement in the biology of these subterranean rodents. Those Argentineans who were taught by him or got to meet him personally were indeed left with numerous grateful memories.

ABSTRACT

We characterize the energy budget for the South American subterranean rodent *Ctenomys talarum* (Talas tuco-tuco), based on new and published data on energy intake (ingestion and digestion) and expenditure (cellular maintenance, thermoregulation, digging activity, movement, pregnancy, lactation and growth). Animals fed a low-quality diet ingested more food, produced more feces and showed lower incidence of coprophagy, lower digestibility, and reduced transit time relative to those fed a high-quality diet. This increase in food intake would assure similar total energy assimilation as a high-quality diet, and demonstrates that tuco-tucos can adjust their ingestive and digestive processes according to the quality of the available food resources. Digging in hard soil was energetically more expensive than digging in soft soil but the net cost of digging an entire burrow system was surprisingly low. We propose that protection against predators and lowered thermoregulatory cost are the main

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advantages of living underground. Energetic demands were higher for reproductive than for non-reproductive females, especially during lactation, the most energetically costly period. Pups started to eat solid food at 7-10 days old, at which point milk production represented only 18% of their energy demands. Pups became independent thermoregulators at 15 days of age. The agreement between calculated daily energy demands and daily energy assimilation (160 KJ) validates our analysis. Possible extrinsic and intrinsic limitations on *C. talarum* energy budget are discussed.

Key words: Energy budget, energy intake, energy expenditure, subterranean rodents, *Ctenomys talarum*

RESÚMEN

En este estudio se describe el presupuesto energético del roedor subterráneo sudamericano *Ctenomys talarum* (tuco-tuco de los Talas), integrando información nueva y ya reportada sobre procesos de obtención (ingestión y digestión) y gasto de energía (mantenimiento celular, termorregulación, excavación, movimiento, preñez, amamantamiento y crecimiento). Los animales alimentados con una dieta de baja calidad ingirieron mayor cantidad de alimento, produjeron mayor cantidad de heces y mostraron menor incidencia de coprofagia, a la vez que presentaron menor digestibilidad y un tiempo de tránsito más breve en relación a aquellos individuos mantenidos bajo una dieta de alta calidad. Este incremento, en la ingesta de alimento de baja calidad, aseguraría una asimilación de energía total similar a la obtenida con una dieta de alta calidad, demostrando que los tuco-tucos son capaces de ajustar sus procesos ingestivos y digestivos de acuerdo a la calidad de los recursos disponibles. La excavación en suelo duro fue energéticamente más costosa que en suelo blando, aunque el costo neto de excavación de una cueva completa fue sorprendentemente bajo. Proponemos que la protección contra la predación y la disminución en los costos de termorregulación representan las principales ventajas de la vida subterránea. Las demandas energéticas de las hembras reproductivas fueron mayores que para las no reproductivas, especialmente durante el amamantamiento de crías, el cual constituye el período energéticamente más costoso. Las crías comienzan a incorporar alimento sólido a los 7-10 días de edad, momento en el cual la producción de leche representa sólo el 18% de sus demandas energéticas. La independencia termorregulatoria es alcanzada en las crías a los 15 días de edad. La concordancia encontrada entre las demandas energéticas diarias y la asimilación diaria de energía (160 KJ) calculadas para un individuo adulto validan nuestro análisis. Se discuten las posibles limitaciones extrínsecas e intrínsecas que operan sobre el presupuesto energético de *C. talarum*.

Palabras clave: Presupuesto energético, obtención de energía, gasto de energía, roedores subterráneos, *Ctenomys talarum*

INTRODUCTION

The maintenance of life requires a continuous flow of energy. The partitioning of available energy between maintenance and reproduction is a dynamic process; priorities of energy allocation to different processes change through the life of an organism and are influenced by changes in environmental conditions and resource availability. The energetic budget of an organism can be understood by the quantitative analysis of energy entering organisms, its pathways within them, and its utilization, conversion, and dispersion (McNab, 2002). Metabolic fuels generally are not available at a constant rate or in sufficient quantity for animals to maintain all physiological processes at an optimal level at all times. However, under environmental conditions resulting in high energetic costs and when food is scarce and/or quality of food is poor, animals can increase efficiency to obtain energy by a combination of ingestive and digestive mechanisms that includes adjustments of food consumption, digesta turnover rate, gut morphology, and digestibility (Cork and Foley, 1991; Bozinovic, 1993; Young Owl and Batzli, 1998). It has been reported that both quality and digestibility of food affect metabolic rates (Batzli, 1985) and, hence, energetic budget: species under low-energy content diets and/or having high digestive costs show low metabolic rates and vice versa (Bozinovic, 1993; Perissinotti, 2003). Therefore, a wide array of intrinsic and extrinsic factors may influence the energetic budget. Animals can use physiological and behavioral mechanisms to maintain a constant flow of metabolic energy to the body and to partition the available energy according to a set of priorities that ensures survival and optimizes long-term reproductive success (Wade and Shneider, 1992).

The principal energetic outputs include expenditures towards maintenance, activity, and production, as well as energy lost by digestive processes. The energy balance between energy intake and output depends on physiology, behavior, ecology, and life history traits in a given environment (Feder et al., 1987). Species may differ in their relation between energy intake and energetic costs because they differ in size, they emphasize different components of a budget, they live under different environmental conditions, or because the cost of daily activities vary with species (McNab, 2002). Some components of an energy budget may be relatively invariant in terrestrial vertebrates, as is the case for maintenance, body temperature regulation, and foraging (Wunder, 1978). In contrast, the energy used for movement may be relatively trivial in some vertebrates whereas in others, such as migratory species or subterranean rodents, it can represent a substantial proportion of the energy budget.

Subterranean rodents live in closed, dark, and dank burrow systems with low primary productivity and limited ventilation (Buffenstein, 2000). Consequently, most share a combination of low basal metabolic rates (BMR), high thermal conductance, broad thermoneutral zones, low body temperatures, and relatively poor thermoregulatory abilities as adaptations to reduce heat storage, water exchange, and energy expenditure (Busch, 1989; Nevo, 1999; Bennett et al., 2000; Zenuto et al., 2002). Because BMR should reflect the rate of biosynthesis (Stevens, 1973; Taigen, 1983; Thompson and Nicoll, 1986), low BMRs would constraint energy use in different energy-demanding processes, thus imposing a ceiling both on total daily energy expenditure (DEE) and sustained metabolic rate, (SusMR; Hammond and Diamond, 1997; Speakman et al., 2003). Sustained metabolic rates are time-averaged metabolic rates, measured in free-ranging animals, maintaining constant body mass over long periods in which metabolism is fueled by food intake rather than energy reserves (Peterson et al., 1990; Hammond and Diamond, 1997).

The low quality of the food items available underground represents a challenge for maintaining energy balance (Buffenstein, 2000). As food is costly to locate, subterranean rodents behave as foraging generalists; nonetheless, they show the capacity to select for different plant species and even plant parts according to their nutritional status (Busch et al., 2000). When the diets of strictly subterranean rodents are compared with those of rodents foraging above ground, the former tend to consume food items of higher nutritional quality and low fiber content (Reichman and Jarvis, 1989; Buffenstein, 2000). The energetic return per foraging effort is maximized in this group of rodents, since digestive efficiencies are high, exceeding those of surface-dwelling rodents (Buffenstein, 2000). Moreover, many subterranean rodents engage in coprophagy (Jarvis and Bennett, 1991; Martino, 2000), relying on microbial fermentation to enhance the extraction and absorption of nutrients (proteins, vitamins) from their diets (Kenagy and Hoyt, 1980).

Ctenomys talarum (Thomas, 1898) are small subterranean rodents found in southern South America, where they inhabit systems of closed galleries parallel to the soil surface (Antinuchi and Busch, 1992). Animals of both sexes and all ages maintain exclusive territories (Busch et al., 1989). They show a polygynous mating system (Zenuto et al., 1999) and care of offspring is strictly maternal (Zenuto et al., 2001). Although individuals of *C. talarum* (Talas tuco-tuco) forage within their tunnels, the majority of foraging bouts occur above ground, and animals must venture away from their tunnels for brief periods to gather vegetation growing on the surface (Busch et al., 2000). Pups exhibit altricial development (Zenuto et al., 2002; Cutrera et al., 2003) and, presumably as a strategy to save energy during lactation, they start to eat solid food after 10 days of age (Zenuto et al., 2002). To date, no studies have provided an energetic "blueprint" for any member of the genus *Ctenomys*.

This paper aims to provide an estimation of the energy budget of the subterranean rodent *Ctenomys talarum*. We synthesize new and published data on the acquisition of energy - ingestion and digestion processes - and in which way this energy is used in different life stages and ambient conditions in this species. We calculated the costs of different activities in the life of a tuco-tuco, including excavation of a complete burrow system, pregnancy, lactation, and growth from birth to independence. We compared the influence of different energy-demanding activities, including maintenance, thermoregulation, growth, reproduction, movement, and excavation under different soil conditions on the daily energetic budget. This evaluation allowed us to analyze which are the more demanding processes in the life of this subterranean rodent and to discuss the possible morphological, ecological, and behavioral adaptations that allow these animals to cope with such costs.

MATERIALS AND METHODS

Animal Capture and Care

Adult *C. talarum* individuals were trapped during their non-breeding season (February - June) and breeding season (July - January) at Mar de Cobo (37° 45′ S, 57° 56′ W), Buenos Aires Province, Argentina, using PVC live traps. All animals were individually housed in plastic cages (0.45 x 0.32 x 0.25 m) with wood shavings for bedding. Diet was composed of a mixture of grasses, sunflower seeds, carrots, sweet potatoes, and lettuce provided *ad libitum*; as these animals do not drink free water, it was not provided. The animal room was maintained at thermoneutrality (25°C) and the light cycle was adjusted to corresponding with seasonal changes.

Measurement of Oxygen Consumption

Oxygen consumption was measured using three kinds of respirometers:

1.-A closed Kalabukhov-Skvortzov respirometer system with a 2 l metabolic chamber (Gorecki, 1975).

2.-A modified closed automatic system, based on the design of Kalabukhov-Skvortzof (Gorecki, 1975). This consists of a double-walled aluminum metabolic chamber with polyurethane between walls, and closed with a 20 mm thick acrylic door that allowed us to observe the animals regularly. A thermocouple was used to measure temperature inside the chamber. Heat was exchanged with the outside chamber automatically by two Peltier intercoolers (Melcor, model CP-1.4-127-06l) connected to a computer and controlled by software developed at Facultad de Ingenieria, Universidad Nacional de Mar del Plata. Ambient temperature inside the chamber was maintained with an accuracy of 0.1°C. Both internal and an external pressure sensors monitored air pressure. Oxygen flow was controlled through two electro-valves. Pressure sensors and electro-valves were connected to a computer and controlled by software. CO_2 and H_2O were removed by Ascarite and Drierite.

3.- A computerized positive-pressure open-flow respirometry system (Sable System, Henderson, NV). Digging and resting chamber systems received dry and CO_2 free air at 3000 ml/min from a flow meter (Cole-Parmer Instrument Company, Vernon Hills, IL), or at 1500 ml/min from a mass flow controller (Sierra Instruments, Monterey, CA). Air was passed through a CO_2-absorbent (IQB®) and water scrubber (Silica Gel) before and after passing through the chamber. Air exiting both chambers was subsampled at 180 ± 10 ml/min and oxygen consumption was obtained from an Oxygen Analyzer FC-1B every 5 s by a Datacan V - PC program (Sable System, Henderson, NV).

Oxygen consumption values were calculated using the equation of Withers (1977). Resting metabolic rate was measured as the 5-min lowest steady-state values from a 20 min trial for pups and from a 90 min trial for adults.

Data are expressed as mass-specific metabolic rate. We converted oxygen consumption to energy values as 20.08 J = 1 ml O_2 (Schmidt-Nielsen, 1994). As animals used in the experiments were not in post-absorptive state, data are estimations of resting metabolic rate (RMR). Throughout this work RMR will be reported as mass specific metabolic rate (M-SRMR). Measurements were conducted during the morning or afternoon since this species showed an arrhythmic pattern of activity (Luna et al., 2000).

Body Temperature Measurement

Body temperature (Tb) in adult tuco-tucos was measured by quickly inserting a thermocouple 2 cm into the rectum; temperature was recorded after readings had stabilized (20 - 30 s). For pups, Tb was measured as pharyngeal temperature.

Energy Budget

Acquisition of Energy: Ingestion and Digestion Processes. Prior to all experiments, male tuco-tucos were maintained for 7 days on a diet composed of a mix of plant species later used in each experiment. Animals were then introduced to a terrarium (0.80 x 0.50 x 0.40 m) completely filled with loamy soil (hardness: 51.15 ± 4.44 Kg/cm^2; humidity:

15%). Since tuco-tucos do not accept pellets for food, two plant species were used as experimental diets: A) *Panicum racemosum* comprised a low quality diet (neutral detergent fiber 68.4%, crude protein 10.7%, caloric content 18.82 ± 0.33 KJ/g), and is highly abundant in natural grasslands were *C. talarum* individuals were trapped; B) *Medicago sativa* comprised a high quality diet (neutral detergent fiber 37.8%, crude protein 17.3%, caloric content 17.53 ± 0.42 KJ/g). Five animals were randomly assigned to each treatment. Food was provided *ad libitum* and lettuce was added to experimental diets to secure water provision for a period of 15 days. At this time, oxygen consumption was measured at thermoneutrality using an open-flow respirometer. On day 16, animals were transferred to metabolic cages for the determination of food consumption and fecal production. We provided a surplus of pre-weighed food at 1 and 12 hr, and remaining food was collected at 12 and 24 hr. Food consumption (available food - remaining food) was corrected for water content. Apparent dry matter digestibility was determined as: (total dry mass of food consumed - dry mass of feces produced)/total dry mass of food consumed (Kenagy et al., 1999). Feces and plants were oven-dried at 70° C for 48 hr to constant mass. Apparent digestibility was also calculated on the basis of energy content; the energy content of plant species as well as feces produced was determined in a calorimeter. Apparent assimilation was calculated as the daily rate of food consumption - daily rate of fecal production. On day 17, animals were deprived of food for 4 hr and then digestive transit time was determined by feeding each animal with their experimental diet. Plants were previously immersed in a colored organic solution; we then recorded the time elapsed between feeding and the production of colored feces. For the determination of incidence of coprophagy (number of feces consumed/number of feces produced) animals were video taped for 24 h on day 18. Body mass of individuals was registered daily, during mornings, to the nearest 0.1 g.

Statistics. We applied a Mann-Whitney *U* test to evaluate the null hypothesis of no differences between nutritional parameters (relative to body mass) calculated for animals under the experimental diets. Pearson's correlation was used to establish the relationship between food consumption and both digestibility and fecal production, and between digestibility and transit time.

Expenditure of Energy: Cellular Maintenance. Oxygen consumption at thermoneutrality was measured in adult non-breeding animals using each of the three kinds of respirometers detailed above.

Expenditure of Energy: Digging. Oxygen consumption was measured at thermoneutrality using a computerized positive-pressure open-flow respirometry system. The digging chamber system consisted of a square acrylic soil collector attached to an acrylic tube (0.11 m dia). A perforated tube containing the soil extracted in the field was placed inside the acrylic tube, leaving an air space between the perforated tube and the outer tube (0.01 m) to permit airflow through the system. A metallic perforated door was added to separate the square acrylic soil collector and the acrylic tube (system volume = 19.1 l). A cylindrical chamber (1.85 l) was used to estimate resting metabolic rate of *C. talarum*.

To allow a complete mixing of the inlet air, the digging chamber was allowed to equilibrate for 30 min. After this equilibration period, we opened the door and the tuco-tuco usually began to burrow within 10 min and continued until it reached the opposite end of the chamber. Data were discarded if animals stopped digging and remained inactive (for 5 min or more) in the respirometry system. Mean digging metabolic rate (DMR) was estimated for each individual in the plateau of oxygen consumption. Oxygen consumption by soil microfauna was negligible. The baseline of the respirometry system was set at 20.95% of oxygen (as suggested by the user guide) before the beginning of each experiment.

We measured Tb before and after each burrow trial. Thermal conductance of burrowing individuals was calculated according to Seymour et al. (1998) as C = MR / (Tb – Ta), where MR is the metabolic rate, Tb is the final body temperature and Ta is the ambient temperature. After each burrowing trial, we estimated the volume of removed soil by the individuals.

Experimental Trials. To estimate the effect of soil hardness on digging metabolic rate, we collected 2 different soil types that occur within the geographical distribution of *C. talarum*: soft soil consisted of gravelly sand (27.40 ± 10.43 Kg/cm^2), whereas hard soil was sandy-loam (36.79 ± 10.65 Kg/cm^2; t = -3.53, p < 0.001). Both types of soil present similar moisture content (3.20 ± 1.26%, t = -1.22, p = 0.23; see Luna and Antinuchi, 2006 ,for details) . For measuring the effect of Ta on digging and resting metabolic rates, the respirometry system was maintained at Ta = 15 ± 1°C, 25 ± 1°C (thermoneutral zone, see Busch 1989), or 35 ± 1°C. To estimate the effect of digging angle on metabolic rate, the metabolic chamber was placed in 3 fixed descendent angles (0°, -25°, and -50° respect to the horizontal plane). For assessing the influence of both ambient temperature and digging angle we used only soft (i.e., gravelly sand) soil. To estimate the mean cost to construct an entire burrow system, we analyzed the data for 15 excavated burrows (7 males, 8 females) mapped by Antinuchi and Busch (1992). For each burrow, we estimated the main tunnel segment length between laterals, the depth of each segment and the length of lateral tunnels. Then, we classified all segments as horizontal (< 40° and popholes) or incline (> 40°). Once all segments were classified, we estimated the mean cost destined to construct an entire burrow system in 2 different approaches, with or without consideration of tunnel slope (Luna and Antinuchi, submitted).

*Statistics***.** We used analysis of covariance (2-way ANCOVA) to test the null hypothesis of no differences in digging or resting metabolic rate between sexes and soil conditions. In these and all subsequent ANCOVAs, we used a fixed model and body mass as a covariate. Two-way ANCOVA was used also to test the null hypothesis of no differences in digging or resting metabolic rate between sexes and ambient temperatures. We used analysis of variance (2-way ANOVA) to test the null hypothesis of no differences in Tb after each burrowing trial, and to evaluate thermal conductance between sexes and among Ta conditions. We used 2-way ANCOVA to test the null hypothesis of no differences in digging metabolic rate between sexes and digging angles. A *t*-test was used to test the null hypothesis of no differences in cost of constructing an entire tunnel system between the conditions of horizontal plane and angles >40°. We used Scheffé or Tukey´s test *a posteriori* to identify differences when ANCOVA or ANOVA results showed statistical differences.

Expenditure of Energy: Different Soil Conditions. Male tuco-tucos were maintained for 15 days in terraria (0.80 x 0.50 x 0.40 m) filled with either sandy soil (hardness: 0.08 ± 0.03 Kg/cm^2) or loamy soil (hardness: 51.15 ± 4.44 Kg/cm^2). Differences in the water holding capacities meant that similar amounts of water provided to terraria represented 5% and 15% of humidity for sandy and loamy soil, respectively. Five animals were randomly assigned to each treatment. Food was provided *ad libitum* and consisted of *Panicum racemosum*, the most abundant plant species in the natural diet of *C. talarum*. Tuco-tucos built burrows in this condition and show the characteristic behavior of gathering plant material from the surface to eat in the tunnels. Animals were removed from their terraria daily to record body mass. At this time we also destroyed their burrow systems to force them to continue to excavate; soil was compacted and hardness controlled using a penetrometer. Oxygen consumption and body temperature were obtained on the days 3, 7, and 15 of treatment.

Statistics. We used ANCOVA (2-way ANCOVA) to test the null hypothesis of no difference in RMR between days of treatment (repeated measures) and soil condition.

Expenditure of Energy: Growth. We monitored 9 litters born in captivity from birth until weaning age (45 days). Body mass and oxygen consumption (using a closed automatic system based in the design of Kalabukhov-Skvortzof) were measured on days 2, 6, 10, 12, 16, 23, 30, 45, and 60 (see Zenuto *et al.*, 2002 for details).

Statistics. We used linear regression to establish the relationship between body mass and age.

Expenditure of Energy: Reproduction. Nine non-reproductive and 13 pregnant females were individually housed in plastic cages (0.45 x 0.32 x 0.25 m) with wood shavings for bedding. Pregnant females were checked daily until pups were born, and the stage of pregnancy was extrapolated from parturition time. RMR was measured using a closed automatic respirometer. Oxygen consumption was recorded in pregnant females at 3 time intervals (<10 d, 10-20 d and >20 d before parturition) and for lactating females it was measured at 2, 6, 10, 12, 16, 23, 30 and 45 days after parturition. Body mass and temperature was registered after each measurement of metabolism (see Zenuto *et al.*, 2002 for details).

Statistics. Because pregnant and lactating females were the same individuals, we used a 1-way repeated measures analysis of covariance (rmANCOVA) to test the null hypothesis of no difference in RMR between pregnant (RMR_p), and lactating females (RMR_{lact}) while 1-way ANCOVA was used to compare RMR between pregnant or lactating and non-reproductive (RMR_{nr}) females. One-way rmANCOVA was used to test the null hypothesis of no differences in RMR within pregnancy and lactation. One-way rmANOVA was used to test the null hypothesis of no difference in M-SRMRs between pregnant ($M\text{-}SRMR_p$) and lactating females ($M\text{-}SRMR_{lact}$), and 1-way ANOVA was used to compare pregnant or lactating and non-reproductive females ($M\text{-}SRMR_{nr}$).

Expenditure of Energy: Thermoregulation. We evaluated oxygen consumption of adult individuals as a function of environmental temperature (5, 10, 15, 20, 25, 30, 35, 40 ^{o}C) using a manual, closed respirometer. Body temperature was measured rectally after each measurement of metabolism.

To calculate the annual cost of thermoregulation we estimated ambient temperature inside burrows using the equation proposed by Altuna (1991), $T_{burrow} = 5.18 + 0.73(Ta)$. We used mean monthly ambient temperature records for Mar del Plata (25 Km distance from Mar de Cobo), obtained online at www.weatherchannel.com.

Oxygen consumption of both pups and adult females was measured in 20-min trials using a computerized positive-pressure open-flow respirometer at 2-3, 6-7, 10-11, 15-16, 30-31, and 45-46 days after pups were born at two different Tas, one within the range of adult thermoneutrality (25°C) and the other below it (19°C) but similar to temperatures measured in burrows under natural conditions (21.5 ± 4°C). We measured oxygen consumption by pups and their mother under 4 different conditions: 1a. single pup alone; 1b. mother alone; 2a. multiple pups (2-3 individuals); 2b. multiple pups and their mother, in the following order: 1a, 1b, 2b, 2a. To calculate mass-specific metabolic rate of pups in groups (condition 2b) we assumed that the whole resting metabolic rate of the female did not differ greatly between grouping conditions 2b and 1b. Under this assumption, mass-specific RMR of pups in groups was calculated as $(RMR_t - RMR_f)/W_p$, where RMR_t is the total RMR (ml O_2/h), RMR_f is the whole female resting metabolic rate (ml O_2/h) and W_p is the sum of pups body weights (g).

We recorded Tb for each animal before (Tbb) and after (Tba) each oxygen consumption measurement trial (pharyngeal temperature for pups <45 days old and rectal temperature for older pups), and from this we obtained the difference ($\Delta Tb = Tbb - Tba$). The effect of grouping condition, age, and Ta were established by comparing ΔTb.

Behavioral Observations. To estimate the energetic costs associated with the observed behaviors, pups in grouping condition 2a and the mother with the pups (2b) were videotaped during the oxygen consumption measurement (JVC model GR-DVL 505). Behavioral observations were conducted while the animals were inside the respirometer only in conditions 2a and 2b.

Statistics. We used a 3-way rmANOVA to evaluate the null hypothesis of no differences in ΔTb of pups of different age, at different Ta (19 and 25 °C), and under different grouping condition (e.g., with and without mothers). The same test was employed to evaluate the hypothesis of no differences in RMR of pups among different ages, Ta, and grouping condition. Simple regression analysis was performed to evaluate the hypothesis of no relationship between RMR and body weight of pups at different Ta (see Cutrera *et al.* 2003). Since no relationship was found between these 2 measures, this allowed us to perform a 3-way rmANOVA, for which only significant interactions were reported.

Throughout this paper we present data as mean ± SD.

RESULTS

Acquisition of Energy: Ingestion and Digestion Processes. Tuco-tucos showed clear differences in nutritional parameters in relation to diet quality. Animals fed with *P. racemosum* ingested more food, produced more feces, displayed lower incidence of coprophagy, and demonstrated lower digestibility and more rapid transit time than those fed with *M. sativa* (Table 1). Number of feces reingested was similar under the 2 diets, whereas the total number of feces produced was different; consequently,

Table 1: Nutritional variables measured for *Ctenomys talarum* under 15 days of treatment with low-quality (*Panicum racemosum*) and high-quality (*Medicago sativa*) diets. Values: mean ± SD. Sample size in parenthesis. Statistics are provided for all comparisons involving body mass.

	Panicum racemosum	*Medicago sativa*	Statistics
Food consumption			
G x day^{-1}	21.17 ± 6.48	12.04 ± 1.85	
KJ x day^{-1}	398.56 ± 122.01	211.20 ± 32.54	
G x day^{-1} x body mass^{-1}	0.16 ± 0.04 (*N* = 5)	0.08 ±0.02 (*N* = 5)	$z = -2.61$, $p = 0.009$
KJ x day^{-1} x body mass^{-1}	2.98 ± 0.69 (*N* = 5)	1.47 ± 0.30 (*N* = 5)	$z = -2.61$, $p = 0.009$
Fecal production			
G x day^{-1}	12.75 ± 3.06	3.75 ± 0.28	
KJ x day^{-1}	236.97 ± 56.91	63.45 ± 7.02	
G x day^{-1} x body mass^{-1}	0.09 ± 0.01 (*N* = 5)	0.02 ± 0.003 (*N* = 5)	$z = -2.61$, $p = 0.009$
Number x day^{-1} x body mass^{-1}	1.66 ± 0.28 (*N* = 5)	0.76 ± 0.16 (*N* = 5)	$z = -2.61$, $p = 0.009$
KJ*day^{-1} x body mass^{-1}	1.77 ± 0.29 (*N* = 5)	0.44 ± 0.07 (*N* =5)	$z = -2.61$, $p = 0.009$
Assimilation			
KJ x day^{-1}	161.59 ± 78 (*N* = 5)	147.74 ± 33.03 (*N* = 5)	
KJ x day^{-1} x body mass^{-1}	1.21 ± 0.51 (*N* = 5)	1.03 ± 0.27 (*N* = 5)	$z = -0.73$, $p = 0.464$

differences in the incidence of reingestion reflected differences in the fecal production (Table 1).

Both food consumption and fecal production were negatively correlated with digestibility ($r = -0.51$, $p < 0.05$ and $r = -0.7$, $p < 0.01$, respectively). In contrast, transit time was positively correlated with digestibility ($r = 0.88$, $p < 0.01$). Animals under both diet treatments maintained or slightly lost body mass but this did not differ between treatments. Moreover, the apparent energy assimilation did not differ between treatments (Table 1). Even though caloric content of food provided in the experiments was quite similar, animals under a high fiber diet showed lower metabolic rates than those under low fiber diet (M-SRMR = 0.69 ± 0.08 ml O_2/gh and 0.84 ± 0.07 ml O_2/gh, respectively; $z = -2.02$, $p = 0.03$).

Expenditure of Energy: Cellular Maintenance. We have published estimations on mass-specific RMR using 3 different methodologies (see Table 2), yielding similar results.

Table 1 (continued).

Digestibility			
Dry matter	0.41 ± 0.09 ($N = 5$)	0.68 ± 0.06 ($N = 5$)	$z = -2.61$, $p = 0.009$
Energy	0.39 ± 0.09 ($N = 5$)	0.69 ± 0.06 ($N = 5$)	$z = -2.61$, $p = 0.009$
Transit time (min)	106.8 ± 31.28 ($N = 5$)	336 ± 39.42 ($N = 5$)	$z = -2.45$, $p = 0.014$
Coprophagy			
Feces produced (P)	295.25 ± 32.26 ($N = 4$)	192.5 ± 43.61 ($N = 4$)	$z = -2.31$, $p = 0.021$
Feces reingested (R)	65.25 ± 28.04 ($N = 4$)	89.5 ± 4.65 ($N = 4$)	$z = -1.44$, $p = 0.148$
Incidence of reingestion (R/P)	0.21 ± 0.07 ($N = 4$)	0.48 ± 0.09 ($N = 4$)	$z = -2.31$, $p = 0.021$

Expenditure of Energy: Digging. We documented no differences in DMR between sexes (2-way ANCOVA, $N = 18$, $F_{1,14} = 0.15$, $p = 0.7$). DMR of individuals in hard soil were higher than those individuals in soft soil (2-way ANCOVA, $N = 18$, $F_{1,14} = 6.90$, $p < 0.02$). We documented no effect in the interaction between sexes and soil conditions (2-way ANCOVA, $N = 18$, $F_{1,14} = 0.47$, $p = 0.51$).

There were no effect of sex and soil conditions on RMR (2-way ANCOVA, $N = 18$, $F_{1,14} = 1.60$, $p = 0.23$, Table 3). RMR did not differ between individuals of hard and soft soils groups (2-way ANCOVA, $N = 18$, $F_{1,14} = 1.83$, $p = 0.20$).

Ambient Temperature. Despite we documented differences in DMR between sexes (2-way ANCOVA, $N = 30$, $F_{1,28} = 10.87$, $p < 0.05$), we found no differences in DMR between sexes within each temperature conditions (Scheffé, $p_{15°C}$, $p_{25°C}$ and $p_{35°C} > 0.05$). Also, we documented differences between in DMR among temperature conditions (2-way ANCOVA, $N = 30$, $F_{2,28} = 27.94$, $p < 0.001$). Digging metabolic rates of individuals exposed to Ta of 15°C was higher than those individuals exposed to 25°C (Scheffé, $p < 0.01$, Table 3). DMR at 35°C was higher than both, at 15°C and 25°C (Scheffé, $p = 0.01$, Table 3).

Table 2: Mass specific resting metabolic rates (M-SRMR, mean ± SD) for individual *Ctenomys talarum*. Sample size in parenthesis.

Method		M-SRMR (ml O_2/gh)	Source
Closed system, based on the design of Kalabukhov-Skvortzov	manual	0.911 ± 0.14 ($N = 3$)	Busch, 1989
	automatic	0.81 ± 0.11 ($N = 9$)	Zenuto et al., 2001
Open flow system, positive pressure		0.94 ± 0.14 ($N = 14$)	Luna et al., 2002.

Table 3: Resting (RMR) and digging (DMR) metabolic rates in individuals of *Ctenomys talarum* digging under various conditions: soft vs. hard soils, at different ambient temperatures in soft soil, and at different digging angles in soft soil.

Variable	Condition	RMR		DMR	
		(ml O2/h)	(ml O2/gh)	(ml O2/h)	(ml O2/gh)
Soil	Soft	114.77 ± 18.22	0.94 ± 0.14	267.59 ± 66.31	2.14 ± 0.42
	Hard	125.73 ± 21.42	0.98 ± 0.07	408.30 ± 145.23	3.18 ± 1.28
Ta	15°C	179.12 ± 41.8	1.39 ± 0.24	426.78 ± 126.00	3.24 ± 0.62
	25°C	116.79 ± 18.71	0.94 ± 0.13	260.24 ± 69.35	2.09 ± 0.58
	35°C	193.58 ± 62.07	1.34 ± 0.22	577.32 ± 164.19	4.13 ± 0.98
	0°	119.99 ± 21.70	0.94 ± 0.15	271.80 ± 59.20	2.10 ± 0.44
Digging angle	-25°	103.47 ± 25.63	0.87 ± 0.13	213.13 ± 26.20	1.71 ± 0.14
	-50°	131.11 ± 30.84	0.96 ± 0.06	354.71 ± 96.46	2.56 ± 0.22

We documented no effect in the interaction between sexes and temperature conditions (2-way ANCOVA, $N = 30$, $F_{2, 28} = 2.58$, $p = 0.09$). In the same way, RMR of individuals exposed to 15°C and 35°C were higher than those at 25°C (2-way ANCOVA, $N = 30$, $F_{2, 28} = 4.43$, $p = 0.02$, Scheffé, $p < 0.01$). No differences in RMR were observed between 15°C and 35°C ($p = 0.58$).

Finally, Tb did not differ between sexes after each burrowing trial and among different Ta conditions (2-way ANOVA, $N = 34$, $F_{2, 31} = 0.92$, $p = 0.41$). Thermal conductance (C) was different at Ta of 35°C compared to those of individuals exposed to 15°C and 25°C (ANOVA, $N = 34$, $F_{2, 31} = 196.48$, $p < 0.01$; Tukey test, 15°C vs. 25°C, $p = 0.75$, 15°C vs. 35°C, $p < 0.01$, 25°C vs. 35°C, $p < 0.01$).

Digging Angle. We documented no differences in DMR between sexes (2-way ANCOVA, $N = 24$, $F_{1, 18} = 4.32$, $p = 0.06$). Digging metabolic rate varied as a function of slope angle (2-way ANCOVA, $N = 24$, $F_{2, 18} = 8.01$, $p < 0.01$, Table 3). Although shallow slopes (-25°) were not energetically different from level slopes (Scheffé, $p = 0.52$), DMR at a slope angle of -50° was greater than either 0° (Scheffé, $p = 0.02$) or -25° (Scheffé, $p = 0.02$, Table 3). We documented no effect of the interaction between sexes and digging angle on DMR (2-way ANCOVA, $N = 24$, $F_{2, 18} = 3.18$, $p = 0.07$).

Even that there were observed differences in RMR between sexes and digging angle (2-way ANCOVA, $N = 24$, $F_{2, 18} = 3.72$, $p = 0.05$), no differences were detected in the Scheffé analysis between this variables (0° vs. -25°, $p = 0.46$; 0° vs. -50°, $p = 0.20$, -25° vs. -50°, $p = 0.08$).

The cost of constructing a burrow in the horizontal plane differed from other in which the natural representation of tunnels >40° was considered ($t = 3.99$, $d.f. = 23$, $p < 0.01$). Thus, the low representation (nearly 6%) of tunnels with angles >40° in excavated burrows (Antinuchi and Busch, 1992) may be a consequence of the high cost to excavate them.

Expenditure of Energy: Different Soil Conditions. We documented effect of soil hardness

(1) from day 3 and no differences across sampling days (2) on RMR of individuals maintained in the same dietary condition (2-way rmANCOVA, $N = 10$, $F(1)_{1,7} = 5.79$, $p = 0.047$, $F(2)_{2,14} = 2.58$, $p = 0.11$).

Expenditure of Energy: Growth. Mean body mass of offspring at 2 days old was 9.83 ± 1.19 g. Body mass at weaning (63.89 ± 9.78 g) represented 53% of adult body mass. Mean M-SRMR of pups up to independence was 1.93 ± 0.30 ml O_2/gh. The relationship between body mass of pups and age (from 2 to 60 d) was $W = 3.74 + 1.31(\text{age})$ (Zenuto et al., 2002); the cost of growth and maintenance of a pup between 2 and 60 days can be calculated as:

$$\text{Cost} = \left(\int_{2}^{60} (1.31 \times \text{age} + 3.74)\, d\,\text{age}\right) \times 1.93 \text{ ml } O_2 g^{-1} h^{-1} \times 24 \text{ h} \times 0.02008 \text{ KJ ml}^{-1} \quad \text{(Eqn. 1)}$$

The energetic cost of a litter of 4 pups (mean litter size in natural populations; Busch et al., 1989; Malizia and Busch, 1991) including daily activity and production until dispersal (nearly 60 days; Malizia et al., 1995) represents 9190.19 KJ (Eq. 1).

Pups were born with their eyes closed, and they opened them partially, but briefly, at 4-6 days of age. At this time they wandered outside the nest following the mother's movements. Milk constitutes their exclusive food although they eat fecal pellets from the substrate. At 7-10 days they opened their eyes and started to eat solid food. During the first 2 weeks, the mother spent 80% of her time at the nest, caring for the offspring, including suckling, retrieving young that wander away, nest maintenance, and carrying food. At this time, pups did not thermoregulate well and were dependent upon contact with the mother for warmth. Weaning was a gradual process that started nearly a month after birth. Thereafter, time suckling diminished until 60 days of age, when the mother frequently chases young away to avoid nursing them (more details see Zenuto et al., 2002).

Expenditure of Energy: Reproduction. Nine *C. talarum* females gave birth in captivity; mean litter size was 4.55 ± 1.25 pups (range = 3-7, 34 pups).

Energetic demands for reproductive females were higher than for non-reproductive females. Lactating females (144.3 ± 37.3 ml O_2/h) showed a 151% increase in their resting metabolic rate relative to non-reproductive females (1-way ANCOVA, $N = 18$, $F_{1,15} = 9.36$, $p < 0.05$). In spite of pregnant females (122.3± 29.8 ml/h) showed 128% increment in relation to non-reproductive females (95.5 ± 12.8 ml O_2/h, $p = 0.053$) no differences were detected (1-way ANCOVA, $N = 23$, $F_{1,19} = 1.71$, $p > 0.05$). Also, no differences in RMR were detected between pregnant and lactating females (1-way rmANCOVA, $N = 9$, $F_{1,7} = 1.78$, $p > 0.3$). Similarly, when mass-specific metabolic rate was considered, oxygen consumption in lactating females (M-SRMR$_{\text{lac}}$ = 1.13 ± 0.31 ml O_2/gh, $N = 9$) was higher than in non-reproductive females (M-SRMR$_{\text{nr}}$ = 0.81 ± 0.11 ml O_2/gh, $N = 9$). On the other hand, we did not detect differences between pregnant and non-reproductive females (M-SRMR$_{\text{p}}$ = 0.85 ± 0.16 ml O_2/gh, $N = 13$; 1-way ANOVA, $F_{1,20} = 0.27$, $p > 0.1$) either between lactating and pregnant females (1-way rmANOVA, $F_{1,8} = 4.22$, $p > 0.05$). Contrary to expected, RMR did not vary through pregnancy (rmANCOVA, $F_{2,22} = 0.04$, $p > 0.1$) or lactation (rmANCOVA, $F_{6,42} = 0.46$, $p > 0.1$). Body temperature was similar among non-reproductive, pregnant, and lactating females (36°C; ANOVA, $F_{2,23} = 1.67$, $p > 0.20$). If we consider the length of each period (95 and 45 days for pregnancy and lactation, respectively), pregnancy represent a total energetic cost of 5600 ± 1360 KJ whereas lactation represents a cost of 3100 ± 800 KJ.

The cost of daily activity and growth of a litter of 4 pups from birth to weaning represents 5247.75 KJ (calculated from Eq. 1 with age = 45) and the energetic cost of producing milk by females during 45 days ((RMR_{lact}- RMR)*45 days*24 hours*0.02008 Kj ml^{-1}) 1058.44 KJ, representing 18% of offspring demands.

Expenditure of Energy: Thermoregulation. Mean Tb for adult *C. talarum* at Ta's ranging from 25 to 35°C was 36.1 ± 0.13°C. Poor thermoregulation was observed in tuco-tucos down to 20°C, although this varied individually: some animals experienced Tb of 27°C or even 20°C at Ta ranging 10 to 15°C. Temperatures below the thermoneutral zone caused a decrease in Tb that can be expressed by the equation: Tb = 25.7+ 0.46 Ta (r = 0.95, Eq. 2). Animals maintained at Ta of 40°C did not experience sweating or panting and died (Fig. 1). The resting metabolic rate was a linear function of ambient temperature from 5 to 25°C and can be expressed as VO_2 = 1.91 - 0.037 Ta (r = 0.74, Eq.

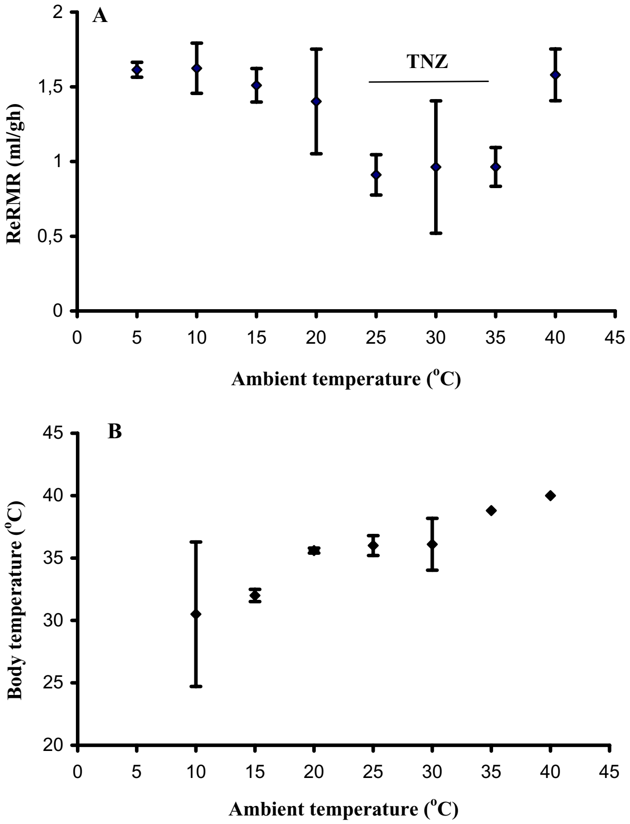

Figure 1: Mass specific metabolic rate (M-SRMR; A) and body temperature (B) as a function of ambient temperature in *Ctenomys talarum*. TNZ = thermoneutral zone. Bars represent one standard deviation of the mean.

3, Busch, 1989).

Age of pups (1), grouping condition (2) and Ta (3) significantly affected ΔTb of pups of *C. talarum* (3-way rmANOVA, $N = 5$, $F(1)_{5,\,120} = 6.65$, $F(2)_{2,\,24} = 15.93$, $F(3)_{1,\,24} = 9.35$, all $p < 0.05$). Additionally, the interactions between grouping condition and Ta and among age, grouping condition and Ta had effect on ΔTb of pups (3-way rmANOVA, $N = 5$, $F(2 \times 3)_{2,\,24} = 10.20$, $F(1 \times 2 \times 3)_{10,\,120} = 2.36$, both $p < 0.05$, see Cutrera et al. 2003).

Pups of *C. talarum* did not thermoregulate independently until they were 15 days old. Before this age, Tb of pups was highly variable (28.1°C - 34.1°C) when they were deprived of contact with their mother or with littermates. Although the Tb of pups fell more slowly while they were in contact with other pups, only the presence of the mother prevented hypothermy in pups (Tukey test, $p < 0.05$, Figs. 2 and 3) at a low Ta (19°C). Huddling with littermates or maternal contact resulted in a significant reduction in the cooling rate of pups at a low Ta relative to that in isolation (Tukey test, $p < 0.05$), but this contact did not have a significant effect at a higher Ta (25°C). As noted above, however, maternal contact was more effective than littermate huddling to prevent pups from cooling, especially when they were < 6 days old (Tukey test, $p < 0.05$). After pups turned 15 days old, the effect of huddling or maternal contact was no longer significant (Tukey test, $p > 0.05$).

RMR of pups of *C. talarum* was significantly affected by their age (1), grouping condition (2) and the interaction between them; however, no statistical differences

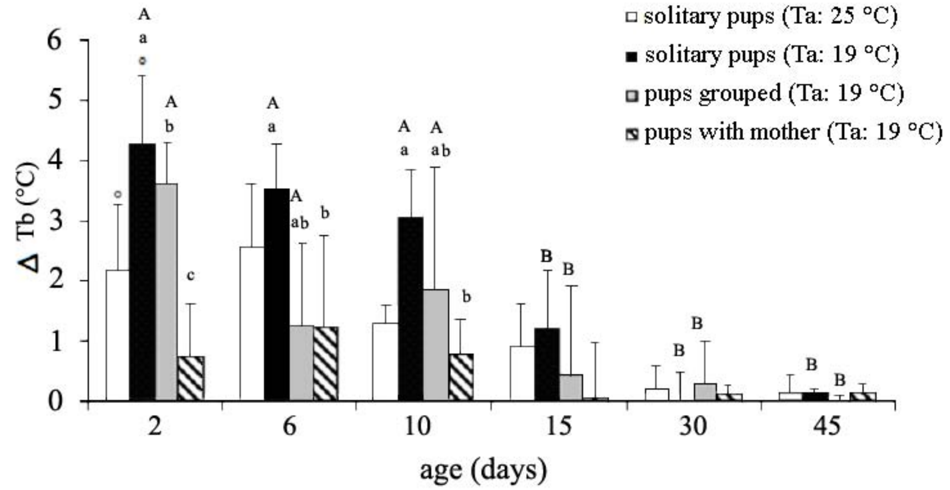

Figure 2. ΔTb of pups of *C. talarum* vs. age in different grouping conditions at a T_a of 19°C and 25°C. $\Delta T_b = T_{bb} - T_{ba}$. Different lowercase letters represent significant differences ($p < 0.05$) among grouping conditions for the same age in pups younger than 15 days of age. Different capital letters represent significant differences ($p < 0.05$) among ages for the same grouping condition. Open circles represent significant differences respect to a Ta of 25°C for the solitary pups. Bars represent one standard deviation of the mean.

The effect of grouping condition on ΔTb of pups older than 10 days is not showed in this figure because it was not statistically significant. For the same reason, the effect of age on ΔTb of pups in contact with their mother is not showed either.

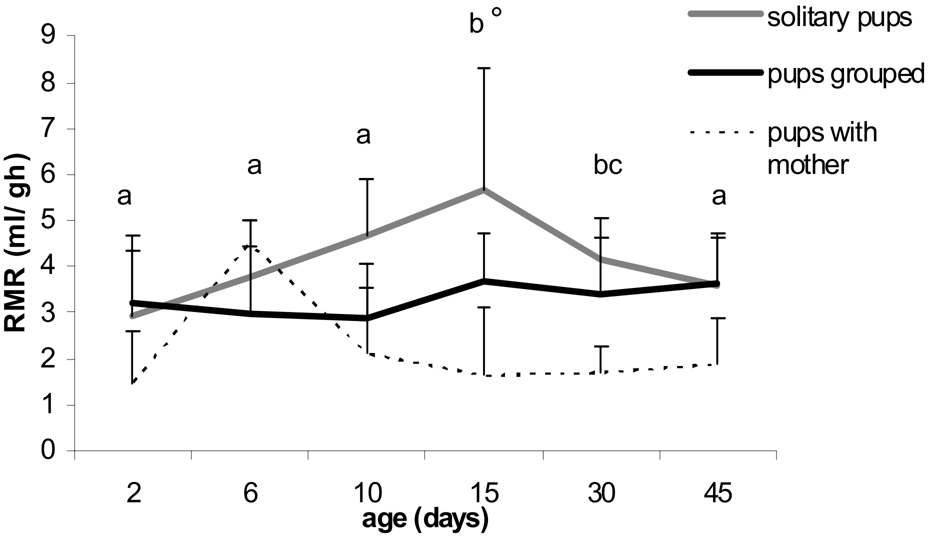

Figure 3. Values of M-SRMR of pups of *C. talarum* vs. age in different grouping conditions. Different letters represent significant differences ($p < 0.05$) among ages for the solitary condition. Open circles represent significant differences ($p < 0.05$) among grouping conditions in 15-day-old pups. Bars represent one standard deviation of the mean.

The effect of grouping condition on M-SRMR of pups younger and older than 15 days is not showed in this figure because it was not statistically significant. For the same reason, the effect of age on M-SRMR of pups in contact with their mother or other pups is not showed either.

were detected in RMR of pups at different Tas (3-way rmANOVA, $N = 5$, $F(1)_{5, 120} = 6.54$, $F(2)_{2, 24} = 37.14$, $F(1 \times 2)_{10, 120} = 3.11$, all $p < 0.05$; $F(3)_{1, 24} = 39.99$, $p(3) > 0.05$, see Cutrera et al. 2003).

Oxygen consumption of pups under three different grouping conditions was similar until they were 15 days old (3.17 ± 1.04 ml O_2/gh). At this age, a peak of M-SRMR was observed in solitary pups (5.68 ± 2.61 ml O_2/gh, Tukey test, $p < 0.05$), possibly reflecting extra energy that was required for physiological thermoregulation. After this age, M-SRMR declined (Tukey test, $p < 0.05$) and did not differ among the different grouping conditions (3.07 ± 0.22 ml O_2/gh, Tukey test, $p > 0.05$). The M-SRMR of pups represented almost 4 times the M-SRMR of a non-reproductive adult (0.81 ± 0.11 ml O_2/gh). Huddling among littermates and maternal contact did not represent a significant reduction in M-SRMR of pups before or after the age of 15 days (Tukey test, $p > 0.05$).

DISCUSSION

Environmental and physiological limitations on individual energy budgets have been proposed as key factors modeling survival and reproductive success. The evolution of life history traits, animal design, optimization of behaviors, and geographical distribution of species are better understood when resource availability and/or physiological constraints are considered. Factors that impose ceilings on sustained metabolic rate include both food supply and physical properties of an animal's body. Physiological constraints can be imposed, either centrally by the rate of food conversion into usable energy, peripherally by the capacity of organs expending energy, or symmorphically, in which both, central and peripheral capacities are co-adjusted (Hammond and Diamond, 1997). For the central limitation hypothesis, input constraints, such us those related to maximum rates of foraging, digestion and absorption, would be engaged in series while outputs (e.g., heat production, mechanical work, growth) would be parallel and independently controlled (see review in Weiner, 1992). Under the peripheral limitation hypothesis, each organ or tissue reaches its own energetic limit and the rate of food conversion into usable energy would be unconstrained (Hammond and Diamond, 1997; Bacigalupe, 2003).

Limits to the capacity to digest and assimilate energy and nutrients from ingested food represent a constraint on metabolic rate in mammals (McNab, 1988). Physiological response to food quality on metabolic rate has been documented in rodents both at interspecific (McNab, 1988; Sakaguchi and Ohmura, 1992) and intraspecific level (Choshniak and Yahav, 1987; Veloso and Bozinovic, 1993; Bozinovic, 1995). Furthermore, physiological and morphological constraints appear to force small mammals to select high-quality food and to limit their forage areas where such food is abundant and suitable (Batzli, 1985; Brown and Nicoletto, 1991). Increased fiber dilutes the concentration of digestible nutrients and energy in the diet (Milton, 1979); consequently, food preferences of rodent herbivores are determined mainly by the protein to fiber ratio as well as other factors such as plant defense compounds. Some species have been shown to decrease ingestion of food items containing high fiber content (Justice and Smith, 1992; Bozinovic, 1995) and / or tannins (Bozinovic, 1997).

Under a low-quality diet (high fiber content) *Ctenomys talarum* not only increased their food intake but also experienced low metabolic rate. As it has been previously observed in this study, an increase in food consumption leads to a more rapid passage of food through the digestive tract which further reduces the digestibility. Reduction in digestibility with high fiber diets may be associated with an increase in gut motility (Demment and van Soest, 1985). Although in this study the low-quality diet may have been accompanied by a shorter digestion period and poorer nutrient uptake, compensation through a higher food intake allowed tuco-tucos to obtain similar net assimilation of energy to that under the high-quality diet. Incidence of fecal ingestion was similar for animals with high- and low-quality diets; this suggests that coprophagy allows animals to obtain essential nutrients rather than to provide energy, at least in conditions of fresh food availability. In contrast to these results, other studies have demonstrated that the incidence of reingestion increased as the quality of food decreases (Kenagy and Hoyt, 1980; Cranford and Johnson, 1989).

Most subterranean rodents gain access to underground plant parts for food by excavating tunnels (Busch et al., 2000). Several North American subterranean rodent species are known to store plant parts (Vleck, 1981; Stuebe and Anderson, 1984). In particular, *Thomomys talpoides* optimize current and future dietary intake eating a winter diet of high-protein items and storing in caches high-energy value items for periods when burrowing in search for food is not possible due to snowing (Stuebe and Anderson, 1984). Even though *C. talarum* excavate and live in burrows, they feed primarily on aerial parts of plants that they collect from the surface during brief aboveground excursions; surface foraging likely is much less costly in energetic terms than subterranean foraging. Nonetheless, subterranean habits imply a close dependence on local variations in resource conditions. Consequently, the ability of tuco-tucos to lower their energetic demands when nutritional conditions (e.g., quality and / or availability of food) in the habitat deteriorate could represent an important advantage in maintaining a balanced energy budget. The energetic costs associated with living underground are assumed to be high; Vleck (1979, 1981) estimated that, depending on soil type, energetic expenditures associated with burrowing may be more than 300 times greater than those required for similar transportation above ground. However, because *C. talarum* are not restricted to burrows for foraging and other activities, they do not dig constantly, supporting the idea that Vleck´s model cannot be generalized to all subterranean rodents (see Contreras and McNab, 1990). *C. talarum* build burrows whose basic structure, once accomplished, appears to vary little, since animals have been recaptured in specific sites repeatedly through all of their lives (nearly 2 years; Busch et al., 1989). Individuals of *C. talarum* spend only 0.27% of its annual budget for building a burrow system that averages 15 m in length (Antinuchi and Busch, 1992). In *Ctenomys* and other subterranean rodents, evidence suggests that burrows are constructed throughout the life of the resident since tunnels are gradually extended as food patches are depleted. Consequently, the impact of burrow construction on daily energy expenditure would be low, even considering the continuous repair and cleaning that likely is necessary. This species also saves energy by constructing most tunnels in the horizontal plane (Luna and Antinuchi, submitted). Moreover, tuco-tucos behave opportunistically, occupying empty burrows when available (Malizia et al., 1995).

On the other hand, tuco-tucos living in soil conditions of different hardness showed differences in their resting metabolic rates and body temperatures (Perissinotti, 2003; this study). Lower metabolic rates and high body temperatures have been found in tuco-tucos maintained for a short period of time (15 days) in compacted soils. This may be the result of lower metabolic rates that reduce heat production under conditions where conduction, convection, and evaporation are limited (i.e., thermal stress hypothesis; McNab, 1966, 1979). Furthermore, harder soils are absolutely more costly to burrow through. Increased energy demands associated with burrowing in hard soil, associated with lower exchange of gases and high heat accumulation, certainly represent a disadvantageous situation for tuco-tucos.

If we consider the energy expenditures for a single *C. talarum* individual in its first year of life, maintenance and growth to independence (ca. 2 months) represents nearly 7% of energetic needs, while maintenance as a subadult and adult demands 53% of the annual energy budget (Table 4A). Once animals disperse from their natal burrow they may build their own burrow system, which costs only 0.26%. Presumably, a small fraction of animals that disperse as adults (Malizia et al., 1995) will assume the cost of digging other burrows. Maintenance of exclusive territories in *C. talarum* requires movement through the burrow system. Luna and Antinuchi (2003) estimated that captive tuco-tucos patrol their entire burrow 13 times/day, spending 0.8% of their annual energy expenditure on this activity. Life underground appears to be a strategy that allows saving a considerable amount of energy allocated to thermoregulation during winter, as observed for other subterranean species (Andersen and MacMahon, 1981). The estimated cost of maintaining Tb inside a burrow represents 31% of the annual budget. Nevertheless, when we calculated the cost of thermoregulation using

Table 4: A) Annual energy budget for adult female *Ctenomys talarum* in the first year of life. B) Daily energetic expenditure during a winter cold day for adult female *Ctenomys talarum* in their first year of life under 3 reproductive states.

A	KJ	%
Burrow construction (15 m)	84.95	0.27
Movements	261.89	0.82
Lactation	1058.3	3.31
Pregnancy	1226.97	3.83
Thermoregulation	9909.98	31.00
Maintenance	17122.14	53.57
Growth	2297.55	7.15
Total	31961.78	

B	KJ/day	Non-reproductive	Pregnant	Lactating
Maintenance	57.07	57.07	57.07	57.07
Thermoregulation	45.57	45.57	45.57 (?)	45.57 (?)
Movements	8.73	8.73	8.73 (or low?)	8.73
Burrow construction (1m)	5.66	5.66	5.66 (or low?)	5.66 (or low?)
Pregnancy	13.63	--	13.63	--
Lactation	23.52	--	--	23.52
Total (KJ/day)		117.03	130.66	140.55

aboveground temperature records, this rose to 34.2%. Therefore, burrows allow tuco-tucos to save nearly 3% of their annual budget. Moreover, heat produced when digging at low ambient temperatures helped *C. talarum* to maintain a more acute body temperature regulation (Luna and Antinuchi, in press). Problems of overheating when digging in sandy soils during summer are avoided through low BMR and both anatomical (e.g., changes in fur density, bare patches) and behavioral (e.g., reduction in digging activity, convectional heat transfer to substrate) mechanisms that allow heat dissipation (Cutrera and Antinuchi, 2004). Consequently, the increase in metabolic rate during digging do not affect body temperature, digging velocity, or energy expenditure in *C. talarum* (Luna and Antinuchi, in press; Cutrera and Antinuchi, 2004). It is possible, especially for pups born early during the reproductive season (e.g., late winter), that burrows together with huddling represent a way for pups to reduce thermoregulatory costs. Maternal contact and littermate huddling did result in a significant reduction in the rate at which pups cooled during the first 2 weeks of their life when they faced ambient temperatures below the range of adult thermoneutrality. This effect disappeared with the onset of physiological thermoregulation. Keeping newborn *Peromyscus* warm had a positive effect on growth rate as well as other aspects of development such as time to thermoregulatory maturity and to opening their eyes and patterns of neural pathways development (Hill, 1983). In *C. talarum* the energy intake of pups must be obtained mainly from early acquisition of solid food starting from 10 days of age, since lactation provides only 18% of their energetic demands. The initial altricial phase in the ontogeny of *C. talarum* represents a stage of great vulnerability and could be a consequence of inability of females to allocate more energy to the reproductive process (BMR-reproduction hypothesis; Thompson, 1992), by their incapacity to increase energy supply (central limitation hypothesis), or to produce new tissues (peripheral limitation hypothesis; Hammond and Diamond, 1997; Bacigalupe, 2003). The risks of altriciality in this species, whose newborns spend most of the time in the protective and thermally stable environment of the burrow in contact with their mother and littermates, are minimized. Thus, burrows and huddling represent possible strategies to allocate more energy to growth. Although lactation is more energetically expensive than pregnancy in most mammals (Thompson and Nicoll, 1986), the reverse appears to be true in *C. talarum* where pregnancy represents the 3.8% of the annual energetic budget of a female, and lactation represents only 3.3% (Table 4A).

Components of the energy budget are additive (Hart, 1952; Hart and Jansky, 1963) but some may be compensatory (Luna and Antinuchi, in press) or may substitute (Webster and Weathers, 1990) for each other. The energy budget we provide here for an individual during its first year of life represents our best estimation according to the present knowledge of *C. talarum* energetics. Although we assumed that components of the energy budget are additive, more information is needed to confirm this; e.g., we lack data on the thermoregulatory capacity of pregnant and lactating females that suffer morphological, physiological, and/or behavioral changes. Female *C. talarum* experience volumetric changes during pregnancy that could affect their thermoregulatory capacity, but we lack data to evaluate if those changes increase or diminish the costs associated with pregnancy (see Zenuto et al., 2002). On the other hand, some data suggest that pregnant or lactating females undertake less digging activity than non-reproductive females, and also exhibit changes in their pelage (Cutrera and Antinuchi, 2004). These behavioral and morphological modifications could represent adjustments to cope with these thermally challenging periods, helping to reduce thermoregulatory costs. When metabolic costs associated with digging and thermoregulation were considered, animals digging in ambient temperatures below or above thermoneutrality showed an additive cost of both components but, at Ta = 15°C digging appears to contribute to maintaining an acute regulation of body temperature when compared with resting animals.

Even considering the energetic limitations and benefits recognized here, it is likely that protection against predators and buffering of thermoregulatory needs constitute the main advantages of living underground. Burrow construction is a surprisingly small portion of the annual energetic budget and thereafter provides a safe refuge to avoid raptors as well as carnivores (Busch et al., 2000; Luna and Antinuchi, 2003).

We estimated the amount of energy used during a winter cold day into a burrow system (e.g., Ta: 11°C) by an adult *C. talarum*. If maintenance, thermoregulation, and construction of one meter (arbitrarily selected) of burrow are included in this calculation, daily energetic budget would be 117 KJ for a non-reproductive individual, 130.7 KJ for a pregnant female, and 140.5 KJ for a lactating female, assuming that females behave similarly in these very different reproductive states (Table 4B). These values represent

2.05, 2.29, and 2.48 times of maintenance cost, respectively, approaching the value of SusMS (sustained metabolic scope = SusMR/RMR) reported for the subterranean rodent *Thomomys bottae* (2.8-3.0; see Hammond and Diamond, 1997). The daily energy budget calculated for *C. talarum* should be interpreted with caution since, as noted above, changes in thermoregulatory capacity in different reproductive states, as well as changes in time budget devoted to different activities, require further research. As we have shown, the daily energetic demands for females in all three reproductive categories could be covered by the daily energy assimilation (160 KJ) calculated for animals fed a plant species (*P. racemosum*) that is part of their natural diet. Moreover, tuco-tucos exhibit the capacity to arrange behavioral and physiological mechanisms responding to variations in food quality.

Nonetheless, these calculations neglect the costs associated with acquisition of food, and do not consider strategies developed by tuco-tucos to cope with natural changes in quantity and quality of food items. Both pre-ingestive (those related to food acquisition) and post-ingestive factors (e.g. changes in assimilation capacities during different reproductive conditions) need to be evaluated to more accurately estimate the energy available for different demanding process. In this regard, *C. talarum* seem to adjust their reproductive activity using environmental cues such that high energy demands of pregnant, lactating, and postpartum females can be attained during the time of higher plant biomass availability (Fanjul et al., 2006). Moreover, births occur during spring and early summer, when thermal conditions are more favorable for altricial pups, securing growth, and progeny survival at a lower cost for both pups and the mother. Use of fat reserves as a complementary strategy to secure energy demands during the more challenging periods may be limited in *C. talarum* due to their small size. Nonetheless, differences in body size between non-reproductive and postparturition females may reflect accumulation of fat reserves in preparation for lactation (Zenuto et al., 2002).

Evidence provided here supports the hypothesis that food and / or nutrient availability has restricted energy acquisition in *C. talarum*, since mechanisms evidently have evolved to optimize the conversion of low quality food to energy. Moreover, reproduction and growth of pups occur when resources are more abundant and thermal conditions are more favorable, demonstrating that the energy budget is adjusted on a seasonal basis. On the other hand, while pregnancy and lactation are expensive periods in most mammal species, such processes are less demanding in *C. talarum*. Even though SusMS has not been evaluated in this species, and despite the relatively low cost of both pregnancy and lactation, estimations of the relationship between energetic costs and maintenance cost during these periods are quite similar to SusMS achieved by other subterranean rodents. Moreover, adaptations that allow heat dissipation (mainly low BMR) may represent a challenge for *C. talarum;* daily energy expenditure in subterranean habitats is expected to be limited, and consequently may restrict the size of organs necessary to supply this energy, which in turn limits resting metabolic rates (Król et al., 2003; Speakman et al., 2003; White, 2003). Consequently, increments in Tb in animals digging in hard soils together with anatomical and behavioral modifications related to heat dissipation found in reproductive females, could be considered as evidence that heat storage limits reproductive output in *C. talarum*. So, different constraints appear to shape the energetic budget throughout the lifespan of *C. talarum* individuals. Detailed experiments (see Bacigalupe, 2003; Speakman et al., 2003) are needed to determine the contribution of food and physiological limitations (namely central, peripheral, and symmorphosis) in imposing the upper limit to sustainable energy budget in *C. talarum*.

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LITERATURE CITED

Altuna C. A.
1991 Microclima de cuevas y comportamiento de homeostasis en una población del grupo *Ctenomys pearsoni* del Uruguay (Rodentia, Octodontidae). Boletín de la Sociedad Zoológica del Uruguay 6:35-46.

Andersen, D. C., and J. A. MacMahon
1981 Population dynamics and bioenergetics of a fossorial herbivore: *Thomomys talpoides* (Rodentia: Geomyidae), in a spruce-fir sere. Ecological Monographs 51:179-202.

Antinuchi, C. D. and C. Busch
1992 Burrow structure in the subterranean rodent *Ctenomys talarum*. Zeitschrift für Säugetierkunde 57:163-168.

Bacigalupe, L.
2003 Energética, diseño animal y limitaciones fisiológicas. Pp 319-332 in Fisiología Ecológica y Evolutiva. Teoría y Casos de Estudio en Animales (Bozinovic, F., ed.). Universidad Católica de Chile, Santiago, Chile.

Batzli, G. O.
1985 Nutrition. Pp. 779-811 in Biology of New World *Microtus* (Tamarin, R. H., ed.). Special Publication 8. American Society of Mammalogist, Lawrence, Kansas.

Bennett, N. C., C. G. Faulkes, and A. J. Molteno
2000 Reproduction in subterranean rodents. Pp. 145-177 in Life Underground: The Biology of Subterranean Rodents (Lacey, E. A., G. Cameron, and J. L. Patton, eds.). The University of Chicago Press, Chicago, Illinois, USA.

Bozinovic, F.
1993 Fisiología ecológica de la alimentación y digestión en vertebrados: modelos y teorías. Revista Chilena de Historia Natural 66:375-382.

1995 Nutritional energetics and digestive responses of an herbivorous rodent (*Octodon degus*) to different levels of dietary fiber. Journal of Mammalogy 76:627-637.

1997 Diet selection in rodents: an experimental test of the effect of dietary fiber and tannins on feeding behavior. Revista Chilena de Historia Natural 70:67-71.

Brown, J. H., and P. F. Nicoletto
1991 Spatial scaling of species composition: body masses of North American land mammals. American Naturalist 138:1478-1512.

Buffenstein, R.
2000 Ecophysiological responses of subterranean rodents to underground habitats. Pp 62-110 in Life Underground: The Biology of Subterranean Rodents (Lacey, E. A., G. Cameron, and J. L. Patton, eds.). The University of Chicago Press, Chicago, Illinois, USA.

Busch, C.
1989 Metabolic rate and thermoregulation in two species of tuco-tuco *Ctenomys talarum* and *Ctenomys australis* (Caviomorpha: Octodontidae). Comparative Biochemistry and Physiology 93:345-347.

Busch, C., C. D. Antinuchi, J.C. del Valle, M. J. Kittlein, A. I. Malizia, A.I. Vassallo, and R. R. Zenuto
2000 Population ecology of subterranean rodents. Pp 183-226 in Life Underground: The Biology of Subterranean Rodents (Lacey, E. A, G. Cameron, and J. L. Patton, eds.). The University of Chicago Press, Chicago, Illinois, USA.

Busch, C., A. I. Malizia, O. A. Scaglia, and O. A. Reig
1989 Spatial distribution and attributes of a population of *Ctenomys talarum* (Rodentia: Octodontidae). Journal of Mammalogy. 70:204-208.

Choshniak, I., and S. Yahav
1987 Can desert rodents better utilize low quality roughage than their non-desert kindred? Journal of Arid Environments 12:241-246.

Contreras L., and B. K. McNab
1990 Thermoregulation and energetics in subterranean mammals. Pp. 1-20 in (Nevo, E., and O.A. Reig, eds.). Evolution of Subterranean Mammals at the Organismal and Molecular Level. Alan R. Liss, New York, New York, USA.

Cork, S. J., and W. J. Foley
1991 Digestive and metabolic strategies of arboreal mammalian folivores in relation to chemical defense in temperate and tropical forest. Pp 133-166 in Plant Defenses against Mammalian Herbivory (Palo, R. T., and C. T. Pobbins, eds.). CRC Press, Boca Ratón, Florida, USA.

Cranford, J. A., and E. O. Johnson
1989 Effects of coprophagy and diet quality on two microtine rodents (*Microtus pennsylvanicus* and *Microtus pinetorum*). Journal of Mammalogy. 70:494-502.

Cutrera A. P., and C. D. Antinuchi
2004 Cambios en el pelaje del roedor subterráneo *Ctenomys talarum*: posible mecanismo térmico compensatorio. Revista Chilena de Historia Natural 77:235-242.

Cutrera, A. P., C. D. Antinuchi, and C. Busch
2003 Thermoregulatory development in pups of the subterranean rodent *Ctenomys talarum*. Physiology and Behavior 79:321-330.

Demment, M. W., and P. J. van Soest
1985 A nutritional explanation for body size patterns of ruminant and non-ruminant herbivores. American Naturalist 125:641-672.

Fanjul, M. S., R. R. Zenuto, and C. Busch
2006 Seasonality of breeding in wild tuco-tucos *Ctenomys talarum* in relation to climate and food availability. Acta Theriologica 51:283-293

Feder, M. E., A. F. Bennett, W. W. Burggren, and R. B. Huey
1987 New Directions in Ecological Physiology. Cambridge University Press, Cambridge, UK.

Gorecki, A.
1975 Respirometry, 10, C, Kalabukhov-Skvortsov respirometer and resting metabolic rate measurement. Pp. 310-313 in Methods for Ecological Bioenergetics, IBP Handbook 24 (Grodzinski, W., R. Z. Klekowski, and A. Duncan, eds.). Blackwell Scientific Publication, Oxford, UK.

Hammond, K. A., and J. Diamond
1997 Maximal sustained energy budget in humans and animals. Nature 386:457-462.

Hart, J. S.
1952 Effects of temperature and work on metabolism, body temperature, and insulation: results with mice. Canadian Journal of Zoology 30:90-98.

Hart, J. S., and L. Jansky.
1963 Thermogenesis due to exercise and cold in warm- and cold-acclimated rats. Canadian Journal of Biochemistry and Physiology 41:629-634.

Hill, R.W.
1983 Thermal physiology and energetics of *Peromyscus;* ontogeny, body temperature, metabolism, insulation, and microclimatology. Journal of Mammalogy 64:19-37.

Jarvis, J. U. M., and N. C. Bennett
1991 Ecology and behavior of the family Bathyergidae. Pp. 66-97 in The Biology of the Naked Mole-rat (Sherman, P. W., J. U. M. Jarvis, and R. D. Alexander, eds.). Princeton University Press, Princeton, New Jersey, USA.

Justice, K. E., and F. A. Smith
1992 A model of dietary fiber utilization by small mammalian herbivores, with empirical results for *Neotoma*. American Naturalist 139:398-416.

Kenagy, G. J., and D. Hoyt
1980 Reingestion of feces in rodents and its daily rhythmicity. Oecologia 44:403-409.

Kenagy, G. J., C. Veloso, and F. Bozinovic
1999 Daily rhythms of food intake and feces reingestion in the degu, an herbivorous Chilean rodent: optimizing digestion through coprophagy. Physiological Biochemistry and Zoology 72:78-86.

Król, E., M.S. Johnson, and J.R. Speakman
2003 Limits to sustained energy intake VIII. Resting metabolic rate and organ morphology of laboratory mice lactating at thermoneutrality. Journal of Experimental Biology 206:4283-4291

Luna, F., and C. D. Antinuchi
2003 Daily movements and maximum speed in *Ctenomys talarum* (Rodentia: Ctenomyidae) in artificial enclosures. Journal of Mammalogy. 84:272-277.

2006 Cost of foraging in the subterranean rodent *Ctenomys talarum*: effect of soil hardness. Canadian Journal of Zoology 84:661-667.

In press Energetics and thermoregulation during digging in the tuco-tuco (*Ctenomys talarum*). Comparative Biochemistry and Physiology - Part A: Molecular and Integrative Physiology.

Luna, F., C. D. Antinuchi, and C. Busch
2000 Ritmos de actividad locomotora y uso de las cuevas en condiciones seminaturales en *Ctenomys talarum* (Rodentia, Octodontidae). Revista Chilena de Historia Natural 73:39-46.

2002 Digging energetics in the South American rodent *Ctenomys talarum* (Rodentia, Ctenomyidae). Canadian Journal of Zoology 80:2144–2149.

Malizia, A. I., and C. Busch
1991 Reproductive parameters and growth in the fossorial rodent *Ctenomys talarum* (Rodentia: Octodontidae). Mammalia 55:293-305.

Malizia, A. I., R. R. Zenuto, and C. Busch
1995 Demographic and reproductive attributes of dispersers in two populations of the subterranean rodent *Ctenomys talarum* (tuco-tuco). Canadian Journal of Zoology 73:732-738.

Martino, N.
2000 Respuestas Nutricionales a Corto Plazo en *Ctenomys talarum* (Rodentia: Octodontidae). Tesis, de Licenciatura Universidad Nacional de Mar del Plata, Mar del Plata, Argentina. 38 pp.

McNab, B. K.
1966 The metabolism of fossorial rodents: A study of convergence. Ecology 47:712-733.

1979 The influence of body size on the energetic and distributions of fossorial and burrowing mammals. Ecology 60:1010-1021.

1988 Complications inherent in scaling the basal rate of metabolism of mammals. Quarterly Review of Biology 63:25-54.

2002 The Physiological Ecology of Vertebrates: A View from Energetics. Cornell University Press, Ithaca, New York, USA. 567 pp.

Milton, K.
1979 Factors influencing leaf choice by howler monkeys: a test of some hypothesis of food selection by generalist herbivores. American Naturalist 114:362-378.

Nevo, E.
1999 Mosaic Evolution of Subterranean Mammals: Regression, Progression and Global Convergence. Oxford University Press, Oxford, UK. 413 pp.

Perissinotti, P. P.
2003 Efecto de la dureza del suelo y la calidad de la dieta sobre la tasa metabólica de reposo en el roedor subterráneo *Ctenomys talarum*. Tesis de Licenciatura. Universidad Nacional de Mar del Plata, Mar del Plata, Argentina. 52 pp.

Peterson, C. C., K. A. Nagy, and J. Diamond
1990 Sustained metabolic scope. Proceedings of the National Academy of Sciences USA 87:2324-2328.

Reichman, O. J., and J. U. M. Jarvis
1989 The influence of three sympatric species of fossorial mole-rats (Bathyergidae) on vegetation. Journal of Mammalogy 70:763-771.

Sakaguchi, E., and S. Ohmura
1992 Fiber digestion and digesta retention time in guinea-pigs (*Cavia porcellus*), degus (*Octodon degus*) and leaf-eared mice (*Phyllotis darwini*). Comparative Biochemistry and Physiology 103:787-791.

Schmidt-Nielsen, K.
1994 Animal Physiology: Adaptation and Environment. Cambridge University Press, Cambridge, New York, USA. 601 pp.

Seymour, R. S., P. C. Withers, and W. W. Weathers
1998 Energetics of burrowing, running, and free-living in the Namib Desert golden mole (*Eremitalpa namibensis*). Journal of Zoology 244:107-117.

Speakman, J. R., T. Ergon, R. Cavanagh, K. Reid, D. M. Scantlebury, and X. Lambin
2003 Resting and daily energy expenditure of free-living field voles are positively correlated but reflect extrinsic rather intrinsic effects. Proceedings of the National Academy of Sciences (USA) 10:14057-14062.

Stevens, E. D.
1973 The evolution of endothermy. Journal of Theoretical Biology 38:597-611.

Stuebe, M. M., and D. C. Anderson
1984 Nutritional ecology of a fossorial herbivore: protein N and energy value of winter caches made by the northern pocket gopher, *Thomomys talpoides*. Canadian Journal of Zoology 63:1101-1105.

Taigen, T. L.
1983 Activity metabolism of anuran amphibians: implications for the origin of endothermy. American Naturalist 121:94-109.

Thompson S. D.

1992 Gestation and lactation in small mammals: basal metabolic rate and the limits of energy use. Pp. 213-259 in Mammalian Energetics: Interdisciplinary Views of Metabolism and Reproduction. Comstock Publishing Associates, Ithaca, New York.

Thompson, S. D., and M. E. Nicoll

1986 Basal metabolic rate and energetics of reproduction in therian mammals. Nature 321:690-693.

Veloso, C., and F. Bozinovic

1993 Dietary and digestive constrains on basal energy metabolism in a small herbivorous rodent. Ecology, 74:2003-2010.

Vleck, D.

1979 The energy cost of burrowing by the pocket gopher *Thomomys bottae*. Physiological Zoology 52:122-136.

1981 Burrow structure and foraging costs in the fossorial rodent *Thomomys bottae*. Oecologia 49:391-396.

Wade, G., and J. Shneider

1992 Metabolic fuels and reproduction in female mammals. Neuroscience and Biobehavioral Reviews 16:235-272.

Webster M. D., and W. W. Weathers

1990 Heat produced as a by-product of foraging activity contributes to thermoregulation by verdins, *Auriparus flaviceps*. Physiological Zoology 63:777-794.

Weiner, J.

1992 Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. Trends in Ecology and Evolution 7:384-388.

White, C.R.

2003 The influence of foraging mode and arid adaptation on the basal metabolic rates of burrowing mammals. Physiological and Biochemical Zoology 76:122-134.

Withers, P. C.

1977 Measurements of VO_2, VCO_2, and evaporative water loss with a flow through a mask. Journal of Applied Physiology 42:120–123.

Wunder, B. A.

1978 A model for estimating metabolic rate of active or resting mammals. Journal of Theoretical Biology 49:345-354.

Young Owl, M., and G. O. Batzli
1998 The integrated processing response of voles to fiber content of natural diets. Functional Ecology 12:4-13.

Zenuto, R. R., C. D. Antinuchi, and C. Busch
2002 Bioenergetics of reproduction and pup development in a subterranean rodent (*Ctenomys talarum*). Physiological and Biochemical Zoology 75:469-478.

Zenuto, R. R., E. A. Lacey, and C. Busch
1999 DNA fingerprinting reveals polygyny in the subterranean rodent *Ctenomys talarum*. Molecular Ecology 8:1529-1532.

Zenuto, R. R., A. I. Vassallo, and C. Busch
2001 A method to study social and reproductive behavior of subterranean rodents in captivity. Acta Theriologica 46:161-170.

EFFECTS OF BIOTIC INTERACTIONS ON SPATIAL BEHAVIOR OF SMALL MAMMALS IN A SEMIARID COMMUNITY IN NORTH-CENTRAL CHILE

EFECTOS DE LAS INTERACCIONES BIÓTICAS SOBRE EL COMPORTAMIENTO ESPACIAL DE PEQUEÑOS MAMÍFEROS EN UNA COMUNIDAD SEMIÁRIDA EN EL NORTE-CENTRAL DE CHILE

John A. Yunger, Peter L. Meserve, and Julio R. Gutiérrez

ABSTRACT

We examined live-trap data of 4 small mammal species for evidence of behavioral responses to predator and/or competitor exclusions in a semiarid thorn scrub community in north-central Chile. The species included an herbivorous hystricognath rodent, *Octodon degus*, a granivorous/herbivorous sigmodontine rodent, *Phyllotis darwini*, and 2 omnivorous/insectivorous sigmodontines, *Abrothrix olivaceus* and *Abrothrix longipilis*. Significant numerical effects of predation on *O. degus* were present during the study; although none were detected on *P. darwini*, previous analyses showed significant but small magnitude effects of predation. Both species had significant effects of predation on survival. We examined effects of biotic interactions on mean distance between successive captures (MDBSC) for consecutive 6-month seasons during a 36-month period during and following an El Niño (ENSO) event in 1991-1994. Time and density were included with predation and competition in 4-way analyses of variance for each species. There was a significant inverse relationship between density and MDBSC for *P. darwini*; this relationship was most pronounced in predator exclusions. There also were inverse relationships between density and MDBSC for *O. degus* and *A. olivaceus*, but only female *O. degus* showed any response to predator exclusion. The mechanisms supporting these movement-density relationships may include sociality for *O. degus*, predation risk for *P. darwini*, and intraspecific agonistic encounters for *A. olivaceus*. *A. longipilis* evidently operates at a different spatio-temporal scale than the other 3 species, and its movements evidently were not affected by density or predator exclusion.

Key words: *Abrothrix longipilis*, *Abrothrix olivaceus*, chaparral, density dependence, El Niño, movement, *Octodon degus*, *Phyllotis darwini*, predator exclusion, rodents

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Pp. 141-164 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

RESUMEN

Examinamos los datos de trampeo vivo de 4 especies de micromamíferos buscando evidencia de respuestas conductuales a exclusión de depredadores y/o competidores en una comunidad arbustiva espinosa semiárida del norte-centro de Chile. Las especies incluyeron un roedor histricognato herbívoro, el degu (*Octodon degus*), un roedor sigmodontino granívoro/herbívoro, la laucha orejuda de Darwin (*Phyllotis darwini*), y dos sigmodontinos omnívoros/insectívoros, la laucha oliva de pastizal (*Abrothrix olivaceus*), y la laucha de pelo largo de pastizal (*Abrothrix longipilis*). Efectos numéricos de depredación sobre *O. degus* estuvieron presente durante el estudio; aunque ninguno fue detectado sobre *P. darwini*, análisis previos mostraron efectos significativos de depredación pero de magnitud pequeña. Ambas especies tuvieron efectos significativos de depredación sobre la sobrevivencia. Se examinaron los efectos de interacciones bióticas en la distancia promedio entre capturas sucesivas (MDBSC) para estaciones sucesivas de 6 meses durante un período de 36 meses y después de un evento El Niño (ENSO) en 1991-1994. El tiempo y la densidad se incluyeron con depredación y competencia en un análisis de varianza de 4 vías para cada especie. Hubo una relación inversa significativa entre densidad y MDBSC para *P. darwini*; esta relación fue más pronunciada en la exclusión de depredadores. Hubo también una relación inversa entre densidad y MDBSC para *O. degus* y *A. olivaceus*, pero sólo las hembras de *O. degus* mostraron alguna respuesta a la exclusión de depredadores. Los mecanismos que sustentan esta relación de densidad-movimiento pueden incluir sociabilidad para *O. degus*, riesgo de depredación para *P. darwini*, y encuentros agonísticos intraespecíficos para *A. olivaceus*. *A. longipilis* opera evidentemente a una escala espacio-temporal diferente a las otras 3 especies, y sus movimientos evidentemente no fueron afectados por la densidad o exclusión de depredadores.

Palabras claves: *Abrothrix longipilis*, *Abrothrix olivaceus*, matorral, dependencia de la densidad, El Niño, exclusión de depredadores, movimiento, *Octodon degus*, *Phyllotis darwini*, roedores

INTRODUCTION

In addition to affecting small mammal numbers and survival, predation can have important behavioral effects (e.g., Kotler, 1984a, 1984b, 1984c; Brown, 1988, 1989, 1992; Brown et al., 1988, 1992; Desy et al., 1990; Lima and Dill, 1990; Kotler et al., 1992; Lima, 1992; Lagos et al., 1995a; Yunger et al., 2002; Yunger, 2004). Perceived predation risk may decrease the area used by prey and the distances moved. Conversely, within a patchy environment, prey using specific microhabitats that provide concentrated resources and/or refuges from predators may increase mobility and areas used with increasing predator risk. In the first case, there is assumed to be a direct relationship between the probability of being detected (and subsequently consumed) by a predator, and prey mobility and foraging behavior. In the second, the advantages of exploiting a patchy resource for food and/or refuge outweigh potential disadvantages of greater movement and/or exposure. When studying such behavior in the field, investigators typically assume that prey can rapidly assess risk vs. energetic gains through proximal cues such as vegetation density, proportion of open habitat, and the relative richness of potential foraging microhabitats.

These foraging strategies are not mutually exclusive. Environmental conditions can play an important role in altering prey responses to their habitat and the presence of predators. This environmental variation can result in 2 broad manifestations that influence foraging: (1) changes in resource availability and (2) fluctuations in population density. Early models of resource availability predicted an inverse relationship between movement and the abundance of food (Cody, 1974; Schoener, 1983), but Ebersole (1980) pointed out that there can be selective pressure not only to obtain necessary energy but also to maximize energy intake. The energy obtained beyond the requirements for basic body maintenance, growth, and reproduction can be directed to reduced intervals between reproductive bouts, increased litter/clutch size, increased growth rates leading to earlier reproductive maturity, and/or large body size favoring the probability of obtaining a mate(s). There are limitations, however, to the area an individual can exploit for procuring resources. As the area used increases, so too does the probability of intra- and interspecific agonistic encounters, and, if the area is a defended territory, the probability of intrusion.

Although most studies have reported an inverse relationship between population density and measures of spatial variation, this pattern is far from universal. The presence or absence of this inverse relationship appears to be independent of the spatial measure used (e.g., home range area, maximum distance across area used, movement between captures). The preponderance of this work is Holarctic and focuses on *Microtus* spp. There have been at least 8 studies on the relationship between density and spatial patterns in *Microtus*; 5 reported an inverse relationship between home range or movement and density (Getz, 1961; Van Vleck, 1969; Krebs, 1970; Abramsky and Tracy, 1980; Ostfeld and Canham, 1995) while 3 did not (Batzli, 1968; Arai and Shiraishi, 1982; Gaines and Johnson, 1982). The inverse relationship between spatial measures and density has also been found for *Peromyscus leucopus* in prairie habitat (Yunger, 2004) and 3 species of heteromyid rodents in a southwestern U.S. desert (Maza et al., 1973), while no relationship was found for *Tamias* in oak woodlands (Mares et al., 1980). Gaines and Johnson (1982) concluded that the lack of a constant inverse relationship may be due to differences in gender and age. Seasonal fluctuations in environmental variables and changes in density among interspecific competitors can also alter spatial-density patterns (Yunger, 2004) or potentially mask intraspecific spatial-density relationships. These patterns need to be tested in other biogeographic regions and with other lineages of mammals.

Several studies have examined behavioral responses of small mammals to varying conditions simulating increased predation risk under semi-natural settings. These have involved introduction of predators into enclosures (e.g., Brown et al., 1988; Kotler et al., 1988), altering light levels as a surrogate for increased actual or perceived predation risk (e.g., Kotler, 1984a, 1984b, 1984c; Vásquez, 1996), and manipulating food levels and distribution to assess relative foraging intensity in different "risk" environments (e.g., Brown, 1988, 1989; Lima and Valone, 1985; Kotler et al., 1992). However, few studies have examined small mammal behavioral responses in natural situations where predators have been excluded. Exceptions include Desy et al. (1990) and Yunger (2004) who analyzed behavioral responses of voles (*Microtus ochrogaster*) and mice (*Peromyscus*) to predator-exclusions, Lagos et al. (1995a, 1995b) who measured changes in microhabitat use by a large caviomorph rodent, *Octodon degus*, in vertebrate predator-exclusions, and Yunger et al. (2002) and Kelt et al. (2004) who utilized foraging experiments and "giving up densities" (GUD's; the level at which small mammals cease to remove a particular resource; *sensu* Brown, 1988, 1989) as indicators of the influence of predators and/or competitors. All of these studies found some effect of predators on home range, movements, or foraging sites of small mammal prey. This included changes in density of 1 species, which reduced movements of a second species (Yunger, 2004), individuals traveling in more direct routes through open sites in the absences of predators (Lagos, 1995a), reduced predator suppression on movements (Desy at al., 1990), and shifts in microhabitat foraging site (Yunger et al., 2002; Kelt et al., 2004). However, there was extensive heterogeneity among these results. Within a given study there were differential responses among species to predator exclusion, with some species exhibiting no effect. One study that included a seasonal component found responses varied over time (Kelt et al., 2004).

A current challenge in mammalian ecology is integration of behavioral responses, territorial defense, movements, and foraging behavior with multiple constraints, such as intra- and interspecific competition, temporal fluctuations in resource availability, and predation risk. In this study we use movement to assess how predation risk, intraspecific variation in density, and interspecific competition act individually and interact collectively on small mammal behavior. This investigation was part of a long-term study of mammalian ecology in north-central Chile (Meserve et al., 1995, 1996, 2003; Yunger et al., 2002; Kelt et al., 2004). The study has provided information on temporal changes in individual small mammal movements at both a long temporal and large spatial scale while experimentally excluding the dominant small mammal competitor and excluding mammalian and avian predators. This semi-arid coastal region of Chile is strongly influenced by El Niño Southern Oscillation (ENSO) events. ENSO events trigger dramatic increases in small mammal densities (Meserve et al., 1995, 1996, 1999, 2003), affording the opportunity to examine the previous experimental manipulations under population fluctuations reaching 1 order of magnitude. This lead to 4 predictions: (1) there would be an inverse relationship between movement and population density of small mammals; (2) prey movements would increase in the absence of predators; (3) smaller, competitively subordinate species would reduce movements in response to increased densities of a large, competitively dominate species; and (4) peak densities resulting from ENSO events would mask any predator or competitor effects.

MATERIALS AND METHODS

Descriptions of the study area were given previously (Meserve et al., 1995, 1996, 1999, 2003). It is located in a relatively homogeneous thorn scrub community ("Quebrada de las Vacas", 240 m elev.) in Parque Nacional Bosque Fray Jorge (71° 40′ W, 30° 38′ S) in the IV Region [Coquimbo] ca. 85 km S La Serena and 350 km N Santiago, Chile near the coast (Fig. 1). The flora of the lower elevation scrub zone includes spiny drought-deciduous and evergreen shrubs and understory herbs on a predominantly sandy substrate, and is termed the *Porlieria chilensis-Proustia pungens-Adesmia_bedwelli* association (Muñoz and Pisano, 1947; Muñoz, 1985; Hoffmann, 1989; Gutiérrez et al., 1993). The area has been protected from grazing and disturbance since 1941. The climate is semiarid Mediterranean with 90% of the mean 110 mm annual precipitation falling in winter months (May-October); summer months are warm and dry. During 1989-1990

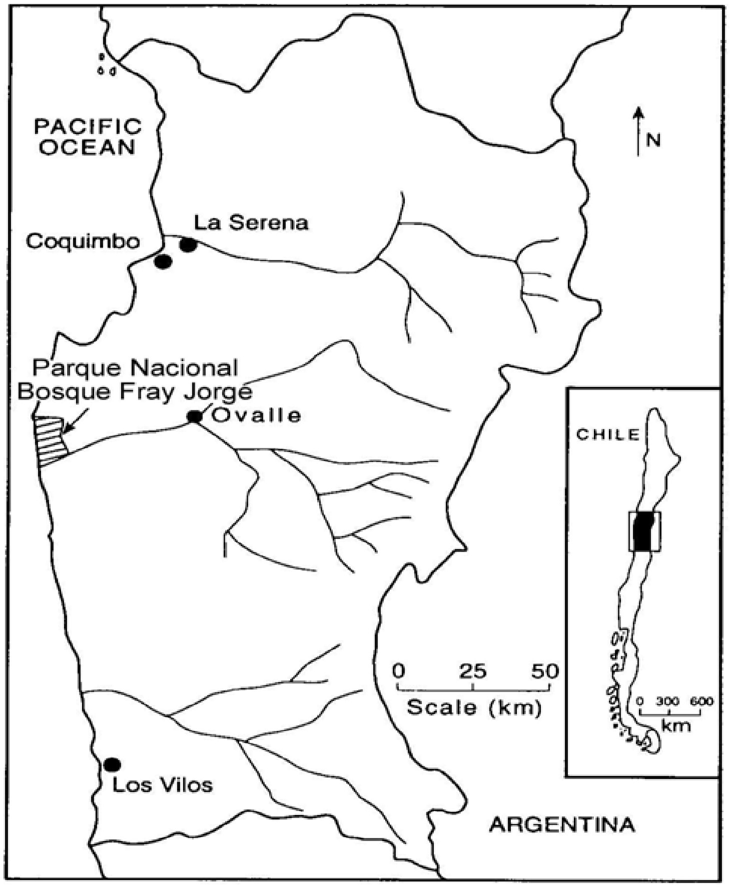

Figure 1. Map of the IV Region (Coquimbo) in north-central Chile showing the location of Parque Nacional Bosque Fray Jorge.

and 1993-1994, rainfall was average to below average (range = 32-89 mm); an ENSO event in 1991-1992 resulted in high rainfall (233 mm, and 229 mm respectively).

Small mammals found in the thorn scrub assemblage include year-around resident "core" species such *Octodon degus* (Octodontidae), and *Phyllotis darwini* (Cricetidae: Sigmodontinae) and a "quasi-core" species (*Abrothrix olivaceus*; Cricetidae: Sigmodontinae) which, although usually resident, undergoes large demographic fluctuations in the thorn scrub. "Opportunistic" species such as *Abrothrix longipilis* (Cricetidae: Sigmodontinae) disappear for varying lengths of time during dry years (Meserve et al., 1999; Milstead, 2000). *O. degus* is strongly herbivorous, *P. darwini* is granivorous/herbivorous, and *A. olivaceus* and *A. longipilis* are omnivorous and insectivorous, respectively (Meserve, 1981a). Other species such as *Oligoryzomys longicaudatus* (Cricetidae: Sigmodontinae), *Thylamys elegans* (Didelphidae), and *Abrocoma bennetti* (Abrocomidae) are sporadic and/or maintain generally low numbers in the thorn scrub (Meserve and Le Boulengé, 1987; Meserve et al., 1995). Predator numbers are particularly high within park boundaries and include the owls *Tyto alba,*

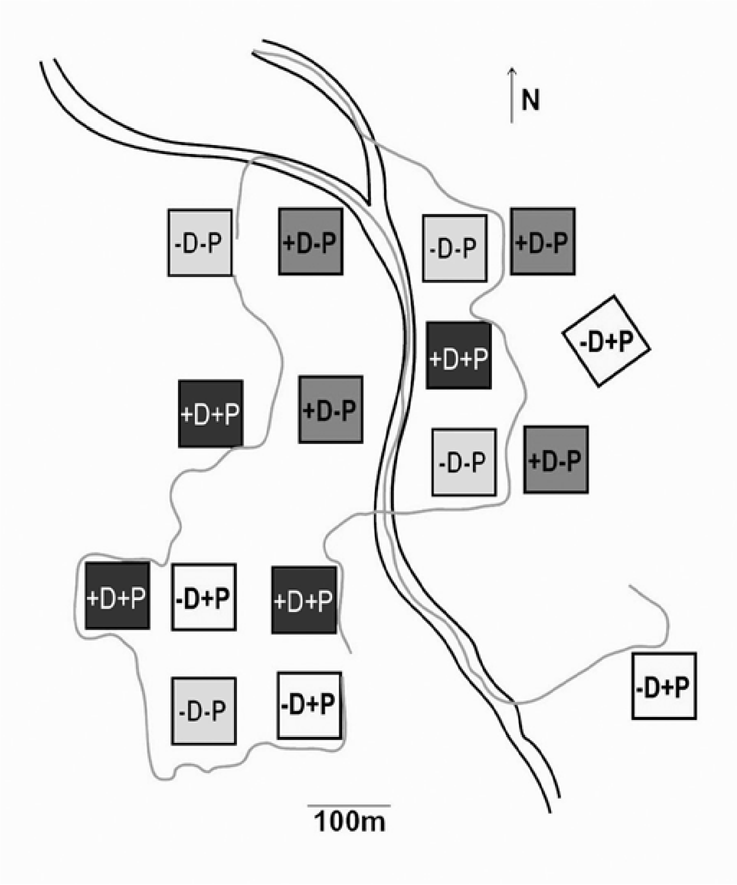

Figure 2. Location of treatments and grids in Quebrada de las Vacas, Parque Nacional Bosque Fray Jorge; symbols and codes as in text. Heavy and lighter shaded lines running among grids indicate locations of access roads and trails among grids, respectively.

Bubo magellanicus, *Speotyto cunicularia*, and *Glaucidium nanum* [sporadic]), and the culpeo fox (*Pseudalopex culpaeus*; Fulk, 1976a; Jaksic et al., 1997; Meserve et al., 1987).

A series of 16 - 75 m x 75 m (0.56 ha) grids have been live-trapped since March 1989 for 4 nights per month with 2 large Sherman-type traps/station (5 x 5 stations, 15 m interval). Animals are marked with ear tags or leg bands, and data taken on tag number, species, sex, weight, reproductive condition, and capture location during handling. Data are analyzed with the CMR (capture-mark-recapture) programs of Le Boulengé (1985; see also Meserve and Le Boulengé, 1987; Meserve et al., 1995). Monthly trappabilities (the mean percentage of the known population that was captured each month) for the first 5 species listed above (except *O. degus*) exceeded 90% (that for degus averaged 65.3 ± 1.6 (SEM)%). We use minimum number known alive (MNKA) estimates per grid for analyses of population trends.

The experiment is a 2 x 2 factorial design with treatments being competition (presence/absence of degu) and predation (presence/ absence; see Meserve et al., 1993a, 1993b, 1995, 1996) and 4 grids randomly assigned to each treatment. For convenience, we term these treatments +D+P (degu and predators present), +D-P (degu present, predators absent), -D+P (degu absent, predators present), and -D-P (degu and predators absent; see Fig. 2).

Differences in density among treatments and temporal changes in density were analyzed with repeated measures analysis of variance (rmANOVA; SAS, 1990) yielding a 2 x 2 within-subjects factorial design. Months were the repeated measures and random variables. Fixed effects were our biotic treatments (degu present/absent and predator present/absent), and density was the independent variable. Inference was based on Type III sum-of-squares. Exclusions began after the May 1989 census; during the pre-test period (March-May), there were no significant differences observed between treatments with respect to densities of *Octodon degus* (rmANOVAs $F = 0.23$, *d.f.* = 1,6, $p = 0.65$) or other principal species (all $F \leq 2.36$, *d.f.* = 1,12, all $p \geq 0.15$; Meserve et al., 1996). We examined pooled spatial results from live-trapping on the grids for successive 6-month time blocks corresponding to principal dry and wet seasons (November-April, and May-October, respectively) from late 1991 through late 1994 (N = 36 months). This period was chosen as it spanned a time of high small mammal captures during and following the 1991-1992 El Niño, thereby facilitating 6 consecutive seasons for comparisons. Mean distance between successive captures (MDBSC, in m, obtained from Program CMR; Le Boulengé, 1985) was used as a measure of movement. As a 6-month season yielded a maximum of ca. 18 (nocturnal) to 24 (diurnal) opportunities for capture, MDBSC was calculated using 10-24 captures per individual.

Treatment effects (competition and predation) were analyzed for each of the first 4 species listed. To avoid pseudoreplication (Hurlbert, 1984), we used mean values per grid because grids were our replicate. Effects of treatment on spatial measures were tested with analysis of covariance (ANCOVA; SAS PROC GLM, SAS, 1990); density and time were included as covariates yielding a 4-way ANCOVA (Table 1). Residuals were inspected for departures from normality using box-plots and normal probability plots (Tukey, 1977). All statistical inferences were based on Type III sum-of-squares with $\alpha = 0.05$.

RESULTS

During the first 32 months of the study (through October 1991) we recorded 8773 captures of 2120 individuals of 8 species. Thereafter, during the focal period of this study (November 1991 through October 1994, N = 36 mo.), we documented 103,637 additional captures of 13,294 individuals of 9 species. Captures of the 4 species considered here (i.e., *O. degus, P. darwini, A. olivaceus, A. longipilis*) comprised 94.4% of all small mammals captured during the focal period.

Numbers of *Octodon degus* were significantly higher in predator-exclusion grids (Fig. 3; rmANOVA's, $F = 7.53$, *d.f.* = 1, 6, $p = 0.034$). However, trends converged in early 1994 suggesting that predation effects were less pervasive when small mammal (and predator) numbers were declining. Predation effects on *Phyllotis darwini* density were not significant (Fig. 3; $F = 0.19$, *d.f.* = 1, 12, $p = 0.670$) although there was a strong trend towards a time x predation interaction ($F = 1.80$, *d.f.* = 1, 35, $p = 0.058$); competition effects (of *O. degus*) also were not significant ($F = 0.04$, *d.f.* = 1, 12, $p = 0.854$). No

Table 1. Covariate model used for the analysis of small mammal mean distance between successive captures (MDBSC). The predator and competitor exclusions were treated as categorical variables, whereas time and density were continuous covariates.

Abrothrix spp., *Phyllotis*	
Source	*d.f.*
Predator	1
Competitor	1
Time	1
Density	1
Predator*Competitor	1
Time*Predator	1
Density*Predator	1
Time*Competitor	1
Density*Competitor	1
Time*Density	1
Time*Predator*Competitor	1
Density*Predator*Competitor	1
Time*Density*Competitor	1
Time*Density*Predator	1
Time*Density*Predator*Competitor	1
ERROR MDBSC:	79

Octodon	
Source	*d.f.*
Predator	1
Time	1
Density	1
Predator*Density	1
Predator*Time	1
Density*Time	1
Predator*Density*Time	1
ERROR MDBSC:	39

significant main treatment effects of competition or predation were found on numbers of *Abrothrix olivaceus* (Fig. 3; predation: $F = 1.00$, *d.f.* = 1, 12, $p = 0.337$; competition: $F = 0.79$, *d.f.* = 1,12, $p = 0.392$). However, a trend towards a time x competition interaction ($F = 1.94$, *d.f.* = 1, 35, $p = 0.065$) suggested that degu effects changed over time. Similar to *A. olivaceus*, *Abrothrix longipilis* exhibited no significant treatment effects (Fig. 3; predation: $F = 1.95$, *d.f.* = 1, 12, $p = 0.188$; competition: $F = 1.65$, *d.f.* = 1, 12, $p = 0.223$). A significant time x predator interaction ($F = 1.98$, *d.f.* = 1, 35, $p = 0.043$), and a trend towards a time x competitor interaction ($F = 1.67$, *d.f.* = 1, 35, $p = 0.097$) suggest differing effects of interactions over time. These trends generally are similar to those of longer-term analyses (Meserve et al., 1996, 1999, 2003); perhaps the most notable difference was a significant predation effect and significant time x predator interactions for *P. darwini* during longer-time periods (i.e., June 1989 through mid-1996; Meserve et al., 1999). There also were strong trends towards statistically significant time x competitor interactions (Meserve et al., 1996, 1999). For *A. olivaceus* and *A. longipilis*, we detected strong trends to statistically significant interactions between time x competition and time x predation (Meserve et al., 1996, 1999).

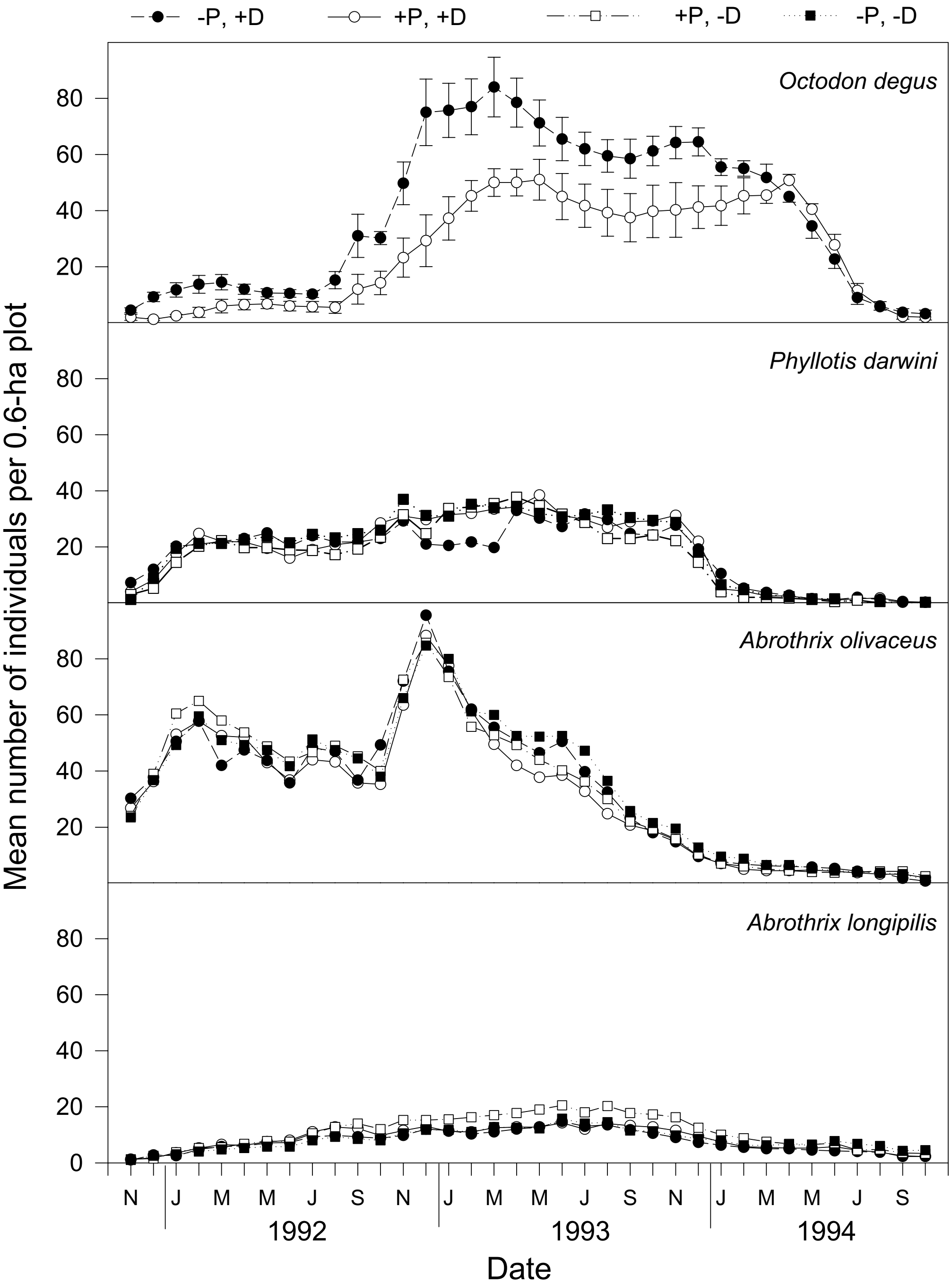

Figure 3. Population trends for *Octodon degus, Phyllotis darwini, Abrothrix olivaceus, and Abrothrix longipilis* from November 1991 through October 1994. Symbols denote treatments (see text for explanation).

Table 2. Summary of 4-way analysis of covariance (ANCOVA) of treatment effects (predation, competition) with density and time included as covariates. Presented are the *F* and *p*-values (in parentheses) associated with each response variable and interaction; degrees of freedom can be found in Table 1. For *Abrothrix longipilis* all values of $p > 0.10$.

	Octodon degus			*Phyllotis darwini*		
	Male	Female	Total	Male	Female	Total
Predator	0.27 (0.608)	1.98 (0.168)	0.20 (0.654)	6.02 (0.017)	0.63 (0.431)	1.70 (0.197)
Competitor	N/A	N/A	N/A	1.73 (0.192)	0.15 (0.698)	0.12 (0.732)
Time	5.83 (0.021)	11.20 (0.002)	5.79 (0.012)	0.55 (0.460)	3.01 (0.087)	1.07 (0.303)
Density	5.52 (0.024)	7.63 (0.009)	7.46 (0.009)	0.27 (0.603)	6.03 (0.016)	1.50 (0.225)
Predator*Competitor	N/A	N/A	N/A	0.32 (0.574)	0.02 (0.901)	0.10 (0.755)
Time*Predator	0.32 (0.576)	4.49 (0.041)	0.54 (0.468)	12.20 (0.001)	5.07 (0.033)	4.69 (0.031)
Density*Predator	0.02 (0.890)	1.84 (0.182)	0.81 (0.374)	6.36 (0.014)	1.24 (0.251)	2.28 (0.135)
Time*Competitor	N/A	N/A	N/A	3.56 (0.063)	0.33 (0.565)	0.21 (0.652)
Density*Competitor	N/A	N/A	N/A	1.31 (0.255)	0.01 (0.949)	0.03 (0.867)
Time*Density	0.08 (0.015)	10.85 (0.002)	10.07 (0.003)	0.01 (0.912)	2.89 (0.093)	0.35 (0.556)
Time*Predator*Competitor	N/A	N/A	N/A	0.39 (0.534)	0.56 (0.459)	0.05 (0.823)
Density*Predator*Competitor	N/A	N/A	N/A	0.34 (0.564)	0.01 (0.944)	0.07 (0.793)
Time*Density*Competitor	N/A	N/A	N/A	1.92 (0.170)	0.01 (0.927)	0.01 (0.967)
Time*Density*Predator	0.08 (0.778)	4.30 (0.045)	1.94 (0.172)	9.65 (0.003)	3.88 (0.050)	4.43 (0.039)
Time*Density*Predator*Competitor	N/A	N/A	N/A	0.43 (0.514)	0.04 (0.850)	0.02 (0.898)

For *O. degus* MDBSC changed significantly over time and with density (Table 2). These significant density, time, and density x time interactions were the result of an inverse relationship between MDBSC and density (Fig. 4). Predators interacted with both time and density to influence the movements of female *O. degus* (Table 2). When

Table 2 (continued).

	Abrothrix olivaceus		
	Male	Female	Total
Predator	0.01 (0.978)	0.03 (0.858)	0.01 (0.929)
Competitor	0.18 (0.668)	0.44 (0.511)	1.33 (0.253)
Time	20.16 (0.001)	10.48 (0.002)	18.08 (0.001)
Density	4.11 (0.046)	0.83 (0.372)	1.92 (0.169)
Predator*Competitor	0.22 (0.639)	0.74 (0.393)	0.37 (0.544)
Time*Predator	0.02 (0.881)	0.01 (0.932)	0.16 (0.689)
Density*Predator	0.01 (0.916)	0.02 (0.891)	0.04 (0.835)
Time*Competitor	0.33 (0.569)	0.96 (0.329)	2.35 (0.129)
Density*Competitor	0.12 (0.731)	0.26 (0.610)	1.17 (0.283)
Time*Density	14.52 (0.001)	4.73 (0.032)	11.34 (0.001)
Time*Predator*Competitor	0.35 (0.555)	0.89 (0.349)	0.48 (0.492)
Density*Predator*Competitor	0.38 (0.550)	0.59 (0.445)	0.28 (0.598)
Time*Density*Competitor	0.27 (0.602)	0.45 (0.503)	1.94 (0.168)
Time*Density*Predator	0.01 (0.917)	0.03 (0.857)	0.07 (0.794)
Time*Density*Predator*Competitor	0.38 (0.541)	0.50 (0.480)	0.18 (0.671)

predators were excluded, there was little change in MDBSC; when predators were present and densities increased, MDBSC declined (Fig 4). This effect occurred at the end of the time series when densities were low.

Phyllotis darwini males showed a significant effect of predation on their MDBSC

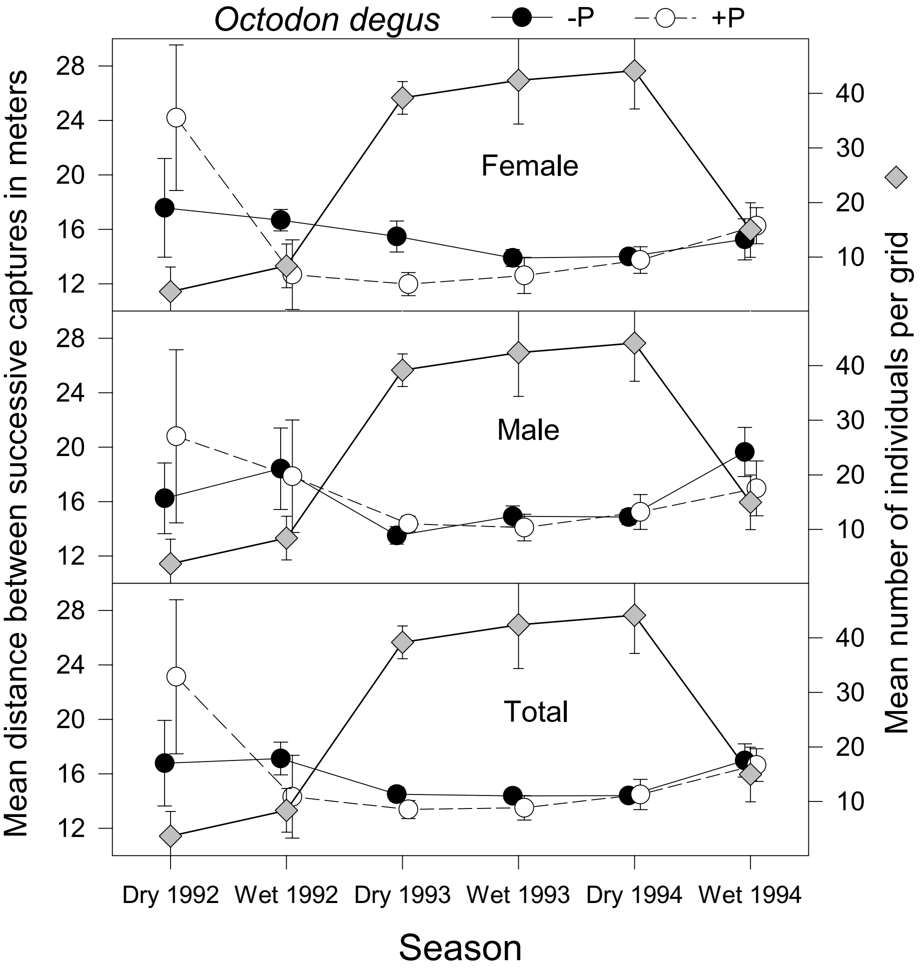

Figure 4. Minimum distance between successive captures (± 1SE, MDBSC) for *Octodon degus* females, males, and all individuals for 6-month periods between November 1991 and October 1994.

with higher values in predator-exclusion plots (Table 2; Fig. 5). For all 3 groups MDBSC changed inversely with density over time; this difference was most pronounced in predator exclusion treatments (Table 2). Thus, *P. darwini* movements were greater under conditions of low density when predators were absent. The exclusion of *O. degus* had no effect on *P. darwini* movements (Table 2).

For *A. olivaceus* there were no significant effects of predation or competition on MDBSC. In all cases MDBSC changed significantly over time (Table 2; Fig. 6). There was a significant effect of density on MDBSC for males (Table 2) but not for females (Table 2). However, all 3 *A. olivaceus* time x density interactions were significant (Table 2); this was a result of MDBSC increasing over time while density decreased (Fig. 6).

For *A. longipilis*, there no significant effects of predation or competition on MDBSC (all $F \leq 0.65$, *d.f.* = 1, 79, $p \geq 0.42$; Fig. 7). Additionally, there were no significant effects of

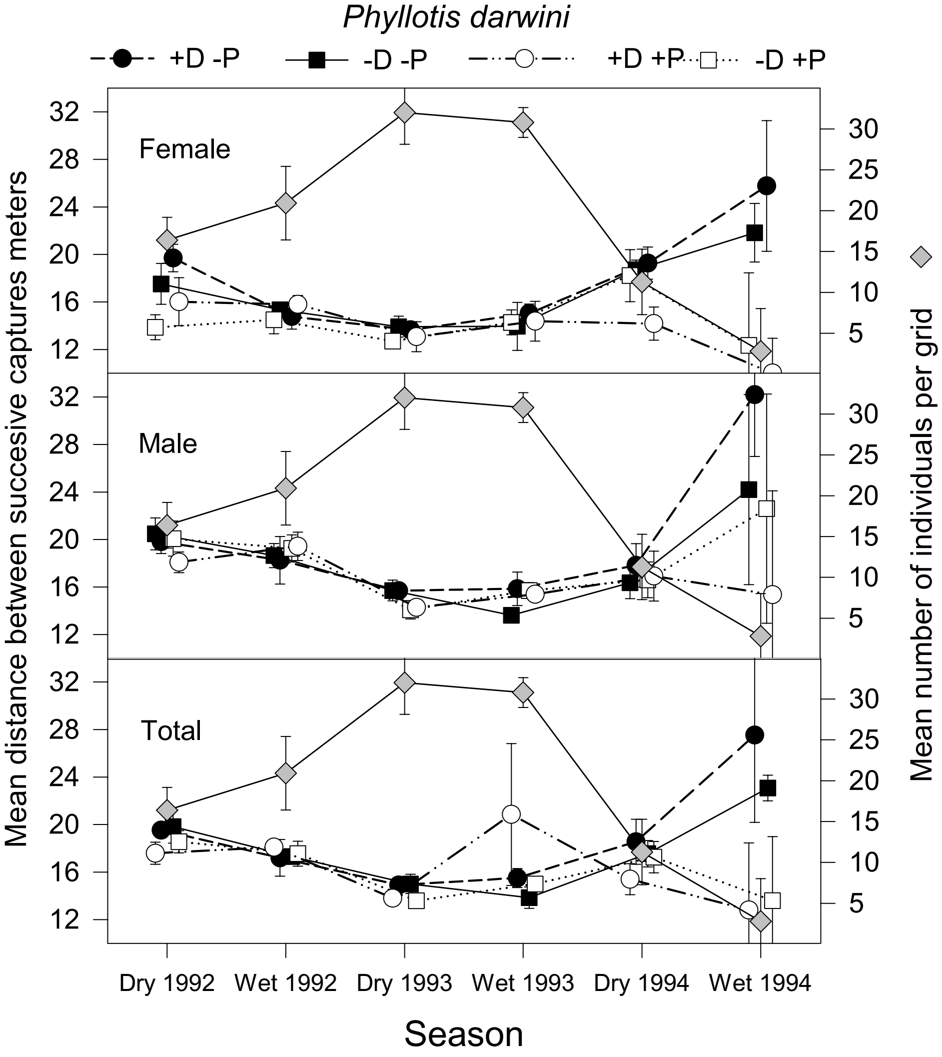

Figure 5. Minimum distance between successive captures (± 1SE, MDBSC) for *Phyllotis darwini* females, males, and all individuals for 6-month periods between November 1991 and October 1994.

either time or density on any spatial measure (all $F \leq 0.65$, *d.f.* = 1, 79, $p \geq 0.42$; Fig. 7).

MDBSC estimates for *O. degus* were ca. 16-32% of linear grid measurements (e.g., widths/lengths, both = 75 m). *P. darwini* had MDBSC estimates that were ca. 16-43% of linear grid measurements. *A. olivaceus* had mean seasonal MDBSC of 15-37% of grid widths/length which tended to increase over time and with declining density. *A. longipilis* had the highest mean seasonal MDBSC estimates of the 4 species ranging from 21 to 37% of the linear grid widths/lengths; there was little change in these measures over time or with density.

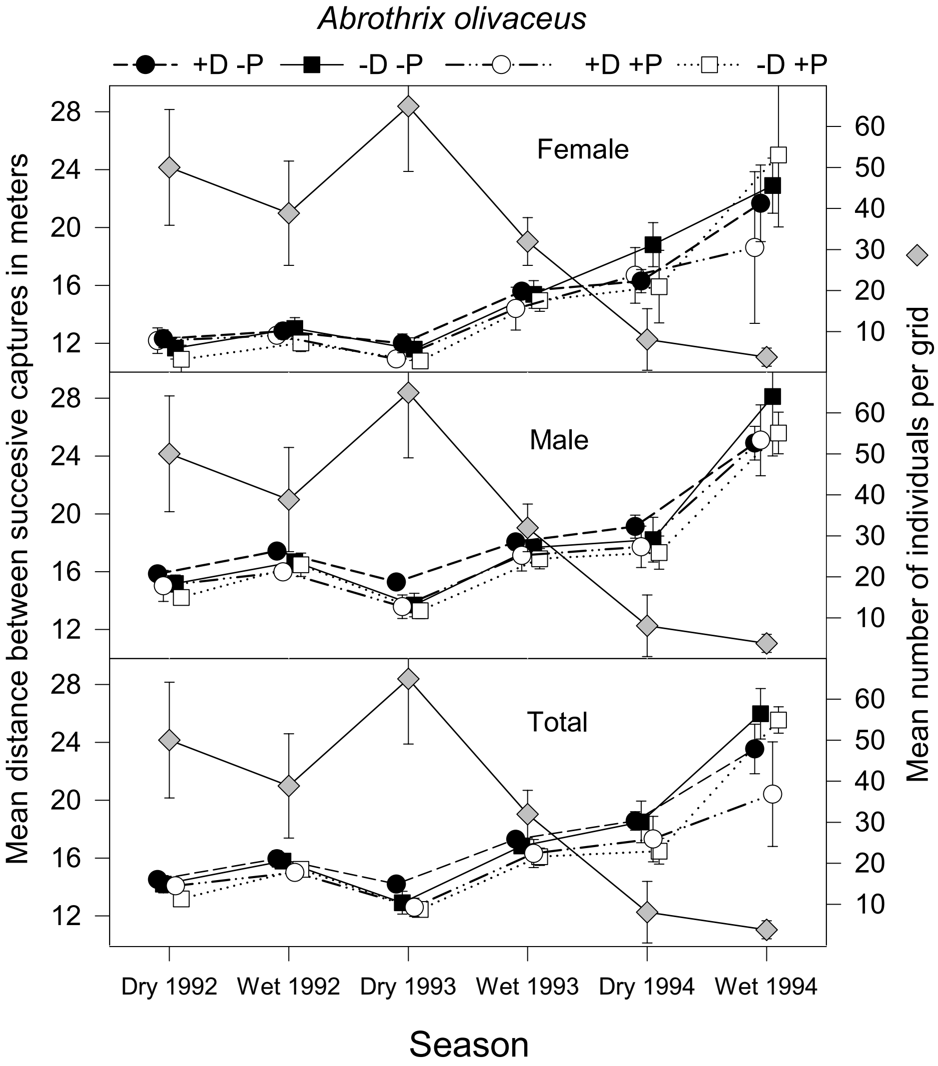

Figure 6. Minimum distance between successive captures (± 1SE, MDBSC) for *Abrothrix olivaceus* females, males, and all individuals for 6-month periods between November 1991 and October 1994.

DISCUSSION

There were no effects of competitor exclusion on movements among the 3 species that are smaller than the diurnal *O. degus*. This was not surprising for *P. darwini*, which is nocturnal; these 2 species rarely come into direct contact. Although Yunger et al. (2002) found no effect of *O. degus* exclusion on *P. darwini* foraging, Kelt et al. (2004) recorded significant increases in foraging by *P. darwini* in the absence of degus. This difference may be attributed to temporal scale of these studies; the latter had a

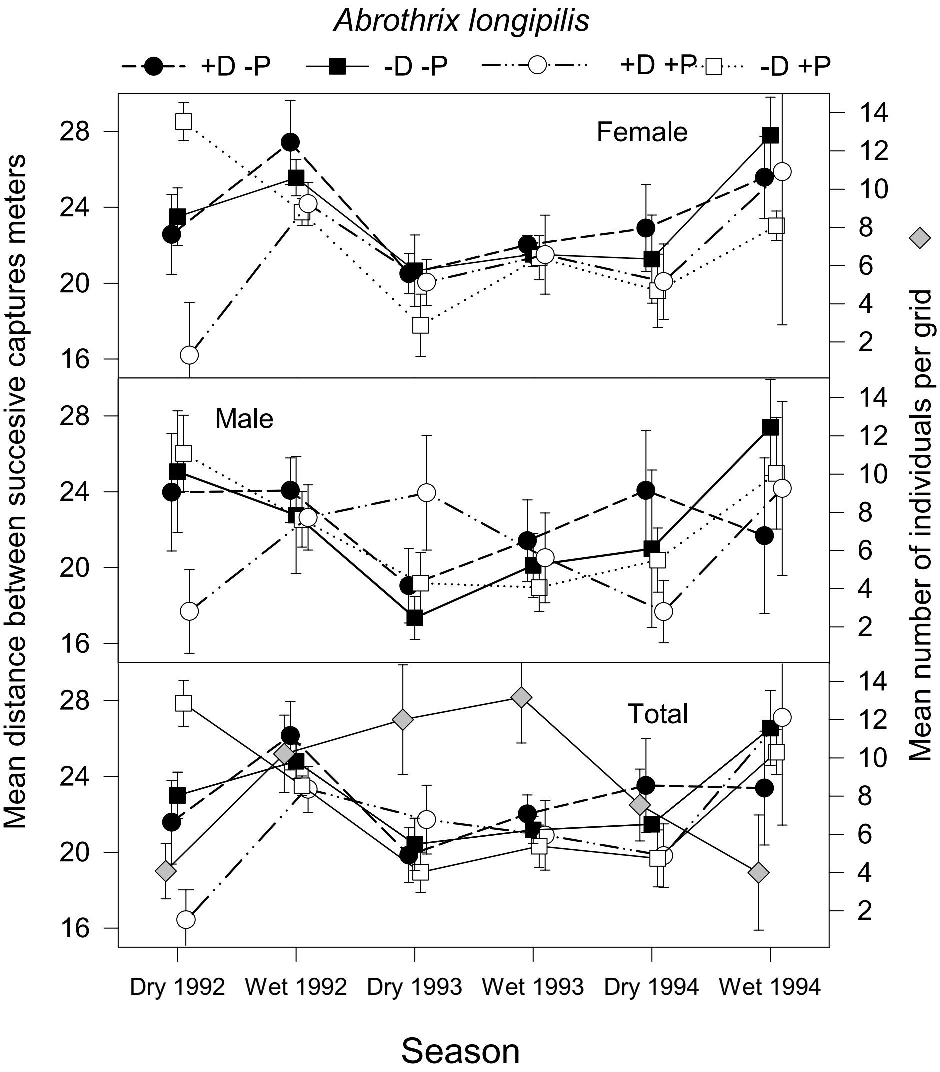

Figure 7. Minimum distance between successive captures (± 1SE, MDBSC) for *Abrothrix longipilis* females, males, and all individuals for 6-month periods between November 1991 and October 1994.

longer duration and potentially greater sensitivity to variation in foraging. Additional work is required to determine the spatio-temporal scale of competition between these 2 species. Based on their natural history, this investigation, and the 2 studies cited above, it appears that interference competition and the direct influence on movements does not occur, but that scramble competition or resource depletion may be occurring. Although there have been no notable numerical effects of *O. degus* exclusion on *A. olivaceus* (Meserve et al., 1996), previous work on foraging behavior has shown that the former species can reduce the giving up densities (GUD) of the latter (Kelt et al., 2004; Yunger et al., 2002). As with *P. darwini*, future work on behavioral interactions between these 2 species needs to resolve the spatio-temporal scale at which significant behavioral interactions occur: is this only when the 2 species come in direct contact over a potential food source, or is *A. olivaceus* moving in such a way as to avoid *O. degus* but not necessarily alter its average distance moved? The opportunistic *A. longipilis* functions at a spatial scale different than *O. degus*. There are periods during which *A. longipilis* is not captured at the study site for several months; during ENSO periods it is regularly captured at the site, reflecting this species' long-term sporadic occurrence (Meserve et al., 2003). *A. longipilis* movements at both short and long temporal scales and movements between grids are significantly greater than *O. degus* (Yunger et al., 2002). Thus, it appears these differences in spatial scale result in no direct effect of *O. degus* on *A. longipilis* movements.

Among the 4 small mammal species in this study, there was extensive temporal variation in movements associated with predator exclusion and changes in densities. Responses to predator exclusion ranged from strong, pervasive effects on both male and female *P. darwini*, to interactions of predation with time and density affecting female *O. degus* movement, to no detectable effects of predators on *A. olivaceus* or *A. longipilis*. Both male and female *O. degus* MDBSC showed a significant inverse relationship with density over time. The same was true for *P. darwini*, although the response was more pronounced on predator exclusion plots. Movements of both male and female *A. olivaceus* changed significantly over time in a density-dependent manner. Similar to the predator exclusion response, *A. longipilis* movements did not change significantly over time, irrespective of density. These graded responses are readily explained by life history characteristics of these species.

O. degus tend to be distributed in areas of high bare ground cover associated with patches of shrubs under which their burrows are located (Meserve, 1981b). Within these areas, MDBSC declined as density increased following the ENSO. Degus are highly social and colonial, and concentrate activity around clusters of burrows and related groups of individuals (Fulk, 1976b; Meserve et al., 1984; Vásquez, 1998). Affinity for other members of the social group or the burrow system itself may prevent degus from making extensive movements away from the family site. As densities increase and space becomes limited, individuals likely reduce overall movements due to aggressive encounters with members of adjacent family groups. A caveat is that food resources remain adequate within this limited area as densities increase. The change in herbaceous plant cover from near zero to 90% following ENSOs (Meserve et al. 2003) suggests this may be the case. Future work should examine changes in *O. degus* spatial patterns following the factorial manipulation of food and density.

Under low densities, female degus had significantly lower MDBSC on predator exclusion plots than predator access plots. Lagos et al. (1995a) found that degus in predator access plots (i.e., +P+D) used open areas less (assessed with smoked tracking plates), had increased daily activity ranges (assessed with fluorescent tracking), and made shorter, more direct movements between shrub patches. Similarly, Yunger et al. (2002) found greater foraging and a trend towards use of open microhabitats by degus in predator exclusion grids (as determined by GUD's). Whereas daily activity ranges and foraging experiments could reflect more subtle patterns of spatial usage than detected by live-trapping, Lagos et al. (1995a) also pooled data over nearly a year; therefore, we expected more similarity between their results and those presented here, which were based on mark-recapture. There also are important energetic and thermoregulatory considerations. Degus limit activity to areas beneath shrubs in summer months regardless of treatment (Lagos et al., 1995b); use of continuous periods would have obscured seasonal differences. Therefore, special attention must be paid to temporal and spatial scales of measurement, and the extent to which individual spatial measures reflect population- vs. individual-level responses to experimental manipulations of biotic interactions.

In the absence of predators, both female and male *P. darwini* showed a strong inverse relationship between movement and density. In view of this significant but small magnitude numerical response to predation, and effects of predation on survival rates (Meserve et al., 1995, 1999), changes in spatial behavior may reflect consequences of increased predation risk. For example, snowshoe hares alter their habitat use due to predation risk, foraging in areas of reduced food availability (Krebs et al., 1995). The increased MDBSC suggested increased spatial usage in the absence of predation. A similar response was reported for prairie voles (*Microtus ochrogaster*) in predator-exclusion plots (Desy et al., 1990). Foraging experiments conducted in summer 1991 showed that *P. darwini* foraged more intensively in predator-exclusion grids (Yunger et al., 2002); Kelt et al. (2004) reported a similar trend in 1999-2001. This species performed more evasive maneuvers to an avian predator model under conditions of a full (vs. new) moon, and that they have significantly higher GUD's (i.e., lower foraging intensity) under artificial full moon light levels (Vásquez, 1994). Yunger et al. (2002) and Kelt et al. (2004) reported a similar effect of moonlight, but only the former reported an effect of cover on *P. darwini* foraging intensity. Increased foraging under shrubs and during a new moon have been inferred as responses to predation risk for gerbils in both the Negev (Kotler, 1984b, Kotler et al., 1991) and Namib Deserts (Hughes et al., 1994), and for heteromyid rodents in the Sonoran Desert (Price et al., 1984). Aviary experiments with owls and *Gerbillus* spp. (Kotler et al., 1991) and field experiments with lanterns and *Dipodomys* spp. (Kotler, 1984c) have confirmed that light levels influence foraging sites and movements between patches. *P. darwini* evidently shares with these other species a variety of behavioral responses to perceived predation risk.

Exclusion of predators had no effect on movement by *A. olivaceus*, and earlier work demonstrated a lack of numerical effects of predation on them (Meserve et al., 1996, 1999). *A. olivaceus* are only occasional prey items for diurnal raptors and foxes (Fulk, 1976a; Meserve et al., 1987; Jaksic et al., 1997). There was a clear and pronounced inverse relationship between movements and density. The inverse correlation between density and MDBSC for *A. olivaceus* may be attributed to a reduction in intraspecific agonistic encounters as reported for *Microtus ochrogaster* (Abramsky and Tracy, 1980).

Changes in density and predator exclusion had no effect on movements by *A. longipilis*. There have also been no numerical effects of predator or competitor exclusion on this species. As with competition, the absence of any response may be attributed to differences in spatial scales. It has also been suggested that *A. longipilis* may travel long distances and "skim" sporadically distributed numerous patches of abundant food (Yunger et al., 2002). Similar results have been found for gerbils in the Negev Desert (Brown et al., 1994) and *Ammospermophilus harrisii* in the Sonoran Desert (Brown, 1989). Associated with the high MDBSC are large long-distance movements for *A. longipilis* at this field site (Yunger et al., 2002). This species also has large home range area in southern temperate rainforests (Rau et al., 1981; Meserve et al., 1991). This lends further support to its characterization as an opportunistic species that persists in more mesic areas such as river bottoms and fog forest habitats during droughts and invades upland thorn scrub after El Niño events (Meserve et al., 1999; Milstead, 2000). Further, its insectivorous diet would predict a larger spatial scale of habitat usage (McNab, 1963; Kelt and Van Vuren, 2001).

Although results for relationships between population density and home range/ movement-density relationships are conflicting (Batzli, 1968; Contreras, 1972; Mares et al., 1980; Arai and Shiraishi, 1982), this study lends support to the general trend of an inverse relationship among a diversity of small mammals (Getz, 1961; Van Vleck, 1969; Krebs, 1970; Maza et al., 1973; Gaines and Johnson, 1982). Three of the 4 species investigated at Fray Jorge conform to this relationship. However, the mechanisms underlying this relationship do not appear to be consistent among the 3 species, and range from sociality for *O. degus*, to intraspecific agonistic encounters for *A. olivaceus*, and predation risk for *P. darwini*.

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LITERATURE CITED

Abramsky, Z., and C. R. Tracy
1980 Relation between home range size and regulation of population size in *Microtus ochrogaster*. Oikos 34:347-355.

Arai, A., and S. Shiraishi
1982 Population ecology of the Japanese field vole (*Microtus montebelli*) in Kyushu. Scientific Bulletin of the Faculty of Agriculture, Kyushu University 36:89-99. (In Japanese, with English summary).

Batzli, G. O.
1968 Dispersion patterns of mice in California annual grasslands. Journal of Mammalogy 49:239-250.

Brown, J. S.
1988 Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology 22:37-47.

1989 Desert rodent community structure: a test of four mechanisms of coexistence. Ecological Monographs 59:1-20.

1992 Patch use under predation risk: I. Models and predictions. Annales Zoologici Fennici 29:301-310.

Brown, J. S., B. P. Kotler, R. J. Smith, and W. O. Wirtz, II
1988 The effects of owl predation on the foraging behavior of heteromyid rodents. Oecologia 76:408-415.

Brown, J. S., R. A. Morgan, and B. D. Dow
1992 Patch use under predation risk: II. A test with fox squirrels, *Sciurus niger*. Annales Zoologici Fennici 29:311-318.

Brown, J. S., B. T. Kotler, and W. A. Mitchell
1994 Foraging theory, patch use, and the structure of a Negev Desert granivore community. Ecology 75:2286-2300.

Cody, M. L.
1974 Competition and the structure of bird communities. Princeton University Press, Princeton, New Jersey. 326 pp.

Contreras, J. R.
1972 Home range in a population of *Oryzomys longicaudatus philippi* (Landbeck) (*Rodentia*, Cricetidae). Physis 31:353-361. (In Spanish, with English summary).

Desy, E. A., G. O. Batzli, and J. Liu
1990 Effects of food and predation on behaviour of prairie voles: a field experiment. Oikos 58:159- 168.

Ebersole, J. P.
1980 Food density and territory size: an alternative model and test on the reef fish *Eupomacentrus leucostictus*. American Naturalist 115:492-509.

Fulk, G. W.
1976a Owl predation and rodent mortality: a case study. Mammalia 40:423-427.

1976b Notes on the activity, reproduction, and social behavior of *Octodon degus*. Journal of Mammalogy 57:495-505.

Gaines, M. S., and M. L. Johnson
1982 Home range size and population dynamics in the prairie vole, *Microtus ochrogaster*. Oikos 39:63-70.

Getz, L. L.
1961 Home ranges, territoriality and movement of the meadow vole. Journal of Mammalogy 42:24-36.

Gutiérrez, J. R., P. L. Meserve, F. M. Jaksic, L. C. Contreras, S. Herrera, and H. Vásquez

1993 Dynamics and structure of vegetation in a Chilean semiarid thorn scrub community. Acta Oecologia 14:271-285.

Hoffmann, A.

1989 Flora Silvestre de Chile: Zona Central. 2nd ed. Ediciónes Fundación Claudio Gay, Santiago, Chile. 255 pp.

Hughes, J. J., D. Ward, and M. R. Perrin

1994 Predation risk and competition affect habitat selection and activity of Namib Desert gerbils. Ecology 75:1397-1405.

Hurlbert, S. H.

1984 Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

Jaksic, F. M., S. I. Silva, P. L. Meserve, and J. R. Gutiérrez

1997 A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South America. Oikos 78:341-354.

Kelt, D. A., P. L. Meserve, L. K. Nabors, M. L. Forister, and J. R. Gutiérrez

2004 Foraging ecology of small mammals in semiarid Chile: the complex interplay of biotic and abiotic effects. Ecology 85:383-397.

Kelt, D. A., and D. H. Van Vuren

2001 The ecology and macroecology of mammalian home range area. American Naturalist 157:637-645.

Krebs, C. J.

1970 *Microtus* population biology: behavioral changes associated with the population cycle in *M. ochrogaster* and *M. pennsylvanicus*. Ecology 51:34-52.

Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Marin, R. Turkington.

1995 Impact of food and predation on the snowshoe hare cycle. Science 269:112-115.

Kotler, B. P.

1984a Effects of illumination on the rate of resource harvesting in a community of desert rodents. American Midland Naturalist 112:383-389.

1984b Harvesting rates and predatory risk in desert rodents: a comparison of two communities on different continents. Journal of Mammalogy 65:91-96.

1984c Risk of predation and the structure of desert rodent communities. Ecology 65:689-701.

Kotler, B. P., L. Blaustein, and J. S. Brown
1992 Predator facilitation: the combined effects of snakes and owls on the foraging behavior of gerbils. Annales Zoologica Fennici 29:199-206.

Kotler, B. P., J. S. Brown, and O. Hasson
1991 Factors affecting gerbil foraging behavior and rates of owl predation. Ecology 72:2249-2260.

Kotler, B. P., J. S. Brown, R. J. Smith, and W. O. Wirtz, III
1988 The effects of morphology and body size on rates of owl predation on desert rodents. Oikos 53:145-152.

Lagos, V. O., L. C. Contreras, P. L. Meserve, J. R. Gutiérrez, and F. M. Jaksic
1995a Effects of predation risk on space use by small mammals: a field experiment with a Neotropical rodent. Oikos 74:259-264.

Lagos, V. O., F. Bozinovic, and L. C. Contreras
1995b Microhabitat use by a small diurnal rodent (*Octodon degus*) in a semiarid environment: thermoregulatory constraints or predation risk? Journal of Mammalogy 76:900-905.

Le Boulengé, E. R.
1985 Computer package for the analysis of capture-recapture data. Acta Zoologica Fennica 173:69-72.

Lima, S. L.
1992 Life in a multi-predator environment: some considerations for anti-predator vigilance. Annales Zoologici Fennici 29:217-226.

Lima, S. L., and L. M. Dill
1990 Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Lima, S., and T. Valone
1985 Foraging-efficiency-predation-risk trade off in the grey squirrel. Animal Behavior 33:155-165.

Mares, M. A., M. R. Willig, and N. A. Bitar
1980 Home range size in eastern chipmunks, *Tamias striatus*, as a function of number of capture: statistical biases of inadequate sampling. Journal of Mammalogy 61:661-669.

Maza, B. G., N. R. French, and A. P. Aschwanden
1973 Home range dynamics in a population of heteromyid rodents. Journal of Mammalogy 54:405-425.

McNab, B. K.
1963 Bioenergetics and the determination of home range size. American Naturalist 97:133-140.

Meserve, P. L.
1981a Trophic relationships among small mammals in a Chilean semiarid thorn scrub community. Journal of Mammalogy 62:304-314.

1981b Resource partitioning in a Chilean semi-arid small mammal community. Journal of Animal Ecology 50:745-757.

Meserve, P. L., J. R. Gutiérrez, L. C. Contreras, and F. M. Jaksic
1993a Role of biotic interactions in a semiarid scrub community in north-central Chile: a long-term ecological experiment. Revista Chilena de Historia Natural 66:224-241.

Meserve, P. L., J. R. Gutiérrez, and F. M. Jaksic
1993b Effects of vertebrate predation on a caviomorph rodent, the degu (*Octodon degus*), in a semiarid thorn scrub community in Chile. Oecologia 94:153-158.

Meserve, P. L., J. R. Gutiérrez, J. A. Yunger, L. C. Contreras, and F. M. Jaksic
1996 Role of biotic interactions in a small mammal assemblage in semiarid Chile. Ecology 77:133-148.

Meserve, P. L., D. A. Kelt, W. B. Milstead, and J. R. Gutiérrez.
2003 Thirteen years of shifting top-down and bottom-up control. BioScience 53:633-646.

Meserve, P. L., B. K. Lang, R. Murua, A. Muñoz, and L. A. González
1991 Characteristics of a terrestrial small mammal assemblage in a temperate rainforest in Chile. Revista Chilena de Historia Natural 64:157-169.

Meserve, P. L., and E. R. Le Boulengé
1987 Population dynamics and ecology of small mammals in the northern Chilean semiarid region. Pp. 413-431 in Studies in Neotropical Mammalogy: Essays in Honor of Philip Hershkovitz (Patterson, B. D., and R. M. Timm, eds.). Fieldiana: Zoology, new series, 39.

Meserve, P. L., R. E. Martin, and J. Rodríguez
1984 Comparative ecology of the caviomorph rodent *Octodon degus* in two Chilean mediterranean-type communities. Revista Chilena de Historia Natural 57:79-89.

Meserve, P. L., W. B. Milstead, J. R. Gutiérrez, and F. M. Jaksic
1999 The interplay of biotic and abiotic factors in a semiarid Chilean mammal assemblage: results of a long-term experiment. Oikos 85:364-372.

Meserve, P. L., E. J. Shadrick, and D. A. Kelt
1987 Diets and selectivity of two Chilean predators in the northern semi-arid zone. Revista Chilena de Historia Natural 60:93-99.

Meserve, P. L., J. A Yunger, J. R. Gutierrez, L C. Contreras, W. B. Milstead, B. K. Lang, K. L. Cramer, S. Herrera, V. O. Lagos, S. I. Silva, E. L. Tabilo, M. A. Torrealba, and F. M. Jaksic.
1995 Heterogeneous responses of small mammals to an El Niño Southern Oscillation event in northcentral semiarid Chile and the importance of ecological scale. Journal of Mammalogy 76:580-595.

Milstead, W. B.
2000 The demographic and genetic structure of arid-land small mammal populations in north-central Chile: Rainfall, refuges and ratadas. Ph.D. Dissertation, Northern Illinois University, DeKalb, Illinois. 147 pp.

Muñoz, M.
1985 Flores del Norte Chico. Dirección de Bibliotecas, Municipalidad de La Serena, La Serena, Chile. 95 pp.

Muñoz, C., and E. Pisano
1947 Estudio de la vegetación y flora de los parques nacionales de Fray Jorge y Talinay. Agricultura Técnica 2:71-190.

Ostfeld, R. S. and C. D. Canham
1995 Density-dependent processes in meadow voles: an experimental approach. Ecology 76:521-532.

Price, M. V., N. M. Waser, and T. A. Bass
1984 Effects of moonlight on microhabitat use by desert rodents. Journal of Mammalogy 65:353-356.

Rau, J., R. Murúa, and M. Rosenmann
1981 Bioenergetics and food preferences in sympatric southern Chilean rodents. Oecologia 50:205-209.

SAS Institute Inc.
1990 SAS/STAT user's Guide, Release 6.0, Volume 2, 4th ed. Cary, North Carolina, USA.

Schoener, T. W.
1983 Simple models of optimal feeding-territory size: a reconciliation. American Naturalist 121:608-629.

Tukey, J. W.
1977 Exploratory Data Analysis. Addison-Wesley, Reading, Massachusetts, USA. 688 pp.

Van Vleck, D. B.
1969 Standardization of *Microtus* home range calculation. Journal of Mammalogy 50:69-80.

Vásquez, R. A.
1994 Assessment of predation risk via illumination level: facultative central place foraging in the cricetid rodent *Phyllotis darwini.* Behavioral Ecology and Sociobiology 34:375-381.

1996 Patch utilization by three species of Chilean rodents differing in body size and mode of locomotion. Ecology 77:2343-2351.

1998 Vigilance and social foraging in *Octodon degus* (Rodentia: Octodontidae). Revista Chilena de Historia Natural 70:557-563.

Yunger, J. A.
2004 Movement and spatial organization of small mammals following vertebrate predator exclusion. Oecologia 139:647-654.

Yunger, J. A., P. L. Meserve, and J. R. Gutiérrez
2002 Small mammal foraging behavior: mechanisms for coexistence and implication for population dynamics. Ecological Monographs 72:561-577.

PHYSIOLOGICAL FLEXIBILITY IN FIELD URINE OSMOLALITY OF RODENTS FROM SEMI-ARID CHILE

FLEXIBILIDAD FISIOLÓGICA EN LA OSMOLARIDAD URINARIA DE CAMPO EN ROEDORES DE CHILE SEMI-ÁRIDO

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Mario Rosenmann[1], and Arturo Cortés

ABSTRACT

We assessed long-term physiological responses in field urine osmolality (Uosm) of 4 murid rodents from semi-arid Chile, as a function of the El Niño Southern Oscillation. In general, all of the rodent species studied showed important temporal fluctuations in their Uosm-values, indicating both seasonal and annual patterns of physiological variability characterized by high Uosm-values during the Austral spring-summer and low Uosm-values during autumn-winter. This pattern was clearly observed during wet years (1991-1992), while during dry years there was an increase in Uosm-values during autumn-winter but not spring-summer. We observed significant effects of year and season on Uosm-values, with a year x season interaction. We demonstrate how flexibility of physiological mechanisms allows small mammals in arid or semi-arid regions to cope with long-term seasonal and annual water variability in their semi-arid habitat. The trends of seasonal water balance during contrasting years (i.e., El Niño vs. dry years) likely is a consequence of plant cover, since this is the principal food and water source for rodents at Fray Jorge.

Key words: El Niño, long-term physiology, water economy, urine concentration, semiarid ecosystems, small mammals, Chile

RESUMEN

Estudiamos las respuestas fisiológicas de largo plazo en la osmolaridad de la orina (Uosm) de cuatro especies de roedores muridos de ambientes semi áridos de Chile en función del fenómeno climático El Niño. En general las cuatro especies muestran importantes fluctuaciones temporales en Uosm, indicando un patrón de variabilidad

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[1] Deceased

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fisiológica anual y estacional caracterizado por valores de Uosm altos durante la primavera-verano austral y valores de Uosm bajos durante otoño-invierno. Este patrón se observó claramente durante los años lluviosos (1991-1992), mientras que durante los años secos se observó un aumento en los valores de Uosm durante otoño-invierno pero no en primavera-verano. Observamos además un efecto significativo de la interacción año y estación sobre Uosm. Finalmente demostramos como la flexibilidad en los mecanismos fisiológicos les permite a los pequeños mamíferos de regiones áridas o semi-áridas tolerar la variabilidad anual y estacional de largo plazo en la disponibilidad de agua en sus habitats semi-áridos. La tendencia de balance de agua estacional durante años contrastantes (i.e., El Niño vs. años secos) parece ser consecuencia de cambios en la cubierta de plantas pues es la fuente de alimento y agua principal para los roedores de Fray Jorge.

Palabras claves: El Niño, fisiologia de largo plazo, economía de agua, concentración de orino, ecosistemas semi-áridas, mamíferos pequeños, Chile

INTRODUCTION

The study of phenotypic flexibility has been a central issue in ecological and evolutionary physiology (Willmer et al., 2000). Indeed, the environmental tuning of an organism's physiology in the field often is hypothesized to be responsible for allowing it to adjust to changing biotic and abiotic conditions, through increases in biological performance (Huey and Berrigan, 1996). This is well-exemplified by desert-dwelling rodents for whom maintaining water homeostasis is challenging (Walsberg, 2000). Rodents from arid and semiarid habitats are faced with the problem of water conservation in conditions where the temporal availability of free water is limited or scarce (Degen, 1997; Bozinovic and Gallardo, 2006). Nevertheless, the physiology of water regulation among desert rodent appears to show remarkable flexibility. The response of small mammals to water deficits and unproductive desert have been investigated intensively (e.g., Schmidt-Nielsen, 1964). However, studies of water economy generally rely heavily on short-term laboratory-oriented experiments (Bozinovic et al., 2003)

Here we examine long-term flexibility in field urine osmolality in an assemblage of arid-zone rodents in temperate South America. To the best of our knowledge, this is the first such study to include dry as well as rainy years associated with the El Niño Southern Oscillation (ENSO) phenomenon. When El Niño occurs, coastal waters warm up during winter months, thereby breaking down thermal inversion, and allowing the intrusion of moist Pacific air masses (Aceituno, 1992; Trenberth, 1997). The ecological effects of ENSO on terrestrial ecosystems of western South America are intense (Jaksic, 2001; Meserve et al., 2003). Indeed, long-term ecological studies have documented that periodic El Niño events have caused several changes in ecological processes and patterns, both at population (Lima et al., 1999, 2002) and community levels (Meserve et al., 1995, 2003; Jaksic, 2001). Since the period of ENSO oscillation is around 6.4 years, long-term studies are essential for understanding such effects across a range of organizational levels, from individuals to communities (Meserve et al., 2003).

Urine osmolality (Uosm in mOsm/kg) reflects the capacity of the kidney for water conservation efficiency by small mammals (e.g., Bozinovic et al., 2003; Gallardo et al., 2005). This capacity has traditionally been used as an estimator of the efficiency of the kidneys for conserving body water, especially in laboratory studies (McNab, 2002). However, this measure has seldom been used as a tool for assessing the water balance stages of small mammals in their natural environments (Cortés et al., 1994). Laboratory studies on water regulation and conservation in small mammals from the arid Mediterranean habitat of north-central Chile, show that the majority of species have maximum concentration capacity > 4,000 mOsm/kg (Bozinovic et al., 1995).

We studied seasonal and yearly long-term acclimatization in the urine osmolality of 4 nocturnal murid rodents, *Abrothrix olivaceus*, *A. longipilis*, *Oligoryzomys longicaudatus*, and *Phyllotis darwini* (for the generic attribution of the former 2 species see Pearson and Smith (1999) and Smith and Patton (1993), respectively). All of these species occur sympatrically at our study site in northern Chile. This site has a semi-arid climate, with highly variable precipitation (Meserve et al., 2003). Although Fray Jorge has a long-term mean of ca. 110 mm of precipitation annually (Meserve et al., 2003), precipitation patterns in the region present large inter-annual variability (e.g., a high rainfall year typically is followed by an intervening 2-3 year period of low or average rainfall). During this study an ENSO event in 1991-1992 resulted in annual rainfall of 233 mm and 229 mm, respectively. In 1993 and 1994 annual rainfall was below average (77 mm and 35 mm, respectively). Consequently, this study was carried out during 2 rainy (1991-1992) and 2 dry (1993-1994) years. Because many arid zone small mammals obtain much or most of their water from plant foods, and precipitation leads to increased green plant growth, which increases environmental water availability to consumers, we predict that: 1) during rainy years, the water economy of rodents in the field will have a marked, seasonal rhythm, presenting moderate Uosm values during the dry seasons (late spring and summer); 2) during dry years, the seasonal, cyclic rhythm will tend to disappear and/or will show evidence of higher levels of water economy (i.e., comparably higher Uosm-values) year round (Cortés et al., 2000) and finally, 3) water balance will be modulated and synchronized by rainfall and consequently primary production, associated with cycles of ENSO events.

MATERIAL AND METHODS

We conducted our study in the Quebrada de Las Vacas (30°38′ S, 71°40′ W, 240 m elevation), in Fray Jorge National Park; Fray Jorge is located along the coast of north-central Chile, 100 km south of La Serena and 400 km north of Santiago. The climate is Mediterranean, and the plant community is characterized by spiny drought-deciduous and evergreen shrubs, 2-3 m in height, with a herbaceous understory. This community has been termed the *Porlieria chilensis-Adesmia bedwellii-Proustia pungens* association (Muñoz and Pisano, 1947). A complete account of the biotic and abiotic conditions of study site is provided by Meserve et al. (2003).

Live trapping of the rodents A. *olivaceus* (*N* = 285 from Autumn 1991 to Spring 1994), *A. longipilis* (*N* = 235 from Autumn 1991 to Summer 1995), *P. darwini* (*N* = 219 from Autumn 1991 to Summer 1995), and *O. longicaudatus* (*N* = 59 from Autumn 1991 to Summer 1994) was conducted using standard (75 x 85 x 240 mm) Sherman traps, placed in two 3 x 10 grids, with 2 traps per station at 10 m intervals. The entire trapping area encompassed 0.30 ha, with adjacent 5 m border strips. Trapping was carried out for 5 consecutive days, using oatmeal as bait. Traps were set near sunset, and checked approximately every 90 minutes until sunrise, minimizing the time that rodents spent in traps. We recognize that factors such as ambient temperature and moisture in the trap may influence the water budget; nonetheless, we made every feasible effort to maintain similar conditions during all our field seasons. All captured rodents were uniquely marked with an ear tag to avoid duplication of urine samples during seasonal sampling.

Urine samples were collected in microhematocrit tubes, which were sealed with parafilm and measured within one hour after collection. All measurements were taken in the field, and urine was collected directly from the genitalia. We measured the total concentration of solids (S = g/100g) in the urine samples, using a field refractometer AO TS Meter/Scientific Instruments (Scientific Instruments) following Cortés and Rosenmann (1989). These data allowed us to estimate urine osmolality as Uosm (mOsm/kg) = 140 $S^{0.984}$ (Cortés and Rosenmann, 1989). Our refractometer measurements (urine samples) were calibrated against a freezing-point osmometer (Advanced Instruments, MA, USA). Previous Uosm values over a single year were presented for *P. darwini* by Gallardo et al. (2005).

All statistical analyses were conducted using S-plus (2000). We evaluated the effects of year and season on the Uosm values of each species using a 2-way analysis of variance (ANOVA). To determine which treatments were significantly different, we utilized the post hoc Tukey test for multiple comparisons. We implemented these comparisons using the *best.fast* command in S-Plus (2000); this method uses the smallest critical point among all the valid methods. Values are listed as means ± 1 SD.

RESULTS

For all 4 species, Uosm-values were greatest in summer and during dry years, reflecting increased water economy at these times (Fig. 1). Interestingly, the magnitudes of these high Uosm-values equalled only 71.0 – 80.7% of the maximum capacity for concentration measured under laboratory conditions (Bozinovic et al., 1995).

All 4 rodent species showed important temporal fluctuations in their Uosm-values, indicating seasonal and inter-annual patterns of physiological variability (Fig. 1). Nevertheless, there were some subtle interspecific differences in seasonal water economy dynamics; specifically, *Phyllotis* retained a stronger seasonal pattern of urine osmolality during drier years than do the other murid rodents at this site, although there was some evidence for convergence after extended drought. During wet years 3 murid species (*A. olivaceus*, *O. longicaudatus*, and *A. longipilis*) exhibited clear seasonal changes in Uosm values (Fig. 1); these were low during autumn and winter (similar to values measured under standard laboratory conditions where food and water are provided *ad libitum*; Bozinovic et al., 1995), but increased in spring and summer (i.e., dry seasons), indicating an increase in water economy due to low environmental water availability (Fig. 1). The seasonal rhythm of water balance for these species tended to disappear during the dry years of 1993-1994, however, which we interpret as indicative of a higher water economy in response to more extreme physiological conditions as perceived by these species.

The seasonal pattern of *Phyllotis*, however, evidently was less markedly impacted by changes in moisture availability. During wet years (1991-1992) this species showed a clear seasonal pattern of water economy, characterized by high Uosm-values during spring-summer and low Uosm-values during autumn-winter. However, during dry

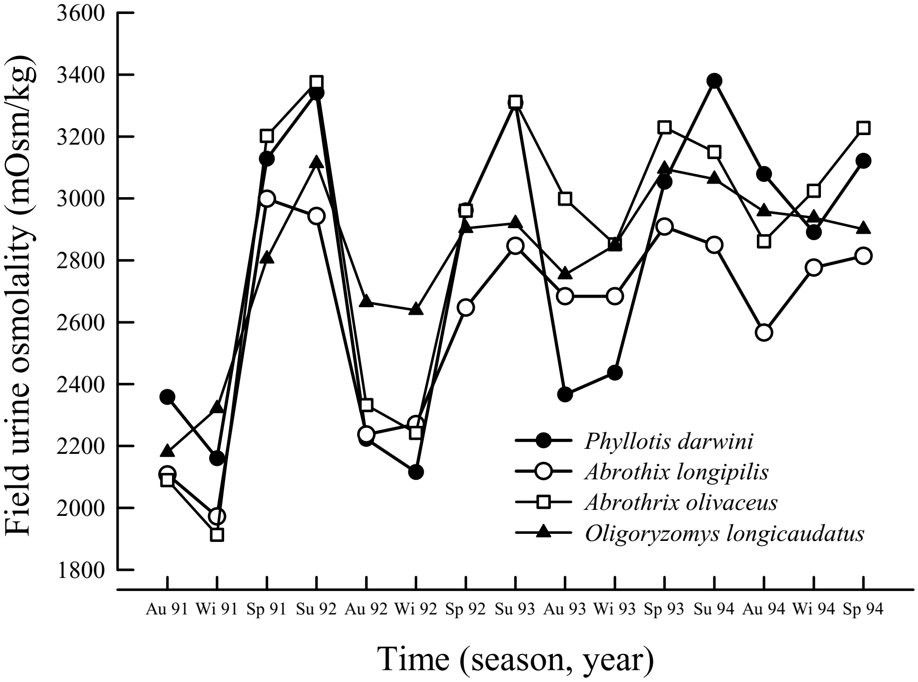

Figure 1. Long term dynamics of field urine osmolality of murid rodents at the semi-arid Fray Jorge National Park. This field study was carried out during 2 rainy, ENSO years (1991-1992) and 2 dry years (1993-1994). Au = autumn, Wi = winter, Sp = spring, and Su = summer.

years (1993-1994) there was an increase in the Uosm-values for autumn-winter, while spring-summer values remained similar to previous years (Fig. 1). Interestingly, however, in winter 1994, after over a year of relative drought, *Phyllotis* appeared to converge on the other rodent species, exhibiting higher urine osmolality even during the more mesic winter season (Fig. 1).

While we observed significant effects of year and season on Uosm-values in *P. darwini*, the year x season interaction was only marginally significant (Table 1). Multiple comparisons showed that spring had significantly higher Uosm-values than autumn and winter ($p < 0.01$), and summer Uosm-values were higher than all other seasons ($p < 0.001$). During 1994 Uosm-values for this species were significantly higher than during other years (1991-1993; $p < 0.01$). The interaction plot (Fig. 2A) shows that Uosm-values were very similar in autumn and winter. Summer values declined from 1991 to 1993, but then increased in 1994, while spring values declined greatly from 1991 to 1992, followed by an increase in 1993, and a slight decline in 1994.

As seen for *P. darwini*, we also observed a significant effect of year, season, and the year x season interaction on Uosm-values for *A. olivaceus* (Table 1). *A posteriori* multiple comparisons showed that spring Uosm-values were significantly higher than both autumn and winter Uosm-values (both $p < 0.01$), and significantly lower than summer values ($p < 0.01$). Furthermore, during 1993 and 1994 Uosm-values for this species were significantly higher ($p < 0.001$) than during other years (1991-1992). The interaction plot

Table 1. Results from the 2-way ANOVA of field urine osmolality for different rodent species inhabiting the semi-arid habitat of Fray Jorge National Park, northern Chile. The residuals serve as expected mean square for all analyses.

Effects/Source of Variation	*d.f.*	*F*-value	*p*
Phyllotis darwini			
Season	3	158.55	< 0.0001
Year	3	3.98	0.0093
Season x year	9	3.49	0.0600
Residuals	134		
Abrothrix olivaceus			
Season	3	76.77	<0.0001
Year	3	14.10	<0.0001
Season x year	8	6.81	<0.0001
Residuals	270		
Oligoryzomys longicaudatus			
Season	3	8.47	0.0002
Year	3	9.39	0.0007
Season x year	8	2.65	0.0180
Residuals	204		
Abrothrix longipilis			
Season	3	38.39	<0.0001
Year	3	20.33	<0.0001
Season x year	9	7.12	<0.0001
Residuals	219		

(Fig. 2B) indicates that autumn and winter Uosm-values tended to increase in parallel throughout the study. In contrast, spring values showed a significant increase during only the driest year (1994), and summer values declined from 1991 to 1993 (we failed to capture any of this species in summer 1994).

Patterns in *O. longicaudatus* were similar to the 2 previous species, with a significant effect of year, season, and the year x season interaction on Uosm-values (Table 1). Post-hoc multiple comparisons showed that spring and summer presented significantly higher Uosm-values than autumn and winter ($p < 0.01$), and summer values were significantly higher than spring ($p < 0.001$). The effect of year appears to be the result of higher Uosm-values during 1993 than during 1991, and during 1994 Uosm-values were significantly higher than during the other years (1991-1993; $p < 0.01$). The interaction

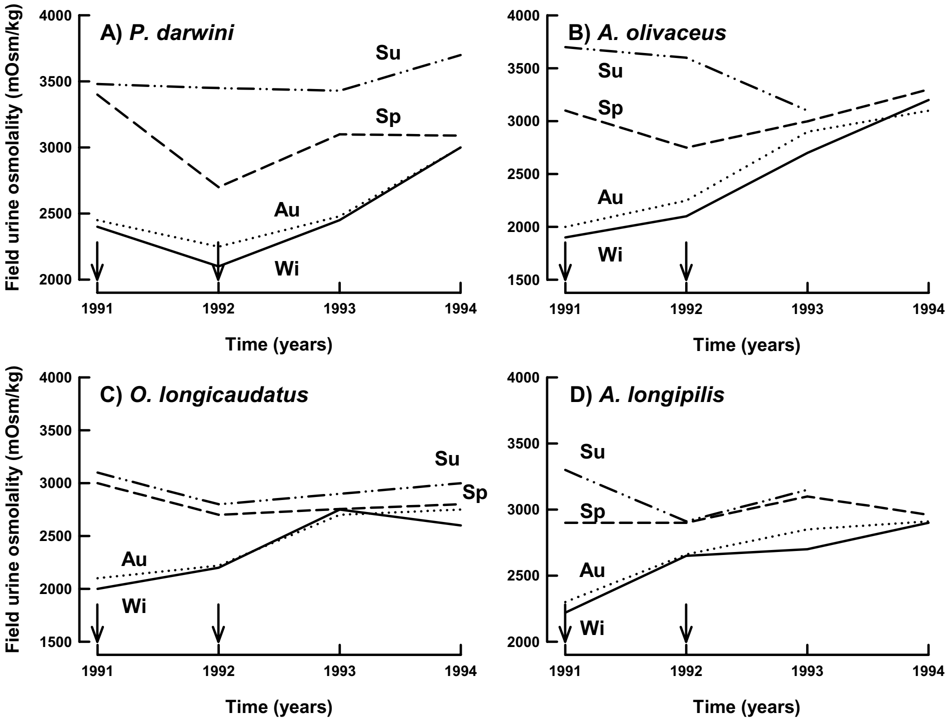

Figure 2. Interaction plots of field urine osmolality between seasons (lines) and years (x-axes) for 4 species of small mammals at the semi-arid Fray Jorge National Park. A) *Phyllotis darwini*, B) *Abrothrix olivaceus*, C) *Oligoryzomys longicaudatus*, and D) *Abrothrix longipilis*. Arrows indicate rainy years. Su = summer, Sp = spring, Au = autumn, and Wi = winter. Vertical arrows indicate rainy years (1991 and 1992)

plot (Fig. 2C) shows that Uosm-values for autumn and winter increased from 1991 to 1993, and declined in 1994. Summer and spring Uosm-values declined from 1991 to 1992 but then remained essentially stable in spring, while increasing slightly in summer.

Finally, *Abrothrix longipilis* also presented a significant effect of year, season, and the year x season interaction term on Uosm-values (Table 1). Multiple comparisons showed that Uosm-values were higher spring and summer than autumn and winter (all p values < 0.01). The significant effect of year appears to be the result of higher Uosm-values during the dry years of 1993 and 1994 than during the wet years of 1991 and 1992. The interaction plot (Fig. 2D) shows that autumn and winter Uosm-values tended to increase from 1991 to 1992 and then more gradually through 1994. In contrast, spring values fluctuated but showed no clear trajectory, and summer values declined from 1991 to 1992, then increased again in 1993; we failed to capture any of this species in summer 1994.

DISCUSSION

Rodents from arid and semi-arid habitats live under conditions where the spatial and temporal availability of free water is limited. Consequently, these species are faced with the problem of water conservation. The response of rodents to unproductive desert environments and water deficits has been intensively investigated in many deserts of the world. However, current understanding of the cellular, systemic and organismal physiology of water economy relies heavily on short-term, laboratory-oriented experiments, which usually focus on responses at isolated levels of biological organization.

Nevertheless, the mechanistic basis of these patterns likely involves seasonal variations in water flux rates as demonstrated by Bozinovic et al. (2003). In addition membrane water channels or aquaporins are more abundant in the kidney cells during summer than during winter (Bozinovic et al., 2003, Gallardo et al., 2005). Several aquaporins are involved in water reabsorption along the renal tubule. Aquaporin-1 is extremely abundant in apical and basolateral membranes of proximal tubule and thin descending loop of Henle. Recently, Gallardo et al. (2005) examined the phenotypic flexibility of field urine osmolality in response to seasonal rainfalls and the experimental expression of renal aquaporins in the leaf-eared mouse *P. darwini*. These authors reported that field urine osmolality was higher in summer than during winter. During the rainy year field urine osmolality in winter was nearly 2,100 mOsm/kg while the mean winter U value of the dry year was 2,600 mOsm/kg. During summer the mean field urine osmolality during the rainy year was 3,321 ± 71.5 mOsm/kg and 3,600 mOsm/kg during the dry year. Nevertheless, dehydration induced an increase in aquaporin protein amount compared to controls and water loaded condition. We hypothesized that the same mechanism is acting in the species of rodents studied here allowing desert rodents to cope with seasonal and yearly water availability in arid habitats.

Thus, the integration of a variety of flexible mechanisms that act at cellular, systemic, and organismal levels allow small mammals in arid regions to cope with seasonal and annual water variability in their semi-arid habitat. The seasonal, cyclic rhythm of the water economy observed in our study of rodents in semi-arid Chile during wet years is consistent with that observed for North American desert heteromyids, such as *Dipodomys merriami*, *Perognathus longimembris*, and *P. fallax* (MacMillen, 1972; MacMillen and Grubbs, 1976).

The seasonal trends in water balance during wet vs. dry years likely are at least partly a function of plant cover, since this is an important food and water source for rodents at Fray Jorge but also may lead to increased ambient humidity (Meserve, 1981; Bozinovic et al., 2003). The abundance and productivity of plants in the semi-arid, Mediterranean environments of north-central Chile are determined by the amount of rainfall (Gutiérrez et al., 1993; Gutiérrez, 2001), which is highly variable both between and within years (di Castri and Hajek, 1976). The response of vegetation to increased pulses of water is very fast (e.g., days to weeks), especially for annual species. In contrast, both small mammals (Meserve et al., 1995, 1999) and predators (Jaksic et al., 1997) exhibit delayed responses to pulses of primary productivity at the study site. This study (see also Bozinovic et al., 2003) demonstrates that precipitation and primary productivity influence the population dynamics of small mammals at a relatively longer temporal scale, in comparison to the more rapid responses observed in physiological acclimatization. Finally, the population dynamics and demography of small mammals and predators in semi-arid Chile is positively correlated with rainfall, which is further correlated with El Niño events (Lima et al., 1999, 2002). Indeed, in our study some species exhibited dramatic fluctuations in their water economy, which were caused by a climatic effect, which, at the same time, may be a product of physiological constraints. This study illustrates that long-term field studies are necessary to fully elucidate the relationship between physiological conditions and precipitation, and to determine the long-term acclimatization responses because of the high between- and within-year variability of rainfall.

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LITERATURE CITED

Aceituno, P.
1992 El Niño, the Southern Oscillation, and ENSO: Confusing names for a complex ocean-atmosphere interaction. Bulletin of the American Meteorological Society 73:483-485.

Bozinovic, F., and P. Gallardo
2006 The water economy of South American desert rodents: from integrative to molecular physiological ecology. Comparative Biochemistry and Physiology C 142:163-172.

Bozinovic, F., P. A. Gallardo, R. H. Visser, and A. Cortés
2003 Seasonal acclimatization in water flux rate, urine osmolality and kidney water channels in free-living degus: molecular mechanisms, physiological processes and ecological implications. Journal of Experimental Biology 206:2959-2966.

Bozinovic, F., M. Rosenmann, F. F. Novoa and R. G. Medel
1995 Mediterranean-type of climatic adaptation in the physiological ecology of rodent species. Pp. 347-362 in Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia (Kalin-Arroyo, M. T., P. H. Zedler, and M. D. Fox, eds.). Springer-Verlag, New York, New York, USA.

Cortés, A., C. Pino, and M. Rosenmann
1994 Balance hídrico del ensamble de micromamíferos de dos localidades de la región mediterránea árida del norte de Chile central: un estudio de campo. Revista Chilena de Historia Natural 67:65-77.

Cortés, A., and M. Rosenmann
1989 A field lab method to determine urine concentration in small mammals. Comparative Biochemistry and Physiology 94A:261-262.

Cortés, A., M. Rosenmann, and F. Bozinovic
2000 Water economy in rodents: evaporative water loss and metabolic water production. Revista Chilena de Historia Natural 73:311-321.

Degen, A. A.
1997 Ecophysiology of Small Desert Mammals. Springer-Verlag, Berlin, Gemrany. 296 pp.

di Castri, F., and E. R. Hajek
1976 Bioclimatología de Chile. Santiago: Editorial Universidad Católica de Chile. 166 pp.

Gallardo, P. A., A. Cortes, and F. Bozinovic
2005 Phenotypic flexibility at the molecular and organismal level allows desert-dwelling rodent to cope with seasonal water availability. Physiological and Biochemical Zoology 78:145-152

Gutiérrez, J. R.
2001 Dynamics of ephemeral plants in the coastal desert of north-central Chile. Pp. 105-124 in Ecology of Desert Environments (Prakash, I., ed.). Zoological Survey of India, Jodhpur, India.

Gutiérrez, J. R., P. L. Meserve, F. M Jaksic, L. C. Contreras, S. Herrera, and H. Vásquez
1993 Structure and dynamics of vegetation in a Chilean semiarid thorn-scrub community. Acta Oecologica 14:271-285.

Huey, R. B., and D. Berrigan
1996 Testing evolutionary hypotheses of acclimation. Pp. 205-237 in Animals and Temperature. Phenotypic and Evolutionary Adaptation (Johnston, I. A., and A. F. Bennett, eds.). Society for Experimental Biology, Seminar Series: 59. Cambridge University Press, Cambridge, Massachusetts, USA.

Jaksic, F. M.
2001 Ecological effects of El Niño in terrestrial ecosystems of western South America. Ecography 24:241-250.

Jaksic, F. M., S. I. Silva, P. L. Meserve, and J. R. Gutiérrez
1997 A long term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South American. Oikos 78:341-354.

Lima M., J. E. Keymer, and F. M. Jaksic
1999 ENSO-driven rainfall variability and delayed density-dependence cause rodent outbreaks in western South America: from demography to population dynamics. American Naturalist 153:476-491.

Lima M., N. C. Stenseth, and F. M. Jaksic
2002 Food web structure and climate effects in the dynamics of small mammals and owls in semiarid Chile. Ecology Letters 5:273-284.

MacMillen, R. E.
1972 Water economy of nocturnal desert rodents. Pp 147-174 in Comparative Physiology of Desert Animals (Maloiy, G. M. O., ed.). Symposium of the Zoological Society of London 31.

MacMillen, R. E., and D. E. Grubbs
1976 The effects of temperature on water metabolism of rodents. Pp. 63-69 in Progress in Animal Biometeorology (Johnson, H. D., ed.). Swets and Zeitlinger, The Hague, The Netherlands.

McNab, B. K.
2002 The physiological ecology of vertebrates: A view from energetics. Cornell University Press, Cornell, New York, USA. 576 pp.

Meserve, P. L.
1981 Trophic relationships among small mammals in Chilean semiarid thorn scrub community. Journal of Mammalogy 62:304-314.

Meserve, P. L., D. A. Kelt, W. B. Milstead, and J. R. Gutiérrez
2003 Thirteen years of shifting "top-down" and "bottom-up" control. BioScience 53:633-646.

Meserve, P. L., W. B. Milstead, J. R. Gutiérrez, and F. M. Jaksic
1999 The interplay of biotic and abiotic factors in semiarid Chilean mammal assemblage: results of a long-term experiment. Oikos 85:362-372.

Meserve, P. L., J. A. Yunger, J. R. Gutiérrez, L. C. Contreras, W. B. Milstead, B. K. Lang, K L. Cramer, S. Herrera, V. O. Lagos, S. I. Silva, E. L. Tabilo, M. Torrealba, and F. M. Jaksic
1995 Heterogeneous responses of small mammals to an El Niño southern oscillation event in northcentral semiarid Chile and the importance of ecological scale. Journal of Mammalogy 76:580-595.

Muñoz, C.P., and E.V. Pisano
1947 Estudio de la vegetación y flora de los parques nacionales de Fray Jorge y Talinay. Agricultura Técnica (Chile) 7:71-190.

Pearson, O. P, and M. F. Smith
1999 Genetic similarity between *Akodon olivaceus* and *Akodon xanthorhinus* (Rodentia: Muridae) in Argentina. Journal of Zoology 247:43-52

Schmidt-Nielsen, K.
1964 Desert Animals: Physiological Problems of Heat and Water. Dover Publications, Inc., New York, New York, USA. 277 pp.

Smith, M. F. and J. L. Patton
1993 The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. Biological Journal of the Linnean Society 50:149-17

S-Plus
2000 Guide to Statistics. Volume 1. Data Analysis Products Division, MathSoft, Seattle, Washington, USA.

Trenberth, K. E.
1997 The definition of El Niño. Bulletin of the American Meteorological Society 78:2771-2777.

Walsberg, G.
2000 Small mammals in hot deserts: some generalizations revisited. BioScience 50:109-120.

Willmer, P., G. Stone, and I. Johnston
2000 Environmental Physiology of Animals. Blackwell Science, Oxford, UK. 644 pp.

RATADA 2001: A RODENT OUTBREAK FOLLOWING THE FLOWERING OF BAMBOO (*CHUSQUEA CULEOU*) IN SOUTHWESTERN ARGENTINA

RATADA 2001: UNA IRRUPCIÓN DE ROEDORES SIGUIENDO AL FLORECIMIENTO DE BAMBÚ (*CHUSQUEA CULEOU*) EN EL SUROESTE DE LA ARGENTINA

Richard D. Sage, Oliver P. Pearson[1], Javier Sanguinetti, and Anita K. Pearson

ABSTRACT

In spring of 2000, *Chusquea culeou* bamboo, the dominant understory plant in Valdivian forest habitat in southwestern Argentina, flowered over a latitudinal range of 100 km and produced a massive amount of seed. Reproductive activity of rodents in the area continued into the subsequent autumn and winter, when rodent numbers reached peak levels and large numbers of drowned rodents appeared on beaches. Owls and foxes reached high numbers, and the mean age in populations of *Oligoryzomys longicaudatus* and *Abrothrix longipilis* declined. In the following (second) spring, reproduction was delayed or suppressed, and by the following (second) autumn populations had declined to unusually low levels. By the third year after the flowering, rodent numbers had returned to levels characteristic of populations in this area.

Oligoryzomys longicaudatus, *Abrothrix longipilis*, *Loxodontomys micropus*, I*renomys tarsalis*, and the introduced *Rattus rattus* increased in numbers following the bamboo bloom; numbers of *Chelemys macronyx* and *Geoxus valdivianus*, species that eat invertebrates, were not affected. These observations strongly imply that the abundance of bamboo seed caused this outbreak, and suggest that food availability is the main factor limiting numbers of rodents in these forests.

Key words. Argentina, bamboo, mast seeding, rodents, population regulation, outbreaks, reproduction, emigration, mortality, obesity, *Chusquea culeou*, *Oligoryzomys*, *Abrothrix*, *Loxodontomys*, *Rattus*, *Irenomys*, *Chelemys*, *Geoxus*.

RESUMEN

Durante la primavera de 2000, la caña *Chusquea culeou*, la planta dominante del sotobosque de los bosques Valdivianos del sudoeste de Argentina, floreció a lo largo

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de un rango latitudinal de 100 km produciendo una gran cantidad de semillas. En el área, la actividad reproductiva de los roedores continuó durante el otoño e invierno siguientes, cuando el número de roedores alcanzó el nivel máximo y una gran cantidad de individuos aparecieron ahogados en las costas de los lagos. El número de zorros y lechuzas aumentó considerablemente, y la edad promedio en poblaciones de *Oligoryzomys longicaudatus* y *Abrothrix longipilis* disminuyó. En la siguiente (segunda) primavera, la reproducción estuvo retrasada o suprimida, y durante el siguiente (segundo) otoño las poblaciones disminuyeron a niveles inusualmente bajos. Para el tercer año luego de la floración, el número de roedores retomó sus valores característicos para las poblaciones de esta área.

Oligoryzomys longicaudatus, *Abrothrix longipilis*, *Loxodontomys micropus*, *Irenomys tarsalis*, y la introducida *Rattus rattus* aumentaron sus números poblacionales luego de la floración masiva de la caña; mientras que para *Chelemys macronyx* y *Geoxus valdivianus*, especies que comen invertebrados, no hubo cambios. Estas observaciones fuertemente implican que la abundancia de semillas de caña fue la causa de la ratada, y sugieren que la disponibilidad de alimento es el factor principal que limita el número de roedores en estos bosques.

Palabras claves. Argentina, caña, semillazón masiva, roedores, regulación poblacional, ratada, reproducción, emigración, mortalidad, obesidad, *Chusquea culeou*, *Oligoryzomys*, *Abrothrix*, *Loxodontomys*, *Rattus*, *Irenomys*, *Chelemys*, *Geoxus*.

INTRODUCTION

Valdivian temperate rainforest dominated by *Nothofagus* trees is a major habitat in southwestern South America (Dimitri, 1959; Veblen et al., 1983, 1996; Wilcox, 1996). Primary understory plants in these forests are bamboos of the genus *Chusquea*, and in Argentine forests the predominant bamboo species is *Chusquea culeou* (E. Desvaux in Gay, 1853). After a long period of vegetative growth, *C. culeou* flowers once, sets seed, and dies. Nearly all bamboo plants in an area flower synchronously, resulting in production of a massive amount of seed and a population explosion among local granivorous rodents. Such outbreaks of mice have been reported from Chile, from other parts of South America, and from Asia, following the gregarious flowering of different species of bamboos (Gunkel, 1948; Seal et al., 1951; Tanaka, 1956, 1957; Janzen, 1976; Murúa et al., 1996; Gallardo and Mercado, 1999). A recent review emphasized our poor understanding of these events (Jaksic and Lima, 2003).

In spring of 2000 a population of *C. culeou* flowered and set seed over a north-south distance of 100 km and east-west distance of 80 km in adjacent parts of Argentina and Chile (Anonymous, 2001a, 2001b; Sanguinetti and García, 2001). The main goal of this paper is to describe the changes in numbers, reproductive behavior, age structure, movements, and mortality of rodent species during this outbreak. In addition, we compare these results with the behavior of these same species from forests where the bamboo remained in the vegetative (green) phase of the life cycle, and suggest what information will be needed for a more predictive understanding of bamboo-induced outbreaks in these forests. Two reports on the responses of rodents to a synchronous flowering of bamboo in Chilean forests (Murúa et al., 1996; Gallardo and Mercado,

1999) involved a different species of *Chusquea*. This is the first analysis of an outbreak in which *C. culeou* is the flowering bamboo species.

MATERIALS AND METHODS

Study Sites and Terminology

Our study area is within Valdivian rainforests along the western border of Argentina, between 39° 52′ S and 40° 35′ S latitude and within the boundaries of Parque Nacional Lanín. The largest town in the area is San Martín de Los Andes (Fig. 1). We collected

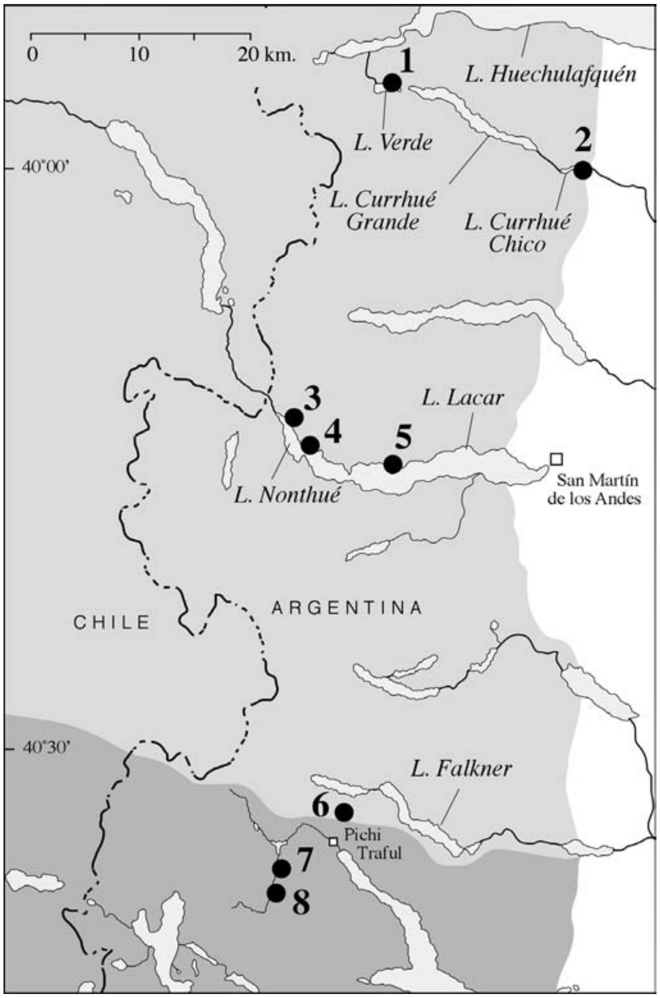

Figure 1. Map showing the area where *Chusquea culeou* bloomed (light stipple) and where it did not (dark stipple) in the western area of Neuquén Province, Argentina, and adjacent parts of Chile. Numbers indicate collection localities.

mice at 8 places and in 2 types of bamboo habitat (Table 1). Six localities (localities 1 – 6) were in the area where a high percentage of bamboo plants flowered (Sanguinetti and García, 2001), and these sites are considered as the flowered-bamboo habitat. The bamboo remained in the vegetative stage at the other 2 localities (localities 7, 8), and these are treated as the green-bamboo habitat. Thus we use 6 replicates for flowered-bamboo and 2 replicates for green-bamboo habitat scores to test for differences between habitat types. While vegetation conditions at the green-bamboo localities contrasted with those where the bamboo flowered, they resembled conditions of baseline rodent populations described by Pearson (2002).

We number the seasons and years of study sequentially, starting from the time the bamboo flowered; thus, Spring-1 corresponds to September through November, 2000, the first year of our study. Seasons in this part of Argentina are: September to November (spring), December to February (summer), March to May (autumn), and June to August (winter).

Trapping Methods, Collections, and Autopsies

We made 5 collections over 3 years; these included Spring-1 (17-22 November 2000), Autumn-1 (29 April – 6 May 2001), Spring-2 (12–24 October 2001), Autumn-2 (3-14 May, 2002), and late Autumn-3 (19 May – 4 June 2003). No samples were taken during Spring-3. We sampled Currhué Chico and Hua Hum during all 5 periods, and Yuco, Traful North, Traful South-1, and Traful South-2 during 3 periods; additionally, we have single collections from Laguna Verde (based on traps) and Lago Nonthué (drowned mice picked up by JS on one day in Spring-2, along a 100-m stretch of beach).

Traplines were set for up to 3 consecutive nights in an area, with 5 to 59 traps per line (Appendix Table 1). Traps were set in late afternoon, picked up the following morning, and reset in a different place that afternoon. Traplines were set in nearly the same places in successive collecting periods. Trap success was calculated as the number of mice caught divided by the number of traps on a trapline, without correcting for traps that were closed and without a mouse. Because traps were moved daily, we treat each nightly trapline as an independent replicate for estimating density by means of trap success for a particular locality, between the 2 habitat types, and among collecting periods. Our measures of trap success were based only on results from live traps (7.5 x 9 x 22.5 cm, Model LFA, H. B. Sherman Traps, Inc.), because only live traps were used during the Autumn-2 collecting period. In other trapping periods we alternately set folding aluminum live traps and Museum Special kill traps (Woodstream Corporation). Traps were baited with a mixture of oat and corn meal and set 5 m apart. A small number of animals were caught in wire mesh live traps (41 x 13 x 13 cm, Model TLT201, Tomahawk Live Trap Co.) and number 0 jump traps (Oneida Victor Co.). During the last 4 trapping periods we also set Sherman traps in standing bamboo, 1– 2.5 m aboveground. These arboreal traps were taped onto thick single canes or groups of smaller canes that were at an approximately horizontal angle, and baited like those on the ground. They were left in place for up to 3 days. Arboreal trap success was calculated separately from the terrestrial trap success described above, and differed somewhat as an index measure because many of the trap nights involved the same trap set in the same place for 2 or 3 nights.

Mice were killed by cervical dislocation, with carbon dioxide, or with an overdose of sodium pentobarbital. All trapped mice were weighed, measured for body length

Table 1. Collecting localities in Neuquén Province, Argentina. General locality names are used throughout the text.

Loc. No.	General Name	Location	Habitat Description	Bamboo Condition
1	Laguna Verde	West of Lago Currhué Grande [71°31′00″W; 39°50′20″S], 1000 m el.	Bamboo in *Nothofagus dombeyi*/*N. obliqua* forest	Flowered
2	Currhué Chico	Around eastern end of Lago Currhué Chico[71°20′00″W; 39°54′20″S], 1050 m el.	Bamboo in *N. antarctica* woodland, and an adjacent grassland	" "
3	Hua Hum	3 km ESE of Seccional Hua Hum [71°38′30″W; 40°8′30″S], 650 m el.	Bamboo in *N. dombeyi*/*N. obliqua* forest	" "
4	Lago Nonthué	Along shoreline of Lago Nonthué, [71°37′30″W; 40°9′10″S], 650 m el.	Dead on beach	" "
5	Yuco	Seccional Yuco [71°31′30″W; 40°10′15″S], 650 m el.	Bamboo in *N. dombeyi*/ *N. obliqua* forest	" "
6	Traful North	3.3 km N, 0.8 km E of jct. Ruta 234 with Río Pichi Traful [71°35′20″W; 40°28′40″S], 950 m el.	Bamboo in *N. dombeyi* forest	Limited flowering
7	Traful South-1	4.6 km S, 5.5 km W of jct. Ruta 234 with Río Pichi Traful [71°39′50″W; 40°31′45″S], 900 m el.	" "	Green (did not flower)
8	Traful South-2	10.8 km S, 5.7 km W of jct. Ruta 234 with Río Pichi Traful [71°39′50″W; 40°34′50″S], 900 m el.	" "	" "

(head and trunk), and examined for tail scars or torn ears. We recorded the presence/absence of scars on the tails and ears of many of the animals. Tail scarring was recorded from nearly all trapped animals, but could not be scored on the drowned mice from Lago Nonthué because the condition of the tail skin on many of the specimens was not good enough to see scars. Tears and holes in the ears remained visible in most of the drowned mice, and we scored ear damage in these and other mice trapped in Spring-2. Upon dissection, the length of a testis was measured, the widths and/or presence of scars in the uteri, and the numbers and lengths (crown-rump length, CRL) of embryos were recorded. Females with enlarged nipples with milk were considered as reproductively active. The amount of intra-abdominal fat was scored with a qualitative index: 0 = small amounts of fat that was restricted to the gonads; 1 = enlarged gonadal fat pads; 2 = enlarged gonadal and mesenteric fat pads; 3 = enlarged pads as well as fat covering the heart and kidneys. In addition to saving the skulls, carcasses from the final 3 collections were preserved in 10% neutral-buffered formalin. Dried tissue was cleaned from the skulls using dermestid beetles. One specimen was donated to the Universidad Nacional del Comahue, S. C. de Bariloche, and the remains of 20 other specimens were lost in the field. All other specimens have been deposited in the Museum of Vertebrate Zoology, University of California, Berkeley, California, USA. The MVZ catalogue numbers for these specimens are: 196312 – 196352, 196841 – 197031, 198850 – 199133, 199656 – 199735, 201039 – 201073, 201079 – 201091, 201109 – 201191, 201193 – 201198, 201201 – 201202.

Age of *Oligoryzomys longicaudatus* and *Abrothrix longipilis* specimens was determined from cusp measurements on molar teeth, as described by Pearson (1975, 1992). Using a video microscope (USB Microscope M2™, Scalar Corp., Tokyo), cusp heights were measured from images on the video screen, corrected for magnification, and grouped into 5 age-class intervals. The intervals (0.10 mm/interval in *Oligoryzomys* and 0.16 mm/interval in *A. longipilis*) were then used to define the 5 age-classes, numbered in order of declining cusp height. Thus age class-1 are young animals with tall cusps and age class-5 are old animals with short cusps.

Rodent Fauna

We collected specimens of 8 species identified as members of the native rodent community in these forests (Pearson, 1983): these included (in descending order of abundance) *Oligoryzomys longicaudatus*, *Abrothrix longipilis*, *A. olivaceus*, *Loxodontomys micropus*, *Irenomys tarsalis*, *Geoxus valdivianus*, *Chelemys macronyx*, and *Aconaemys porteri*. In addition we caught specimens of *Octodon bridgesii*, *Phyllotis xanthopygus*, *Reithrodon auritus*, and the non-native *Rattus rattus*. Many aspects of the life histories of the native species in forests with a mature but non-flowering bamboo understory are known (Pearson and Pearson, 1982; Pearson, 1983, 2002; Murúa and González, 1986; Murúa et al., 1986, 1987, 1996; Patterson et al., 1989, 1990; Kelt, 1994, 2000).

Analyses

Analyses were conducted with SPSS 11.0® (SPSS Inc., Chicago, IL), and included single- and 2-factor analysis of variance (ANOVA), analysis of covariance (ANCOVA), and Spearman rank correlation; results were considered significant at $p \leq 0.05$. Throughout the text we present mean values followed by standard errors. Analysis of variance and covariance were used to assess effects of independent variables. Darlington and Smulders (2001) discussed the statistical advantages of ANCOVA for studies of the 'condition' of animals. Cusp height (as a proxy variable for age) was treated as a covariate when testing for the effects of time or habitat on the response variables of interest. One output in the SPSS General Linear Model analysis is the least-squares means of the dependent variable adjusted for the covariance structure of the main effects and interactions. These adjusted means are presented throughout the text. When no mice were caught in a trapline (0% success) a 'dummy value' of 0.01 mice was entered.

RESULTS

General Patterns of Bamboo Flowering, Amounts of Seed, and Rodent Numbers

The length of the vegetative stage of the life cycle of *C. culeou* is not well established. The last major flowering in the area of our study was in 1938 (Sanguinetti and García, 2001), indicating a life span of 62 years for this population of *C. culeou*. When *C. culeou* flowered in Argentina in 2000, it also flowered in adjacent areas of Chile, as reported in the newspaper El Diario Austral de Valdivia (Anonymous, 2001a, 2001b). In Spring-1 an estimated 98% of bamboo plants in the study area were in bloom, with much pollen in evidence (Plate 1A). By late in Summer-1 (February, 2001) seeds had formed and were beginning to drop to the forest floor. In Autumn-1 seed fall was heavy and bamboo leaves were dead on the canes (Plate 1B). In Spring-2 there were still some seeds on the surface of the ground and many bamboo leaves had fallen. Seedlings were abundant. By Autumn-2 no seeds remained on the surface, the dead bamboo canes were leafless, and seedlings up to 20 cm tall were abundant. Seedlings remained abundant to the end of our study and the dead canes became increasingly brittle and sagged towards the ground.

To estimate the amount of bamboo seed available to rodents, we counted and weighed fertile seeds (caryopses) on 6 representative bamboo culms collected in Autumn-1. The 6 culms held an average of 6,799±3,143 [range 1,112 – 21,454] well-formed seeds, and the mean dry weight of an individual seed was 7.3±0.58 mg [5.4 - 9.3 mg]. Since there may be up to 120,000 live culms/ha in similarly dense bamboo habitat (Pearson et al., 1994), we estimate that as many as 81,000 fertile seeds/m^2, weighing up to 0.59 kg may have been available to animals in bamboo thickets at this time.

By Summer-1, rodents were noticeably abundant. Forest residents reported that their cats and dogs started bringing mice into their homes. During our visit in Autumn-1 we saw rodents in the afternoon while setting traps, caught them within minutes of setting the traps, and watched many active animals in the bamboo thickets at night. Later in Autumn-1, rodents began to enter houses and outbuildings. A family living near Hua Hum abandoned their home in Winter-1 because the number of mice indoors became intolerable (Monica Sosa, pers. comm.). Rodents were still abundant in Spring-2, and carcasses washed up on the shores of lakes in the region by the thousands. But, at this time they were not as active in the forest as in Autumn-1. Unlike Autumn-1, no mice were observed while setting traps during the Autumn-2 and Autumn-3 collecting periods.

Species Abundances

A total of 757 animals were collected. *Oligoryzomys* was the most abundant species collected, forming 41% of the total collection, followed by *A. longipilis* (29%), *A. olivaceus* (13%), *Loxodontomys* (9%), *Rattus* (3%), *Irenomys* (1.5%), *Geoxus* (1.2%), and *Chelemys* (0.9%). *Oligoryzomys* and *A. longipilis* were the only species collected at all sites. Ten specimens (5 *Aconaemys porteri*, 3 *Octodon bridgesii*, 1 *Phyllotis xanthopygus*, and 1 *Reithrodon auritus*) will not be considered further because of limited captures and/or their atypical occurrence in the forest habitat (*Octodon*, *Phyllotis*, and *Reithrodon*). Numbers of all other species collected at each locality and in each period are listed in Appendix Table 2.

Plate 1. The bamboo understory on a hillside at the Hua Hum locality (A) in Spring 1 when the plants were alive and flowering and (B) after they had died in Autumn 1. Oliver P. Pearson in (A) and Anita K. Pearson in (B) for scale.

The relative abundances of the rodent species changed over time and habitat (Table 2). In the flowered bamboo habitat *Oligoryzomys* was 2-3 times more common than *A. longipilis* in 3 of the 5 collecting periods. Only during Autumn-1 and Autumn-3 did *A. longipilis* become as abundant as *Oligoryzomys*. In the green bamboo habitat *A. longipilis* was twice as abundant as *Oligoryzomys* in Autumn-2 and Autumn-3, but *Oligoryzomys* was the more common species in Spring-2. *Rattus* increased to its greatest relative abundance in the flowered bamboo during Autumn-2, when they composed one-quarter of all animals collected. At the same time *A. longipilis* declined in relative abundance while *Oligoryzomys* remained common. *Rattus* was not collected in Autumn-3. *Abrothrix olivaceus* was relatively uncommon (about 10% of the collection) in the flowered bamboo, but in Autumn-3 became equally as common (31%) as *Oligoryzomys* and *A. longipilis*; at the same time its abundance in the green bamboo habitat remained low (11%). The semifossorial taxa, *Geoxus* and *Chelemys*, remained uncommon in our traps in all periods and localities (Appendix Table 2).

Trap Success and Abundance

Overall trap success on the ground was 29% (546 animals during 1888 trap nights; Appendix Table 1). An ANOVA showed significant main effects of trap type ($F = 29$, $d.f. = 1, 78$, $p < 0.001$), collecting period ($F = 15$, $d.f. = 4, 78$, $p < 0.001$), and bamboo habitat

Table 2. Relative abundances of four rodent species, measured as the proportion of the total sample of mice trapped during each collecting period in flowered and green bamboo habitats, Neuquén Province, Argentina. Drowned mice from Lago Nonthué are not included in the calculations for the flowered bamboo habitat in Spring-2. Trapping in green bamboo habitats did not begin until Spring-2.

Collecting period	Sample size: Flowered/Green	*Oligoryzomys longicaudatus*		*Abrothrix longipilis*		*Abrothrix olivaceus*		*Rattus rattus*	
		Flowered	Green	Flowered	Green	Flowered	Green	Flowered	Green
Spring-1	41/--	0.71	--	0.22	--	0.02	--	0	--
Autumn-1	188/--	0.37	--	0.43	--	0.15	--	0.005	--
Spring-2	263/40	0.47	0.52	0.16	0.32	0.08	0.10	0.05	0
Autumn-2	43/35	0.49	0.26	0.16	0.49	0.07	0.14	0.26	0
Autumn-3	110/27	0.31	0.22	0.32	0.48	0.31	0.11	0	0

(*F* = 6.9, *d.f.* = 1, 78, $p = 0.01$) on trap success. In the same analysis two interaction effects were significant (both $p < 0.001$): trap x period (*F* = 14, *d.f.* = 3, 78) and period x bamboo (*F* = 8.7, *d.f.* = 2, 78). Mean trap success was lower with live than kill traps (0.26 ± 0.021 and 0.51 ± 0.025, respectively). Analysis using only results with live traps showed a highly significant main effect ($p < 0.001$) of collecting period (*F* = 7.8, *d.f.* = 4, 46) and of the period x bamboo interaction (*F* = 10, *d.f.* = 2, 46), but a non-significant effect ($p = 0.25$) for bamboo habitat alone (*F* = 1.4, *d.f.* = 1, 46).

In the flowered bamboo habitat trap success increased from spring to autumn in the first year (10% to 51%) but decreased over the same seasons in the second year (44% to 12%) (Table 3). The actual increase in density from Spring-1 to Autumn-1 was probably greater than 5-fold, since a deficiency of open traps probably limited the number of captures at each station. By Autumn-3, trap success had increased to 24%, which is close to autumn trap success in baseline populations (29.3%; Pearson, 2002). Trap success differed between green and flowered habitats. Whereas trap success in flowered bamboo habitats dropped from Spring-2 to Autumn-2, it increased from 23% to 34% during this period in the green bamboo woods. In Autumn-3, trap success was higher in the flowered (24%) than in the green (8%) bamboo habitat.

Drowning Rodents

A conspicuous feature of the outbreak was the large number of drowned rodents on lake shores. Residents and park rangers first noticed this during Winter-1. We observed drowned animals at Lago Nonthué (150 mice in 100 m of beach) and at Lago Currhué Grande (325 carcasses in 100 m) in Spring-2 (Plate 2A, B, and C). In mid-October, 2001, a man reported being within sight of drowned mice for most of the day as he sailed on 50 km-long Lago Lacar (pers. comm. to JS). At campsites and towns near lakes the drowned rodents caused considerable concern among both campers and civic leaders because of fears of infection with a hantavirus (Andes virus) that has caused fatalities in these areas (Baro et al., 1999; Calderon et al., 1999; Lazaro et al., 2000).

The drowned mice retrieved from the beach at Lago Nonthué differed in species composition from the rodents trapped in nearby woods (Table 4). *Oligoryzomys* was abundant in both collections. While *A. longipilis* was the second most abundant rodent

Table 3. Mean frequency of live-trap success in 54 trap lines over time and bamboo habitat. The values reported with means are standard errors, and the numbers of trap lines per collecting period/habitat are shown within parentheses. Trapping in green bamboo habitats did not begin until Spring-2.

Collecting period	Flowered bamboo	Green bamboo
Spring-1	0.10±0.061 (5)	--
Autumn-1	0.51±0.068 (4)	--
Spring-2	0.44±0.043 (10)	0.23±0.051 (7)
Autumn-2	0.12±0.043 (10)	0.34±0.068 (4)
Autmn-3	0.24±0.043 (10)	0.08±0.068 (4)

Plate 2. (A, B, C). Drowned rodents (mostly *O. longicaudatus*) along the western shore of Lago Currhué Grande in Neuquén Province, 16 October 2001. (D) Picking up drowned rodents from the beach at San Martín de Los Andes. The workers are wearing filter masks because of concern about possible infection with a hantavirus that occurs in one species of the drowned mice (*O. longicaudatus*).

Table 4. The percent species composition and numbers (in parentheses) of drowned mice picked up on the beach at Lago Nonthué compared to those trapped in the nearby woods at Hua Hum in the same (Spring-2) collecting period.

Species	Lago Nonthué	Hua Hum
Oligoryzomys longicaudatus	37 (43)	55 (40)
Abrothrix longipilis	1 (1)	38 (28)
Abrothrix olivaceus	3 (4)	1 (1)
Loxodontomys micropus	43 (50)	4 (3)
Rattus rattus	10 (12)	0
Irenomys tarsalis	6 (7)	0
Geoxus valdivianus	0	1 (1)
Totals	(117)	(73)

in the forest sample (39%), it was rare (1%) among the drowned mice. Conversely, *L. micropus* was abundant in the lake collection (42%) and rare in forest (4%) samples. Substantial numbers of *I. tarsalis* were present among the drowned animals (7%) but were not collected at all in the forest during the same time; similarly, *R. rattus* was present in the lake sample (10%) but absent in the nearby Hua Hum collection. However, mutilation of some snap-trapped rodents in Spring-2 at Hua Hum suggested that black rats were present at this trapping site.

Public health concerns about the drowned rodents prompted the municipal government of San Martín de Los Andes to remove the carcasses from their 400-m public beach every morning (Plate 2D). Between October, 2001 and February, 2002 the municipal workers picked up 11,245 mice, an average of 110 per day. Over this 4-month period there were noticeable declines in the number of animals retrieved in weeks 3, 7, and 12 (Fig. 2). Each of these declines were associated with full moon phases (in the middle of weeks 3 and 7, and the last night of week 11, thereby immediately preceding week 12). We conducted a stepwise multiple regression analysis on the relationship between the numbers of mice picked up each week (dependent variable) and two independent variables: (1) week number and (2) a proxy variable for the relative amount of moonlight during that week (0 for the new moon, 0.5 for first and last quarter moons, and 1 for the full moon phase). The best-fit regression [(number of mice picked up = 2227 – 129 (week) – 849 (moon phase)] was highly significant ($F = 22$, $d.f. = 2, 13$, $p < 0.001$). The time variable (week) explained most of the variation in numbers ($r^2 = 0.64$), but inclusion of lunar phase into the regression model significantly increased ($p = 0.02$) its explanatory power by 14% ($r^2 = 0.78$). Thus, fewer mice washed up on the beach in weeks when the nights were brightest. This could reflect reduced activity on bright nights; rodents in other systems are known to reduce their activity during the full moon (Price et al., 1984; Abramsky et al., 1990; Yunger et al., 2002; Kelt et al., 2004).

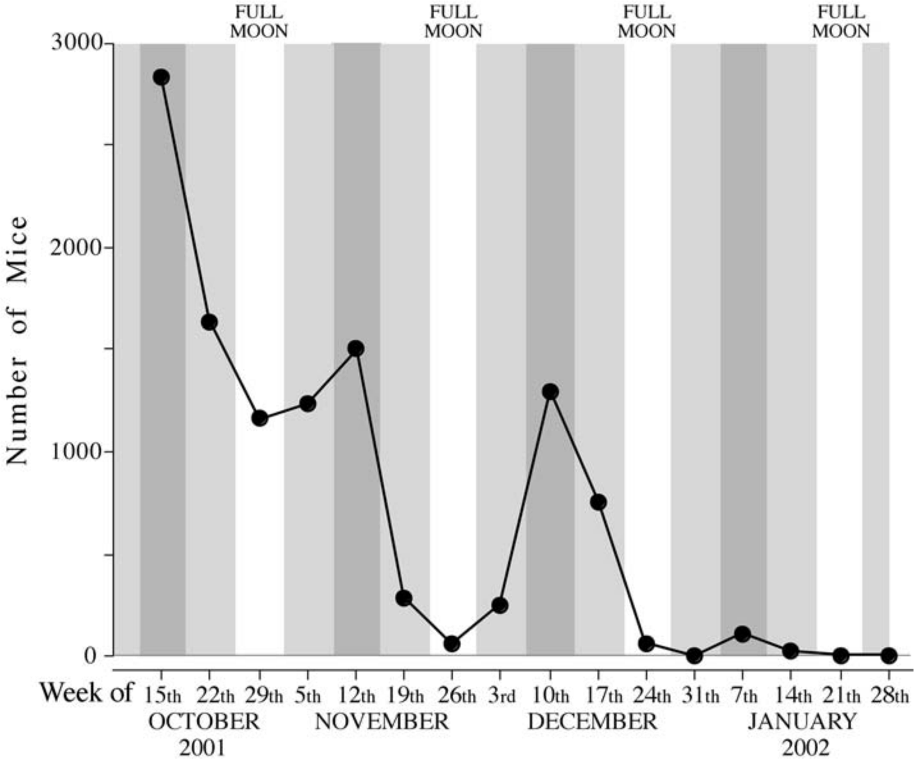

Figure 2. Weekly numbers of drowned rodents picked up by municipal workers on the shore of Lago Lacar at San Martin de Los Andes. The clear columns mark the weeks of the full moons.

Tooth Wear and Age Structure

Mean cusp height of the *Oligoryzomys* sample was 0.46 ± 0.005 mm (range: 0.17 - 0.67 mm). Comparable values for *A. longipilis* were 0.78 ± 0.012 mm (range: 0.22 – 1.04 mm). No difference was detected across gender (*Oligoryzomys* $F = 1.4$, *d.f.* = 1, 304, $p = 0.20$; *A. longipilis* $F = 3.3$, *d.f.* = 1, 211, $p = 0.07$). However, relationships between tooth wear and measurements of body size differed between the 2 species. In *Oligoryzomys* the correlation of cusp height with body length ($r_s = 0.06$, $p = 0.3$) and with body weight ($r_s = -0.02$, $p = 0.8$) was not significant. In *A. longipilis*, cusp height was significantly correlated with body length ($r_s = -0.23$, $p = 0.001$) and body weight ($r_s = -0.22$, $p = 0.001$).

Tooth-wear age categories differed over collecting period and bamboo habitat, and between the 2 species (Table 5). Mean age declined by 43% in *Oligoryzomys* (age class 3.5 to 2.0) and by 52% in *A. longipilis* (age class 3.1 to 1.5) from Spring-1 to Autumn-1 in the flowered bamboo habitat, reflecting continued breeding and recruitment of young animals during this interval. Mean age increased 20% over the first winter in *Oligoryzomys* populations (2.0 to 2.5) but remained stable and young among *A. longipilis* in Autumn-1 and Spring-2 (1.5 vs. 1.6, Table 5). In Spring-2, the youngest *A. longipilis* (age class-1) predominated in the collections (Table 5). Unlike the first year, mean ages of animals of both species increased rather than decreased from Spring-2

Table 5. Mean age class and frequency (based on tooth wear) in *Oligoryzomys longicaudatus* and *Abrothrix longipilis* samples over time and in flowered and green bamboo habitats, Neuquén Province, Argentina.

Collecting period	Bamboo habitat	Mean±SE (*N*)	Age class 1	2	3	4	5
Oligoryzomys longicaudatus							
Spring-1	flowered	3.5±0.18 (29)	0.07	0.07	0.21	0.59	0.07
Autumn-1	flowered	2.0±0.08 (69)	0.20	0.68	0.07	0.04	
Spring-2	flowered	2.5±0.06 (118)	0.02	0.51	0.42	0.05	0.01
“	green	2.7±0.13 (21)		0.38	0.57	0.05	
Autumn-2	flowered	3.3±0.12 (21)		0.05	0.62	0.33	
“	green	3.1±0.20 (9)		0.11	0.67	0.22	
Autumn-3	flowered	2.9±0.11 (33)		0.24	0.61	0.15	
“	green	2.8±0.17 (6)		0.17	0.83		
Abrothrix longipilis							
Spring-1	flowered	3.1±0.20 (9)		0.11	0.67	0.22	
Autumn-1	flowered	1.5±0.10 (80)	0.64	0.29	0.01	0.05	0.01
Spring-2	flowered	1.6±0.10 (40)	0.52	0.40	0.08		
“	green	3.8±0.26 (13)		0.08	0.31	0.38	0.23
Autumn-2	flowered	3.1±0.34 (7)		0.14	0.71		0.14
“	green	2.6±0.27 (17)	0.06	0.53	0.23	0.06	0.12
Autumn-3	flowered	2.2±0.10 (34)	0.03	0.82	0.09	0.06	
“	green	2.5±0.31 (13)		0.77	0.08		0.15

to Autumn-2 (24% in *Oligoryzomys* and 48% in *A. longipilis*, Table 5). These Autumn-2 animals were the oldest of the 3 autumn populations. In Autumn-3 individuals of both species were still, on average, older than those of Autumn-1. During the second and third years the mean ages of the species varied in different ways in the two habitats. Mean age of *Oligoryzomys* populations exhibited parallel trajectories in both habitats, ageing through Summer-2 and being relatively old in Autumn-3 (Table 5). In contrast, the mean age of *A. longipilis* populations in the green bamboo habitat declined over Summer-2 while neighboring populations in the flowered bamboo habitat increased in age (Table 5). For *Oligoryzomys* there was a significant effect of collecting period ($F = 35$, $d.f. = 4, 298$, $p < 0.001$), and non-significant effects of bamboo habitat ($F = 0.06$, $d.f. = 1, 298$, $p = 0.8$) and the interaction of period x bamboo ($F = 0.6$, $d.f. = 2, 298$, $p = 0.6$). For *A. longipilis* there were highly significant effects of collecting period ($F = 13$, $d.f. = 4, 205$, $p < 0.001$), bamboo habitat ($F = 16$, $d.f. = 1, 205$, $p < 0.001$), and their interaction ($F = 22$, $d.f. = 2, 205$, $p < 0.001$).

Age structure of *Oligoryzomys* in the sample of drowned mice from Lago Nonthué was not different from that of the contemporary population in the nearby Hua Hum forest (1-way ANOVA; $F = 2.9$, $d.f. = 1, 75$, $p = 0.10$).

Reproduction

Females. In Spring-1 the majority of captured animals were reproductively active (Table 6). Nine of 15 female *Oligoryzomys* were pregnant with fetuses up to 24 mm CRL, and 2 were lactating. Four of 5 female *A. longipilis* collected at this time showed signs of active reproduction: 2 females had small fetuses (5 and 10 mm CRL), another had 3 small uterine bumps, and a fourth was lactating. The single female *L. micropus* in the Spring-1 collection had corpora lutea and uterine swellings, indicating an early pregnancy.

In Autumn-1 many mice were reproductively active. Most (86%) female *Oligoryzomys* were pregnant, including 7 of 10 mice in the youngest age class. Average litter sizes were larger than in the previous spring (6.9 versus 5.4; Table 7). Two females were carrying 11 embryos, which equals the maximum reported for this species (Pearson, 1983), and a third mouse had 10 embryos. One pregnant female (in age

Table 6. Percentages of reproductively active female mice (i.e., with fetuses or lactating) of four species from the flowered and green bamboo habitats, Neuquén Province, Argentina. The number of females in each sample is shown within parentheses.

Collecting Period	*Oligoryzomys longicaudatus*		*Abrothrix longipilis*		*Abrothrix olivaceus*		*Loxodontomys micropus*	
	Flowered	Green	Flowered	Green	Flowered	Green	Flowered	Green
Spring-1	60 (15)		100 (5)		—		100 (1)	
Autumn-1	8 (29)		15 (48)		15 (13)		80 (5)	
Spring-2	0 (55)	0 (7)	10 (21)	100 (4)	0 (10)	0 (2)	5 (19)	0 (1)
Autumn-2	0 (11)	0 (3)	—	0 (10)	0 (5)	0 (3)	—	—
Autumn-3	9 (11)	0 (1)	0 (11)	0 (4)	0 (15)	0 (1)	—	0 (2)

class-1) had the highest cusp height that we measured in the entire sample of female *O. longicaudatus*, demonstrating that precocial, young-of-the-year breeding occurs in this species when conditions are favorable. Only 14% of the 48 female *A. longipilis* were pregnant in Autumn-1. But as was the case with *Oligoryzomys*, mean litter size was larger in Autumn-1 than in Spring-1 (3.9 vs. 3.3, Table 7) in *A. longipilis*. Twelve non-pregnant mice had prominent nipples, indicating recent pregnancies. Two of these 12 were old (class-4) and the other 10 were young (age class-1 and -2). Among the pregnant mice 3 were in age class-1 and 3 were in age class-2. The youngest of the pregnant females had a cusp height of 0.96 mm, the sixth tallest teeth among 85 females measured. As with *Oligoryzomys*, this dental information shows that precocial reproduction was taking place in this late-autumn population of *A. longipilis*. In a study of the reproductive biology of this species Pearson (1992) found no evidence of late season breeding by young-of-the-year females. Four of the 5 *L. micropus* were pregnant in Autumn-1, with a mean litter size of 6.2±0.63 and a range of 5 - 8. The 8 embryos increases the maximum litter size reported for this species by 1 (Pearson, 1983). The fifth animal had enlarged uteri and prominent nipples, suggesting that she had recently bred. Two of 13 female *A. olivaceus* were pregnant (with 5 and 6 embryos), and 4 non-pregnant mice with enlarged uteri and prominent nipples had recently finished breeding. The remaining 7 *A. olivaceus* were nulliparous, with threadlike uteri.

In summary, *A. longipilis* exhibited a lower level of reproductive activity (14%) than in *O. longicaudatus* (86%) in Autumn-1 samples, suggesting that *A. longipilis* was ending the autumnal breeding, while this was continuing in *O. longicaudatus*. The high percentage (80%) of pregnant *Loxodontomys* indicates that, like *Oligoryzomys*, it continued its autumnal breeding season. *Abrothrix olivaceus*, with a low percentage of pregnancies, was behaving like the congeneric *A. longipilis* and ending its breeding season.

In Spring-2, despite dissecting more than 6 times as many mice as in Spring-1, we found no signs of reproduction (Table 6). All female *Oligoryzomys* had threadlike, translucent uteri, indicating that this species had not begun to breed in either bamboo habitat. The reproductive behavior of *A. longipilis* differed from that of *Oligoryzomys* in Spring-2. While only 2 of 21 females from the flowered bamboo habitat were pregnant, all 4 from the green bamboo were reproductively active (3 were pregnant, and one had an enlarged uterus with scars). The 2 pregnant animals from the flowered area were older (class-2 and –3) individuals, while 14 of the reproductively inactive animals

Table 7. Litter sizes in *Oligoryzomys longicaudatus* and *Abrothrix longipilis* over time in the flowered bamboo habitat, Neuquén Province, Argentina. Mean litter size and standard error are followed by the range [ ] and sample size ( ).

Collecting period	*Oligoryzomys longicaudatus*	*Abrothrix longipilis*
Spring-1	5.4±0.50 [2 – 7] (9)	3.3±0.67 [2 – 4] (3)
Autumn-1	6.9±0.42 [4 – 11] (24)	3.9±0.34 [3 – 5] (7)
Spring-2	No data	4.5 [4, 5] (2)
Autumn-3	7 (1)	No data

were class-1 individuals. The 4 reproductively active animals from green bamboo localities also were older animals (age classes 3 to 5). Thus, in Spring-2 only the oldest *A. longipilis* females showed signs of early breeding in both habitats. Zero of 10 female *A. olivaceus* were pregnant in the Spring-2 collection, and threadlike uteri were recorded for most specimens. There were also no signs of embryos or corpora lutea in 20 *L. micropus*. The uterine horns of 7 *R. rattus* were 1 – 2 mm wide, but no corpora lutea were seen; uterine scars present in 2 *R. rattus* suggested earlier pregnancies. Five *Irenomys* showed no signs of reproductive activity. In summary, there was much less reproductive activity recorded in Spring-2 than in Spring-1, and where observed (in *A. longipilis*) it was restricted to older animals.

In Autumn-2 no animals showed signs of reproductive activity. In Autumn-3 one of 12 female *Oligoryzomys* was pregnant, indicating that some breeding extended into this autumn. Intense autumnal breeding was only observed in Autumn-1.

Testis Size. Mean testis length in *Oligoryzomys* declined over the study period in the flowered bamboo habitat (Table 8). Length was greatest in Spring-1, when 60% of females were breeding (Table 6) and mean age was greatest (Table 5). The mean length in Autumn-1 was smaller than in Spring-1, although the percentage (88%) of females that were breeding then was the highest found during our study (Table 6). The distribution of testis length in this Autumn-1 sample of 41 males was bimodal (kurtosis = -1.3), with modes at 4 and 7 mm. Testis length among the 7 oldest mice (in age classes-3 to -5) ranged from 6 to 8 mm. Testis length among the 21 youngest mice (in age class-1) ranged from 3 to 9 mm. Six of these animals had testis lengths between 7 and 9 mm, suggesting that sexual maturity can be reached at a very young age when conditions are favorable. In Spring-2 mean testis length further declined from that in the previous autumn (Table 8), even though the animals were now older (Table 5). Mean length in Spring-2 was significantly lower than in Spring-1 ($p = 0.005$ in a Tamhane T2 test for post hoc multiple comparisons among testis lengths from all 5 periods). Testis size was smallest in Autumn-2 and only slightly larger in Autumn-3 (Table 8). Means of these 2 autumn samples were both significantly smaller than that observed in Autumn-1 ($p < 0.001$ for Autumn-1 vs. -2 and $p < 0.001$ for Autumn-1 vs. -3 in the same multiple comparison tests described above). These small testes in the

Table 8. Mean testis length (mm) and standard error for *Oligoryzomys longicaudatus* and *Abrothrix longipilis* over time and in flowered and green bamboo habitats, Neuquén Province, Argentina. Means are adjusted to a standard body length of 103 mm for *O. longicaudatus* and 107 mm for *A. longipilis*. Sample sizes are within parentheses.

Collecting period	*Oligoryzomys longicaudatus*		*Abrothrix longipilis*	
	Flowered	Green	Flowered	Green
Spring-1	6.4±0.31 (14)	--	13.0±0.97 (4)	--
Autumn-1	5.3±0.18 (41)	--	7.1±0.34 (33)	--
Spring-2	4.9±0.14 (69)	5.7±0.30 (15)	3.6±0.43 (21)	9.4±0.69 (9)
Autumn-2	3.3±0.36 (10)	3.6±0.47 (6)	3.8±0.73 (7)	4.3±0.73 (7)
Autumn-3	3.6±0.25 (23)	4.3±0.52 (5)	4.2±0.42 (24)	4.1±0.65 (9)

Autumn-2 and -3 males occurred when females were also not reproductively active (Table 6). The length pattern in the green bamboo habitat during the second and third years paralleled that in the flowered habitat: they were largest in Spring-2, smallest in Autumn-2, and intermediate sized in Autumn-3 (Table 8). No significant difference existed between mean size in these 2 habitats when only the males from the last 3 collecting periods were compared ($F = 2.3$, $d.f. = 1, 122$, $p = 0.13$).

Changes in testis size in *A. longipilis* in the flowered bamboo habitat were similar to that in *Oligoryzomys*: largest in Spring-1 and declining through Autumn-3 (Table 8). Lengths in the Autumn-1 sample were bimodally distributed, as was also the case with the *Oligoryzomys* at this time. The modes for the *A. longipilis* were at 4 and 12 mm. The 3 oldest males (age classes 4 and 5) had testes 12 mm long. Five of the 22 youngest (age class-1) animals had testes between 10 and 12 mm long, suggesting that they too had reached sexual maturity. Mean length declined to its smallest value in Spring-2 (Table 8), when all but 1 *A. longipilis* had testes between 3 and 6 mm in length. Mean length remained small in Autumn-2 and -3. A notable difference in testis size was observed in Spring-2 between animals from the flowered and green bamboo habitats. At this time the 9 males from the green bamboo had testes ranging in length from 10 to 12 mm, while only 1 of 21 *A. longipilis* from the flowered bamboo had a testis in that length range. However, the animals with large testes in the green bamboo were much older than the animals in the flowered habitat (Table 5), and their greater ages may be the reason for their larger testes. Testis size in animals from green bamboo habitat declined to the same small size as Autumn-2 and -3 males in the flowered habitat.

Body Conditions

Fatness. The amount of fat varied among individuals as a function of species, time, and habitat. A striking feature of some mice was their great amount of intra-abdominal fat. In the fattest animals (class-3), the fat completely covered the heart, kidneys, testes/uteri, and lower intestines. We only recorded 20 such animals (19 *Oligoryzomys* and 1 *L. micropus*), and all were collected in Spring-2 in the flowered bamboo habitat. None of 214 *A. longipilis* was in a fat class higher than 1. The average 'fatness' of *Oligoryzomys* and *A. longipilis* was reversed in Spring-2 in the 2 habitats: in flowered bamboo, 0-class individuals were less frequent (47%) in *Oligoryzomys* and more so (93%) *A. longipilis*, whereas the respective percentages were 67 and 46 (Table 9) in the green bamboo. On average the *Oligoryzomys* were fatter than *A. longipilis* in the flowered habitat (1.1 vs. 0.07) and leaner (0.3 vs. 0.5) in the green bamboo habitat (Table 9); suggesting more efficient use of bamboo seeds by *Oligoryzomys* than *Abrothrix*.

Standardized Weight Changes. We compared weights of mice across time and habitats to test for possible beneficial effects of the bamboo seed on body condition, assuming that a heavier animal was in better condition than a lighter one of the same size and age. The standardized weights across time and habitat in *Oligoryzomys* and *A. longipilis* were examined with ANCOVA using body length as a covariate of body size and cusp height as a covariate of age. Sex was not a significant variable in either species. Age (molar cusp height) was not a significant covariate in *Oligoryzomys* but was statistically important ($p < 0.01$) in *A. longipilis*. Body weight was significantly associated ($p < 0.001$) with body length for both species. Finally, collecting period was a significant factor ($p < 0.001$) for both species but bamboo habitat was not.

Table 9. Frequencies of intra-abdominal fat scores in *Oligoryzomys longicaudatus and Abrothrix longipilis* trapped in different habitats in Spring-2, Neuquén Province, Argentina**.** Class values range from small amounts of fat restricted to gonads (0) to enlarged pads plus fat covering kidneys and heart (3). Mean and standard error are reported, with sample size (*N*) in parentheses.

Species	Bamboo Habitat	Frequency of fat-class scores				Mean
		0	1	2	3	
Oligoryzomys	Flowered	0.47	0.14	0.2	0.19	1.1±0.14 (79)
“ “	Green	0.67	0.33	0	0	0.3±0.10 (21)
Abrothrix	Flowered	0.93	0.07	0	0	0.07±0.041 (41)
“ “	Green	0.46	0.54	0	0	0.5±0.14 (13)

In the flowered habitat the heaviest *Oligoryzomys* (estimated weight 39 g at the standardized body length of 99 mm) were collected in Spring-1 (Table 10). Despite their weight all of these animals had virtually no fat (class-0). The estimated mean body weight in Autumn-1 was 32 g, representing an 18% decline from Spring-1. From Autumn-1 to Spring-2 body weights did not change in the flowered bamboo habitat, even though obese animals (class-3) were present in the latter period (Table 9). By Autumn-2, however, the standardized weight of these flowered-bamboo animals had declined another 6 g, to 29 g, and reaching their lightest standardized weight recorded during the study (Table 10). This was also the period when overall abundance of rodents was at its lowest level (Tables 2 and 3). In the next year (Autumn-3) standardized weight had increased to 28 g, but it was still 12% lower than the 32-g weight of the

Table 10. Estimated mean body weight (g) at different times and in different bamboo habitats for *Oligoryzomys longicaudatus* and *Abrothrix longipilis*, Neuquén Province, Argentina. Estimated weights are at adjusted mean body length of 99 mm in *Oligoryzomys* and 107 mm in *A. longipilis*. Mean and standard error are reported, with sample size (*N*) in parentheses.

Collecting Period	Bamboo Habitat	*Oligoryzomys longicaudatus*	*Abrothrix longipilis*
Spring-1	flowered	39±0.9 (29)	39±1.5 (9)
Autumn-1	“ “	32±0.6 (69)	36±0.5 (80)
Spring-2	“ “	32±0.6 (78)	32±0.7 (39)
“ “	green	29±1.1 (21)	31±1.4 (13)
Autumn-2	flowered	26±1.1 (21)	29±1.7 (7)
“ “	green	28±1.6 (9)	32±1.1 (17)
Autumn-3	flowered	28±0.9 (34)	30±0.8 (34)
“ “	green	28±2.0 (6)	31±1.2 (13)

Autumn-1 animals. The animals in the green bamboo habitat in Spring-2, Autumn-2, and Autumn-3 were always lighter in weight than those in the flowered bamboo during the time (Autumn-1 and Spring-2) when there was much seed available (Table 10). But these green bamboo animals were heavier than those in the flowered bamboo in Autumn-2, the time when the rodents had declined to their lowest abundances during the study (Tables 2 and 3).

Abrothrix longipilis exhibited similar temporal patterns in standardized weight. The heaviest animals were collected in Spring-1, after which weights declined (Table 10). There was a 3 g decline (9%) in mean body weight from Spring-1 to Autumn-1. Body weights declined another 10% over the winter, to 32 g in Spring-2. From Spring-2 to Autumn-2, the standardized weight of *A. longipilis* continued to decline by another 3 g (9%). Similar to *Oligoryzomys*, we documented a difference in the amount of weight loss in *A. longipilis* during the second growing season between the flowered and green bamboo habitats (Table 10). Spring-2 animals in flowered areas averaged slightly (albeit not significantly) heavier (1 g) than those in the green bamboo habitat, but in Autumn-2 the green bamboo mice weighed 3 g more (also not significant). Although the patterns of reversals in weight were similar in *Oligoryzomys* and *A. longipilis*, the differences approached statistical significance only in the former species. Our data suggest there was an overall decline of about 30% in estimated body weight over the course of the study in both species and this was not closely linked to the abundance of bamboo seed.

Tail Scars and Torn Ears. We examined the patterns of scars on the tails and torn ears on the assumption that these wounds were the results of fights between mice and/or signs of escape from predators. Males had a higher frequency than females of at least 1 tail scar in both *Oligoryzomys* (0.42 (N = 159) vs. 0.34 (N = 110)) and *A. longipilis* (0.56 (N = 113) vs. 0.29 (N = 102)). The difference between sexes was highly significant in *A. longipilis* (F = 16, *d.f.* = 1, 214, p < 0.001) but not in *Oligoryzomys* (F = 1.6, *d.f.* = 1, 268, p = 0.2). In *A. longipilis* there was a highly significant effect of age class on the presence/absence of a tail scar (F = 5.6, *d.f.* = 4, 209, p = > 0.001), with the frequency increasing nearly monotonically from 0.25 in age class-1 to 0.78 in age class-5 animals. There was a near significant age effect in *Oligoryzomys* (F = 2.1, *d.f.* = 4, 268, p = 0.08), but the intermediate age classes of -2, -3, and -4 had the highest frequencies of tail scarring (0.48, 0.36, and 0.46, respectively) while the youngest and oldest animals had lower frequencies. The frequency of scarring changed across time and habitats (Table 11). We examined the effects of species, sex, age class based on tooth wear, bamboo condition, and collecting period on scarring patterns with ANCOVA, using age class as a covariate. The significant main effects were collecting period (F = 22, *d.f.* = 4, 4.9, p = 0.003), bamboo condition (F = 6.5, *d.f.* = 1, 2.7, p = 0.092), and age (F = 6.7, *d.f.* = 1, 447, p = 0.010) and the only significant interaction term was between collecting period and species (F = 7.9, *d.f.* = 4, 5.8, p = 0.016). In the flowered bamboo habitat scarring frequencies in both species were low in Spring-1, when animals were relatively old (Table 5) and population densities were low (Tables 2 and 3). Levels of scarring in *Oligoryzomys* were low in all 3 autumn collections (Table 11), even though densities and ages of autumn animals differed among years. In Autumn-1 the densities were high and the animals were young, while in Autumn-2 and Autumn-3 the densities were comparatively lower (Tables 2 and 3) and the animals were older (Table 5). The highest incidence of tail scars occurred among Spring-2 animals, when densities were

Table 11. Mean frequency of mice with at least one scar on tail among trapped *Oligoryzomys longicaudatus* and *Abrothrix longipilis* across collecting periods and bamboo conditions, Neuquén Province, Argentina. Mean and standard error are reported, with sample size (*N*) in parentheses.

Collecting Period	Bamboo Condition	*Oligoryzomys longicaudatus*	*Abrothrix longipilis*
Spring-1	flowered	0.08±0.078 (29)	0.33±0.137 (9)
Autumn-1	" "	0.19±0.050 (69)	0.11±0.046 (81)
Spring-2	" "	0.64±0.046 (78)	0.73±0.064 (41)
" "	green	0.78±0.089 (21)	1.00±0.114 (13)
Autumn-2	flowered	0.34±0.091 (21)	0.86±0.155 (7)
" "	green	0.52±0.137 (9)	0.53±0.100 (17)
Autumn-3	flowered	0.19±0.072 (34)	0.49±0.069 (35)
" "	green	0.29±0.168 (6)	0.50±0.119 (12)

still high but beginning to decline. At this time large numbers of *Oligoryzomys* were drowning in the nearby lakes. These scarred Spring-2 mice were older than those of the preceding autumn (Table 5) and were not reproductively active (Table 6, 8).

Abrothrix longipilis differed in a number of ways from *Oligoryzomys* with respect to scarring. Frequency of scars in the former species was lower in Autumn-1 than Spring-1 (Table 11), even though densities were higher. Many of these autumn *A. longipilis* were very young and perhaps they had not yet reached the age where fighting starts in this species. By Spring-2 the incidence of tail scars was 3 times higher than in Autumn-1, and the animals were somewhat older (Table 5) and densities were still high. Some feature of the social or predatory environment may have changed in the interval between Autumn-1 and Spring-2, leading to this increased amount of wounding. But unlike in *Oligoryzomys*, the high frequency of tail scars in *A. longipilis* was not associated with drownings during Spring-2. In Autumn-2 the frequency of tail scars reached the highest level that we recorded in the flowered bamboo (Table 11); at this time the abundance of *A. longipilis* had dropped to its lowest level, and these animals were as old as those from Spring-1 (Table 5). By Autumn-3 scarring had declined to a moderate level, among mice that now were younger but more abundant than in the preceding year.

In green bamboo the patterns of tail scarring were similar in both species, declining continuously from Spring-2 to Autumn-3 (Table 11). But in Spring-2 the scarred *Oligoryzomys* were of middle-age, while more than half of the *A. longipilis* individuals were in the oldest 2 age classes and the sample had the highest mean age among our collections (Table 5). By Autumn-2 the frequency of scarring in both species had declined although density had increased from the preceding spring. The Autumn-2 *Oligoryzomys* were older, and *A. longipilis* younger, than in Spring-2. In Autumn-3 the incidence of tail scarring was lower in *Oligoryzomys* and about the same in *A. longipilis* as it was in the preceding autumn. The ages of these Autumn-3 animals were similar to those in Autumn-2 (Table 5).

In summary, the frequency of tail scarring showed a complicated relationship with age, species, and population density. One consistent trend in these 2 species was the 3- to 6-fold increase in scarring during Winter-1, which was the time when the populations reached their peak densities and rodents began leaving the forest habitat in large numbers.

Mice were both abundant and drowning in Spring-2, and we compared whether fighting (torn ears) was at the same level in the mice that drowned and the nearby flowered habitat. For 3 species the frequency of torn ears was higher among the drowned than the trapped animals: *Oligoryzomys*, 25% of 36 animals (drowned in L. Nonthue) vs. 10% of 59 animals (collected in flowered bamboo habitat); *A. longipilis*, 50% of 2 vs. 18% of 34; *Loxodontomys*, 41% of 46 vs. 0% of 4. Drowned mice had significantly higher frequencies of torn ears than live-trapped mice (ANOVA, $F = 5.0$, $d.f. = 1, 175$, $p = 0.03$), suggesting that near the time when mouse densities were declining from their peak levels, the mice entering the water had suffered more wounding than those remaining in the forest.

Arboreal Activity

We observed rodents climbing on seed-laden bamboo canes in Autumn-1 using night-vision binoculars. This prompted us to set arboreal lines of live traps to determine which species were foraging in bamboo. With 294 trap-nights over 28 arboreal trap lines, the weighted mean trap success per trap line was 0.12 ± 0.023 (range: 0 - 0.46). Trap success ranged from 0 to 30% (Table 12) and was not significantly influenced by collecting period, bamboo habitat, or the interaction of these 2 factors (ANOVA, all $p > 0.05$). The highest success was in one line of traps in flowered bamboo in Autumn-1, which also was the time of greatest trap success on the ground (Table 3). Arboreal trap success declined to 12% and 15% in the flowered bamboo in Autumn-2 and -3, when there was no more seed on the dead canes. Trap success in Spring-2 was notably lower in the green bamboo (0%) than in the flowered bamboo (15%), when some bamboo seed still remained on the flowered stalks (Table 12).

We caught 40 mice in arboreal traps and identified 39 of them (one escaped): 25 *O. longicaudatus* in the flowered bamboo habitat and 1 in the green bamboo; 4 *A. longipilis* in the flowered and 5 in the green bamboo habitats; 1 *A. olivaceus* in each habitat, and

Table 12. Trap-success frequency in 28 arboreal trap lines over time and bamboo habitat, Neuquén Province, Argentina. Means and standard errors are reported, with numbers of trap lines shown in parentheses.

Collecting Period	Flowered Bamboo	Green Bamboo
Autumn-1	0.30 (1)	--
Spring-2	0.15±0.042 (7)	0 (4)
Autumn-2	0.12±0.057 (5)	0.12±0.073 (3)
Autumn-3	0.15±0.057 (5)	0.10±0.073 (3)

2 *R. rattus* in the flowered bamboo. The predominance of *Oligoryzomys* (67%) was not surprising as it was the most abundant species present and is known to be somewhat arboreal (Contreras, 1972; Pearson, 1983). Likewise, to catch *R. rattus* up in the canes was not unexpected, as two of its common names (roof rat and climbing rat) refer to its arboreal behavior. The 2 *Abrothrix* species are primarily terrestrial, yet both were also caught up in the canes. *Oligoryzomys* was the most common rodent caught in arboreal traps in the flowered bamboo (78%), whereas *A. longipilis* was the most common in the green bamboo habitat (71%). The difference in abundance of these 2 species between the 2 habitats was highly significant (Mann-Whitney U-test, $z = -3.5$, $p < 0.001$).

Predator Abundances

During Autumn-1 barn owls (*Tyto alba*) were abundant, and were heard calling every night near our campsites. Park Ranger Monica Sosa reported that during Winter-1 owls commonly flew in front of her headlights at night near Yuco (Locality 5), and that dead barn owls were found in Summer-2. In Spring-2 a few barn owls were heard by one of us (RDS) while camped at Hua Hum and Currhué Chico, whereas in Autumn-2 only 1 barn owl was heard calling during 7 nights at the same sites, and in Autumn-3 a barn owl was heard only once during 4 nights of camping at Hua Hum and Currhué Chico. Based on these qualitative observations and accounts, the abundance of this generalist nocturnal predator appears to have closely paralleled that of the rodents. In a separate study one of us (JS) has been monitoring a series of scent stations near Lago Currhué Grande, and observed a 30% increase in the number of Andean red fox, or culpeo (*Pseudalopex culpaeus*) visiting scent-stations in Summer-2 compared with visits in the (pre-flowering) summer of 1998.

DISCUSSION

Ratada-2001*: Its Cause and Structure*. Both large and small fluctuations in numbers of rodents in Valdivian rainforest have been reported and their varying causes are becoming better understood (see below). We have described a large fluctuation in the vicinity of San Martín de Los Andes over a 3-year period from 2000 to 2003. The most notable features of this cycle to the general public were the invasion of human dwellings by the rodents and their drownings in lakes in 2001; thus, we name this the *Ratada-2001*. The cycle, however, was initiated in the spring (October) of 2000 almost certainly by the flowering and production of a massive amount of seed. That the ratada was ultimately caused by the production of bamboo seed rather than some other factor is supported by the close correspondence between the areas where the bamboo flowered and where mice invaded buildings or drowned in high numbers (Plate 2A, B, and C).

When *C. culeou* began to flower in Spring-1 rodent populations were in the low phase of the annual cycle (Fig. 3), and densities were similar to those of baseline populations (Pearson, 2002). Numbers increased during the breeding season of Spring-1 and Summer-1. Bamboo seed matured in late Summer-1 and began falling to the ground. Seed was abundant on the ground in Autumn-1, and probably became an *ad libitum* food resource for mice until Spring-2. Derting (1989) found that with *ad libitum* food supplies, young *Sigmodon hispidus* grew more rapidly and reached first estrus at an earlier date than did individuals with a more limited food supply. The abundance of very young (age class-1) and pregnant *Oligoryzomys* and *A. longipilis* in our Autumn-1 sample suggests that a similar acceleration to reproductive age occurred in late Summer-1. Such precocial reproduction provides a fitness advantage to the individual female and contributes importantly to the size of the population at the end of the breeding season (Lambin and Yoccoz, 2001). Because of the abundance of bamboo seed, reproduction in 4 of the native rodents continued at a high intensity through Autumn-1, and the breeding season was 3 months longer than typical. Extension of the breeding season due to a superabundance of food was reported for *Oligoryzomys* in Chile (Murúa et al., 1986; Gonzáles et al., 1989). A similar extension of breeding occurs in some Northern Hemisphere species reaching high densities (e.g. Jensen, 1982; Pucek et al., 1993). If generation times of these Argentine species are similar to rodents like *Microtus agrestis* (6 weeks), *Mus domesticus* (7 weeks), and *Rattus norwegicus* (8 weeks) (Cockrum, 1962), then 1 to 2 more cycles could have occurred in the season when the bamboo flowered. Our data show that litter sizes in *Oligoryzomys* were larger than normal during this final part of the breeding season. Because of the likely shortened generation time plus larger litter sizes, the population growth rate (R) during these 'extra' rounds of breeding was higher than normal and led to the final population growth of the rodents to outbreak (plague) numbers.

In early Winter-1 reproduction ended, populations reached their highest densities, and the decline phase began (Fig. 3). Three lines of evidence suggest an immediate start to this decline. In late Winter-1 park rangers reported seeing high numbers of owls, permanent residents within Parque Nacional Lanín reported rodent invasions of their buildings, and rodents began to drown in large numbers. All 3 of these factors (predation, emigration, and drowning) should have contributed to declining rodent numbers. We infer that the decline phase lasted from Winter-1 into Summer-2 based on the beach records at Lago Lacar (Fig. 2), and was due to continued mortality from drowning, predation, and low recruitment during the second season. Evidence for low recruitment was the virtual absence of breeding female *Oligoryzomys* or *A. longipilis* in Spring-2 (Table 6), the scarcity of young animals (Table 5), and low numbers of *A. longipilis* in the Autumn-2 collections (Table 2, Appendix Table 2). Absence of young animals suggests that little reproduction occurred during the last half of Summer-2, and low autumnal numbers indicates little recruitment during the second breeding season. Delayed maturation plus a late start and short duration of the breeding season is commonly observed in rodent cycles after peak densities are reached (Krebs and Myers, 1974: Hansson and Henttonen, 1985; Fitzgerald et al., 2004).

One possible reason for delayed, or reduced, reproduction in the flowered bamboo habitat in Spring-2 was that over-wintered animals were comparatively younger than the Spring-1 population of the previous year when there was probably no autumn (and winter) breeding. Evidence consistent with this hypothesis comes from comparing *A. longipilis* from the flowered and green bamboo habitats in Spring-2. Four of 4 females from the green habitats, but only 2 of 20 from the flowered habitats, were reproductively active, and mice from green bamboo habitat were older than those from the flowered bamboo habitat (Table 5). Autumn breeding is uncommon (Pearson, 1992, 2002), so Spring-2 females in the green bamboo likely had been born during Summer-1, and were >6 months old. In the flowered bamboo habitat we know that breeding continued into early Winter-1, so the Spring-2 population included disproportionately more females that were about 4 months old. However, the observation that precocial (young-of-the-

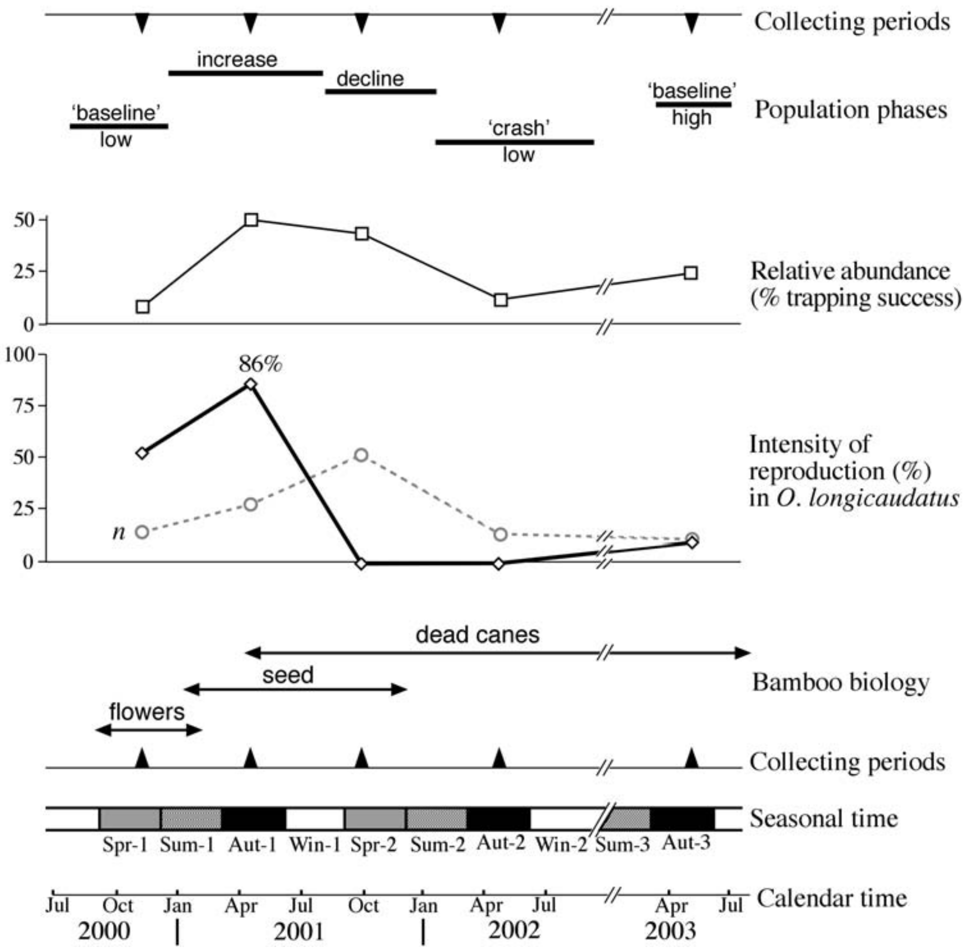

Figure 3. Chronology of Ratada-2001. The chart shows major events in the phenology of the flowering bamboo and rodent populations with respect to the 5 collecting periods, the passage of the annual seasons, and the calendar dates. The graph of the intensity of reproduction in *O. longicaudatus* shows the percentage of females that were reproductively active in a sampling period, with *N* indicating the number of animals autopsied.

year) female *A. longipilis* were breeding in Autumn-1 contradicts the hypothesis that females in the flowered bamboo habitat were 'too young' (at about 4 months of age) to breed in Spring-2.

Why *Oligoryzomys* females in both habitats were not in breeding condition in Spring-2 is unknown. The explanation in flowered bamboo habitats could be the same as for *A. longipilis*, that they were mostly winter-born and 'too young' when we sampled in Spring-2. This could also be the reason for lack of reproduction in the females from the green bamboo habitat, as the animals in this habitat also consisted of young animals (Table 5). But this argument is also contradicted by the extremely young (age class-1) and pregnant *Oligoryzomys* in Autumn-1.

Two other, more general speculations about the apparent reduction (or failure) of reproduction in *Oligoryzomys* and *A. longipilis* in the second year in the flowered bamboo habitat are suggested from the body conditions of the Spring-2 animals. Many of the *Oligoryzomys* at this time were obese (Table 9), and tail scars (Table 11) and torn ears (see Results) were frequent in both species. Fertility is frequently reduced in obese laboratory rodents (Coleman and Hummel, 1967; Good et al., 1997; Hellman, 1967). Such a side-effect of obesity might explain why these forest rodents did not have high reproductive success during the second breeding season after the bamboo flowered in their habitat. The high level of wounds in Spring-2 probably resulted from fighting during this time of high densities. If this is true, then the animals that had lived through the high density conditions existing from Autumn-1 to Spring-2 had been experiencing chronic stress for more than 1 generation due to fighting. Prenatal stress of the mother negatively affects the fertility of her offspring in various mammalian taxa, including rodents (Ward, 1972; Herrenkohl, 1979; Pollard and Dyer, 1985; Marchlewska-Koj et al., 2003), canids (Osadchuk et al., 2003), and humans (de Zegher and Ibáñez, 2004); and similar effects may have developed in the *Oligoryzomys*, *A. longipilis*, and other rodents living under the stress of high densities during the peak phase of this outbreak. Experimentally induced prenatal stress in laboratory rats (Pollard, 1986; Holemans et al., 1998; Francis et al., 1999) and nutritional deprivation of pregnant humans (Duncan and Scott, 2004) resulted in detrimental effects in offspring lasting at least 2 generations after the application of the stress. Such intergenerational transmission could amplify these negative, prenatal effects on reproductive ability of the forest rodents and have demographic consequences. Reproductive failure likely played a major role in the crash at the end of *Ratada-2001*, and determining its cause should be a major goal of future studies of rodent outbreaks when *C. culeou* flowers in other areas.

The outbreak ended and populations returned to 'control' conditions in terms of population size and structure sometime during the third season after the bamboo flowered (Fig. 3). By Autumn-3 rodent populations in flowered bamboo habitat were twice as abundant as during the Autumn-2 low (Table 3). The age-structure of both *Oligoryzomys* and *A. longipilis* populations had shifted toward younger age (Table 5), which suggests that reproduction had been successful in the third breeding season. Additional evidence for this return to normal conditions was the increase in relative numbers of *A. longipilis* trapped in Autumn-3 (32% of the period total) compared to their low abundance (16% of the period total) in Autumn-2 (Table 2).

The Rattus rattus *Outbreak – A Different Story*. In 20 years of trapping 2 of the authors (OPP and AKP) had never collected *R. rattus* in the native forests, and so our collection of many specimens of this species in this habitat was completely unexpected. Not only was the outbreak of this species surprising, but its timing appears to have differed from that of the native species. Our earliest indication of the presence of rats in the native habitat came in Autumn-1, when we found that a number of our snap-trapped mice at Hua Hum had been badly chewed. *Rattus* are known to do this to trapped specimens and it constituted indirect evidence of their presence at this time. These damaged animals were only found in traps placed in a small marshy area at the study site. One *Rattus* was trapped at Currhué Chico in Autumn-1, but at that time we presumed that this was only a stray from a population in buildings of a government outpost about 5 km away. In Spring-2 however, rats comprised 10% of the drowned mice picked up on the beach (Table 4). We continued to find badly chewed mice in the same small area at Hua Hum where this had happened in Autumn-1, but we did not trap any rats. Only in Autumn-2 did we catch many *Rattus*. At this time rats were captured well away from the marshy area at Hua Hum, including high up on the hillside and in arboreal traps. And during this period, when autumn trapping success reached its lowest level (Table 3), we captured this species at Currhué Chico, Hua Hum, and Yuco, where they comprised one-third of the 33 animals that we collected from these 3 localities (Appendix Table 2).

Our success in trapping this species from many areas within the flowered bamboo habitat suggests that, of our 5 collecting periods, they were most abundant in Autumn-2. One of us (JS) trapped *Rattus* during Summer-2 in the forests near Lago Currhué Grande (near Locality 1) and at Lago Huechulafquén (approximately 20 km NW of Locality 2); animals were captured in native forests and far from human dwellings. During Summer-2 tourists at campsites and landholders within Parque Nacional Lanín reported sightings of rats to park rangers. This is further evidence of the extensive occupation of the native forests by this rodent, and that numbers were highest in the second year after the bamboo flowered.

These trapping records and observations indicate that the dynamics of the *Rattus* population was different from that of the native species. Peak numbers of the rats was reached in Summer-2 or Autumn-2, 6 to 9 months after the native mice reached their highest abundance. Given that the rats established dense populations only in the areas of Parque Nacional Lanín where the bamboo had flowered, it appears that their ability to expand their local distribution away from urbanized areas was in some way directly linked to the flowering of the bamboo. *Rattus rattus* was the most abundant native rodent species during bamboo-associated outbreaks in the forests of Assam, India (Seal et al., 1951) and Japan (Tanaka, 1957), so a similar response to a bamboo seeding in its introduced range in South America is not surprising. However, the factors causing the time of peak rat abundance to differ from that of the native species are unknown. If our interpretation is correct that the rats reached their highest densities in the second summer or autumn, then their presence among the drowned animals in Spring-2 disagrees with a hypothesis that rodents were drowning because of their efforts to disperse to less crowded habitats. If the dispersal hypothesis was correct for the *Rattus*, then one would predict that they would have continued drowning through Spring-2, Summer-2, and into Autumn-2, which was not observed nor reported to the park rangers. The rise and fall of black rats in the Valdivian forests of Argentina remains largely mysterious.

Comparisons of the Ratada-2001 *and Baseline Populations*. Based on 20 years of field data on *Oligoryzomys* and *A. longipilis* in this general region, Pearson (2002) described the normal population structure of these species and emphasized their general long-term stability. Similar studies of *Oligoryzomys* and *A. longipilis* in Chile have shown that numbers of these species regularly fluctuate, albeit with low amplitudes, linked to fluctuations in oceanic weather systems (Murúa et al., 2003a, 2003b). During years of high seed production by forest trees, however, Chilean populations of *Oligoryzomys* regularly undergo large and rapid increases in number (Gonzáles et al., 1989). A comparison of biological features in the Baseline and *Ratada-2001* populations may clarify which factors become important in shifting these populations to outbreak levels rather than staying within their normal system of low-amplitude, weather-linked fluctuations (Table 13).

Baseline populations increase in numbers from a springtime low to an autumn high in the normal annual cycle. The increase from 16 to 30% in overall trap success of the Baseline population reflects a normal doubling of the population size, and contrasts with the ca. 5-fold or greater increase (10 to 51%) between Spring-1 and Autumn-1 in the ratada population (Table 13). This difference could result from an increased breeding effort per female in the form of larger litter sizes, and/or a continual buildup in the percentages of breeding females during the reproductive season. In comparison to the Baseline average, mean litter size in the *Ratada-2001* population of *Oligoryzomys* was one-half embryo higher in Spring-1, and during the extended reproductive season in Autumn-1 the mean increased to 2 embryos above Baseline (Table 13).

In contrast, there was no significant difference in reproductive output between female *A. longipilis* in *Ratada-2001* and Baseline populations. The Autumn-1, ratada females increased their average litter sizes by only one-half embryo over the Spring-1 females, and by only one-tenth of an embryo over the long-term average of the Baseline females (Table 13). Also the range in numbers of embryos/litter of this species did not change in the ratada population during this increase phase of the population, whereas it did increase in *Oligoryzomys* (Table 13). This stability in reproductive values in *A. longipilis* may reflect an inability of this species to respond reproductively to changes in food availability. The unusual ovulatory cycle of *A. longipilis* (Pearson, 1992) may be related to this apparent inability to vary litter size in this species. Both *Oligoryzomys* and *A. longipilis* increased in numbers during the outbreak, but evidently by different means; *Oligoryzomys* increased individual reproductive effort whereas *A. longipilis* employed some other means, perhaps by precocial breeding of summer-born females who would not normally have bred until the following spring.

Age structure of the *Ratada-2001* and the Baseline populations differed most notably in their spring populations. Both types of populations were similar in having relatively few old animals (4 and 7%, respectively) in autumn. In spring, however, 40% of Baseline populations of *Oligoryzomys* and *A. longipilis* were older animals (Table 13); comparable percentages in the Spring-2 *Ratada-2001* populations were 6% and 0%, respectively. This downwards shift in age reflected continued recruitment from the extended Autumn-1 breeding season during the outbreak.

The *Ratada-2001* and the Baseline populations also differed in density changes over the winter period. Nearly half of Baseline populations fail to survive from Autumn to Spring (Table 13). During Ratada-2001 however, trap success only dropped 7% from Autumn-1 to Spring-2, leading to an estimated 87% over-winter survival. The ratada populations continued breeding and increased in size after our Autumn-1 sampling, which likely is the reason we did not record declines in Spring-2. In contrast, Baseline populations finish breeding before the autumn sampling period, at which time they are close to peak densities and may already be starting their normal, intra-annual decline.

In summary, Baseline and Ratada-2001 populations differed in the timing of breeding; Baseline populations experienced a short season, whereas Ratada-2001 populations had an extended season during the increase phase but little or no breeding during the decline phase. As a result of these different breeding regimes the spring and autumn age structures differed between these 2 populations: Baseline populations were characterized by a predominance of old animals in spring and young animals in autumn, whereas during Ratada-2001 we observed a predominance of young animals

Table 13. Comparisons of biological features in Baseline and *Ratada-2001* Populations. Information in the table is from Pearson (2002) and this report, respectively.

Feature	Baseline Populations	*Ratada-2001* Populations
Abundance in spring vs. autumn, based on percent trap success*	Spring = 16	Spring-1 = 10 Spring-2 = 44
	Autumn = 30	Autumn-1 = 51 Autumn-2 = 12 Autumn-3 = 24
Reproduction (litter size)**	*O. l.* = 4.9±0.23 (2 – 11)	*O. l.* (Spring-1) = 5.4±0.5 (2 – 7) *O. l.* (Autumn-1) = 6.9±0.42 (4 – 11)
	A. l. = 3.8±0.11 (2 – 5)	*A. l.* (Spring-1) = 3.3±0.67 (2 – 4) *A. l.* (Autumn-1) = 3.9±0.34 (3 – 5)
Spring age structure (percent in older segment of population)***	*O. l.* = 40	*O. l.* = 6
	A. l. = 41	*A. l.* = 0
Autumn age structure (percent in older segment of population)***	*O. l.* = 7	*O. l.* = 4
	A. l. = 28	*A. l.* = 6
Overwinter mortality (percent) ****	47	14

* Percentages for the overall Baseline population are from Pearson (2002:197), and for the *Ratada-2001* populations they are from Table 3.

** Information for the Baseline Populations comes from Table 1 in Pearson (2002), and for the *Ratada-2001* Population from Table 7.

*** This percentage was estimated for the Baseline populations of *Oligoryzomys* from Fig. 2A in Pearson (2002) using the oldest 2 of the 5 age categories, and for *A. longipilis* using the oldest 4 of the 11 categories. For the *Ratada-2001* populations the values were compiled from Table 6 using age classes IV and V.

**** In this table the percent overwintering mortality was calculated as 1 – (spring/autumn trapping abundance). The comparison done for the *Ratada-2001* Populations is of the Spring-2/Autumn-1 abundance in the flowered bamboo habitats.

during both the autumn and spring of the increase and peak phases and the high numbers of old animals in the autumn of the crash phase.

Comparison of the Ratada-2001 *with Another Local Outbreak*. An outbreak occurred in 1997 in forests south of the present study area, and was not caused by the flowering of bamboo (Pearson, 2002; Table 14). Neither unusual climatic conditions nor an unusually large seed production by a forest tree species was thought to explain this outbreak (Pearson, 2002). While the latitudinal extent of the 1997 ratada was 3 times greater than that of the bamboo-induced *Ratada-2001*, the high numbers of mice were distributed spottily compared to the uniformly high numbers throughout the flowered bamboo region during *Ratada-2001*. This could imply that the stimulus for *Ratada-1997* was patchily distributed compared to the uniformly high production of bamboo seeds in forests from Lago Huechulafquén to Lago Falkner (Sanguinetti and García, 2001).

Both outbreaks shared the feature of an extended breeding season before peak densities were reached (Table 14). Trap successes were equally high in the spring following the winter peak, suggesting that peak densities were similar in both outbreaks. Body condition of peak-stage animals, as measured by fat scores, was also similar (Table 14), including the same difference in amount of fat between *Oligoryzomys* (high) and *A. longipilis* (low scores). Large numbers of mice drowned during the decline phase in both of these outbreaks, and the drownings occurred in approximately the same period of time, i.e. late winter and into spring (Table 14). The high fat levels observed in drowned *Oligoryzomys* suggest that they had not left the forest habitat because of starvation. Not only were the Spring-2 ratada animals fat, but at the same time that they were drowning there was still bamboo seed on the forest floor and on stalks of the dead plants. A high fat index has not been clearly related to a high nutritional condition in other rodents (Batzli and Esseks, 1992; Krebs and Singleton, 1993), and perhaps the drowning of fat mice in these 2 outbreaks indicates that they too were not in a good nutritional state. Species composition of the drowned rodents in the 2 outbreaks was also similar (Table 14): *Oligoryzomys* was the predominant species, followed by *L. micropus*, and few *A. longipilis*. In both outbreaks the relative abundance of drowned rodents and those trapped in nearby woods differed (Table 14); *A. longipilis* was common in the forest and rare in the drowned sample while the reverse was the case for *L. micropus*. The abundance of drowned *L. micropus* during both outbreaks is puzzling in light of their apparent rarity inside the forests. Trap shyness probably is not the explanation for the low catch of forest *L. micropus*, as we have caught many of them in more open habitats to the east of the forest. Other possible explanations for the different frequencies of drowned versus trapped *L micropus* and *A. longipilis* might be that (1) *A. longipilis* are better swimmers than *L. micropus* and drown less frequently, or (2) that when overall rodent densities rise individual *L. micropus* leave the forests before *A. longipilis*. Under this second hypothesis even uncommon species might try to leave the forest when overall rodent densities are high. This hypothesis also may explain why *I. tarsalis*, a decidedly uncommon species in traps, also appeared among the drowned animals (Table 4).

Another feature common to the ratadas of 1997 and 2001 was the reduced level of reproduction in the season following the peak. Judging by the inactive and/or immature condition of the ovaries of Spring-2 animals in *Ratada-2001*, reproduction in that season was delayed and possibly reduced. The 1997 outbreak collections were made in late spring and early summer, when reproductive activity usually is obvious, but at that time gonads were inactive (Pearson, 2002). To some ecologists the lack of reproduction by microtine rodents during the decline phase of demographic cycles is considered the central problem to understanding rodent population cycles (Christian, 1950; Boonstra, 1994).

A notable difference between the 2 outbreaks was the absence of *R. rattus* during the 1997 outbreak, whereas they became a dominant species in the forest fauna during *Ratada-2001*. This apparently was a real difference, as *R. rattus* also were present

Table 14. Similarities and differences in features of two rodent outbreaks (in 1997 and 2001) in southwestern Argentina. The information in the table is from Pearson (2002) and this report, respectively.

Features of Outbreak	Ratada-1997	Ratada-2001
Initiated by bamboo flowering	No	Yes
Latitudinal extent of outbreak	300 km	100 km
Extended breeding season in previous year	Yes (implied from ages of drowned animals)	Yes (observed in Autumn-1)
Percent trap-success in spring of peak density	*43, 62, & 63	**Live traps: 47 (range: 30-75; *N* = 7) Snap traps: 60 (range: 36-67; *N* = 7)
Body condition of animals	*O. longicaudatus*: most were fat *A. longipilis*: few were fat	*O. longicaudatus*: most were fat *A. longipilis*: fewer were fat
Rattus rattus	None observed	Became abundant
Drownings	Spring	Late winter to mid-summer
Relative species abundance among drowned animals	*O.l. > L. m. >> A. l.*	*O. l. > L. m. >> A. l.= A. o.*
Relative species abundance of trapped animals	****O. l. > A. l. >> A. o. > L. m.*	*O. l. > A. l. >> L. m.= A. o.*
Female breeding condition in season following peak density	Non-reproductive in late spring (1997)	Non-reproductive in early Spring-2 (2001)

* Pearson (2002) presented the combined success of equal numbers of live and snap traps. We present values from his Table 1 for November trappings at Lago Espejo Chico and Parque Nacional Los Alerces.

** Success values are means for Spring-2 collections from flowered bamboo habitats, computed from information in Appendix Table 2.

*** Abundances of rodent species trapped at Lago Espejo Chico on 5 and 24 November, 1997 were calculated from the records in the field catalogue of OPP.

among the drowned Lago Nonthué animals in 2001 but absent from the drowned (beach) collection in 1997. Furthermore, black rats were caught in the woods during the second outbreak but not in the earlier one, even though the same traps and the same trapping methods were used on both occasions.

In summary, these 2 outbreaks show many similarities in the responses of the main species: an extended breeding season in the autumn preceding the peak density; large stores of fat; periods of mass drownings; and lack of breeding during the reproductive season in which the decline phase occurred. The major difference between the 2 outbreaks was that one did not involve the flowering and masting of a bamboo species, whereas the other was caused by this botanical event.

Comparison of the Ratada-2001 *with Chilean Bamboo Ratadas*. Two bamboo-induced ratadas in the Valdivian forest ecosystem in Chile were described by Murúa et al. (1996) and Gallardo and Mercado (1999). A notable difference between the ratadas in the 2 countries was the time lag between the onset of bamboo flowering and the peak in rodent densities (Table 15). In our study this happened about 10 months after the *C. culeou* bamboo flowered. However, in Chile this peak occurred 18 to 21 months (i.e., in "Autumn-2", using the terminology describing the seasons of the Ratada-2001 outbreak) after the quila bamboo (*C. quila*) flowered. This evidently occurred because the ripe seed of quila is not available to the rodents until the second season after flowering (i.e., in "Summer-2"); in the study area of Murúa et al. (1996) the peak in rodent density occurred a few months after most of the year-old seed had fallen to the ground. The intensive reproduction by the rodents needed to reach this high Autumn-2 density must have occurred late in the second growing season, because in Autumn-1, when seeds were still on the plants (González and Donoso, 1999), populations of both *O. longicaudatus* and *A. olivaceus* were at typical densities (Murúa et al., 1996). We suggest 2 possible reasons for this delay in intensive reproduction in these Chilean rodents. First, rodents may not climb up quila canes as readily as they do colihue canes because the former grow high into the forest canopy whereas the latter remain in the understory. Thus, the seeds on the canes may be unavailable in sufficient amounts in Autumn-1 to allow breeding by the mice; in Chile these seeds apparently do not become an *ad libitum* food supply to the mice until they fall to the ground in Summer-2 (González and Donoso, 1999). A second possibility might be that the seeds are unpalatable while they are still on the plant. Studies of the levels of arboreal activity of the Chilean rodents and the palatability of the retained seeds are needed to learn why the rodents do not begin breeding in the season that the quila bamboo flowers. Another possible difference between the *C. culeou* and *C. quila* ratadas is the season(s) when the peak densities and declines take place. In our study area, peak rodent densities occurred in winter and the decline took place over the subsequent spring and early summer. From the limited information on Chilean ratadas, it appears that the peak density is reached in autumn and the decline occurs during the winter. Murúa et al. (1996) observed an abrupt decline, from an estimated 244 animals / ha to 0 animals / ha over a 3-month period of 'Winter-2' (using our notation for seasons during an outbreak) at their study site in Peulla. Only after more of these bamboo-caused outbreaks are described will we be able to assess how the peaks and declines in rodent populations differ depending on the species of bamboo causing the outbreak.

One similarity in Chilean and Argentine ratadas appears to be which rodent species increased in numbers during the outbreaks in the 2 countries. The most common species in all but one of the Chilean outbreaks was *Oligoryzomys* (Table 15). The apparent exception was at Peulla in July, 1995, where 93% of the animals were *A. olivaceus* according to Murúa et al. (1996). However, there seems to be a contradiction about the most common species at Peulla, because Ruiz and Simeone (2001) reported that more than 90% of 140 prey items that they identified from the feces of Kelp Gulls

Table 15. Behaviors of rodents in bamboo-caused ratadas in Argentina (this study) and in Chile. Information on the Chilean outbreaks at San Martín and Peulla are from Murúa et al. (1996), and at Puyehue, Queilen, and Yaldad are from Gallardo and Mercado (1999). Mauro E. Gonzales (pers. comm.) said that bamboo flowered at Yaldad in the spring of 1993, not the spring of 1992 as stated in Gallardo and Mercado (1999). We use the name *C. quila* for the bamboo that flowered in Chile, as suggested by M. E. Gonzales (pers. comm.).

	Outbreaks			
	This study	San Martín	Peulla	Puyehue (P), Queilen(Q), Yaldad (Y)
Species flowering	*C. culeou*	*C. quila*	*C. quila*	*C. quila*
Season of peak density (time from initial spring flowering to ratada	Winter-1 (approx. 10 months post-flowering)	Autumn-2 (approx. 18 months post-flowering)	Winter-2 (approx. 21 months post-flowering)	P: Winter (18-21 mos. post-flowering) Q & Y: Autumn-2 (approx. 18 mos. post-flowering)
Autumn breeding	Yes	--	Yes	--
Time of steepest decline	Winter-1 through Spring-2	Winter-2 (after Autumn-2	Winter-2	Not studied
Relative species diversity at peak density	*O.l.* > *A. l.* >> *A. o.* = *L. m.*	*O. l.* >> *A. o.*	*A. o.* >> *O. l.*	P: primarily *O. l.* Q: *O. l.* >>> *A. o.* Y: *O. l.* > *A. o.*
Condition of gonads at peak and in decline	Inactive in both sexes	--	--	Q: Inactive in both sexes Y: Inactive in both sexes
Autumn breeding before peak	Yes	--	Yes	--

(*Larus dominicanus*) collected in May, 1995 in the same area were *Oligoryzomys* and only 2% were *A. olivaceus*. The predominance of *Oligoryzomys* reported in most of the bamboo-induced ratadas may be because this species is the most granivorous of the Valdivian forest rodents (Pearson, 1983; Meserve et al., 1988), pre-adapting it to be the most efficient species in digesting and metabolizing bamboo seed.

Another difference following the flowering of *C. culeou* and *C. quila* may be the rarity of mass drownings during quila-ratadas. Neither Murúa et al. (1996) nor Gallardo and Mercado (1999) mentioned mass drownings in the outbreaks that they studied. But a report of aggregations of gulls feeding on dead mice along the banks of the Rio Peulla (Ruiz and Simeone, 2001) suggests that this phenomenon did occur in some areas. The absence or reduction of drownings during quila ratadas might be related to the water temperatures when the populations peak and start to decline; water temperatures at the time of the autumn peak of *quila*-ratadas would not be as cold as when *culeou*-ratadas reach their peak later in the winter and so most of the Chilean mice might not be overcome by hypothermia and survive their swim after entering the water.

Neither Murúa et al. (1996) nor Gallardo and Mercado (1999) mentioned the presence of *R. rattus* in the Chilean outbreaks, although the species has been reported from natural habitats in central Chile (Simonetti, 1983). The absence of this species would be another difference between *quila*- and *culeou*-ratadas. Gunckel (1948) quoted a report on a 1780 ratada in Valdivia, Chile, in which Ambrosio Higgins referred to drowned animals as "pericotes," which in Argentina is a vernacular name for *R. rattus*. Unfortunately there is no verification that he was using this vernacular name in the same way, rather than in reference to rodents of another species. Higgins also wrote of the flowering of "colihue" bamboo, and this raises the possibility that the "pericote" drownings he mentioned really involved *R. rattus* following the flowering of *C. culeou* rather than *C. quila*.

Predicting Ratadas in the Valdivian Forests. A recent review of rodent outbreaks in South America (Jaksic and Lima, 2003) presents a confusing picture of the frequency and distribution of bamboo ratadas in the Valdivian forest ecosystem. There are 2 reasons for this confusion. The first is that there is a poor understanding of the flowering biology of species of *Chusquea*, in spite of its distribution and importance (Judziewicz et al., 1999). Second, there have been only 2 studies of flowerings and subsequent ratadas with sufficient information about the species of bamboo and the time and place of flowering to be helpful (Murúa et al., 1996; Gallardo and Mercado, 1999). The paucity of information on the reproductive biology of *Chusquea* species is understandable in light of the decadal-long vegetative phase of the life cycle of these bamboos. Many reports of flowerings and of subsequent ratadas have been anecdotal remarks by visiting chroniclers, or a local event sufficiently noteworthy to be reported in a newspaper. Bamboos of different species have different generation times, and even within recognized species, local populations may flower in different years (Janzen, 1976). From the phenology of the flowering and seeding patterns of the Chilean and Argentine *Chusquea* we know that there are differences among species in seed dehiscence, and this has important consequences on the timing of subsequent rodent outbreaks. Recognition of this difference in seeding strategy between these 2 bamboo species clarifies why the lag between flowering and ratadas ranges from 1 to 2 years. Since the seed-holding strategies are still only known for 2 of the 12 species of *Chusquea* in the Valdivian forest (Judziewicz et al., 1999), we lack critical pieces of knowledge needed to predict the time when a ratada will occur after a particular species flowers.

Another aspect of the life histories of the Valdivian chusqueas that complicates the development of a predictive model of ratadas is lack of synchrony in flowering within the same nominal "species." Cohorts of *C. quila* flowered in different places in Chile over a 3-year period in the 1990s (Gallardo and Mercado, 1999; Jaksic and Lima, 2003). Each of these year cohorts occupied a relatively large geographical area, and a ratada developed 2 years after each cohort flowered. A similar pattern of spatially asynchronous flowering over large ranges apparently exists within *C. culeou*, as the cohort that flowered in 2000 covered about one-fifth of the 550 km long, total distribution of this species in Argentina. Even within the same area there can be cohorts that flower on different cycles. Within our study area there are 2 morphotypes of *C. culeou*. The tall (approximately 4 m high) plants flowered in 2000, while the partially sympatric shorter (2-3 m height) plants have remained green. Presumably these year- and morphological-cohorts will flower at different times and produce ratadas in different areas, but as yet we are ignorant about these temporal and geographic sequences. In Chile there may be more than one species of bamboo growing at the same locality, each on a different flowering regime. This sympatry further complicates the timing of local rodent outbreaks. The significance of this taxonomic, temporal, and geographical variability among bamboos has not been appreciated for its importance to the timing and location of ratadas. A consequence of this variability in the life cycles of the many species and populations of bamboos is that flowering and the associated rodent outbreaks may appear to be haphazard across the full range of *Chusquea*, even though this is not the case. Much more careful study of the reproductive biology of the Chilean and Argentinean chusqueas is needed before we can have a predictive science of bamboo-associated outbreaks throughout the Valdivian forest ecosystem. The current lack of predictability has important consequences for a wide range of human activities, including public health campaigns (i.e. planning for possible outbreaks of rodent-associated diseases), negative effects on tourism, and opportunities by biologists to plan studies of these uncommon events.

SUMMARY AND CONCLUSIONS

Beyond their impacts on public health and the tourism industry, how do bamboo ratadas fit into our understanding of what regulates population size in rodents? Two environmental factors (food and predation) had major impacts in *Ratada-2001*, but at different times during the outbreak. The superabundance of seed in Summer-1 and Autumn-1 certainly was the most important environmental factor promoting the increase phase that led to the high densities achieved by *Oligoryzomys*, *A. longipilis*, and *R. rattus*. The extended individual reproductive performances and/or precocial breeding of females directly caused the population densities to reach high levels. Superabundant food may also have caused a marked increase in the numbers of *L. micropus* and *I. tarsalis*, if their presence among the drowned mice in Spring-2 indicates high density and not a pathological behavior. Because there were still bamboo seeds on the ground and mice were still fat in Spring-2 while mice were dying in the lakes, we doubt that a shortage of food was an important factor causing the decline phase. Predation probably was unimportant in limiting or stopping the increase phase in

Summer-1 and Autumn-1, but may have played a major role during the decline and crash phases from Winter-1 to Autumn-2. The increased numbers of predatory birds and mammals from Winter-1 into Summer-2 probably lowered the survival chances of each individual mouse. We don't know how important this factor is, however, compared to the mortality that resulted from individuals drowning in the lakes, and we lack an explanation for the drownings. If the drownings are an incidental consequence of a dispersal 'drive', then this individual performance factor may have played a major direct role in causing population densities to decline in Spring-2 and Summer-2. We do know from the observations made by the park rangers that mice were crossing the roads and entering houses at the time that they began drowning in the lakes, but it remains to be shown that the mice that drowned were dispersing and not in the water because of a pathological condition that might be associated with their obesity and/or repressed reproductive condition. In this ratada the environmental factors of weather and habitat probably had much smaller impacts than food and predation on determining the maximal and minimal sizes of the populations.

Although another bamboo-induced ratada caused by the flowering of *C. culeou* is unlikely to happen in this particular part of the Valdivian woods during the next 60 years, we think it would be a mistake to dismiss these outbreaks as merely idiosyncratic and without instructive value. The kind of outbreak described here is infrequent within our temporal reference frame, but they are of regular occurrence. Since the Holocene began, 12,000 years ago, it is highly likely that there may have been as many as 200 or more such flowerings and associated ratadas in our study area; we know that a bamboo-induced ratada happens about every 12 to 14 years somewhere within the Valdivian forest ecosystem (Jaksic and Lima, 2003). If other cohorts of *C. culeou* each occupy similar percentages (one-fifth) of the total range of this species in Argentina as the one that flowered in 2000, then there may be as many as 4 more flowerings of the tall morphotype in the near future. Such flowerings represent what Diamond (1986) called 'natural perturbation experiments,' where an *ad libitum* amount of food is added to the environment over a large area. From this perspective, each of the future bamboo flowerings offer ecologists a natural experimental system in which to test ideas concerning (1) What limits populations?; (2) What prevents further population growth?; and (3) What limits density in habitats of different quality? These are the questions that Krebs (2002) considers most important for understanding the general process of population regulation and limitation.

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APPENDIX TABLE 1

Weighted mean success (percent) with live (L) or snap (S) traps on the ground, Neuquén Province, Argentina. Number of mice captured and the number of traps set in a trapline during each night of a collecting period are shown within parentheses. No traps were set at some localities during different collecting periods. We did not correct our results for traps that were closed or sprung and empty.

	Flowered bamboo habitats					Green bamboo habitats	
Collecting period	Laguna Verde	Currhué Chico	Hua Hum	Yuco	Traful North	Traful South-1	Traful South-2
Spring-1	L = 5% (2/40) S = 2% (1/40)	L = 28% (11/40) S= 25% (10/40)	L = 6% (4/50, 2/50) S = 3% (3/50, 0/50)	L = 7% (3/45) S = 7% (3/45)	--	--	--
Autumn-1	--	L = 62% (27/45, 4/5) S = 74% (36/45, 1/5)	L = 18% (9/50) S = 56% (28/50)	L = 45% (18/40) S = 49% (19/39)	--	--	--
Spring-2	--	L=43% (9/16, 4/9, 5/14, 3/10) S = 54% (10/16, 4/11, 5/8)	L = 54% (15/20, 7/20, 5/10) S = 64% (13/21, 14/21, 14/21, 6/10)	--	L = 36% (5/14, 4/7, 3/12) S = 73% (7/8, 4/7, 5/7)	L = 18% (2/14, 2/12, 1/12, 4/12) S = 36% (2/8, 4/6, 2/7, 2/7)	L = 29% (6/14, 4/14, 2/14) S = 42% (4/8, 4/8, 2/8)

Appendix Table 1 (continued)							
Autumn-2	--	L = 10% (3/40, 3/40, 6/41)	L = 7% (2/14, 1/36, 5/59)	L = 10% (6/40, 0/20)	L = 19% (7/21, 5/41)	L = 27% (6/20, 6/25)	L = 41% (9/20, 10/26)
Autumn-3	--	L = 33% (7/29, 9/20) S = 50% (3/6)	L = 8% (2/12, 1/20, 0/7) S = 82% (6/6, 5/6, 3/5)	L = 29% (9/20, 4/15) S=100% (6/6, 6/6)	L = 29% (6/19, 5/20, 3/12) S = 78% (5/6, 9/12)	L = 3% (1/13, 0/20) S = 64% (3/5, 4/6)	L = 12% (2/20, 3/20) S = 58% (5/9, 6/10)

APPENDIX TABLE 2

Total number of individuals and numbers and sex of 8 species of rodents collected during 5 periods in Neuquén Province, Argentina. The general name of each site is as given in Table 1. The sample size in each collecting period is shown inside parentheses and separated from one another with a slash (/) mark, i.e. (Spring-1/Autumn-1/Spring-2/Autumn-2/ Autumn-3). A dash (-) for the Spring-2 period at Yuco indicates that no trapping was done then. Collections were made only once at Laguna Verde (Spring-1) and Lago Nonthué (Spring-2). At Traful North, Traful South-1, and Traful South-2 collections were made in Spring-2, Autumn-2, and Autumn-3, and the information shown is for these 3 periods.

Species	Sex	Laguna Verde	Currhué Chico	Hua Hum	Lago Nonthué	Yuco	Traful North	Traful South-1	Traful South-2
Oligoryzomys longicaudatus (313)	f	0	49 (11/15/14/7/2)	34 (2/12/16/2/2)	20	8 (2/1/-/1/4)	9 (5/1/3)	4 (3/0/1)	6 (3/3/0)
	m	1	65 (8/31/16/5/5)	50 (4/9/24/3/10)	23	9 (1/1/-/1/6)	9 (6/1/2)	13 (8/2/3)	13 (7/4/2)
Abrothrix longipilis (217)	f	2	24 (1/13/3/0/7)	36 (1/19/15/0/1)	1	17 (1/16/-/0/0)	5 (2/0/3)	12 (3/7/2)	6 (1/3/2)
	m	0	18 (0/8/2/2/6)	27 (1/10/13/0/3)	0	18 (3/15/-/0/0)	26 (6/5/15)	9 (4/1/4)	16 (5/6/5)
Abrothrix olivaceus (101)	f	0	22 (0/12/5/0/5)	5 (0/1/0/0/4)	1	4 (0/0/-/0/4)	8 (4/2/2)	4 (1/3/0)	2 (1/0/1)
	m	0	13 (0/8/4/0/1)	13 (1/8/1/0/3)	3	11 (0/0/-/0/11)	9 (4/1/4)	1 (1/0/0)	5 (1/2/2)

Appendix Table 2 (continued).									
Loxodontomys micropus (67)	f	0	5 (1/4/0/0/0)	2 (0/1/1/0/0)	18	0	0	1 (1/0/0)	3 (1/0/2)
	m	0	1 (0/0/1/0/0)	2 (0/0/2/0/0)	32	0	1 (1/0/0)	1 (0/1/0)	1 (0/1/0)
Rattus rattus (24)	f	0	1 (0/0/0/1/0)	2 (0/0/0/2/0)	7	2 (0/0/-/2/0)	0	0	0
	m	0	1 (0/1/0/0/0)	4 (0/0/0/4/0)	5	2 (0/0/-/2/0)	0	0	0
Irenomys tarsalis (12)	f	0	0	0	5	0	1 (0/0/1)	1 (0/0/1)	0
	m	0	1 (0/0/0/0/1)	2 (1/1/0/0)	2	0	0	0	0
Geoxus valdivianus (9)	f	0	1 (0/1/0/0/0)	1 (0/0/0/0/1)	0	1 (0/1/-/0/0)	2 (0/0/2)	0	0
	m		1 (0/0/0/0/1)	2 (0/0/1/0/1)	0	0	0	1 (0/1/0)	0
Chelemys macronyx (7)	m	0	0	1 (0/0/0/1/0)	0	0	1 (0/0/1)	2 (0/2/0)	3 (1/0/2)
Locality totals:		3	202	181	117	72	71	49	55

LITERATURE CITED

Abramsky, Z., M. L. Rosenzweig, B. Pinshow, J. S. Brown, B. P. Kotler, and W. A. Mitchell

1990 Habitat selection: an experimental field test with two gerbil species. Ecology 71:2358-2369.

Anonymous

2001a Horda de roedores apareció en Maihue. El Diario Austral de Valdivia, 25 August, pp. A12-13.

2001b Invasión de colilargos llegó al Lago Riñihue. El Diario Austral de Valdivia, 24 August, pp. A17.

Baro, M., J. Vergara, and M. Navarrete

1999 Hantavirus en Chile: revisión y análisis de casos desde 1979. Rev. Med. Chil. 127:1513-1523.

Batzli, G. O., and E. Esseks

1992 Body fat as an indicator of nutritional conditions for the brown lemming. Journal of Mammalogy 73:431-439.

Boonstra, R.

1994 Population cycles in microtines: the senescence hypothesis. Evolutionary Ecology 8:196-219.

Calderon, G., N. Pini, J. Bolpe, S. M. Levis, J., E. Segura, N. Guthmann, G. Cantoni, J. Becker, A. Fonollat, C. Ripoll, M. Bortman, R. Benedetti, M. Sabattini, and D. Enria

1999 Hantavirus reservoir hosts associated with peridomestic habitats in Argentina. Emerging Infectious Diseases 5:792-797.

Christian, J. J.

1950 The adreno-pituitary system and population cycles in mammals. Journal of Mammalogy 31:247-259.

Cockrum, E. L.

1962 Introduction to Mammalogy. The Ronald Press Co., New York, New York, USA. 116 pp.

Coleman, D. L., and K. P Hummel

1967 Studies with the mutation, diabetes, in the mouse. Diabetologia 3:238-248.

Contreras, J.

1972 El home range en una población de *Oryzomys longicaudatus philippi* (Landbeck) (Rodentia, Cricetidae). Physis (Buenos Aires) 31:353-361.

Darlington, R. B., and T. V. Smulders.
2001 Problems with residual analysis. Animal Behaviour 62:599-602.

de Zegher, F., and L. Ibáñez.
2004 Novel insights into the endocrine-metabolic and reproductive consequences of prenatal growth restraint in girls. Girls-born-small become women-born-small. Verhandelingen - koninklijke academie voor geneeskunde van belgie 66:353-382.

Derting, T. L.
1989 Metabolism and food availability as regulators of production in juvenile cotton rats. Ecology 70:587-595.

Diamond, J.
1986 Overview: laboratory experiments, field experiments, and natural experiments. Pp. 3-22 in Community Ecology (Diamond, J., and T. J. Case, eds.). Harper & Row, Publishers, New York, New York, USA.

Dimitri, M. J.
1959 Aspectos fitogeograficos del Parque Nacional Lanín. Anales de Parques Nacionales 8:95-122.

Duncan, C. J., and S. Scott
2004 The key role of nutrition in controlling human population dynamics. Nutrition Research Reviews 17:163-175.

Fitzgerald, B. M., M. G. Efford, and B. J. Karl
2004 Breeding of house mice and the mast seeding of southern beeches in the Orongorongo Valley, New Zealand. New Zealand Journal of Zoology 31:167-184.

Francis, D., J. Diorio, D. Liu, and M. J. Meaney
1999 Nongenomic transmission across generations of maternal behavior and stress responses in the rat. Science 286:1155-1158.

Gallardo, M. H., and C. L. Mercado
1999 Mast seeding of bamboo shrubs and mouse outbreaks in southern Chile. Mastozoología Neotropical 6:103-111.

González, L. A., R. Murúa, and C. Jofré
1989 The effect of seed availability on population density of *Oryzomys* in southern Chile. Journal of Mammalogy 70:401-403.

González, M. E., and C. Donoso
1999 Producción de semillas y hojarasca en *Chusquea quila* (Poaceae: Bambusoideae), posterior a su floración sincrónica en la zona centro-sur de Chile. Revista Chilena de Historia Natural 72:169-180.

Good, D. J., F. D. Porter, K. A. Mahon, A. F. Parlow, H. Westphal, and I. R. Kirsch
1997 Hypogonadism and obesity in mice with a targeted deletion of the Nhlh2 gene. Nature Genetics 15:397-401.

Gunckel, H.
1948 La floración de la quila y del colihue en la Araucania. Ciencia e Investicación. 4:91-95.

Hansson, L., and H. Henttonen
1985 Regional differences in cyclicity and reproduction in *Clethrionomys* species: are they related? Annales Zoologici Fennici 22:277-288.

Hellman, B.
1967 Some metabolic aspects of the obese-hyperglycemic syndrome in mice. Diabetologia 3:222-229.

Herrenkohl, L. R.
1979 Prenatal stress reduces fertility and fecundity in female offspring. Science 206:1097-1099.

Holemans, K., L. Aerts, and F. A. Van Assche
1998 Fetal growth and long-term consequences in animal models of growth retardation. European Journal of Obstetrics, Gynecology and Reproductive Biology 81:149-156.

Jaksic, F. M., and M. Lima
2003 Myths and facts on ratadas: bamboo blooms, rainfall peaks and rodent outbreaks in South America. Austral Ecology 28:237-251.

Janzen, D. H.
1976 Why bamboos wait so long to flower. Annual Review of Ecology and Systematics 7:347-391.

Jensen, T. S.
1982 Seed production and outbreaks of non-cyclic rodent populations in deciduous forests. Oecologia 54:184-192.

Judziewicz, E. J., L. G. Clark, X. Londono, and M. J. Stern
1999 American Bamboos. Smithsonian Institution Press, Washington, D.C., USA. 392 pp.

Kelt, D. A.
1994 The natural history of small mammals from Aisén Region, southern Chile. Revista Chilena de Historia Natural 67:183-207.

2000 Small mammal communities in rainforest fragments in central and southern Chile. Biological Conservation 92:345-358.

Kelt, D. A., P. L. Meserve, L. K. Nabors, M. L. Forister, and J. R. Gutiérrez
2004 Foraging ecology of small mammals in semiarid Chile: the complex interplay of biotic and abiotic effects. Ecology 85:383-397.

Krebs, C. J.
2002 Beyond population regulation and limitations. Wildlife Research 29:1-10.

Krebs, C. J., and J. H. Myers
1974 Population cycles in small mammals. Advances in Ecological Research 8:267-399.

Krebs, C. J., and G. R. Singleton
1993 Indices of condition for small mammals. Australian Journal of Zoology 41:317-323.

Lambin, X., and N. G. Yoccoz
2001 Adaptive precocial reproduction in voles: reproductive costs and multivoltine life-history strategies in seasonal environments. Journal of Animal Ecology 70:191-200.

Lazaro, M. E., A. J. Resa, C. M. Barclay, L. Calanni, L. Samengo, L. Martinez, P. J. Padula, N. Pini, M. B. Lasala, B. Elsner, and D. A. Enria
2000 Sindrome pulmonar por Hantavirus en el sur andino argentino. Medicina (Buenos Aires) 60:289-301.

Marchlewska-Koj, A., M. Kruczek, J. Kapusta, and E. Pochroń
2003 Prenatal stress affects the rate of sexual maturation and attractiveness in bank voles. Physiology and Behavior 79:305-310.

Meserve, P. L., B. K. Lang, and B. D. Patterson
1988 Trophic relationships of small mammals in a Chilean temperate rainforest. Journal of Mammalogy 69:721-730.

Murúa, R., and L. A. González
1986 Regulation of numbers in two Neotropical rodent species in southern Chile. Revista Chilena de Historia Natural 59:193-200.

Murúa, R., L. A. González, M. González, and C. Jofré
1996 Efectos del florecimiento del arbusto *Chusquea quila* Kunth (Poaceae) sobre la demografía de poblaciones de roedores de los bosques templados frios del sur Chileno. Boletín de la Sociedad de Biología de Concepción, Chile 67:37-42.

Murúa, R., L. A. González, and M. Lima
2003a Second-order feedback and climatic effects determine the dynamics of a small rodent population in a temperate forest of South America. Population Ecology 45:19-24.

2003b Population dynamics of rice rats (a Hantavirus reservoir) in southern Chile: Feedback structure and non-linear effects of climatic oscillations. Oikos 102:137-145.

Murúa, R., L. A. González, and P. L. Meserve
1986 Population ecology of *Oryzomys longicaudatus philippii* (Rodentia: Cricetidae) in southern Chile. Journal of Animal Ecology 55: 281-293.

Murúa, R., P. L. Meserve, L. A. González, and C. Jofré
1987 The small mammal community of a Chile and temperate rain forest: lack of evidence of competition between dominant species. Journal of Mammalogy 68:729-738.

Osadchuk, L. V., B. O. Braastad, A. L. Hovland, and M. Bakken
2003 Handling during pregnancy in the blue fox (*Alopex lagopus*): the influence on the fetal gonadal function. General and Comparative Endocrinology 132:190-197.

Patterson, B. D., P. L. Meserve, and B. K. Lang
1989 Distribution and abundance of small mammals along an elevational transect in temperate rainforests of Chile. Journal of Mammalogy 70:67-78.

1990 Quantitative habitat associations of small mammals along an elevational transect in temperate rainforests of Chile. Journal of Mammalogy 71:620-633.

Pearson, A. K., O. P. Pearson, and I. A. Gomez
1994 Biology of the bamboo *Chusquea culeou* (Poaceae: Bambusoideae) in southern Argentina. Vegetatio 111:93-126.

Pearson, O. P.
1975 An outbreak of mice in the coastal desert of Peru. Mammalia 39: 375-386.

1983 Characteristics of a mammalian fauna from forests in Patagonia, southern Argentina. Journal of Mammalogy 64:476-492.

1992 Reproduction in a South American mouse, *Abrothrix longipilis*. Anatomical Record 234:73-88.

2002 A perplexing outbreak of mice in Patagonia, Argentina. Studies on Neotropical Fauna and Environment 37:187-200.

Pearson, O. P., and A. K. Pearson
1982 Ecology and biogeography of the southern rain forests of Argentina. Pp. 129-142 in Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, University of Pittsburg Special Publications Series 6, Pittsburgh, Pennsylvania, USA.

Pollard, I.
1986 Prenatal stress effects over two generations in rats. Journal of Endocrinology 109:239-244.

Pollard, I., and S. L. Dyer
1985 Effects of stress administered during pregnancy on the development of fetal testes and their subsequent function in the adult rat. Journal of Endocrinology 107:241-245.

Price, M. V., N. M. Waser, and T. A. Bass
1984 Effects of moonlight on microhabitat use by desert rodents. Journal of Mammalogy 65:353-356.

Pucek, Z., W. Jędrzejewski, B. Jędrzejewska, and M. Pucek
1993 Rodent population dynamics in a primeval deciduous forest (Białowieża National Park in relation to weather, seed crop, and predation. Acta Theriologica 38:199-232.

Ruiz, J., and A. Simeone
2001 Feeding by Kelp Gulls on rodents during a mouse outbreak at an island area in southern Chile. Waterbirds 24:118-120.

Sanguinetti, J., and L. García
2001 Floración masiva de *Chusquea culeou* en el Parque Nacional Lanín. Unpublished report (January), pp. 1-19, Administración de Parques Nacionales.

Seal, S. C., S. C. Ghosal, and P. N. Bose
1951 Notes on the bamboo flowering, migration of rats and their unusual mortality in certain districts of North Assam. Calcutta Medical Journal 48:149-155, 195-199.

Simonetti, J. A.
1983 Occurrence of the black rat (*Rattus rattus*) in central Chile. Mammalia 47:131-132.

Tanaka, R.
1956 Fluctuation in vole populations following the widespread synchronous flowering of bamboo-grasses on Mt. Turugi. Bulletin of Kochi Women's College 4:61-68.

1957 An ecological review of small-mammal outbreaks with special reference to their association with the flowering of bamboo grasses. Bulletin of Kochi Women's College 5:20-30.

Veblen, T. T., C. Donoso, T. Kitzberger, and A. J. Rebertus
1996 Ecology of southern Chilean and Argentinean *Nothofagus* forests. Pp. 293-353 in The Ecology and Biogeography of *Nothofagus* Forests (Veblen, T.T., R. S. Hill, and J. Read, eds.). Yale University Press, New Haven, Connecticut, USA.

Veblen, T. T., F. M. Schlegel, and J. V. Oltremari
1983 Temperate broad-leaved evergreen forests of South America. Pp. 5-31 in Temperate Broad-leaved Evergreen Forests Of South America (Ovington, J. D., ed.). Elsevier, Amsterdam, The Netherlands.

Ward, I.
1972 Prenatal stress feminizes and demasculinizes the behavior of males. Science 175:82-84.

Wilcox, K.
1996 Chile's Native Forests. NW Wild Books, Bellingham,Washington, USA. 148 pp.

Yunger, J. A., P. L. Meserve, and J. R. Gutiérrez
2002 Small-mammal foraging behavior: mechanisms for coexistence and implication for population dynamics. Ecological Monographs 72:561-577.

TROPHIC RELATIONSHIPS WITHIN A HIGHLAND RODENT ASSEMBLAGE FROM MANU NATIONAL PARK, CUSCO, PERU

RELACIONES TRÓFICAS DENTRO DE UN ENSAMBLE DE ROEDORES DE ALTURA EN EL PARQUE NACIONAL DEL MANU, CUSCO, PERÚ

Sergio Solari

I did not have an opportunity to met Dr. Oliver Pearson; my first approach to him was through his classical papers on highland rodents. Although I am not a "rodent person", I became familiar with these references as I developed this research. My former advisor, Víctor Pacheco, put 3 of those papers on my desk after our first field trip to Acjanaco: "Mammals of the highlands of southern Peru" (1951), "A taxonomic review of the rodent genus Phyllotis*" (1958), and "The diversity and abundance of vertebrates along an altitudinal gradient in Peru" (1978). Eventually, I made use of more of his papers for new projects and was always impressed by how clearly he wrote about his many and broad interests. His knowledge and enthusiasm in regard to the small mammals, so evident in his writings, has been a permanent motivation for my research; I only hope this paper may properly express my gratitude for his enormous contribution to our knowledge on the Neotropical mammal fauna.*

ABSTRACT

Analysis of stomach contents were performed for 5 species of sigmodontine rodents from a highland assemblage at Manu National Park, Peru (3400-3500 m), including *Akodon subfuscus*, *A. torques*, *Oxymycterus paramensis*, *Phyllotis osilae*, and *Oligoryzomys* sp. Indices of niche breadth and overlap were calculated, and interspecific and intraspecific variation were assessed with analysis of variance. Consumption of arthropods (adults and larvae) was predominant in the akodontines, comprising >60% of diet by volume. *Phyllotis osilae* had the greatest niche breadth, whereas *O. paramensis* had the least niche breadth and the lowest coefficient of variation (arthropod larvae, 18.1%). Niche overlap was higher between species of *Akodon* (0.98), and lower between *P. osilae* and *O. paramensis* (0.25). Differences among the 5 species, as well among the 3 most abundant ones, were statistically significant, with all variables showing significant differences in univariate tests. Considering either season or gender, and their interaction with

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taxonomic diversity (i.e., species), differences were not significant among *Oxymycterus* and the 2 *Akodon* species. Intraspecific differences were found only for *A. subfuscus*, which showed seasonal variation, mostly in consumption of vascular plant tissue. These findings confirm that local patterns of resource use depend on resource availability, and that food is rarely a key factor for ecological segregation in these rodent assemblages. Rather, habitat segregation appears to be the main mechanism to reduce competition in this and other rodent assemblages in South America.

Key words: Trophic niche, ecology, highland rodents, Akodontini, Peru

RESUMEN

Análisis de contenidos estomacales fueron llevados a cabo para 5 especies de roedores sigmodontinos de un ensamble altoandino en el Parque Nacional Manu, Perú (3400-3500 m), incluyendo *Akodon subfuscus*, *A. torques*, *Oxymycterus paramensis*, *Phyllotis osilae*, y *Oligoryzomys* sp. Indices de amplitud y sobreposición de nichos fueron calculados, y la variación interespecífica e intraespecífica fueron evaluadas mediante análisis de varianza. El consumo de artrópodos (adultos y larvas) fue predominante en los akodontinos, comprendiendo >60% del volumen de la dieta. *Phyllotis osilae* tuvo la mayor amplitud de nicho, mientras que *O. paramensis* tuvo la menor amplitud de nicho y el menor coeficiente de variación (larvas de artrópodos, 18.1%). La sobreposición de nichos fue más alta entre especies de *Akodon* (0.98), y más baja entre *P. osilae* y *O. paramensis* (0.25). Las diferencias entre las 5 especies, así como entre las 3 más abundantes, fueron estadísticamente significativas, con todas las variables mostrando diferencias significativas en las pruebas univariadas. Considerando únicamente estaciones o sexo, y su interacción con la diversidad taxonómica (i.e., especies), las diferencias fueron no significativas entre *Oxymycterus* y las dos especies de *Akodon*. Diferencias intraespecificas fueron encontradas solo para *A. subfuscus*, el cual mostró variación estacional, principalmente en el consumo de tejido vascular. Estos hallazgos confirman que los patrones locales de uso de recursos dependen de la disponibilidad de recursos, y que el alimento es raramente un factor clave para la segregación ecológica en estos ensambles de roedores. Mas bien, la segregación de habitat parece ser el mayor mecanismo para reducir la competencia en éste y otros ensambles de roedores en Sudamérica.

Palabras claves: Nicho trófico, Ecología, Roedores Alto Andinos, Akodontini, Perú

INTRODUCTION

Empirical studies show that animals partition environmental resources along 3 basic axes: space, food, and time (Pianka, 1973). Food habits may be critical for niche segregation (Glanz, 1984; Gliwicz, 1987), but the importance of this niche axis depends on the local availability of food resources and microhabitats (Schoener, 1974; M'Closkey, 1976; Meserve et al., 1988). Active niche segregation during community assembly may allow for species coexistence (Goodyear, 1992), but segregation also plays a role in the reduction of interspecific competition and subsequently, in maintenance of community equilibrium (Brown et al., 1986; Vitt et al., 2000).

The degree and extent of competition between 2 species may be influenced by their morphological and ecological similarity (Pianka, 1973). Closely related species might be more likely to compete with each other for a limiting resource when they occur in sympatry than in allopatry (Wolff, 1996). Competition is reduced through spatially variable niche parameters, geographic variation in the diet of a species is a valuable test of the extent of this plasticity (Pizzimenti and De Salle, 1980; Meserve et al. 1988).

A valid approach to the study of ecological communities is to focus on a taxonomic group, in this case I will refer to the assemblage (see Patterson et al., 2003) of sigmodontine rodents, to test hypotheses concerning community processes. Studies of ecological relationships in rodent assemblages of South America are not extensive; in Peru these include works by Dorst (1958, 1971, 1972a, 1972b), Pearson and Ralph (1978), and Pizzimenti and De Salle (1980, 1981). However, research in Chile (Meserve, 1981; Rau et al., 1981; Glanz, 1984; Meserve et al., 1988; Kelt et al., 1994), Argentina (Dalby, 1975; Pearson, 1983; Suarez and Bonaventura, 2001), and other countries (for reviews see Glanz, 1982 and O'Connell, 1982) have increased our knowledge of trophic relationships, with 2 main findings: (1) levels of insectivory vary geographically among similar assemblages, and (2) local patterns of resource use depends of the availability of resources.

As part of a project to assess biological diversity in the highlands of Manu National Park, I sampled small mammals in habitats surrounding the Puesto de Vigilancia Acjanaco. Among the 5 sigmodontine species recorded, 3 mice of the tribe Akodontini were the most abundant (*Akodon subfuscus*, *A. torques*, and *Oxymycterus paramensis*); captures of 2 other species (*Phyllotis osilae* and *Oligoryzomys* sp.) were insufficient for some analyses. Here, I analyze the diet of these 5 species and interpret these results in terms of assemblage structure. Given the abundance of Akodontines, the equilibrium of this assemblage may ultimately depend on the way their niches are related.

STUDY AREA AND METHODS

The study area is located in the highland grasslands ("pajonal") of Manu National Park, Paucartambo Province, on the humid Puna of the Cordillera Oriental, Cusco, Peru. The habitat extends as a narrow strip, ranging from 3300 to 3800 m, and intergrades on its lower boundary with the montane cloud forest (Cano et al., 1995). Dominant vegetation includes bunchgrasses of the genera *Calamagrostis*, *Festuca*, and *Stipa* (Poaceae). These bunches cover 0.25-0.75 m2, are about 1 m tall, and are interspersed with small forbs such as *Werneria*, *Hypochaeris*, and *Senecio* (Asteraceae), *Geranium* (Geraniaceae), and *Gentiana*, *Gentianella*, and *Halenia* (Gentianaceae). An additional element was patches of the shrub *Baccharis* spp. (Asteraceae), which occurred throughout the study area (Cano, 1994).

Sampling was conducted near Puesto de Vigilancia Acjanaco (71° 22′ W, 13° 07′ S), 32 km NE (by road) Paucartambo, at about 3450 m. Daily mean temperature ranged from 6 to 15 °C, and relative humidity was approximately 30%. A dry season occurs from June to August, and most precipitation falls from December to April (Cano et al., 1995). Trapping was conducted in both dry (August and September 1990, July 1991) and wet (March 1991) seasons to include seasonal climatic variation in the area.

Three trapping grids were established, with 5 lines of 12 stations each, separated by 8-10 m. At each station I placed 1 Victor snap trap, and a single Sherman live trap was placed at every other station. These 90 (60 Victor and 30 Sherman) traps were baited and checked twice daily (morning and evening), and trapping periods lasted 2 weeks. Stomachs were preserved in 70% ethanol.

For dietary analysis, each stomach was opened and the contents washed over a silk screen and physically homogenized (Meserve, 1981). Empty or almost empty stomachs were not considered. Stomach contents were boiled and cleared in a 10% sodium hydroxide solution (Hansson, 1970). Two subsamples, one containing large fragments and another with smaller parts, were taken from each stomach for analyses. Large fragments were examined and quantified from 10 optic fields using a stereomicroscope at 40X, using percent cover as a measure of volume. For the smaller fragments, 1 aliquot was spread over a microscope slide and covered with a cover slip; 10 optic fields at 100X were used to examine and quantify the composition of this subsample. For both quantifications, cover was approximated to the nearest 5%. Subtotals were pooled in a single estimate of trophic preferences for each specimen. Percentages of total identified material were taken as a measure of food volume in diet (Gebczynska and Myrcha, 1966); this is considered to be more reliable than unadjusted frequencies of occurrence (Hansson, 1970).

Results of this analysis were tabulated and summarized for each individual, along with information about species, sex, date (season), and time of capture (e.g., morning vs. evening). Average diets according to these categories were calculated for all the rodents, although 2 species had too few captures to determine any sort of variation. For the sake of comparisons, only 6 categories are used in subsequent analyses: arthropod larvae, adult arthropods, monocot epidermis, dicot epidermis, vascular plant tissues, and other (e.g., unidentified, seeds, pollen). To document degrees of specialization I calculated the coefficient of variation (CV) for each main food item for each species; I consider CV values below 25% as indicatives of some preference for those food items.

I assessed patterns of resource use and similarity between diets using indices of niche breadth and overlap (see Krebs, 1989), respectively. Niche breadth was estimated with Levins' Index (Levins, 1968) as follows:

$$B = 1 / \Sigma p_j^2,$$

where p_j is the proportion of resource j in the diet. Levins' index varies between a minimum (1) and a maximum breadth (N food categories, 6 in this case).

By using percent of volume of each item I obtained overlap indices, which may indicate degree of competition for such specific resource category (Sale, 1974). I used Pianka's Symmetric Overlap Index and the Modified Morisita's Index. Pianka's Index (Pianka, 1973) is calculated as:

$$O_{jk} = \Sigma p_{ij}p_{ik} / \sqrt{\ } \Sigma p_{ij}^2 \Sigma p_{ik}^2,$$

and the Morisita's Index (Horn, 1966) as:

$$C_H = 2 \Sigma p_{ij}p_{ik} / \Sigma p_{ij}^2 + \Sigma p_{ik}^2,$$

where, p_{ij} and p_{ik} are the proportion of the food category i in the diet of species j or k.

Overlap indices (OI) are considered to be high for values above 0.75, and low if below 0.50.

Multivariate analyses of variance (MANOVA) were used to assess variation across species, season, and gender, as well as their interaction. In the case of intraspecific variation, the MANOVA tests included season and gender variation, as well as their interaction. Between-subjects effects (univariate test) were evaluated when significant differences occurred in the MANOVA tests. Differences were considered significant at $p < 0.05$. All statistical analyses were performed using MINITAB 12.

RESULTS

A total of 118 animals was collected, representing 5 sigmodontine species: *Oligoryzomys* sp. B, *Phyllotis osilae*, *Akodon subfuscus*, *A. torques*, and *Oxymycterus paramensis* (Pacheco et al., 1993). The most abundant species were *A. subfuscus* and *A. torques* (35% of total captures) and *O. paramensis* (26%), which would be expected for this habitat (Dorst, 1971; Pearson and Ralph, 1978; O'Connell, 1982; Reig, 1986). Captures of *Oligoryzomys* sp. B and *Phyllotis osilae* were insufficient to allow some analyses, but statistical differences in diet between and within species could be detected.

For the analyses of stomach contents only 67 individuals were considered, because samples of *Akodon* spp. from 1990 were not included. High proportions of arthropod (adults plus larvae) consumption were recorded for all 3 Akodontines (Fig. 1), with a mean of 59.3% for *Akodon subfuscus*, 65.46% for *A. torques*, and 72.96% for *Oxymycterus paramensis*. On the other hand, *Oligoryzomys* sp. B had an apparent tendency towards omnivory, with a high proportion of seeds and arthropods, and *Phyllotis osilae* had more than 64% of its diet composed by plant material (Table 1).

Oxymycterus paramensis was primarily insectivorous, feeding mainly on arthropod larvae (57.3%, Table 1), with a greater consumption among males, and also during the wet season (Table 2). Adult arthropods were the second item of importance (Table 1). This species was predominantly insectivorous, with a clear specialization towards consumption of arthropod larvae (Table 2). The total proportion of plant material was even less than of adult arthropods (Table 1).

Akodon torques also was insectivorous, with arthropod larvae comprising the main proportion of its diet (39.3%, Table 1), and more so for males than females (Table 2). The consumption of adult arthropods by this species showed some variation between males and females, and between seasons (Table 2). This percentage was slightly higher than that of plant material (Table 1).

For *Akodon subfuscus*, consumption of adult arthropods (29.9%) was very similar to that of arthropod larvae (Table 1). These categories showed little variation among sexes or seasons (Table 2), although plant material was more important than for all other akodontines, comprising 26% of the total volume (Table 1).

We only captured 2 individuals of *Phyllotis osilae* during our sampling. Both showed strong dependence on plant material, comprising over 64% of the diet. Vascular plant tissue was the most important single category (Table 1).

Two samples were also available for *Oligoryzomys* sp. B, but they were so dissimilar that even general insights to the diet of this species are tenuous. However, arthropod larvae were consistently high in both individuals, with a mean consumption of 39.5%, followed by total plant material (Table 1). Stomach contents of 1 individual contained

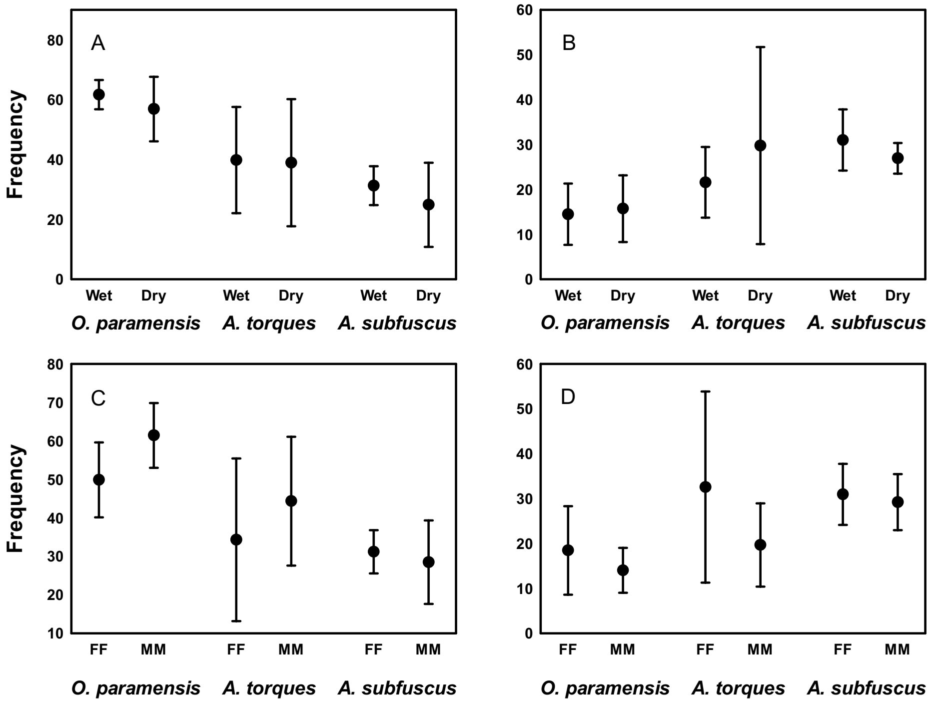

Figure 1. Seasonal and gender-related variation in consumption of arthropods (mean + 1 SD) for 3 species of akodontine rodent. A: Seasonal (wet vs. dry) variation in arthropod larvae. B: Seasonal (wet vs. dry) variation in adult arthropods. C: Sexual (females vs. males) variation in arthropod larvae. D: Sexual (females vs. males) variation in adult arthropods.

33% seeds.

To avoid spurious results using the coefficient of variation (CV), only species with more than 10 stomachs were included; this constrained analysis to only 3 species. The lowest CVs for *O. paramensis* corresponded to arthropod larvae (18.1%), for *A. subfuscus*, this was adult arthropods (20.9%) and, for *A. torques*, no category showed CV values < 25%.

Use and Overlap of Food Resources

Based on these data, niche breadth using Levins' metric (Krebs 1989) ranged from 2.65 in *O. paramensis* to 4.53 in *A. subfuscus* (Table 1). Levins' values tend to a maximum when resources are used in similar proportions, which is the case when species do not discriminate among resources. Thus, on a relative scale, these values suggest that within this assemblage *O. paramensis* acts as a "specialist," and *A. subfuscus* as a "generalist."

Niche overlap measures ranged from low (0.25, between *O. paramensis* and *P. osilae*) to quite high (0.98, between *A. torques* and *A. subfuscus*). High overlap is indicative of

Table 1. Food habits for the 5 rodent species (sample size) of the highland assemblage in Manu National Park. Weight and percent consumption of each food category expressed as mean (standard deviation). Niche breadth based on Levins' index.

		Arthropods				Vascular		Niche
Species	Weight	Larvae	Adults	Monocot	Dicot	Plant Tissue	Others	Breadth
O. paramensis	64.87	57.34	15.62	4.64	3.94	4.69	13.77	2.65
(*N* = 31)	(15.89)	(10.41)	(7.26)	(2.92)	(2.19)	(2.18)	(6.59)	
A. torques	27.25	39.34	26.13	6.26	6.63	8.13	13.51	3.90
(*N* = 18)	(3.64)	(19.19)	(17.26)	(3.29)	(4.42)	(5.48)	(10.10)	
A. subfuscus	25.68	29.46	29.86	8.88	6.33	10.85	14.62	4.53
(*N* = 14)	(7.05)	(9.14)	(6.24)	(6.29)	(1.69)	(4.34)	(5.21)	
P. osilae	34.00	0.0	2.30	22.70	14.80	26.60	33.60	3.88
(*N* = 2)	(2.12)	(--)	(1.27)	(6.65)	(13.29)	(18.95)	(40.16)	
Oligoryzomys sp. B	19.50	39.50	6.90	12.50	3.80	8.50	28.80	3.73
(*N* = 2)	(0.71)	(9.19)	(8.63)	(13.15)	(0.85)	(4.95)	(25.17)	

Table 2. Variation of food habits for 3 akodontine rodents in the Peruvian highlands. Percent consumption is expressed as mean consumption (standard deviation) of each food category, according to gender and season.

	Arthropods				
	Larvae	Adults	Monocot	Dicot	Vascular Plant Tissues
			Oxymycterus paramensis		
Males ($N = 20$)	61.45 (8.42)	14.05 (5.00)	3.90 (2.11)	4.10 (2.00)	4.42 (2.07)
Females ($N = 11$)	49.88 (9.75)	18.48 (9.85)	5.98 (3.75)	3.65 (2.57)	5.19 (2.38)
Wet ($N = 3$)	61.67 (4.88)	14.50 (6.84)	3.27 (1.81)	3.00 (1.80)	3.97 (1.26)
Dry ($N = 28$)	56.88 (10.78)	15.74 (7.42)	4.78 (3.00)	4.04 (2.23)	4.77 (2.26)
			Akodon torques		
Males ($N = 9$)	44.36 (16.73)	19.68 (9.29)	6.12 (2.78)	6.88 (4.99)	8.01 (5.86)
Females ($N = 9$)	34.32 (21.12)	32.59 (21.28)	6.39 (3.91)	6.39 (4.07)	8.26 (5.42)
Wet ($N = 8$)	39.81 (17.74)	21.59 (7.87)	5.83 (3.02)	5.38 (1.36)	9.21 (5.80)
Dry ($N = 10$)	38.96 (21.22)	29.77 (21.94)	6.60 (3.63)	7.64 (5.74)	7.27 (5.36)
			Akodon subfuscus		
Males ($N = 9$)	28.49 (10.83)	29.24 (6.24)	9.61 (7.72)	6.00 (1.17)	11.27 (4.09)
Females ($N = 5$)	31.20 (5.61)	30.96 (6.82)	7.56 (2.51)	6.92 (2.41)	10.10 (5.16)
Wet ($N = 10$)	31.28 (6.49)	31.02 (6.86)	7.09 (1.93)	5.91 (1.36)	9.01 (3.04)
Dry ($N = 4$)	24.90 (14.05)	26.95 (3.42)	13.35 (11.11)	7.38 (2.19)	15.45 (3.78)

similarity between the diets of those species, and may suggest possible competition for food between them. In general, these values (Table 3) support the idea that the akodontine rodents have similar, insectivorous diets.

Trophic Relationships in the Assemblage

Interspecific relationships: I used MANOVA to evaluate differences in use of food

Table 3. Niche overlap for species-pairs, based on their food habits. Two indices (Pianka's and Morisita's) are shown.

Species pair	Pianka's	Morisita's
O. paramensis - A. torques	0.94	0.93
O. paramensis - A. subfuscus	0.85	0.82
O. paramensis - P. osilae	0.25	0.25
O. paramensis - Oligoryzomys sp.	0.90	0.89
A. torques - A. subfuscus	0.98	0.97
A. torques - P. osilae	0.38	0.38
A. torques - Oligoryzomys sp.	0.87	0.87
A. subfuscus - P. osilae	0.48	0.48
A. subfuscus - Oligoryzomys sp.	0.83	0.82
P. osilae - Oligoryzomys sp.	0.59	0.59

resources among species, seasons, and sexes. The category "others" was excluded because its composition was neither regular nor comparable, but the original volumetric percentages of all other categories were retained to reduce correlation between variables. Differences among species were significant (Wilk's Lambda = 0.219, $F = 4.76$, *d.f.* = 20, 163, $p < 0.001$), but no other factors and no 2- or 3-way interactions were significant (all Wilk's Lambda > 0.77, all $p > 0.19$). All the variables showed significant differences ($F > 4.2$, *d.f.* = 4, $p < 0.005$) among species. Additional analyses excluded *P. osilae* and *Oligoryzomys* sp. B, due to small sample sizes, but differences were still significant (Wilk's Lambda = 0.384, $F = 5.76$, *d.f.* = 10, 94, $p < 0.001$) among the 3 akodontines, but also between seasons (Wilk's Lambda = 0.76, $F = 2.96$, *d.f.* = 5, 47, $p < 0.025$). There was a strong trend ($p = 0.52$) for an interaction between species, season, and gender. All the 5 variables showed significant differences ($F > 3.4$, *d.f.* = 2, $p < 0.04$) among species, but only 1 variable (monocots; $F > 4.2$, *d.f.* = 4, $p < 0.005$) among seasons. In the case of the interaction "species x season x gender", 2 variables (adult arthropods and monocots) showed significant differences.

Intraspecific relationships: I also evaluated seasonal and sexual variation, as well as their interaction, within the 3 species with adequate sample sizes, using MANOVA tests. Of these, only *A. subfuscus* exhibited seasonal variation (Wilk's Lambda = 0.12, $F = 8.69$, *d.f.* = 5, 6, $p = 0.01$); with vascular plant tissue showing significant differences ($F = 13.85$, *d.f.* = 1, $p < 0.005$) , because of large consumption during the dry season (Table 2). The other 2 species, *O. paramensis* (Wilk's Lambda > 0.8, $p > 0.6$) and *A. torques* (Wilk's Lambda > 0.56, $p > 0.25$) did not show significant variation in either season or gender, or the interaction of these factors. Although males of *O. paramensis* ate more arthropod larvae than females did (Table 2), this variation was not significant.

DISCUSSION

This highland rodent assemblage is dominated by akodontines, which were more abundant than any other group, and their dominance did not change between sampling periods or seasons. Feeding habits were similar to previous reports (Pizzimenti and De Salle, 1980; Glanz, 1982; O'Connell, 1982, Suarez, 1994), and confirmed that *Oxymycterus paramensis* is almost strictly insectivorous. Additionally, both species of *Akodon* were strongly insectivorous, albeit to a lesser extent than *Oxymycterus*. *Akodon subfuscus* showed only a slight specialization for an insectivorous diet, without clear preference for larvae or adult arthropods, whereas *A. torques* may be regarded as a generalist species not relying on any particular food resource. Although samples were limited for both *Phyllotis osilae* and *Oligoryzomys* sp. B, the analyses verified their roles as herbivorous (see Dorst, 1971, 1972b) and omnivorous-insectivorous, respectively.

The use of the coefficient of variation (CV) as an index of preference suggested a marked dependence of *O. paramensis* on arthropod larvae, and additionally, pointed to *A. subfuscus* as reliant on adult arthropods. Indices of niche breadth and niche overlap also suggest that *O. paramensis* was a dietary specialist, distinct from other species in the assemblage, with a large prevalence of arthropod larvae in its diet. Specialization towards insectivory by other species of *Oxymycterus* has been documented by Hershkovitz (1994) and Suarez (1994). No other species in this study showed a similar predilection for a particular food category.

Niche overlap values were above 0.75 for several pair of species, indicating high dietary similarity (Table 3). Although this may be interpreted as indicative of shared resource use and lack of competition (Sale, 1974), it may also be possible that high overlap implies the potential for strong competition that has not yet led to divergence in resource utilization. Alternatively, species might distinguish and partition resources more finely than detected with the 6 dietary categories employed here. In the case of *A. torques* and *A. subfuscus*, for example, the high overlap in diet might be reduced through low overlap in another axis of their ecological niches.

Statistical analyses were weakened by the small sample sizes for 2 of the 5 species in the assemblage (*P. osilae* and *Oligoryzomys* sp.). However, it was evident that species in this assemblage either were moderately to very strong insectivores (*Oxymycterus*, *Akodon*) or were omnivorous-herbivorous (*Phyllotis*, *Oligoryzomys*). When considering all the species within this assemblage, arthropod larvae showed significant differences in every comparison, with *O. paramensis* and *P. osilae* exhibiting maximal and minimal consumption of this item, respectively. Species of *Akodon* were primarily insectivorous, averaging 70-90% arthropods in their diets (Pizzimenti and De Salle, 1980; Meserve et al., 1988; Suarez and Bonaventura, 2001), and this study supports previous reports (Dorst, 1971, 1972b; Pizzimenti and De Salle, 1980) that *P. osilae* is an herbivore that mostly depends on leafy vegetation.

Only *A. subfuscus* showed significant variation across seasons. Pizzimenti and De Salle (1980) reported gender variation in *O. paramensis*, but indicated that females usually consumed more insects than males. Those differences were not statistically significant, but were implied to be biologically important. On the other hand, my data suggest that an increased consumption of vascular plant tissue by *A. subfuscus* occurred during the dry season, and that males of *O. paramensis* ate more arthropod larvae than conspecific females (Fig. 1). Statistical support was only obtained for seasonal variation in *A. subfuscus*. Seasonal variation in food habits of akodontine rodents appears to be determined by the energetic budget of the species (Pizzimenti and De Salle, 1980; Glanz, 1984; Meserve et al., 1988), while sexual variation may be related to resource availability, or be dependent on life history traits, like cost of reproduction (Suarez, 1994).

High overlap along 1 or more niche axes may be compensated with low overlap on others (Husar, 1976; Holt, 1987). Thus, rodent species may segregate according to body size (Brown et al., 1986; Gliwicz, 1987). Species in this assemblage differed significantly in weight ($F > 45$, *d.f.* = 4, 62, $p < 0.001$), although pairwise comparisons failed to segregate *A. subfuscus* and *A. torques* (Table 1); this is consistent with the limited segregation between these 2 species in food habits. Other authors have indicated that temporal activity may be an important niche axis on which species segregate (Dorst, 1958; Bruseo and Barry, 1995), but data from this study are insufficient to test this temporal hypothesis, as traps were checked only twice a day.

Whereas food is rarely considered a prominent factor for niche segregation, specific habitat regularly is (Meserve et al., 1988; Suarez and Bonaventura, 2001). Sympatric rodent species often use different microhabitats (Dueser and Shugart, 1978; Glanz, 1982; Patterson et al., 1990; Kelt et al., 1994, 1999) suggesting it may be a primary mechanism to reduce niche overlap and competition. Whitford (1976) and Zegers and Ha (1981) suggested that differential habitat use was a principal resource structuring rodent assemblages, although these authors included some scansorial species. Habitat segregation has been reported for *A. subfuscus* and *A. torques* in Peru (Patton and Smith, 1992), with the latter being more abundant in dense moss mats within the montane forests, and the former in adjacent clumps of tall lush grassland. Unpublished data (S. Solari) suggest that similar segregation occurs in this assemblage as well.

Reig (1986) argued that the generalist food habits and flexibility of habitat preference of akodontine rodents was a principal factor leading to their wide success in South America. This group is mostly Andean in distribution, and contributes enormously to the local diversity in Puna and páramo habitats. Pizzimenti and De Salle (1980, 1981) also attributed the greater abundance and broader distribution of Andean rodents to omnivorous habits, although their data pertained mostly to small to medium phyllotines; they noted that many akodontines were primarily insectivorous, an observation supported by this study. Nevertheless, Pizzimenti and De Salle (1980, 1981) recognized that varying capabilities to use different resources in different environments was the key to the success of the omnivore guild, at least in Peru. However, my data generally support the hypothesis of Meserve et al. (1988), which suggested that resource availability has influenced local patterns of resource use more than has evolutionary specialization, and that the former mechanism is more influential in structuring South American small mammal assemblages.

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LITERATURE CITED

Brown, J. H., D. W. Davidson, J. C. Munger, and R. S. Inouye
1986 Experimental community ecology: the desert granivore system. Pp. 41-62, in Community Ecology (Diamond, J., and T. J. Case, eds.). Harper & Row, New York, New York, USA.

Bruseo, J. A., and R. E. Barry, Jr.
1995 Temporal activity of syntopic *Peromyscus* in the Central Appalachians. Journal of Mammalogy 76:78-82.

Cano, A.
1994 Synopsis de la flora Fanerogámica altoandina del Parque Nacional Manu, Cusco. Master Thesis, Universidad Nacional Mayor de San Marcos, Lima. 224 pp.

Cano, A., K. R. Young, B. Leon, and R. B. Foster
1995 Composition and diversity of flowering plants in the upper montane forest of Manu National Park, southern Peru. Pp. 271-280 in Biodiversity and Conservation of Neotropical Montane Forests (Churchill, S. P., H. Balslev, E. Forero, and J. L. Luteyn, eds.). The New York Biological Garden, Bronx, New York, USA.

Dalby, P. L.
1975 Biology of Pampa rodents, Balcarce area, Argentina. Publications of the Museum, Michigan State University, Biological Series 5:199-272.

Dorst, J.
1958 Contribution a l'etude ecologique des rongeurs des haut plateaux peruviens. Mammalia 22:547-565.

1971 Nouvelles recherches sur l'ecologie des rongeurs des haut plateaux peruviens. Mammalia 35:515-547.

1972a Premieres recherches sur la densité, la biomasse et la spécialisation écologique de quelques rongeurs des hautes Andes du Pérou. Comptes Rendus Academie des Sciences, Biologies 274:940-942.

1972b Morphologie de l'estomac et regime alimentaire de quelques rongeurs des hautes Andes de Perou. Mammalia 36:647-656.

Dueser, R. D., and H. H. Shugart, Jr.
1978 Microhabitats in a forest-floor small mammal fauna. Ecology 59:89-98.

Gebczynska, Z., and A. Myrcha
1966 The method of quantitative determining of the food composition of rodents. Acta Theriologica 11:385-390.

Glanz, W. E.
1982 Adaptive zones of Neotropical mammals: a comparison of some temperate and tropical patterns. Pp. 95-110 in Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Special Publication Series, Pymatuning Laboratory of Ecology, Vol. 6. University of Pittsburgh, Linesville, Pennsylvania, USA.

1984 Ecological relationships of two species of *Akodon* in central Chile. Journal of Mammalogy 65:433-441.

Gliwicz, J.
1987 Niche segregation in a rodent community of Africa dry savanna. Journal of Mammalogy 68:169-172.

Goodyear, N. C.
1992 Spatial overlap and dietary selection of native rice rats and exotic black rats. Journal of Mammalogy 73:186-200.

Hansson, L.
1970 Methods of morphological diet micro-analysis in rodents. Oikos 21:255-266.

Hershkovitz, P.
1994 The description of a new species of South American hocicudo, or long-nose mouse, genus *Oxymycterus* (Sigmodontinae, Muroidea), with a critical review of the generic content. Fieldiana: Zoology, 79:1-43.

Holt, R. D.
1987 On the relation between niche overlap and competition: the effect of incommensurable niche dimensions. Oikos 48:110-114.

Horn, H. S.
1966 Measurement of "overlap" in comparative ecological studies. American Naturalist 100:419-424.

Husar, S. L.
1976 Behavioral character displacement: evidence of food partitioning in insectivorous bats. Journal of Mammalogy 57:331-338.

Kelt, D. A., P. L. Meserve, and B. K. Lang
1994 Quantitative habitat associations of small mammals in a temperate rainforest in southern Chile: empirical patterns and the importance of ecological scale. Journal of Mammalogy 75:890-904.

Kelt, D. A., P. L. Meserve, B. D. Patterson, and B. K. Lang
1999 Scale dependence and scale independence in habitat associations of small mammals in southern temperate rainforests. Oikos 85:320-334.

Krebs, C. J.
1989 Ecological Methodology. Harper & Row, New York, New York, USA. 654 pp.

Levins, R.
1968 Evolution in Changing Environments: Some Theoretical Explorations. Princeton University Press, Princeton, New Jersey, USA. 120 pp.

M'Closkey, R. T.
1976 Community structure in sympatric rodents. Ecology 57:728-739.

Meserve, P. L.
1981 Trophic relationship among small mammals in a Chilean semiarid thorn scrub community. Journal of Mammalogy 62:304-314.

Meserve, P. L., B. K. Lang, and B. D. Patterson
1988 Trophic relationships of small mammals in a Chilean temperate rainforest. Journal of Mammalogy 69:721-730.

O'Connell, M. A.
1982 Population biology of North and South American grassland rodents: a comparative review. Pp. 167-185 in Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Special Publication Series, Pymatuning Laboratory of Ecology, Vol. 6. University of Pittsburgh, Linesville, Pennsylvania, USA.

Pacheco, V., B. D. Patterson, J. L. Patton, L. H. Emmons, S. Solari, and C. F. Ascorra
1993 List of mammal species known to occur in Manu Biosphere Reserve, Peru. Publicaciones del Museo de Historia Natural, UNMSM (A) 44:1-12.

Patterson, B. D., P. L. Meserve, and B. K. Lang
1990 Quantitative habitat association of small mammals along an elevational transect in temperate rainforest of Chile. Journal of Mammalogy 71:620-633.

Patterson, B. D., M. R. Willig, and R. D. Stevens
2003 Trophic strategies, niche partitioning, and patterns of ecological organization. Pp. 536-579 in Bat Ecology (Kunz, T. H., and M. B. Fenton, eds.). Chicago, University of Chicago Press, Chicago, Illinois, USA.

Patton, J. L., and M. F. Smith
1992 Evolution and systematics of Akodontine rodents (Muridae: Sigmodontinae) of Peru, with emphasis on the genus *Akodon*. Pp. 83-103 in Biogeografía, Ecología y Conservación del Bosque Montano en el Perú (Young, K. R., and N. Valencia, eds.). Memorias del Museo de Historia Natural, UNMSM 21:1-227.

Pearson, O. P.
1983 Characteristics of a mammalian fauna from forests in Patagonia, southern Argentina. Journal of Mammalogy 64:476-492.

Pearson, O. P., and C. P. Ralph
1978 The diversity and abundance of vertebrates along an altitudinal gradient in Peru. Memorias del Museo de Historia Natural "Javier Prado" 18:1-97.

Pianka, E. R.
1973 The structure of lizard communities. Annual Review of Ecology and Systematics 4:53-74.

Pizzimenti, J. J., and R. De Salle
1980 Dietary and morphometric variation in some Peruvian rodent communities: the effect of feeding strategy on evolution. Biological Journal of the Linnean Society 13:263-285.

1981 Factors influencing the distributional abundance in two trophic guilds of Peruvian cricetid rodents. Biological Journal of the Linnean Society 15:339-354.

Rau, J., R. Murua, and M. Rosenmann
1981 Bioenergetics and food preferences in sympatric southern Chilean rodents. Oecologia 50:205-209.

Reig, O. A.
1986 Diversity patterns and differentiation of high Andean rodents. Pp. 404-439 in High Altitude Tropical Biogeography (Vuilleumeier, F., and M. Monasterio, eds.). Oxford University Press, New York, New York, USA.

Sale, P. F.
1974 Overlap in resource use, and interspecific competition. Oecologia 17:245-256.

Schoener, T. W.
1974 Resource partitioning in ecological communities. Science 185:27-39.

Suarez, O. V.
1994 Diet and habitat selection of *Oxymycterus rutilans* (Rodentia: Cricetidae). Mammalia 58:225-234.

Suarez, O. V., and S. M. Bonaventura
2001 Habitat use and diet in sympatric species of rodents of the low Parana delta, Argentina. Mammalia 65:167-176.

Vitt, L. J., S. S. Sartorius, T. S. C. Avila-Pires, M. C. Esposito, and D. B. Miles
2000 Niche segregation among sympatric Amazonian teiid lizards. Oecologia 122:410-420.

Whitford, W. G.
1976 Temporal fluctuations in density and diversity of desert rodent populations. Journal of Mammalogy 57:351-369.

Wolff, J. O.
1996 Coexistence of white-footed mice and deer mice may be mediated by fluctuating environmental conditions. Oecologia 108:529-533.

Zegers, D. A., and J. C. Ha
1981 Niche separation of *Peromyscus leucopus* and *Blarina brevicauda*. Journal of Mammalogy 62:199-201.

MAMMALS, AMPHIBIANS, AND REPTILES OF THE BOLIVIAN HIGH ANDES: AN INITIAL COMPARISON OF DIVERSITY PATTERNS IN *POLYLEPIS* WOODLANDS

MAMÍFEROS, ANFIBIOS, Y REPTILES DE LOS ALTOS ANDES DE BOLIVIA: UNA COMPARACIÓN INICIAL DE PATRONES DE DIVERSIDAD EN BOSQUES DE *POLYLEPIS*

Teresa Tarifa, James Aparicio E., and Eric Yensen

While working on the mammals and herpetofauna of Polylepis *woodlands, we felt the enchantment of the high Andean environment, its people, and their history. This environment also moved Oliver P. Pearson. The knowledge he produced in countries adjacent to Bolivia has served us well, and we appreciate this and the person he was. We dedicate this paper to his memory in appreciation of his many contributions to the vertebrate biology of the high Andes.*

ABSTRACT

Mammals, amphibians, and reptiles of the Bolivian high Andes are poorly known. We collected specimens of the 3 groups in 11 *Polylepis* woodlands. We compared diversity patterns of amphibians, reptiles, and mammals to learn if they were similar to one another and if one taxonomic group could serve as an umbrella for the others in conservation planning. We found a number of new distributional records for mammals, amphibians, and reptiles; new records for amphibians and reptiles are reported herein. Mammals were most diverse, whereas amphibian and reptile diversities were low. None of the groups' diversities correlated with each other, suggesting that conservation areas should be selected based upon a variety of taxa rather than any single umbrella group.

Key words: mammals, amphibians, reptiles, *Polylepis*, Bolivia, high Andes, species diversity, diversity patterns, umbrella species, biogeography

RESUMEN

Los mamíferos, anfibios y reptiles de las alturas andinas de Bolivia son todavía poco

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conocidos, por lo que colectamos ejemplares de los tres grupos en 11 zonas boscosas de *Polylepis*. En este trabajo, comparamos entre sí los patrones de diversidad de anfibios, reptiles y mamíferos para determinar si un grupo taxonómico podría servir de indicador para otros en la planificación de la conservación. Encontramos varios nuevos registros de distribución para estos taxones; aquellos nuevos para anfibios y reptiles se reportan en este trabajo. Los mamíferos fueron el grupo más diverso, mientras que la diversidad de anfibios y reptiles fue baja. Las diversidades de los distintos grupos no mostraron correlaciones, lo cual sugiere que las áreas de conservación deberían seleccionarse en base a diversos taxones, en lugar de en base a un único taxón indicador.

Palabras claves: mamíferos, anfibios, reptiles, *Polylepis*, Bolivia, altoandino, diversidad de especies, patrones de diversidad, "especies paraguas", biogeografía

INTRODUCTION

Woodlands dominated by trees of *Polylepis* spp. (Rosaceae) occur in the high Andes from Venezuela to northern Argentina, and once covered perhaps 20% of the high Andes of Bolivia. These small evergreen trees (1-20 m, usually 2-6 m tall in Bolivia) occur in isolated stands above the "normal" treeline (ca. 3000 m elevation) and extend from there up to 5200 m, forming the highest-elevation woodlands in the world (Eckholm, 1975; Ellenberg, 1979; Fjeldså, 1987, 2002a; Kessler, 1995a, 1995b, 2002; Rada et al., 2001; Argollo et al., 2004).

These woodlands vary in diversity, structure, and composition, but all are dominated by at least 1 *Polylepis* species. On the eastern slopes of the Andes (called yungas in Bolivia and herein), the woodlands lie just above the high diversity cloud forests of the Amazon Basin; in interior valleys, they occur above dry tropical deciduous woodlands; in the altiplano (the arid, 3500-4200 m elevation plateau between the eastern and western cordilleras), *Polylepis* woodlands occur in patches that do not contact other forest types but instead are adjacent to high elevation shrub and/or grass-dominated communities known as puna (Fjeldså, 2002a; Kessler, 2002).

Polylepis woodlands provide critical habitats for high-Andean birds in an otherwise treeless region. Throughout their range from Venezuela to Argentina, *Polylepis* woodlands are utilized by 214 species of birds, of which 51 are strongly associated with them, 14 are dependent, and 7 of the dependents are endangered or vulnerable (Frimer and Nielsen, 1989; Fjeldså, 1992, 1993, 2002b).

Birds are frequently used as an "umbrella group" to protect entire biotas (Wilcox, 1982; Diamond, 1986; Fjeldså, 1990; Bibby et al., 1992; Remsen and Parker, 1995; Long et al., 1996; Fjeldså and Rahbek, 1997). This is because they are well-known taxonomically, highly detectable during the day and thus readily censused, and a speciose group that shows geographic patterns well (Fjeldså, 2000; Canaday and Rivadeneyra, 2001). Using detailed records of bird distribution in the high Andes, Fjeldså (1992, 1993, 2002b; Fjeldså & Kessler 1996) has proposed that areas with high avian endemism should be priority areas for conservation. He located 7 centers of endemism in the Andes from Ecuador to Argentina that would protect most of the avifauna of the high-elevation *Polylepis* woodlands, and presumably the rest of the fauna as well. Two of these centers of endemism occur in Bolivia: one near La Paz and the other on the edge of the Cochabamba Basin (Fjeldså, 2002b).

We wondered if these woodlands were as important to other vertebrates as to birds, and began our initial investigation in 1992. The available data for mammals occurring in *Polylepis* woodlands in Bolivia is still limited to our studies (Yensen and Tarifa, 1993, 2002; Tarifa and Yensen, 2001), and recent studies on *Oxymycterus paramensis* (Rodentia: Muridae) populations (Vargas, 2001), Andean bear (T*remarctos ornatus*) habitat use (Azurduy and Velez, 2001), and a comparison of the structure of 2 small, non-volant mammal communities (Moya Soto, 2003).

We recently presented data (Yensen and Tarifa, 2002) suggesting that Fjeldså's (1993) proposed reserves would not be adequate to conserve mammalian diversity. In our study, mammal species lists differed greatly from one site to another (high beta diversity), suggesting that many small reserves spread over a larger area would be more effective for small, non-volant mammals. Fjeldså (2002b) has pointed out that the lack of agreement between bird and mammal patterns may result from inadequate knowledge of true mammalian distributions. Only additional mammal collecting will resolve this issue, but there is a previously unpublished data set that bears upon the question.

While mammal distributions in the high Andes are poorly known relative to birds, there are no published data at all on reptiles or amphibians associated with *Polylepis* woodlands. We (TT and EY) did our field work with mammals in collaboration with JA who simultaneously collected reptiles and amphibians at most of the same sites, and we present here a comparison of diversity patterns among the 3 groups in order to answer the following questions: 1) Which species of amphibians, reptiles, and mammals occur in *Polylepis* woodlands? 2) Are the diversity patterns of amphibians and reptiles similar to those of mammals? 3) Would protected areas proposed for mammals or birds serve equally well to protect amphibian and reptile diversity? In addition, this paper provides the first description of the herpetofauna of *Polylepis* woodlands and reports a number of new distributional records.

METHODS

We selected 11 *Polylepis* woodlands between 3200 and 4600 m elevation in the high Andes of Bolivia, located from near the Peruvian border to near the Argentine border, and extending over 863 km north to south. The woodlands were separated from each other geographically by 50 to 308 km (nearest-neighbor distance, mean = 140.3 km; Fig. 1 and Appendix I). All were fragmented, and fragments varied in size from 1.2 to > 300,000 (median = 300) ha. Time since fragmentation varied from < 10 to 100+ years (Table 1).

Localities were recorded in the field using road distances from major landmarks; latitude and longitude were obtained using a Garmin XL12 GPS unit, and sites were located on topographic maps after return from the field. Precipitation in each woodland was estimated from isopleths in Montes de Oca (1989), Kessler (1995c), and data in Liberman (1986).

We sampled mammals, amphibians, and reptiles in 23 fragments in the 11 woodlands. The fragments were in close proximity (<1 to 29 km, median = 7.1 km distant) and judged to have been components of the same pre-fragmentation woodland.

Non-volant small mammals (all < 500 g except *Lagidium viscacia*) were trapped in

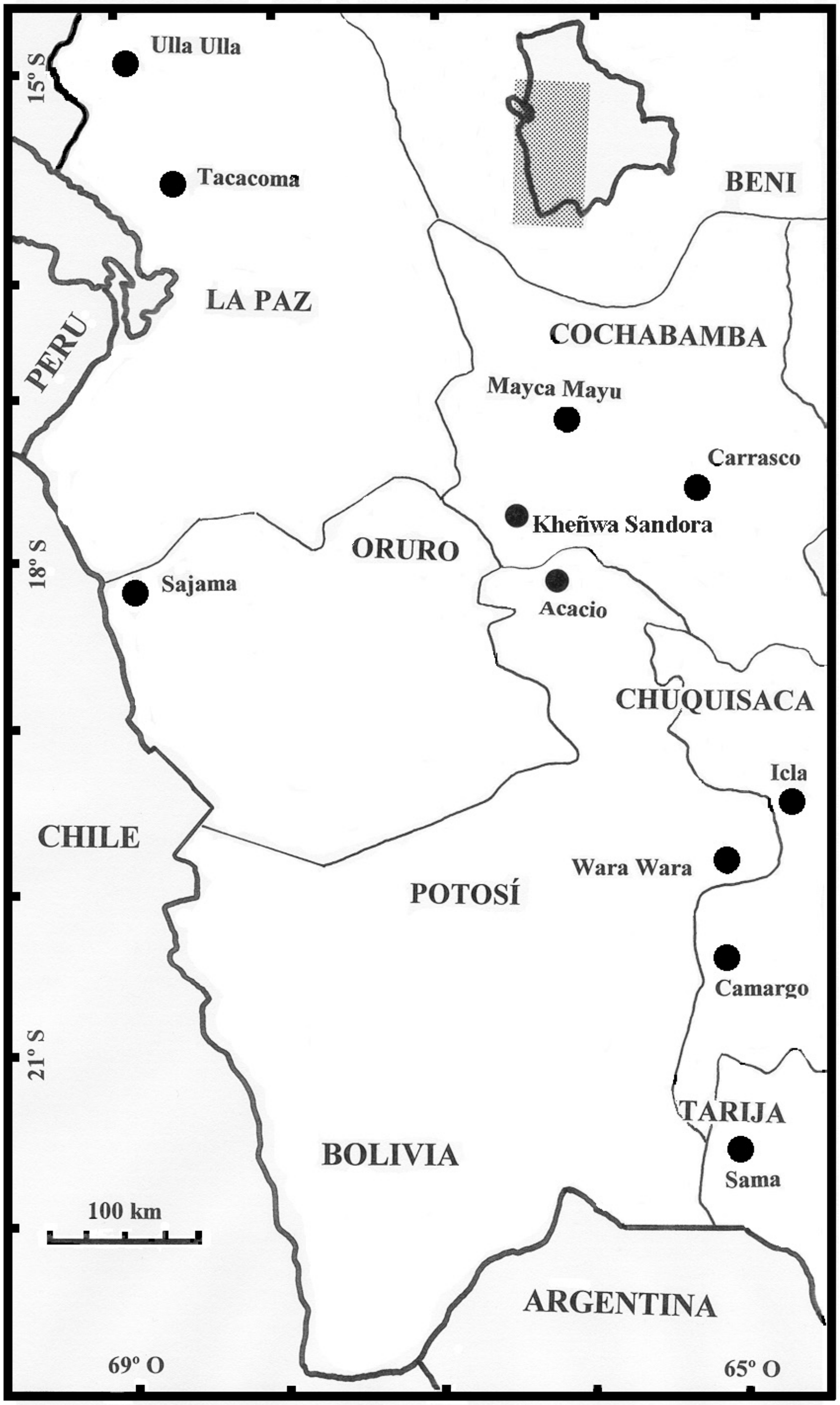

Figure 1. Location of the woodlands studied in the high Andes of Bolivia.

Table 1. Characteristics of *Polylepis* woodland study areas. Age indicates time since fragmentation and isolation refers to distance to nearest fragment.

Site	Elevation (m)	Precipitation (mm)	Fragment Size (ha)	Age (yr)	Isolation (km)	Adjacent Habitat
Ulla Ulla	3800	1200	6	?	1-10	Puna
Tacacoma	3800	1100	150	<20	0-1	Puna, Yungas
Mayca Mayu	3300-3400	1200	4	<20	0-1	Puna, Yungas
Carrasco	3200-3700	1200	150	<10	1-10	Puna, Yungas
Kheñwa Sandora	3700	800	>2000	<20	1-10	Puna
Sajama	4240-4600	350	>1000	>100	1-10	Puna
Acacio	3500-3700	900	300	?	1-10	Puna
Icla	3700-3800	800	1000-3000	<20	1-10	Puna
Wara Wara	3700	500	700	?	1-10	Puna, Valle Seco
Camargo	3200-3600	500	>30,000	?	10+	Puna, Valle Seco
Sama	4000	400	>1000	>100	1-10	Puna

Museum Special, Victor, Sherman, and Tomahawk traps baited with oatmeal, vanilla, and peanut butter; sardines were added to the mixture for half of the traps. Traps were placed at 10-15 m intervals in transects of 50 traps set inside *Polylepis* woodland. Trapping transects were often modified due to the ruggedness of the terrain (slopes of 45° - 80°), fragment size, and shape. Traps were set in late afternoon and checked in early morning. Voucher specimens were prepared as standard study skins and skulls, or preserved in formaldehyde with the skull cleaned separately, and deposited in the Colección Boliviana de Fauna [CBF], La Paz, Bolivia.

The nomenclature of some rodents in the genus *Phyllotis* is still tentative, pending further taxonomic work. The revisions of this genus (Pearson, 1958; Steppan 1993, 1995, 1997) included few Bolivian specimens. In the central Bolivian Andes, we found 3 entities of *Phyllotis* which were distinct from known taxa and not defined taxonomically at present. We refer to them herein as *P.* cf. *osilae* "A", *P.* cf. *osilae* "B", and *P.* cf. *xanthopygus* after the species they most closely resembled. *Phyllotis osilae* and *P. o. phaeus* are distinct ecologically (Pizzimenti and de Salle, 1980), and Anderson (1997) treated *P. chilensis* as a full species, whereas Steppan (1997) treated it as a subspecies of *P. xanthopygus*. Until the taxonomic issues are resolved, we elected to treat all of these entities as full species in our data analyses. This could potentially inflate the species lists and estimates of beta diversity (see below), but would not affect other results. Mammalian nomenclature follows Wilson and Reeder (2005).

We collected specimens of amphibians and reptiles by hand during diurnal and nocturnal searches of the most likely places where they could be encountered. Collected specimens were preserved using standard methods, deposited in the CBF, and identified using determined material therein, taxonomic keys, and descriptions (Donoso-Barros, 1966; Gallardo, 1987; Peters and Donoso-Barros, 1970; Cei, 1980, 1993; Veloso and Bustos, 1982; Aparicio, 1993). Nomenclature follows de la Riva et al. (2000) for amphibians and Dirksen and de la Riva (1999) for reptiles.

Species diversity was calculated using the information theory index ($H' = -\Sigma\, p_{\mathrm{i}} \log_{10} p_{\mathrm{i}}$) and the inverse of the Simpson index ($D_{\mathrm{s}} = 1/\Sigma\, p_{\mathrm{i}}^{2}$), where p_{i} is the proportion of the *i*th species. The information theory index is a Type I index, which is more sensitive to changes in rare species in the community. The inverse of the Simpson index is a Type II index, which is more sensitive to changes in the most abundant species (Peet, 1974). We used both measures to ensure that observed diversity patterns were not overly influenced by rare or abundant species (Krebs, 1989). However, because D_{s} is sensitive to small sample sizes, we used an unbiased estimator, which is less affected by sample size: $D_{\mathrm{s}}^{*} = 1/\Sigma\, [n_{\mathrm{i}}(n_{\mathrm{i}}\text{-}1)/N(N\text{-}1)]$, where n_{i} is the number of individuals of each species and N is the total individuals in the sample (Ludwig and Reynolds, 1988).

In order to compare the statistical significance of H' values among sites and taxa, we used the formula, $H' = (N \log_{10} N - \Sigma\, n_{\mathrm{i}} \log_{10} n_{\mathrm{i}})/N$ (Lloyd et al., 1968), then tested for statistical significances of H' values among samples using modified *t*-tests (Hutcheson, 1970; Zar, 1984), where $t = (H'_{1} - H'_{2}) / \sqrt{(s^{2}_{1} + s^{2}_{2})}$, and $s_{\mathrm{i}}^{2} = (\Sigma\, n_{\mathrm{i}} \log_{10}^{2} n_{\mathrm{i}} - [\Sigma\, n_{\mathrm{i}} \log_{10} n_{\mathrm{i}}]^{2} / N) / N^{2}$. Degrees of freedom for each test were calculated using the formula, $\nu = (s^{2}_{H'1} + s^{2}_{H'2})^{2} / (([s^{2}_{H'1}]^{2} / n_{1}) + ([s^{2}_{H'2}]^{2} / n_{2}))$ (Zar, 1984).

For mammals, we used data reported in Yensen and Tarifa (2002) to compare mammals with amphibians and reptiles. The H' values for mammals reported here differ from those reported earlier because in this paper we use common instead of natural logarithms to facilitate *t*-tests of significance. To compare H' values calculated using $\log_{10}$ with those using natural logs, the conversion factor is 2.302585.

We used the Bray-Curtis similarity coefficient to compare sites, where percent similarity = $2\, w / (A + B)$, w is the number of species in common, and A and B are the total number of species at each site (Ludwig and Reynolds, 1988). Statistical analyses were conducted using SYSTAT 10.0 (Wilkinson 2000), PC-ORD 4.0 (McCune and Mefford, 1999), and a hand calculator. Systat 10.0 did not give exact p values for Spearman rank correlations; multiple Spearman rank correlations were adjusted with Bonferroni corrections. All correlations were based upon the 8 woodlands where all 3 taxonomic groups were collected. Beta diversity was calculated using a Mantel test in PC-ORD. This technique compares paired matrices of geographic and species composition distances among sites using the Sorensen distance measure, $1 - [2\, w / (A + B)]$. We used 1000 Monte Carlo iterations to calculate p values, although Mantel's asymptotic approximation gave similar results.

RESULTS

Field work was conducted in July-August 1995, June-August 1996, July 1999, and August 2000. For completeness, data from *Polylepis* woodlands in the Western Cordillera (Sajama National Park: Yensen and Tarifa, 1993; Aparicio, 1996; Tarifa, 1996) and also from Ulla Ulla (Apolobamba Natural Area of Integrated Management: Tarifa, 1997; Aparicio, 1999) were included in the analyses.

We trapped a total of 6198 trap-nights for mammals in *Polylepis* woodlands and caught 426 individuals of 31 species for 6.87% trap success. Including large and medium-sized mammals documented and observed, we recorded a total of 39 species. A list of mammals occurring in *Polylepis* woodlands was published elsewhere (Tarifa and Yensen, 2001; Yensen and Tarifa, 2002). In the comparisons below, we refer only to small, non-volant mammals (Table 2). We omitted medium and large mammals from inter-site and inter-taxonomic comparisons because they have large home ranges and use many habitat types.

The recent availability of a series of specimens of the marsupial genus *Thylamys* in the CBF and a revision of this genus (Solari, 2003) has enabled us to re-identify some specimens. The *Thylamys* collected at Acacio are considered *T. venustus* herein, adding an additional species to the mammalian fauna of *Polylepis* woodlands (Tarifa and Yensen, 2001). The substitution of *T. venustus* for *T. pallidior* at Acasio does not change the diversity patterns reported earlier (Yensen and Tarifa, 2002). Moya Soto (2003) and other workers have recently shown us specimens which will add 2 more species to the list for *Polylepis* woodlands. However, these were not from woodlands studied by us, and their addition does not change the diversity patterns reported herein.

We spent a total of 335.6 person-hours searching for amphibians and reptiles (mean = 32.4, range 16.5 - 56.3 person-hours/woodland), and in several places local residents also contributed specimens. Approximately equal amounts of time were devoted to nocturnal and diurnal collecting. In total, we captured 94 individuals of 7 species of amphibians (Table 3) and 77 individuals of 8 species of reptiles (Table 4). No herpetologists were able to participate in the field work at Camargo and no reptiles were collected there; amphibian collections by EY were incidental to mammal trapping and may be incomplete. At Mayca Mayu, no reptiles could be collected, but JA saw *Liolaemus* lizards there. At Sajama, there is no surface water inside the *Polylepis* woodlands, and no amphibians were found, although they were collected in other habitats nearby (Aparicio, 1996). These sites were eliminated from some analyses.

New Distributional Records for Amphibians and Reptiles. Records below are from *Polylepis* woodlands unless otherwise specified. A new species to science and a number of distributional records resulted from the fieldwork (Appendix II). A frog (*Phrynopus* n. sp.) was found at Tacacoma by Claudia Cortez who collected 17 specimens on 3 July 1995 in an irrigation ditch carrying water from the *Polylepis* woodland to nearby fields. It is currently being described (I. de la Riva, pers. comm.).

The lizard *Liolaemus fittkaui*, a species endemic to Bolivia, was previously known only from the type locality (Tiraque, Tiraque Province, Cochabamba Department). This study extends its known range 85 km WSW to Pusuq'huni (Kheñwa Sandora woodland; Appendix I), Arque Province, Cochabamba Department. Pusuq'huni is a relatively large fragment (ca. 1000 ha) of *Polylepis* woodland at 3700 m elevation. The trees reached 4 m tall forming an open woodland with a grassy understory on the SW side of a steep, rocky canyon ca. 500 m deep. We observed lizards on rocks in the canyon, and local residents brought 5 specimens to us on 15 August 2000. No other lizard species was seen at Pusuq'huni, although *L. alticolor* was found at our "Km 80" locality 3 km to the NW.

The snake *Tachymenis* cf. *elongata* was collected while driving though a sparse *Polylepis* woodland enroute to a collecting locality. This is the first record of this species in Bolivia and we report it here. The specimen was seen crossing the road and

Table 2. Small and medium-sized mammals documented in *Polylepis* woodlands. Symbols: Ull = Ulla Ulla, Tac = Tacacoma, May = Mayca Mayu, Car = Carrasco, Khe = Kheñwa Sandora, Saj = Sajama, Aca = Acacio, Icl = Icla, War = Wara Wara, Cmg = Camargo, Sam = Sama.

Species	Woodland											
Marsupials	Ull	Tac	May	Car	Khe	Saj	Aca	Icl	War	Cmg	Sam	Σ
Thylamys pallidior	-	-	-	-	1	4	-	-	1	3	-	9
*Thylamys venustus**	-	-	-	-	-	-	7*	-	-	-	-	7
Murid Rodents												
Abrothrix andinus	-	-	-	1	-	-	-	-	-	-	-	1
Abrothrix jelskii	2	-	-	-	-	1	-	-	-	-	-	3
Akodon aerosus	-	-	-	1	-	-	-	-	-	-	-	1
A. albiventer	-	-	-	-	-	8	-	-	6	-	6	20
A. boliviensis	3	-	-	-	-	-	-	1	-	-	-	4
A. fumeus	-	1	-	39		-	-	-	-	-	-	40
A. kofordi	-	-	-	1	-	-	-	-	-	-	-	1
A. lutescens	2	-	-	1	5	-	3	-	-	-	-	11
A. subfuscus	-	27	8	2	1	-	-	-	-	-	-	38
Andinomys edax	-	-	-	1	2	-	1	-	-	-	-	4
Calomys lepidus	-	-	-	-	-	-	-	1	-	-	-	1
Chinchillula sahamae	-	-	-	-	-	1	-	-	-	-	-	1
Microryzomys minutus	1	-	-	-	-	-	-	-	-	-	-	1
Necromys amoenus	-	-	-	-	-	-	-	1	-	-	-	1
Oligoryzomys sp. B	-	1	1	9	-	-	2	-	-	1	-	4
O. destructor	2	-	-	-	-	-	-	-	-	-	-	2

Table 2 (continued).	Ull	Tac	May	Car	Khe	Saj	Aca	Icl	War	Cmg	Sam	Σ
Oxymycterus hiska	-	1	-	-	-	-	-	-	-	-	-	1
O. paramensis	-	-	1	9	5	-	16		-	-	-	31
Phyllotis osilae osilae	-	-	1	5	-	-	-	-	-	-	-	6
P. osilae phaeus	12	13	-	-	-	-	-	-	-	-	-	25
P. cf. *osilae* A	-	-	-	-	27	-	22	-	-	-	-	49
P. cf. *osilae* B	-	-	-	-	-	-	-	18	-	-	-	18
P. xanthopygus	-	-	-	-	-	-	-	-	22	-	17	39
P. x. chilensis	-	-	-	-	-	54	-	-	-	-	-	54
P. cf. *xanthopygus*	-	-	-	-	-	-	-	-	-	36	-	36
Thomasomys n.sp.	-	-	-	1	-	-	-	-	-	-	-	1
Caviomorph Rodents												
Cavia tschudii	-	1	-	-	-	-	-	-	-	-	-	1
Galea musteloides	-	-	-	-	-	-	-	3	-	-	-	3
Lagidium viscacia	1	-	-	-	-	2	-	-	-	-	-	3
No. individuals	23	44	11	70	41	70	51	24	29	40	23	426
No. species	7	6	4	11	6	6	6	5	3	3	2	30
Trap-nights	204	467	93	528	1267	1770	329	287	374	438	441	6198
Spp/100 trap-nights	3.4	1.3	4.3	2.1	0.5	0.3	1.8	1.7	0.8	0.7	0.5	0.48

*Change in identification from Tarifa and Yensen (2001) and Yensen and Tarifa (2002).

Table 3. Amphibians documented in *Polylepis* woodlands. Symbols: Ull = Ulla Ulla, Tac = Tacacoma, May = Mayca Mayu, Car = Carrasco, Khe = Kheñwa Sandora, Saj = Sajama, Aca = Acacio, Icl = Icla, War = Wara Wara, Cmg = Camargo, Sam = Sama.

	Woodland											
Species	Ull	Tac	May	Car	Khe	Saj	Aca	Icl	War	Cmg[1]	Sam	Σ
Bufo spinulosus	*[2]	-	5	2	5	*[2]	-	3	2	4	6	27
Gastrotheca marsupiata	-	-	4	-	-	-	-	-	-	-	-	4
Hyla albonigra	-	-	-	-	-	-	2	-	-	1	-	3
H. andina	-	-	10	-	-	-	-	-	-	1	-	11
Pleurodema marmoratum	6	-	-	-	-	*[2]	-	-	-	-	2	8
Phrynopus sp. nov. [3]	-	17	-	-	-	-	-	-	-	-	-	17
Telmatobius marmoratus	3	-	3	-	1	*[2]	3	7	1	1	5	24
No. individuals	9	17	22	2	6	0	5	10	3	7	13	94
No. species	2	1	4	1	2	0	2	2	2	4	3	7
Collecting Effort (hr)[4]	26.6	35.5	56.3	16.9	25.9	45.1	32.4	40.1	16.5	12.0	28.3	335.6

[1] Amphibian collecting at Camargo was done opportunistically by EY and may not be complete.
[2] Asterisk indicates that the species was collected outside *Polylepis* woodland, but in the study area.
[3] One of several new species of *Phrynopus* currently being described.
[4] Includes time spent searching for reptiles except at Camargo.

Table 4. Reptiles documented in *Polylepis* woodlands. Symbols: Ull = Ulla Ulla, Tac = Tacacoma, May = Mayca Mayu, Car = Carrasco, Khe = Kheñwa Sandora, Aca = Acacio, Icl = Icla, War = Wara Wara, Cmg = 30 km N Camargo, Saj = Sajama, Sam = Sama.

	Woodland											
Species	Ull	Tac	May	Car	Khe	Saj	Aca	Icl	War	Cmg[1]	Sam	Σ
Opipeuter xestus	-	-	-	1	-	-	-	-	-	-	-	1
Proctoporus bolivianus	3	20	-	-	-	-	-	-	-	-	-	23
Liolaemus alticolor	-	-	-	6	1	4	1	7	1	-	2	22
L. fittkaui	-	-	-	-	5[2]	-	-	-	-	-	-	5
L. islugensis	-	-	-	-	-	-	-	-	-	-	18	18
L. ornatus	-	-	-	-	-	-	-	-	2	-	-	2
L. signifer	*[3]	-	-	-	-	3	-	-	-	-	-	3
Tachymenis peruviana	*	1	-	1	-	-	-	-	-	-	1	3
No. individuals	3	21	-	8	6	7	1	7	3	-	21	77
No. species	1	2	-	3	2	2	1	1	2	-	3	8
Collecting Effort (hr)[4]	26.6	35.5	56.3	16.9	25.9	45.1	32.4	40.1	16.5	0	28.3	323.6

[1] Reptile collecting was not done at Camargo; none were found at Mayca Mayu despite searching.
[2] Second record for Bolivia; endemic species.
[3] Asterisk indicates that the species was collected outside *Polylepis* woodland, but in the study area.
[4] Includes time spent searching for amphibians.

captured by hand in the Cordillera de Cochabamba about 200 m N of the village of Sapanani, Chapare Province, Cochabamba Department (17° 20.5′ S, 66° 03.6′ W; 3640 m elevation) by JA on 16 July 1996. The habitat was an open shrubland of *Polylepis* 1-3 m tall with introduced *Eucalyptus* planted among *Polylepis* and adjacent to cropland.

We documented range extensions within Bolivia for 3 amphibians. Claudia Cortez collected 5 specimens of the frog *Telmatobius marmoratus* in a seasonal stream at Sama; this was the first record for Tarija Department (Avilés Province). Collecting at other woodlands resulted in provincial records for Nor Cinti (Camargo, Chuquisaca Department) and Zudañes (Icla, Chuquisaca Department), Linares (Wara Wara, Potosí Department) and Charcas (Acacio, Potosí Department). The distribution of *Bufo spinulosus* was extended to Tarija Department (Sama, Avilés Province). New provincial records for this species include Chapare (Mayca Mayu, Cochabamba Department) and Totora (Carrasco, Cochabamba Department), Linares (Wara Wara, Potosí Department), and Zudañes (Icla, Chuquisaca Department). *Pleuroderma marmoratum* has a wide distribution in the high Andes. Claudia Cortez collected 2 specimens at Sama in a seasonal stream. This extends its known distribution to Tarija Department (Avilés Province).

We found range extensions within Bolivia for 4 species of lizards. *Liolaemus alticolor* is a widely distributed lizard of the high Andes, but our collections were the first records for Tarija Department (Sama, Avilés Province) and Chuquisaca Department (Icla, Zudañes Province). Provincial records include Linares (Wara Wara, Potosí Department), Ibañes (Acacio, Potosí Department), and Totora (Carrasco, Cochabamba Department). *Liolaemus ornatus* also is widely distributed in the high Andes of Bolivia, but our collections extend its known distribution to Tarija Department (Sama, Avilés Province, in puna habitat not *Polylepis*) and Linares Province (Wara Wara, Potosí Department). *Liolaemus islugensis* was previously known only in Potosí Department in southwestern Bolivia, and this was the first record for Tarija Department (Sama, Avilés Province). *Opipeuter xestus* is endemic to yungas forests between 1000-3000 m elevation on the east slopes of the Andes in central Bolivia. Our specimen from Carrasco is the highest recorded for the species (3850 m). This lizard, like some species of yungas mammals (Yensen and Tarifa, 2002), also occurs in *Polylepis* woodlands where they are adjacent to yungas woodlands.

Alpha Diversity. *Polylepis* woodlands had significantly more species of mammals than amphibians or reptiles (means = 5.4, 2.1, and 1.9 species/woodland; Wilcoxon signed ranks tests, $z = -2.405$, $p = 0.016$ and $z = -2.830$, $p = 0.005$, respectively) but the number of amphibian and reptile species were not significantly different from each other ($z = -0.640$, $p = 0.522$; Table 5, Fig. 2). Also the diversity indices (H') were higher for mammals than amphibians or reptiles ($H' = 0.423$, 0.280, and 0.154, respectively; Table 5). The difference between mammals and reptiles was significant (Wilcoxon signed ranks test, $z = -2.934$, $p = 0.003$), whereas mammals and amphibians were not significantly different from each other ($z = -1.689$, $p = 0.091$), although the p-value may indicate a trend. H' values for amphibians and reptiles did not differ significantly from each other ($z = -1.007$, $p = 0.314$), paralleling the results with species number.

Using an index more sensitive to species evenness, D_s^*, mammals and amphibians were more diverse than reptiles in the 11 woodlands (mean $D_s^* = 2.198$, 2.299, and 1.574, respectively), as with the other indices. However, mammal and amphibian diversities did not differ significantly from each other (Wilcoxon signed ranks test, $z =$

Table 5. Species diversity of mammals, amphibians, and reptiles in *Polylepis* woodlands in Bolivia. S = number of species; H' = Shannon-Wiener diversity index; D_s* = unbiased estimator for samples of D_s, the inverse of the Simpson index; Ma = mammals, Am = amphibians, and Re = reptiles.

	S			H'			D_s*		
Woodland	Ma	Am	Re	Ma	Am	Re	Ma	Am	Re
Ulla Ulla	7	2	1	0.658	0.276	0.000	3.51	2.00	1.00
Tacacoma	6	1	2	0.436	0.000	0.083	2.21	1.00	1.11
Mayca Mayu	4	4	*	0.385	0.555	*	1.96	3.61	*
Carrasco	11	1	3	0.655	0.000	0.320	2.93	1.00	1.87
Kheñwa Sandora	6	2	2	0.485	0.196	0.196	2.20	1.50	1.50
Sajama	6	0	2	0.363	*	0.297	1.65	0.00	2.33
Acacio	6	2	1	0.595	0.292	0.000	3.39	2.50	1.00
Icla	5	2	1	0.379	0.265	0.000	1.77	1.88	1.00
Wara Wara	3	2	2	0.283	0.276	0.276	1.65	3.00	3.00
Camargo	3	4	*	0.166	0.501	*	1.23	3.50	*
Sama	2	3	3	0.249	0.440	0.218	1.68	3.00	1.36
Mean Diversity	5.4	2.1	1.9	0.423	0.280	0.154	2.198	2.299	1.574

* Not collected

-0.178, $p = 0.859$). This was due to the fact that even though there were fewer species of amphibians, their species abundances were more even than those of the mammals, and this resulted in similar values of D_s* for the two groups. The mean reptile D_s* was significantly lower than that of mammals ($z = -2.045$, $p = 0.041$) but not amphibians ($z = -1.481$, $p = 0.139$).

Although H' and D_s* gave slightly different results, the 3 measures of diversity (S, H', D_s*) were nevertheless highly correlated with each other. For mammals, Spearman rank correlations of S, H', and D_s* in the 11 woodlands were all highly significant ($r_s = 0.757$ to 0.952; $p < 0.01$ to < 0.001). We found similarly high correlations among amphibian diversities ($r_s = 0.939$ to 0.968; all $p < 0.001$) and reptile diversities ($r_s = 0.831$ to 0.916; all $p < 0.001$).

We used H' and S to further explore patterns of diversity among mammals, amphibians, and reptiles at each site and among woodlands. In a given woodland, H' of mammals, amphibians, and reptiles frequently differed (Fig. 2). At several sites we collected either 0 or 1 species of reptile or amphibian ($H' = 0$), which eliminated many possible comparisons. However, 8 mammal-amphibian, 6 mammal-reptile, and 3 reptile-amphibian comparisons were possible. Of these 17 comparisons, 9 were significantly different (Table 6). This shows that the diversity of the 3 groups frequently differed significantly in the same woodland.

Among woodlands, the diversities of mammals, amphibians, and reptiles also differed significantly, and each group had a different pattern (Fig. 2). For mammals,

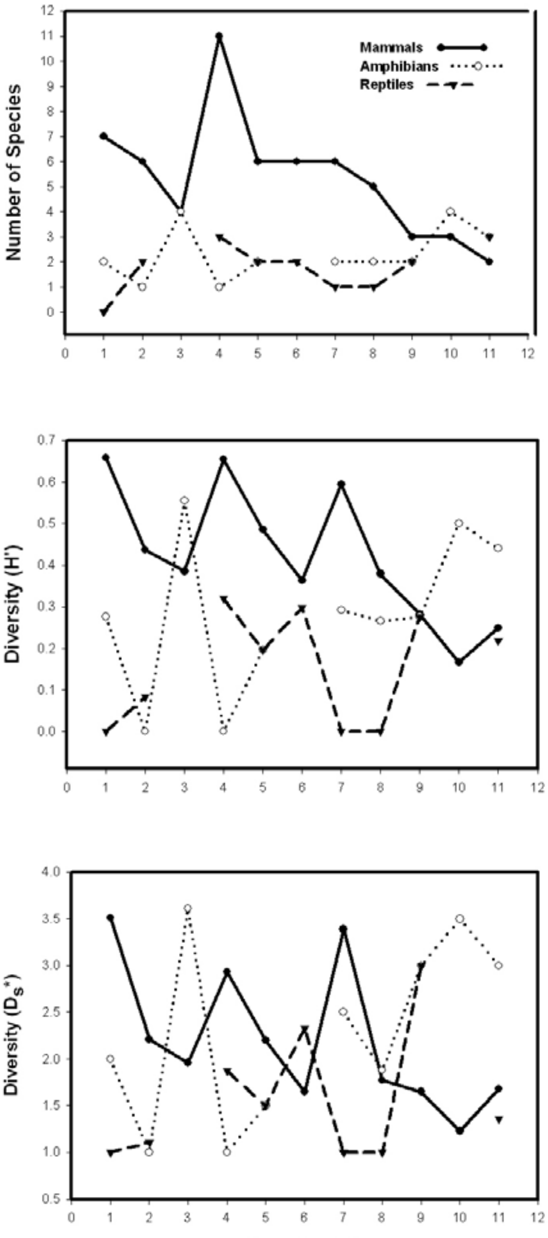

Figure 2. Comparison of mammal, amphibian, and reptile diversities in Bolivian *Polylepis* woodlands: Above, species richness (*S*) in the 11 woodlands sampled; Center, *H'* patterns for mammals, amphibians, and reptiles for each woodland; Below, D_s* patterns for the 3 groups in each woodland. Woodland numbers are as in Appendix I.

Table 6. Results of *t*-tests for intra-site diversity differences in *H′* among amphibians, reptiles, and mammals. Values indicate *t* and significance level.

Site	Mammals - Amphibians	Mammals - Reptiles	Amphibians - Reptiles
Ulla Ulla	**3.93*****	(**7.75*****)	**5.84*****
Tacacoma	(**7.10*****)	**4.09**^{3***}	1.38
Mayca Mayu	1.32	-	-
Carrasco	(**10.64*****)	**2.78***	(**2.68***)
Kheñwa Sandora	**2.27***	**2.27***	0
Sajama	-	1.05	-
Acacio	**5.02*****	(**12.86*****)	(**7.55*****)
Icla	1.06	(**4.07*****)	(**4.98*****)
Wara Wara	0.07	0.07	0
Camargo	**2.65***	-	-
Sama	**3.12****	0.35	**2.39***

Parentheses = comparisons between pairs of samples, one of which had a single species.
Bold = $p < 0.1$ or less, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

H′ differed significantly (*t*-tests) at 27 of the 55 pairs of woodlands (Table 6), indicating that many of the differences in diversities among sites were real. Amphibian *H′* values differed at 14 of 28 pairs of woodlands where comparisons were possible, also indicating some real patterns of variability among woodlands. However, diversities of reptiles did not differ significantly among woodlands; only 1 of 24 comparisons was significant, and that one was nearly significant at $p < 0.1$; we did not adjust for experiment-wise error rates, however, so this could have been a Type I error (Sokal and Rohlf, 1995). Thus reptile diversities probably differed little among woodlands, unlike mammals and amphibians.

As an additional test of the independence of the diversity patterns of the 3 taxonomic groups, we wished to determine if diversities of mammals, amphibians, and reptiles were correlated with each other among sites. Spearman rank correlations among *S*, *H′*, and D_s^* for mammals, amphibians, and reptiles across sites were all negative (r_s = –0.093 to –0.690). However, none of the correlations were significant with the exception of species richness (*S*) for mammals and amphibians ($p < 0.05$). The lack of positive correlations and the tendency toward negative correlations is an additional indication that the 3 taxonomic groups have independent diversity patterns. This suggests that each group responds differently to the underlying environmental variables.

Environmental Variables. We next looked for correlations between mammal, amphibian, and reptile diversity and environmental variables that might have affected the diversity patterns. One would expect diversity of the 3 groups to increase with precipitation and fragment size, and to decrease with time since fragmentation and elevation.

Precipitation was positively correlated with all measures of mammal diversity (*S*, *H'*, D_s*; $r_s = 0.951$, 0.904, and 0.880, respectively; all $p < 0.001$). Sites progressively closer to yungas woodlands received increasing amounts of precipitation and had higher mammal diversity. Amphibian diversities were negatively correlated with precipitation (*S*, *H'*, D_s*; $r_s =$ -0.730; -0.537, and -0.665; $p < 0.05$, < 0.05, and ~0.1, respectively). Although amphibian diversity typically increases with precipitation in other areas, we did not find this in our study. In arid regions, several *Polylepis* woodlands studied had permanent or semi-permanent streams, and this probably is more important than differences in precipitation. Reptile diversities were not significantly correlated with precipitation (*S*, *H'*, D_s*; $r_s = -0.300$, -0.210, and -0.284; $p > 0.2$, >0.5, and > 0.0.2), possibly because they are less dependent on water.

Fragment size was negatively correlated with mammal diversity (*S*, *H'*, and D_s*, $r_s = -0.604$, -0.582 and -0.648, $p < 0.1$, < 0.05 and < 0.1, respectively), but not amphibian ($r_s = 0.269$, 0.069, and 0.038; $p > 0.2$, > 0.5, and > 0.5) or reptile diversities ($r_s =$ 0.041, 0.052, and 0.172; all $p > 0.5$). Although the lack of correlation between fragment size and species diversity may seem contrary to the expected pattern, the woodlands in high precipation areas near yungas have been highly fragmented in recent years resulting from intense, small-scale agriculture (Table 1). Precipitation and fragment size were also negatively correlated ($r_s = -0.841$, $p < 0.005$). Areas with high precipitation have the densest human populations and nearly all *Polylepis* woodlands have been converted to agriculture. Remaining fragments were small but occurred in an area with a rich species pool. In contrast, in more arid areas of the high Andes, fragments were larger but inhabited by a smaller species pool (Yensen and Tarifa, 2002). Many fragments near yungas appeared to be totally impacted by edge processes and no interior core area remained (Laurance and Yensen, 1991). No measure of diversity was correlated with elevation (mammal *S*, *H'*, and D_s*, $r_s = -0.288$, -0.281, and -0.038 ($p > 0.2$, > 0.2, and > 0.5, respectively; amphibian *S*, *H'*, and D_s*, $r_s = 0.310$, 0.259, and 0.136; $p > 0.2$, > 0.2, and > 0.5, respectively; reptiles *S*, *H'*, and D_s*, $r_s = -0.013$, -0.262, and -0.406; $p > 0.5$, > 0.2, and > 0.2, respectively).

Beta Diversity. Our data demonstrated large differences in species composition among the different *Polylepis* woodlands (Tables 2-4). To make comparisons among groups, we used only the 8 woodlands where all groups were collected. Beta diversities reported earlier for mammals (Yensen and Tarifa, 2002) were recalculated for these 8 woodlands.

Species turnover among woodlands was highest for mammals (mean similarity = 14.5%, *N* = 28 comparisons among woodlands). Reptiles had intermediate similarity among woodlands (mean = 35.6%), and amphibian species were most similar (mean = 45.1%, Table 7). These similarities reflect the sizes of the species pools, the widespread distribution of 2 amphibians (*Bufo spinulosus* and *Telmatobius marmoratus*) and 1 lizard (*Liolaemus alticolor*), and perhaps less habitat specificity among the few amphibians and reptiles at high elevation in comparison with the more speciose mammals.

As another measure of beta diversity, we used a Mantel test with the Sorensen distance measure. The standardized Mantel statistic for mammals ($r = -0.395$, $p = 0.033$) indicated significant species turnover with distance. For reptiles, turnover was even higher ($r = -0.647$, $p = 0.015$). However, for amphibians, species appear to be either very widespread or very local, leading to no significant correlation among interwoodland

Table 7. Results of t-tests comparing species diversity (*H'*) among *Polylepis* woodlands (lower left half of matrix). Percent similarity in species (Bray-Curtis) among 8 study areas where all 3 taxonomic groups were sampled (upper right half of matrix). Similarity is based upon species presences and absences. Column abbreviations for woodlands match names in rows.

Site	Ulla	Taca	Mayc	Carr	Kheñ	Saja	Acac	Icla	Wara	Cmg	Sam
Mammals											
Ulla Ulla	-	15.4	-	11.1	15.4	-	15.4	16.7	0	-	0
Tacacoma	**2.12***	-	-	35.3	16.7	-	16.7	0	0	-	0
Mayca Mayu	1.85	0.38	-	-	-	-	-	-	-	-	-
Carrasco	0.01	**2.52****	**1.99**	-	47.1	-	47.1	0	0	-	0
Kheñwa San	1.57	0.64	0.72	**1.85**	-	-	66.7	0	22.2	-	0
Sajama	**2.88****	0.90	0.15	**3.49*****	1.35	-	-	-	-	-	-
Acacio	0.65	2.05*	1.62	0.81	1.31	**3.14****	-	0	0	-	0
Icla	**2.21***	0.51	0.04	**2.49***	0.91	0.15	**2.08***	-	0	-	0
Wara Wara	**3.62*****	**1.79**	0.75	**4.39*****	**2.20***	0.97	**4.15*****	0.87	-	-	80.0
Camargo	**4.80*****	**3.21****	1.63	**5.82*****	**3.52*****	**2.41****	**5.80*****	**1.95**	1.42	-	-
Sama	**4.33*****	**2.52****	1.06	**5.50*****	**2.90****	1.59	**5.56*****	1.27	0.46	1.18	-

Table 7 (continued).

Amphibians											
Ulla Ulla	-	0	-	0	50.0	-	50.0	50.0	50.0	-	80.0
Tacacoma	*	-	-	0	0	-	0	0	0	-	0
Mayca Mayu	**4.32*** **	*	-	-	-	-	-	-	-	-	-
Carrasco	*	*	*	-	66.7	-	0	66.7	66.7	-	50.0
Kheñwa San	0.69	*	**3.12***	*	-	-	0	100.0	100.0	-	80.0
Sajama§	-	-	-	-	-	-	-	-	-	-	-
Acacio	0.26	*	**4.50*** **	*	0.85	-	-	50.0	50.0	-	40.0
Icla	0.16	*	**4.20*** **	*	0.20	-	0.41	-	100.0	-	80.0
Wara Wara	0.00	*	**3.39*** **	*	0.60	-	0.18	0.11	-	-	80.0
Camargo	**1.84**	*	0.44	*	**1.97**	-	1.75	**1.89**	1.61	-	-
Sama	**2.46***	*	**1.84**	*	**2.11**	-	**2.49***	**2.51***	**2.38**	0.51	-

Table 7 (continued).

Reptiles											
Ulla Ulla	-	66.7	-	0	0	-	0	0	0	-	0
Tacacoma	1.38	-	-	40.0	0	-	0	0	0	-	40.0
Mayca Mayu†	0.00	0.00	-	-	-	-	-	-	-	-	-
Carrasco	*	1.77	-	-	40.0	-	50.0	50.0	40.0	-	66.7
Kheñwa San	*	0.92	-	0.78	-	-	66.7	66.7	50.0	-	40.0
Sajama	*	-	-	0.20	0.92	-	-	-	-	-	-
Acacio	0.00	1.38	-	2.68	*	*	-	100.0	66.7	-	50.0
Icla	0.00	1.38	-	2.68	*	*	0.00	-	66.7	-	50.0
Wara Wara	*	**1.90**	-	0.30	0.60	0.24	*	*	-	-	40.0
Camargo†	-	-	-	-	-	-	-	-	-	-	-
Sama	*	1.33	-	0.71	0.16	0.93	*	*	0.51	-	-

§ No amphibians found in woodland, but occurred nearby.
† Reptiles not sampled.
* Samples with just 1 species at 1 of the pair of woodlands ($H' = 0$).
Bold = $p < 0.1$ or less (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

similarities and distance (r = -0.240, p = 0.216).

Gamma Diversity. For mammals, we documented cases of geographic replacement in mice of the abundant genus *Phyllotis* and in the small marsupial *Thylamys*. We found only 1 taxon of *Phyllotis* per site but frequent geographic replacement (Yensen and Tarifa, 2002). Similarly, *Thylamys venustus* replaced *T. pallidior* in the eastern Andes (Tarifa et al., unpublished). Thus 9 of 31 species (29%) were involved in geographic replacements.

Amphibian species were geographically widespread (Duellman, 1979; de la Riva et al., 2000), except for a new species of *Phrynopus* which was found at only 1 locality. We found no other cases of geographic replacement using range maps constructed by JA from data in the CBF, Duellman et al. (1997), and de la Riva et al. (2000). Lack of species turnover was another indication that the amphibian species pool is limited to a handful of species adapted to the rigorous conditions of the high Andes.

Among reptiles, we documented 2 apparent cases of geographic replacement in *Liolaemus* lizards (*L. ornatus* – *L. fittkaui* and *L. ornatus* – *L. islugensis*) using range maps constructed by JA from data in the CBF and Dirksen and de la Riva (1999). There was also a possible case of replacement among the snakes *Tachymenis peruviana* and *T.* cf. *elongata*. Thus 3 of 8 species (38%) were involved in geographic replacement.

Gamma diversity was an important component of intersite variability for mammals and reptiles but not amphibians. The low gamma diversity in amphibians was consistent with the results of the Mantel test showing lower turnover in amphibians.

DISCUSSION

Bolivia's rich lowland herpetofauna decreases gradually in species diversity along an elevational gradient up to the upper limit of yungas forest (ca. 3000 m elevation), then decreases abruptly to a low level in the treeless highlands (Duellman, 1979). Although the high Andean herpetofauna of Bolivia is still poorly known, by all accounts it is composed of relatively few species (Duellman, 1979; Cadle and Patton, 1988; Duellman et al., 1997; Aparicio, 1999; Dirksen and de la Riva, 1999; de la Riva et al., 2000; Aparicio and Rios, 2002). In a long-term study of a 100 km^2 area between 3700-4280 m elevation in the puna, Aparicio (1993) reported 5 species of amphibians and 4 reptiles, all of which we found in *Polylepis* woodlands. In the high Andes, a given community would be expected to have a maximum of 5 to 7 species of amphibians and reptiles (Cadle and Patton, 1988); we found from 2 to 6 species per woodland, which is consistent with this estimate.

In the high Andes, amphibian and reptile species richness is limited by extreme climatic variation, which occurs year-round. The species that can survive in this harsh environment must have adaptations which allow them to (1) maintain an active body temperature in a region where the mean annual temperature is ca. 10° C (Montes de Oca, 1989), (2) ensure that eggs and juveniles do not dessicate during the day or freeze during the night, and (3) have few dietary specializations so that they can utilize whatever prey are available (Donoso-Barros, 1966).

There currently are 186 species of amphibians recorded from Bolivia, 18% of which are endemic, but the eventual total is expected to reach much higher. The known fauna has increased 66% between 1990 and 2000, but only 1 of the species added was from the high Andes (de la Riva et al., 2000). Using data in de la Riva et al. (2000), we noted 4 distributional patterns in the amphibian fauna of the Bolivian high Andes: (1) widespread species endemic to the high Andes (*Bufo spinulosus*, *Telmatobius marmoratus*, and *Pleuroderma marmorata*), (2) species that also occur in humid montane yungas forests (*Gastrotheca marsupiata* and *Hyla andina*), (3) species shared with inter-Andean dry valleys (*Hyla albonigra* and *Pleuroderma cinereum*), and (4) high-Andean aquatic endemics (*Telmatobius culeus* restricted to Lake Titicaca and *T. huayra* endemic to Potosí).

Although the number of amphibian species per woodland (1-4) may seem low because we collected in the dry season when there was relatively less amphibian activity, we found all of the species known to occur in the Bolivian high Andes between 3200 to 4600 m, and we added 1 species (*Phrynopus* n. sp.) to the high Andean fauna. Further, Aparicio and Rios (2002) collected in the Ulla Ulla region during the wet season and found similar results at high elevations (no more than 3 amphibian and 3 reptile species per community) suggesting that the community is the same, and small, in both wet and dry seasons. Potential additions to the list of amphibian species utilizing *Polylepis* woodlands would be more new species of *Phrynopus* and *Telmatobius*, because there are a number of narrow endemics and undescribed species in these genera (JA, in preparation; I. de la Riva, personal communication). *Pleuroderma cinerea* was a possibility at the lowest elevation woodlands adjacent to the dry interior valleys (e.g., Wara Wara).

For reptiles, the list of species utilizing *Polylepis* woodlands likely is close to complete. However, the common snake *Tachymenis peruviana* probably is present at most sites yet was rarely recorded in our survey, likely because it occurs at low densities and is less active in the dry season. *Liolaemus alticolor* and *L. signifer* could occur at 1 or 2 more woodlands between La Paz and Potosí, but not in Tarija Department. *L. islugensis* and *L. fittkaui*, 2 Bolivian endemics, and *L. ornatus* are known from very few sites, and we extended their small ranges.

We calculated the number of species of amphibians and reptiles that potentially could be expected to occur at each woodland based on their known geographic distributions. Even if all the species that could potentially occur in a woodland were in fact present, which is unlikely due to the degradation of the sites, the geographic pattern of species richness would not change greatly. Amphibian and reptile diversities would still be consistently low, differ from each other at several sites, and show little resemblance to the mammalian pattern (Fig. 3).

Agricultural conversion, forest fragmentation and degradation, and pollution have negative effects on the amphibians of Bolivia (de la Riva et al., 2000). We observed this in *Polylepis* woodlands as well. In more degraded woodlands, formerly permanent streams were intermittent or completely dry. These woodlands are important for maintenance of watersheds in the high Andes (Yensen and Tarifa, 2002). At Sajama, where there was no surface water inside the woodlands at any time of the year, there were no amphibians, even though 3 species occurred outside the woodland along the nearby Sajama River.

Amphibians depend more upon water than the presence or absence of trees *per se*, but surface water depends in turn upon the amount of tree cover, density of grasses and herbs in the understory, amount of remaining topsoil, fragment size, precipitation, and topography. The local absence of any amphibian species from the limited pool may be a symptom of habitat degradation.

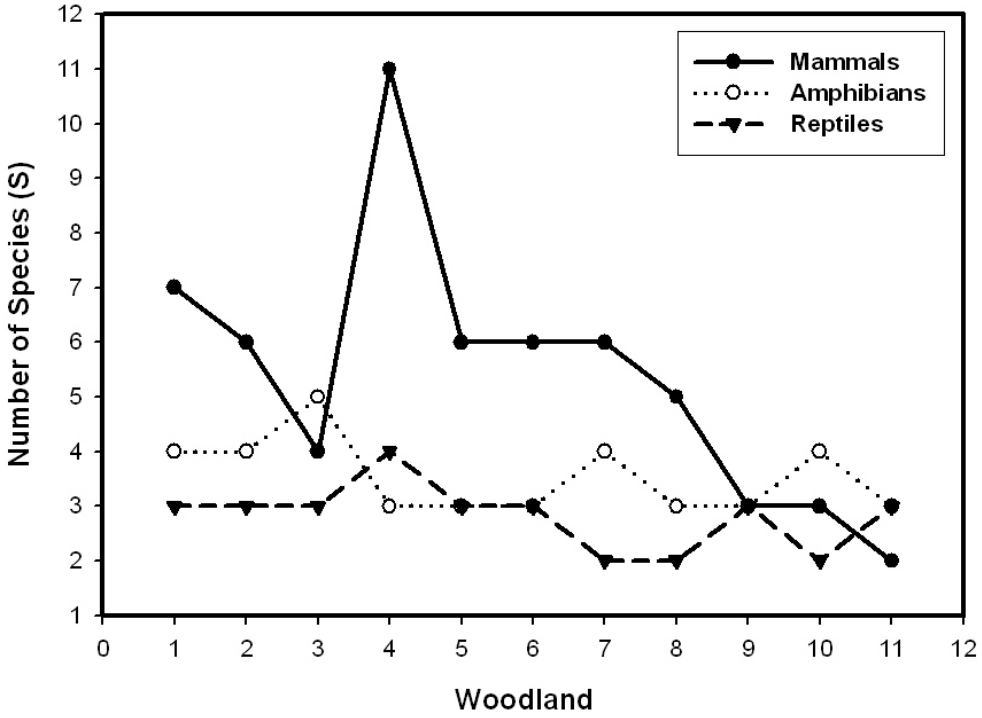

Figure 3. Patterns of species richness including amphibians and reptiles that potentially could occur in the woodlands studied. The addition of hypothetical species did not result in concordant patterns among taxonomic groups (see text). Woodland numbers are as in Appendix I.

To definitively answer the question of whether or not birds can be a successful umbrella group for high-Andean amphibians, reptiles, and mammals, we will need still more data on the distributions of these latter groups. However, the initial data from this study indicate that any group with high beta diversity probably would not be well protected by using birds as an umbrella because there is too much geographic species turnover to protect it with a small number of sites. Rather, a system of small reserves in different watersheds would be more appropriate. As one example of a group that would require a number of reserves, there appear to be many cryptic species of frogs of genus *Phrynopus* with very limited distributions (J. Aparicio, in preparation; I. de la Riva, personal communication).

The high Andes generally are considered to have low biological diversity (Pearson, 1978; Duellman, 1979; Cadle and Patton, 1988), whereas the tropical eastern slopes of the Andes constitute one of the planet's megadiversity "hotspots" (Mittermeier et al., 1998). Conservation strategies protecting "hotspots" have been advocated as the most efficient means of conserving biodiversity (Mittermeier et al., 1998, 2000; Myers et al., 2000). However, this strategy has been questioned as overly simplistic (Jepson and Canney, 2001). In Bolivia, highland ecosystems are degrading much more rapidly than the more sparsely populated tropics (Ministerio de Desarrollo Sostenible y Planificación, 2001; Ibisch et al., 2003). If human edeavors depend upon functional ecosystems (Pirot et al., 2000; Tilman, 2000; Huynen et al., 2004), and these in turn depend upon maintenance of biological diversity, then we must conserve biodiversity in populated areas, not just in "hotspots" (Kinzig et al., 2002).

Conservation programs in the high Andes are urgently needed to maintain ecosystem services and other benefits of biodiversity. *Polylepis* woodlands play an especially important role in this regard, because they help maintain watersheds, promote soil fertility, and provide firewood, herbal medicines, and other benefits (Fjeldsa and Kessler, 1998; Yensen and Tarifa 2002). Although the ecological roles of most species in *Polylepis* woodlands are still unknown, maintaining existing biodiversity must be a high priority for ecosystem functions such as stability, productivity, and nutrient retention (Tilman, 1999, 2000).

The mammals, amphibians, and reptiles of the high Andes are all endemic to the region (Cadle and Patton, 1978). Conservation of a tropical "hotspot" is virtually certain to be inadequate to protect these taxa, nor will it help maintain ecosystem services in the high Andes. One of the best ways to protect the rich biodiversity of the sparsely populated tropics is by maintaining the ecological sustainability of populated areas in the highlands to reduce the need for people to migrate from degraded highlands down to more pristine lowlands in order to survive.

The high rates of amphibian endemism in the tropical lowlands (de la Riva et al., 2000) suggest that amphibians could be used as an umbrella group to provide protection for other valuable biological resources. However, despite this potential, amphibians frequently are ignored due to lack of knowledge about their taxonomy, distribution, and conservation status. Further, their low diversity would argue against this. Mammals likewise have relatively limited distributions, poorer dispersal ability, and ranges limited by barriers (Yensen and Tarifa, 2002), and thus one could argue that they also have potential as a good umbrella group, and protecting all of them would require more than just a few sites.

While it would be nice to have complete data on distribution patterns for amphibians, reptiles, and mammals, we need to use a variety of information in making conservation decisions rather than relying on a single group as a "shortcut." It seems to us that an even better option than umbrella groups would be to sponsor interdisciplinary field surveys which include data on as many groups as possible prior to arriving at conservation decisions. If the lack of agreement among distributional patterns of birds, mammals, amphibians, and reptiles is in fact real, it suggests that we need to rethink the umbrella group approach to evaluating areas of conservation priority in the high Andes (at least) and place more effort in less easily observed groups which may also be information-rich. We should also place more effort in protecting a wider diversity of areas.

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APPENDIX 1: GAZETTEER OF LOCALITIES

Woodlands and specific collecting localities listed from north to south. The woodlands are shown in Fig. 1.

Geographic Area	Collecting Locality	Coordinates (Lat., Long.)	Fragment Size (ha)
1. Ulla Ulla	1. Sorapata	15° 01′, 68° 55′	2
	2. La Curva	15° 06′, 69° 01′	2
	3. Pelechuco	14° 49′, 69° 04′	2
2. Tacacoma	4. Tacacoma	15° 36′, 68° 39′	140
	5. Quiyabaya	15° 37′, 68° 41′	10
3. Mayca Mayu	6. Mayca Mayu	17° 05′, 66° 06′	1
	7. Espital Mayu	17° 05′, 66° 05′	3
4. Carrasco	8. Mojón	17° 30′, 65° 25′	75
	9. Cocapata	17° 34′, 65° 18′	30
	10. Monte Punku	17° 34′, 65° 17′	45
5. Kheñwa Sandora	11. Km 80	17° 40′, 66° 29′	>1000
	12. Pusuq'huni	17° 45′, 66° 27′	>1000
6. Sajama	13. Quebrada Kohuiri	18° 08′, 68° 57′	>1000

	14. Cerro Inchu Askata	18° 02′, 68° 56′	contiguous with 13
	15. Cerro Comisario	18° 11′, 68° 55′	contiguous with 13
7. Acacio	16. Acacio	18° 06′, 66° 13′	300
8. Icla	17. Mesa Pata	19° 34′, 64° 39′	1000-3000
	18. Potolo	19° 34′, 64° 40′	contiguous with 17
9. Wara Wara	19. Wara Wara	19° 49′, 65° 08′	700
10. Camargo	20. 31-36 km N Camargo	20° 19-22′, 65° 07-08′	>30,000
	21. Río Honda	20° 25′, 65° 08′	contiguous with 20
	22. 22-24 km N Camargo	20° 25-26′, 65° 08′	contiguous with 20
11. Sama	23. Cerro Kewiñal	21° 42′, 65° 09′	>1000

APPENDIX 2: SPECIMENS EXAMINED FOR AMPHIBIAN AND REPTILE DISTRIBUTIONAL RECORDS

Amphibians:

Phrynopus n. sp.(La Paz Department, Larecaja Provice): CBF 2129-2145.

Telmatobius marmoratus (Tarija Department, Avilés Province): CBF 3042-3046; (Chuquisaca Department, Nor Cinti Province): CBF 3050; (Chuquisaca Department, Zudañes Province): CBF 2119-2124, 2128; (Potosí Department, Linares Province): CBF 2108-2109, 2110, 3032.

Bufo spinulosus (Tarija Department, Avilés Province): CBF 3036-3041; (Cochabamba Department, Chapare Province): CBF 3029-3030; (Cochabamba Department, Totora Province): CBF 3047-3048; (Potosí Department, Linares Province): CBF 2111-2112; (Chuquisaca Department, Zudañes Province): CBF 2125-2127.

Pleuroderma marmoratum (Tarija Department, Avilés Province): CBF 3034-3035.

Reptiles:

Liolaemus fittkaui (Cochabamba Department, Tiraque Province): TTS 904-905, EY 1803-1805.

Tachymenis cf. *elongata* (Cochabamba Department, Chapare Province): CBF 1843.

Liolaemus alticolor (Tarija Department, Avilés Province): CBF 1786-1787; (Chuquisaca Department, Zudañes Province): CBF 1564, 1568, 1570-1574; (Potosí Department, Linares Province): CBF 1567; (Potosí Department, Ibañes Province): CBF 1838; (Cochabamba Department, Totora Province): CBF1839-1842.

Liolaemus ornatus (Tarija Department, Avilés Province): CBF 1784; (Potosí Department, Linares Province): CBF 1566, 1569.

Liolaemus islugensis (Tarija Department, Avilés Province): CBF 1767-1784, 1786-1787.

Opipeuter xestus (Cochabamba Department, Totora Province): CBF 1531.

LITERATURE CITED

Anderson, S.
1997 The mammals of Bolivia. Bulletin of the American Museum of Natural History 231:1-652.

Aparicio, J.
1993 Herpetofauna de Huaraco un ecosistema Andino en el Altiplano Central de Bolivia. Ecología en Bolivia: Documentos, Serie Zoología 4:1-38.

1996 Herpetofauna. Pp. 19-23 in Diagnostico sobre la fauna de vertebrados, Plan de Manejo del Parque Nacional Sajama (Tarifa, T. ed.). Contrato de Préstamo del Banco Interamericano de Desarrollo No. 840/SF-BO. 88 + 38 pp.

1999 Herpetofauna de la Reserva Nacional de Fauna Altoandina Ulla Ulla, Departamento de La Paz (Bolivia). Revista Boliviana de Ecología 5:13-23.

Aparicio, J., and J. N. Rios
2002 Herpetofauna de Montañas: Parque Nacional y Área Natural de Manejo Integrado Apolobamba, La Paz – Bolivia. Memorias de la III Reunión Regional de Selvas de Montaña. San Salvador de Jujuy, Argentina. Interactive CD.

Argollo, J., C. Soliz, and R. Villalba
2004 Potencialidad dendrocronológica de *Polylepis tarapacana* en los Andes Centrales de Bolivia. Ecología en Bolivia 39:5-24.

Azurduy, C., and X. Velez
2001 Nota sobre la presencia, uso e importancia de los bosques de *Polylepis* como parte del hábitat del oso andino (*Tremarctos ornatus*) en la cuenca alta del río Cañón. Revista Boliviana de Ecología y Conservación Ambiental 9:79-84.

Bibby, C. J., N. J. Collar, M. J. Crosby, M. F. Heath, C. Imboden, T. H. Johnson, A. J. Long, A. J. Stattersfield, and S. J. Thirgood
1992 Putting biodiversity on the map: priority areas for global conservation. International Council for Bird Preservation, Cambridge, UK. 90 pp.

Cadle, J. E., and J. L. Patton
1988 Distribution patterns of some amphibians, reptiles, and mammals of the eastern Andean slope of Southern Peru. Pp. 225-244 in Proceedings of a workshop on Neotropical distribution patterns (Heyer, W. R., and P. E. Vanzolini, eds.). Academia Brasileira de Ciências, Rio de Janeiro, Brasil.

Canaday, C., and J. Rivadeneyra
2001 Initial effects of a petroleum operation on Amazonian birds: terrestrial insectivores retreat. Biodiversity and Conservation 10:567-595.

Cei, J. M.
1980 Amphibians of Argentina. Monitore zoologico Italiano, Monografia 2:1-609.

1993 Reptiles del noroeste, noreste y este de la Argentina. Herpetofauna de las selvas subtropicales, puna y pampas. Museo regionale di scienze naturali (Torino, Italy), Monografie 14:1-949.

Diamond, J.
1986 The design of a nature reserve system for Indonesian New Guinea. Pp. 485-503 in Conservation biology: the science of scarcity and diversity. (Soulé , M. E., ed.). Sinauer Associates, Sunderland, Massachusetts, USA.

Dirksen, L., and I. de la Riva
1999 The lizards and amphisbaenians of Bolivia (Reptilia, Squamata): checklist, localities, and bibliography. Graellsia 55:199-215.

de la Riva, I., J. Köhler, S. Lotters, and S. Reichle
2000 Ten years of research on Bolivian amphibians: Updated checklist, distribution, taxonomic problems, literature and iconography. Revista Española de Herpetologia 14:19-164.

Duellman, W. E.
1979 The herpetofauna of the Andes: patterns of distribution, origin, differentiation, and present communities. Pp. 371-459 in The South American herpetofauna: Its origin, evolution, and dispersal (Duellman, W. E., ed.). University of Kansas Museum of Natural History, Monograph 7.

Duellman, W. E., I. de la Riva, and E. R. Wild
1997 Frogs of the *Hyla armata* and *Hyla pulchella* groups in the Andes of South America, with definitions and analyses of phylogenetic relationships of Andean groups of *Hyla*. University of Kansas Museum of Natural History, Scientific Papers 3:1-41.

Donoso-Barros, R.
1966 Reptiles de Chile. Ediciones de la Universidad de Chile, Santiago, Chile. 458 pp.

Eckholm, E.P.
1975 The deterioration of mountain environments. Science 189:764-770.

Ellenberg, H.
1979 Man's influence on tropical mountain ecosystems in South America. Journal of Ecology 67:401-416.

Fjeldså, J.
1987 Birds of relict forests in the high Andes of Peru and Bolivia. Zoological Museum, University of Copenhagen, Copenhagen, Denmark. 80 pp.

1990 The conservation of biological diversity: using birds to set priorities. Pp. 157-175 in Environmental concerns: an inter-disciplinary exercise (Hansen, J. A., ed.). Elsevier Applied Science, London, England.

1992 Biogeographic patterns and evolution of the avifauna of relict high-altitude woodlands of the Andes. Steenstrupia 18:9-62.

1993 The avifauna of the *Polylepis* woodlands of the Andean highlands: the efficiency of basing conservation priorities on patterns of endemism. Bird Conservation International 3:37-55.

2000 The relevance of systematics in choosing priority areas for global conservation. Environmental Conservation 27:1-9.

2002a *Polylepis* forests – vestiges of a vanishing ecosystem in the Andes. Ecotropica 8:111-123.

2002b Key areas for conserving the avifauna of *Polylepis* forests. Ecotropica 8:125-131.

Fjeldså, J., and M. Kessler
1996 Conserving the biological diversity of *Polylepis* woodlands of the highland of Peru and Bolivia: A contribution to sustainable natural resource management in the Andes. NORDECO, Copenhagen, Denmark. 250 pp.

Fjeldså, J., and C. Rahbek
1997 Species richness and endemism in South American birds: Implications for the design of networks of nature reserves. Pp. 466-482 in Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities (Laurance, W. F., and R. O. Bierregaard, Jr., eds.). University of Chicago Press, Chicago, Illinois, USA.

Frimer, O., and S. M. Nielsen
1989 The status of *Polylepis* forests and their avifauna in Cordillera Blanca, Peru. Zoological Museum University of Copenhagen, Copenhagen, Denmark. 58 pp.

Gallardo, J.
1987 Anfibios Argentinos: Guía para su identificación. Librería Agropecuaria, Buenos Aires, Argentina. 98 pp.

Huynen, M. M. T. E., P. Martens, and R. S. DeGroot.
2004 Linkages between biodiversity loss and human health: a global indicator analysis. International Journal of Environmental Health Research 14:13-30.

Hutcheson, K.
1970 A test for comparing diversities based on the Shannon formula. Journal of Theoretical Biology 29:151-154.

Ibisch, P. L., A. Carretero, S. G. Beck, S. Cúellar, S. D. Espinoza, and N. V. Araujo
2003 El caso de los bosques andinos. Pp. 272-285 in Biodiversidad: la riqueza de Bolivia: estado de conocimiento y conservación (Ibisch, P. L., and G. Mérida, eds.). Editorial FAN, Santa Cruz de la Sierra, Bolivia.

Jepson, P., and S. Canney
2001 Biodiversity hotspots: hot for what? Global Ecology & Biogeography 10:225-227.

Kessler, M.
1995a The genus *Polylepis* (Rosaceae) in Bolivia. Candollea 50:131-171.

1995b Present and potential distribution of *Polylepis* (Rosaceae) forests in Bolivia. Pp. 281-294 in Biodiversity and conservation of Neotropical montane forests (Churchill, S. P. , H. Balslev, and E. Forero, eds.). New York Botanical Garden, New York, New York, USA.

1995c *Polylepis*-Wälder Boliviens: Taxa, Ökologie, Verbreitung und Geschichte. Dissertationes Botanicae 246, J. Cramer, Berlin.

2002 The "*Polylepis* problem": where do we stand? Ecotropica 8:97-110.

Kinzig, A. P., S. W. Pacala, and D. Tilman (eds.)
2002 Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions. Monographs in Population Biology 33, Princeton University Press, Princeton, New Jersey, USA. 365 pp.

Krebs, C. J.
1989 Ecological Methodology. Harper and Row, New York, New York, USA. 654 pp.

Laurance, W. F., and E. Yensen
1991 Predicting the impact of edge effects in fragmented habitats. Biological Conservation 55:77-92.

Liberman, M.
1986 Microclima y distribución de *Polylepis tarapacana* en el Parque Nacional del Nevada Sajama, Bolivia. Documents Phytosociologiques, noveau serie 10:235-276.

Lloyd, M., J. H. Zar, and J. R. Karr
1968 On the calculation of information-theoretical measures of diversity. American Midland Naturalist 79:257-272.

Long, A. J., M. J., Crosby, A. J. Stattersfield, and D. C. Wege
1996 Towards a global map of biodiversity: patterns in the distribution of restricted-range birds. Global Ecology and Biogeography Letters 5:281-304.

Ludwig, J. A., and J. F. Reynolds
1988 Statistical Ecology: A Primer on Methods and Computing. John Wiley and Sons, New York. 337 pp.

McCune, B. and M. J. Mefford
1999 PC-ORD for Windows. Multivariate analysis of ecological data, version 4.0. MjM Software, Gleneden Beach, Oregon, USA.

Ministerio de Desarrollo Sostenible y Planificación
2001 Estrategia Nacional de Conservación y Uso Sostenible de la Biodiversidad. Ministerio de Desarrollo Sostenible y Planificación, La Paz, Bolivia. 193 pp.

Mittermeier, R. A., N. Myers, P. R. Gill, and C. G. Mittermeier (eds.)
2000 Hotspots: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions. Distributed for CEMEX, Mexico City, and Conservation International, New York by University of Chicago Press, Chicago. 431 pp.

Mittermeier, R. A., N. Myers, J. B. Thomsen, and G. A. B. da Fonseca
1998 Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. Conservation Biology 12:516-520.

Montes de Oca, I.
1989 Geografia y Recursos Naturales de Bolivia. Second edition. Editorial Educacional del Ministerio de Educacion y Cultura, La Paz, Bolivia. 574 pp.

Moya Soto, K. S.
2003 Comparación de Comunidades de Micromamíferos en Bosques de Kewiña (*Polylepis besseri*). Licenciatura Thesis, Universidad Mayor de San Simón, Cochabamba, Bolivia. 84 pp.

Myers, N., R. A. Mittermeier, G. A. B. da Fonseca, and J. Kent
2000 Biodiversity hotspots for conservation priorities. Nature 403:853-858.

Pearson, O.
1958 A taxonomic revision of the rodent genus *Phyllotis*. University of California Publications in Zoology 56:391-496.

Pearson, O. P., and C. P. Ralph
1978 The diversity and abundance of vertebrates along an altitudinal gradient in Peru. Memorias del Museo de Historia Natural "Javier Prado" 18:1-97.

Peet, R. K.
1974 The measurement of species diversity. Annual Review of Ecology and Systematics 5:285-307.

Peters, J., and R. Donoso-Barros
1970 Catalogue of the Neotropical Squamata. Part II. Lizards and amphisbaenians. U. S. National Museum Bulletin 297:1-293.

Pirot, J.-Y., P.-J. Meynell, and D. Elder.
2000 Ecosystem Management: Lessons from Around the World: A Guide for Development and Conservation Practitioners. IUCN, Gland Switzerland and Cambridge, UK. 132 pp.

Pizzimenti, J. J., and R. de Salle
1980 Dietary and morphometric variation in some Peruvian rodent communities: The effect of feeding strategy on evolution. Biological Journal of the Linnean Society 13:263-285.

Rada, F., C. García-Núñez, C. Boero, M. Gallardo, M. Hilal, J. González, F. Prado, M. Liberman-Cruz, and A. Azócar
2001 Low-temperature resistance in *Polylepis tarapacana*, a tree growing at the highest altitudes in the world. Plant, Cell and Environment 24:377-381.

Remsen, J. V., Jr., and T. A. Parker, III
1995 Bolivia has the opportunity to create the planet's richest park for terrestrial biota. Bird Conservation International 5:181-199.

Salazar-Bravo, J., E. Yensen, T. Tarifa, and T. L. Yates
2002 Distributional records of Bolivian mammals. Mastozoología Neotropical 9:70-78.

Sokal, R. R., and F. J. Rohlf
1995 Biometry: The Principles and Practice of Statistics in Biological Research. Third edition. W. H. Freeman and Company, New York, New York, USA. 887 pp.

Solari, S.
2003 Diversity and distribution of *Thylamys* (Didelphidae) in South America, with emphasis on species from the western side of the Andes. Pp. 82-101 in Predators with Pouches: The Biology of Carnivorous Marsupials (Jones, M., C. Dickman, and M. Archer, eds.). CSIRO, Sydney, Australia.

Steppan, S.
1993 Phylogenetic relationships among the Phyllotini (Rodentia: Sigmodontinae) using morphological charaters. Journal of Mammalian Evolution 3:187-213.

1995 Revision of the tribe Phyllotini (Rodentia: Sigmodontinae), with a phylogenetic hypothesis for the Sigmodontinae. Fieldiana: Zoology, new series 80:1-112.

1997 Phylogenetic analysis of phenotypic covariance structure. I. Contrasting results from matrix correlation and common principal component analyses. Evolution 51:571-586.

Tarifa, T.
1996 Mamíferos. Pp. 38-48 in Diagnostico sobre la fauna de vertebrados, Plan de Manejo del Parque Nacional Sajama (Tarifa, T., ed.). Contrato de Préstamo del Banco Interamericano de Desarrollo No. 840/SF-BO.

1997 Mamíferos. Pp. 43-72 in Plan de Manejo Reserva Nacional de Fauna Ulla Ulla, Informe Tecnico, vol. II: aspectos biologicos. Ministerio de Desarrollo Sostenible y Medio Ambiente, Direccion Nacional de Conservacion de la Biodiversidad, La Paz, Bolivia.

Tarifa, T., and E. Yensen
2001 Mamíferos de los bosques de *Polylepis* en Bolivia. Revista Boliviana de Ecología y Conservación Ambiental 9:29-44.

Tilman, D.
1999 The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80:1455-1474.

2000 Causes, consequences and ethics of biodiversity. Nature 405:208-211.

Vargas, R.
2001 Abundancia y Estructura Poblacional de *Oxymycterus paramensis* en Fragmentos de Bosque de *Polylepis besseri* en la Localidad de Sacha Loma, Provincia Mizque, Cochabamba. Licenciatura thesis, Universidad Mayor de San Simón, Cochabamba, Bolivia.

Veloso, A., and E. Bustos (eds.)
1982 La Vegetación y los Vertebrados Ectotérmicos del Transecto Arica – Lago Chungara. ROSTLAC, Montevideo, Uruguay. 327 pp.

Wilcox, B. A.
1982 In situ conservation of genetic resources: determinants of minimum area requirements. Pp. 639-647 in National parks, conservation, and development: the role of protected areas in sustaining society (McNeely, J. A., and K. R. Miller, eds.). Smithsonian Institution Press, Washington, D.C., USA.

Wilkinson, L.
2000 SYSTAT 10.0. SPSS, Inc., Chicago, Illinois, USA.

Wilson, D. E., and D. A. Reeder (eds.)
2005 Mammal Species of the World: A Taxonomic and Geographic Reference. Third edition. Johns Hopkins University Press, Baltimore, Maryland, USA. 2142 pp.

Yensen, E., and T. Tarifa
1993 Reconocimiento de los mamíferos del Parque Nacional Sajama. Ecología en Bolivia 21:45-66.

2002 Mammals of Bolivian *Polylepis* woodlands: guild structure and diversity patterns in the world's highest woodlands. Ecotropica 8:145-162.

Zar, J. H.
1984 Biostatistical Analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA. 718 pp.

PATTERNS OF SMALL MAMMAL SPECIES RICHNESS IN MEDITERRANEAN AND TEMPERATE CHILE

PATRONES EN LA RIQUEZA DE ESPECIES DE PEQUEÑOS MAMÍFEROS EN LAS REGIONES MEDITERRÁNEA Y TEMPLADA DE CHILE

Hernán L. Cofré, Horacio Samaniego, and Pablo A. Marquet

ABSTRACT

While it is widely accepted that species richness and rarity are non-randomly distributed across time, space, and taxa, it is by no means evident which are the factors affecting the distribution patterns of both attributes. In this study we analyze richness and rarity patterns of small mammals (rodents and marsupials) in Mediterranean and Temperate Chile. We test for the effect of environmental factors that may explain richness and endemism variability after accounting for spatial autocorrelation. We also analyze the relationship between species traits and correlates of rarity (density and range size) after accounting for phylogenetic relatedness. Our results show that energy input and to a lesser degree glaciations may explain richness pattern of small mammals from forest habitats in Chile, whereas glaciations and topographic heterogeneity are associated with endemicity patterns. Both factors may explain the high richness found at 37° S and the low values at the southernmost tip of the continent. When phylogenetic relatedness was accounted for, the number of vegetation types was the only ecological trait significantly associated with density and latitudinal range. Our results reinforce the importance of energy availability and productivity in determining patterns in biodiversity.

Key words: Chile, diversity, mammals, Mantel test, rarity, macroecology, phylogenetic effects

RESUMEN

Si bien la idea de que la riqueza y la rareza específica tienen una distribución no aleatoria con relación al tiempo, el espacio, y la taxonomía, no es para nada evidente cuáles son los factores que afectan los patrones de distribución de aquellos dos atributos. En este estudio analizamos los patrones de riqueza y rareza de pequeños mamíferos (roedores

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y marsupiales) en Chile mediterráneo y templado. Ponemos a prueba el efecto de los factores ambientales en la variación en riqueza y endemismo luego de dar cuenta de la autocorrelación espacial. También analizamos la relación entre rasgos específicos y correlatos de la rareza (densidad y tamaño del rango de distribución) luego de dar cuenta del parentesco filogenético. Nuestros resultados muestran que la cantidad de energía y, en menor grado, el efecto de las glaciaciones, pueden explicar los patrones de riqueza de los pequeños mamíferos en los habitats boscosos en Chile, mientras que las glaciaciones y la heterogeneidad topográfica están asociadas a los patrones de endemismo. Ambos factores pueden explicar la alta riqueza encontrada a 37° S y los bajos valores en el extremo sur del continente. Cuando se tuvo en cuenta el parentesco filogenético, el número de tipos vegetacionales fue el único factor ecológico asociado significativamente con la densidad y el rango latitudinal. Nuestros resultados refuerzan la importancia de la disponibilidad de energía y la productividad en la determinación de los patrones de biodiversidad.

Palabras claves: Chile, diversidad, mamíferos, test de Mantel, rareza, macroecología, efectos filogenéticos

INTRODUCTION

Spatial patterns of variability in species richness have been reported for centuries. Recently, however, they have gained renewed attention, driven by the urgent need to improve our understanding of processes underlying its generation and maintenance (e.g., Ceballos and Brown, 1995; Rosenzweig, 1995; Hubbell, 2001; Blackburn and Gaston, 2003; Gaston, 2003) at local, regional, and global scales (e.g., Ricklefs and Schluter, 1993; Brown, 1995; Gaston 2000). Unfortunately, and despite decades of research, no simple general answer to the question of the determinants of species diversity at any single scale, let alone to explain how the different scales interact to the formation of biodiversity patterns, is yet available (Hubbell, 2001; Whittaker et al., 2001). One way of improving our understanding of factors determining spatial changes in diversity is by expanding the traditional scope of analysis beyond the quantification of species numbers to encompass associated traits such as abundance, geographic range, and body size, and how they may contribute to the observed patterns (Arita and Figueroa, 1999; Kaspari et al., 2000; Jetz and Rahbek, 2002; Marquet et al., 2004; Ruggiero and Kitzberger, 2004; Vázquez and Gaston, 2004). Although this phenomenological approach can be criticized as lacking a solid theoretical foundation and by its limited predictability and generality, it may nevertheless allow us to at least identify those factors that might need to be included and/or accounted for in a general theory of biodiversity.

Numerous studies have assessed species richness, endemicity, and rarity across geographical areas in the context of identifying priority areas for the conservation of biodiversity (Prendergrast et al., 1993; Ceballos and Brown, 1995; Williams et al., 1996; Arita et al., 1997; Dobson et al., 1997; Kerr, 1997; Ceballos et al., 1998; Baquero and Tellería, 2001). However, few of these studies have assessed how environmental factors and life history traits affect patterns of species richness and rarity (Ceballos and Brown, 1995; Baquero and Tellería, 2001; Ruggiero and Kitzberger, 2004). On the other hand, rarity has been recognized as an indicator of extinction risk and provides a concrete basis for identification of threatened species (Diamond, 1984; Rabinowitz et al., 1986; Pimm et al., 1988; Arita et al., 1990; Arita, 1993; Manne et al., 1999; Purvis et al., 2000; Manne and Pimm, 2001; Cardillo et al., 2004). In spite of this, little consensus exists about the factors that best predict species abundance and/or range distribution (Bevill and Louda, 1999; Murray et al., 2002; Gaston, 2003).

In this chapter, we attempt to answer some questions related to the richness and rarity of small mammals from the Mediterranean and Temperate zones of Chile. Specifically, we ask if spatial patterns in the distribution of small mammal species are congruent with the spatial distribution of endemicity, and if there is any congruence among the environmental and historical factors that may explain patterns in species richness and rarity.

MATERIALS AND METHODS

Study Area and Taxonomic Group

According to Armesto et al. (1996) native forests in Chile occur between 30° and 55° S. In this gradient of 25 degrees of latitude, we can find two main kinds of forest: Sclerophyllous forest (31° - 36°) and Temperate rain forest (36° - 55°) (see also Armesto et al., 1996; Amigo and Ramírez 1998). In the Mediterranean region (mostly Sclerophyllous forests), mean annual precipitation ranges between 200 and 1000 mm and occurs mostly in winter. The average annual maximum temperature ranges between 12° and 16°C, and the minimum is rarely below 0°C. On the other hand, the Temperate region experiences mean annual rainfall from 800 to 4000 mm, and average annual maximum temperatures between 7° and 14°C (Di Castri and Hajek, 1976; Amigo and Ramírez, 1998).

Our study area extends from 30° to 55° S and from sea level to 2500 m. We used a geographic information system (GIS) to divide the study area to 274 half-degree quadrants. We selected 50 quadrants that satisfied the requirements of being located only in the Sclerophyllous or Temperate forest ecoregions, and not overlapping with the Patagonian or Andean steppe ecoregions. This general approach has been widely used in a broad range of ecological studies to map species richness (e.g. Arita et al., 1990, 1997; Kerr and Packer, 1997; Ceballos et al., 1998; Baquero and Telleria, 2001; Hawkins and Porter, 2003; Rodríguez and Arita, 2004; Ruggiero and Kitzberger, 2004; Tognelli and Kelt, 2004). Our species pool includes 33 small mammal species (<500 g) inhabiting forest in Mediterranean and Temperate zones of Chile (Table 1). Taxonomy follows Yañez and Muñoz-Pedreros (2000), although we consider *Abrothrix xanthorhinus* to be a junior synonym of *A. olivaceus* following Smith et al. (2001).

Variables and Statistical Methods

Variables. The dependent variables in all diversity analyses were species richness and endemicity. Species richness was determined by tallying the number of species whose geographic range overlapped each half-degree quadrant. Endemicity was quantified using the following index:

Table 1. Small mammals species found in forest habitats in Mediterranean and Temperate Chile. Type of forest: MF = Mediterranean forest, TF = Temperate forest.

Family	Species	Type of forest
Didelphidae	*Thylamys elegans*	mainly MF / marginally TF
Caenolestidae	*Rhyncholestes raphanurus*	TF
Microbiotheriidae	*Dromiciops gliroides*	Marginally MF / mainly TF
Muridae	*Oligoryzomys longicaudatus*	MF / TF
	Oligoryzomys magellanicus	TF
	Akodon hershkovitzi	TF
	Akodon lanosus	TF
	Akodon markhami	TF
	Abrothrix olivaceus	MF / TF
	Abrothrix sanborni	TF
	Abrothrix longipilis	MF / TF
	Geoxus valdivianus	marginally MF / mainly TF
	Chelemys megalonyx	MF
	Chelemys macronyx	marginally TF
	Pearsonomys annectens	TF
	Phyllotis darwini	MF / marginally TF
	Phyllotis xanthopygus	marginally TF
	Loxodontomys pikumche	marginally MF
	Loxodontomys micropus	TF
	Irenomys tarsalis	marginally MF / TF
	Reithrodon physodes	marginally TF
	Euneomys chinchilloides	marginally TF
Chinchillidae	*Chinchilla lanigera*	marginally MF
Octodontidae	*Octodon degus*	MF
	Octodon bridgesi	MF / TF
	Octodon lunatus	MF
	Octodon pacificus	TF
	Spalacopus cyanus	MF
	Aconaemys fuscus	TF
	Aconaemys sagei	TF
	Aconaemys porteri	TF
Ctenomyidae	*Ctenomys maulinus*	marginally MF/TF
Abrocomidae	*Abrocoma bennetti*	MF

$$I_e = \frac{\sum_{i=1}^{n_s} 1/R_i}{n_s}$$

where R_i represents the latitudinal range for species i (Gaston, 1994) and n_s corresponds to the total number of species per site (s). This type of index has been used to study patterns of congruence in the spatial distribution of endemism and species richness (e.g., Williams et al., 1996; Arita et al., 1997; Baquero and Tellería, 2001). However, we also use it to evaluate the relationship between endemism and environmental variables. In order to assess the effect of the environment on species richness we considered 6 environmental variables for each quadrant: the normalized difference vegetation index (NDVI), the mean Elevation (Elevation), the mean daily temperature (Temperature), mean daily precipitation (Precipitation), the number of vegetation types (Vegetation Types), and the history of Glaciation. This last variable is a binary variable that indicates whether or not a quadrant was covered by ice during the last glacial maximum (Mercer, 1983; see also Vuilleumier, 1971; Villagrán et al., 1996). NDVI is a measure of "greenness" that is obtained from images developed by the National Oceanic and Atmospheric Administration's Advanced Very High Resolution Radiometer satellite (NOAA AVHRR). NDVI appears to correlate strongly with plant biomass, primary productivity, and actual evapotranspiration (e.g., Box et al., 1989; Hobbs, 1995; Paruelo et al., 1998, 2001) and has been broadly used as a surrogate of productivity in studies of avian and mammal diversity (Fraser, 1998; Acevedo and Currie, 2003; Hurlbert and Haskell, 2003; Hawkins, 2004; Hurlbert, 2004; Tognelli and Kelt 2004). The NDVI data used here corresponds to the mean value (from April 1992 to March 1993) for each half-degree quadrant and was obtained from http://edcsns17.cr.usgs.gov/1KM/. The same procedure was used to obtain the mean elevation based on 30 arc-second map produced by the United States Geological Survey (available at http://edcdaac.usgs.gov/gtopo30/hydro/sa_dem.asp). Mean daily temperature and mean daily precipitation were obtained from the 1961-1990 databases available at the IPCC Data Distribution Center (http://ipcc-ddc.cru.uea.ac.uk). The number of vegetation types in each quadrant was obtained by counting the variety of vegetation types in each quadrant following Gajardo (1994).

To assess the relationship between rarity and life-history traits, species were classified according to body size, mean litter size, diet, habitat breadth, activity period (diurnal vs. nocturnal), life form or habit (terrestrial vs. fossorial), and sociability (social vs. non-social). We defined rarity based on density and range size of species (Gaston 1994). We compiled data on density, latitudinal range, diet, body mass, habitat use, and life history traits using published literature (e.g., Mann, 1978; Pearson and Pearson, 1982; Pearson, 1983, 1984; Reise and Venegas, 1987; Johnson et al., 1990; Meserve and Jaksic, 1991; Meserve et al., 1991; Jiménez et al., 1992; Redford and Eisenberg, 1992; Kelt, 1994; Murúa, 1996; Spotorno et al., 1998, 2001; Cofré and Marquet, 1999; Muñoz and Yañez, 2000; Saavedra and Simonetti, 2000, 2001, 2003; Ebensperger and Cofré, 2001). Density of each species was defined as the mean of values reported in the literature. The geographic range of each species was defined by latitudinal extent (sensu Gaston, 1994; see also Gillespie, 2002). Habitat breadth was assessed by counting the occurrence of each species in different types of habitat. We followed Murúa (1996) for most species habitat occurrences. For species endemic to the Mediterranean region, habitat occurrence was assigned by a literature review

(Mann, 1978; Jaksic, 1997; Muñoz and Yañez, 2000 and reference therein). We then tallied the number of vegetation types in which each species may be found. To analyze the role of trophic status we created 2 dummy variables (Draper and Smith, 1998; Zar, 1999) – herbivory and insectivory; based on published studies, all species were characterized as herbivore ("herbivory" = 1, "insectivory"= 0), omnivore ("herbivory" = 1, "insectivory" = 1), or insectivore ("herbivory" = 0, "insectivory" = 1). Habits were defined as either terrestrial or fossorial. Mean body mass (g), latitudinal range size, and litter size were $\log_{10}$ transformed for all statistical analyses. Density was expressed as $\log_{10}$ (mean regional density +1).

Statistical Analyses. To explore the univariate relationship between rarity and species attributes, we applied regression analysis or ANOVA, depending on trait type. To assess the extent to which the observed variance in density and latitudinal range may be explained by a combination of species´ attributes we applied a multiple regression analysis with backward elimination and stepwise forward selection methods (Zar, 1999). In the backward procedure, the least significant variables were removed until 2 criteria were met: first, explained variance (R^2) was maximal, and second, all the variables in the model were significant ($p < 0.1$; Draper and Smith, 1998; Zar, 1999). Variables already in the model that lost their significance during the process were deleted. The stepwise forward selection procedure was stopped when no remaining variable was significant ($p < 0.1$), if added to the model. Both analyses were performed separately, and we selected the model (forward vs. backward procedure) which explained the greatest amount of variance. Because multiple regressions may fail to identify significant independent variables when multicollinearity is present, we examined the tolerance values in this procedure. Tolerance is computed as $1-R^2$ for a regression between a given independent variable and all other independent variables (Legendre and Legendre, 1998; Draper and Smith, 1998; Zar, 1999; Graham, 2003). As a rule of thumb, multicollinearity is indicated by tolerance values <0.20. In this study, all tolerance values were >0.5; therefore all variables had a small redundancy or large contribution to the regression.

Because our analysis involves comparisons across different species, it is possible that species can share traits because of shared ancestry (Felsenstein, 1985; Harvey and Pagel, 1991). To assess the contribution of phylogenetic relatedness on traits potentially associated to rarity, we used the Signed Mantel test (Böhning-Gaese et al., 2000; Böhning-Gaese and Oberrath, 2001; Oberrath and Böhning-Gaese, 2002), which is an extension of the traditional Mantel test (Mantel, 1967; Smouse et al., 1986; Legendre et al., 1994; Taylor and Gotelli, 1994). A Mantel test assesses the correlation between the elements of 2 distance matrices (Manly, 1986). To construct each matrix, each trait x species combination is compared with all the other species. Thus, for each variable (dependent and independent), the distance data on N sampling units (small mammal species) are represented by an $N \times N$ matrix with $N(N - 1) / 2$ different paired distances. We constructed two $\mathbf{Y}$ matrices describing the dissimilarity (distance) in regional density and latitudinal range, respectively, an $\mathbf{X}_1$ matrix with the phylogenetic distance among species (= taxonomic distance; Oberrath and Böhning-Gaese 2002), and $\mathbf{X}_2 \ldots \mathbf{X}_n$ matrices representing the dissimilarities in the other attributes among species. The Mantel test determines the statistical relationship between these matrices. In the univariate version of the test each of the matrices representing the predictor variables were assessed separately. For the multivariate analysis we used the same independent predictor variables as identified by the multiple regression procedure. In Mantel tests, the regression of the individual values in the matrices yields the partial regression coefficients b_1 and b_{2n} and the respective *t*-values (Smouse et al., 1986). A valid significance level for each variable (the Mantel significance level) is then derived by comparing the original *t*-value with a null distribution of *t*-values constructed by Monte Carlo randomization. For each permutation, the $\mathbf{X}_1$ and $\mathbf{X}_{2,\ldots,n}$ matrices are held constant and the species in the Y matrix are randomly permuted (Smouse et al., 1986; Oberrath and Böhning-Gaese, 2001). To construct the null distribution of *t*-values we used 2000 randomizations.

To study the univariate relationship between community traits (endemicity and richness) and environmental variables, we also applied Poisson or linear regression analyses for richness and endemicity respectively. In multivariate models for species richness and endemicity we examined the extent to which the observed variance may be explained by only two historical or environmental variables to avoid the effect of multicollinearity and overfitting (e.g. Currie and Fritz 1993; Van Rensburg et al., 2002). Model selection was based on the Akaike Information Criterion (Akaike 1973). For simple and multiple Poisson regression analyses, model fit was assessed by analyzing the deviance table using a Chi-square approximation (Dalgaard 2002) in the R statistical software (R Development Core Team 2005). In the multivariate analysis of endemicity, the dichotomous variable Glaciation was entered as a dummy variable.

To test for the potential effect of spatial autocorrelation and properly control for its effect on environmental and community traits (endemicity and richness) we again employed the Signed Mantel test (Legendre and Legendre, 1998; Oberrath and Böhning-Gaese, 2001; Lemoine and Böhning-Gaese, 2003). We constructed two dissimilarity Y matrices (as distances of richness and endemicity index, respectively), an $\mathbf{X}_1$ matrix with the spatial distance among sites, and $\mathbf{X}_{2,\ldots,n}$ matrices representing dissimilarities in environmental traits. Valid significance levels for each X-variable (the Mantel significance level) were derived by comparing the original *t*-value with a null distribution of *t*-values obtained from 2000 Monte Carlo randomizations (Oberrath and Böhning-Gaese, 2001). Geographic distance between sites was calculated using the Great-Circle distance calculator available in the Fields package (Nychka 2004) of the R statistical software (R Development Core Team 2005).

When necessary, variables were transformed to be as close to normality as possible. Specifically, Temp was $\log_{10}$ transformed and NDVI, Number of vegetation types, and Elevation were square root transformed. Unless stated otherwise, all regular statistical methods were implemented with Statistica 5.1 for Windows (StatSoft Inc., Tulsa, Oklahoma, USA).

RESULTS

Richness, Endemicity, and Environmental traits

Species richness showed the classic latitudinal pattern with a monotonic decrease from high values at low latitudes to low values at high latitudes (Fig. 1a). Nevertheless, the highest richness values were found between 35° and 40° S (see also spatial patterns in Fig. 2). On the other hand, the endemicity index shows a decreasing trend from 30° to 50° S punctuated by peaks at 38° and 52° S and a steep increase at the tip of the

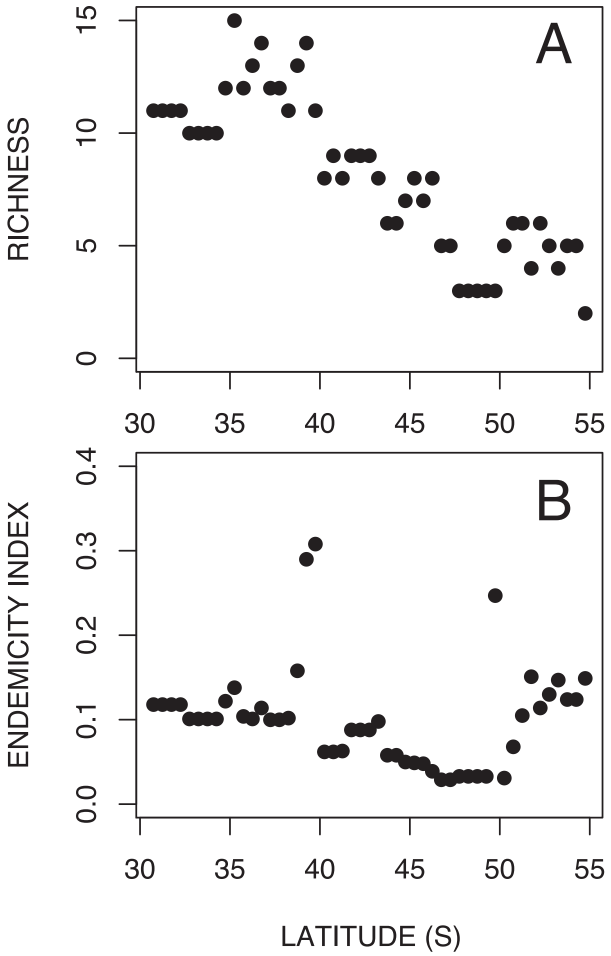

Figure 1. Mammal species richness (a) and endemicity (b; I_e) in each 0.5° (lat/long) quadrant, as a function of latitude, in Mediterranean and Temperate Chile (30° - 55° S).

continent (Fig. 1b; see also Fig. 2).

Univariate analyses show that all 6 environmental and historical variables were statistically associated with species richness (Table 2). NDVI, Temperature, and Glaciation showed the strongest relationship with richness (i.e., large deviance and low AIC; see also Fig. 3). Endemicity also showed a strong association with all environmental and historical variables (Table 2), but with the number of vegetation types. Elevation, Temperature, and Glaciation were the variables that best predicted endemicity (Fig. 4).

The best 2-variable regression model for species richness variation included the positive effects of NDVI and Temperature (Table 3) a measure of productive energy available for consumers and of solar energy availability respectively (Evans et al.

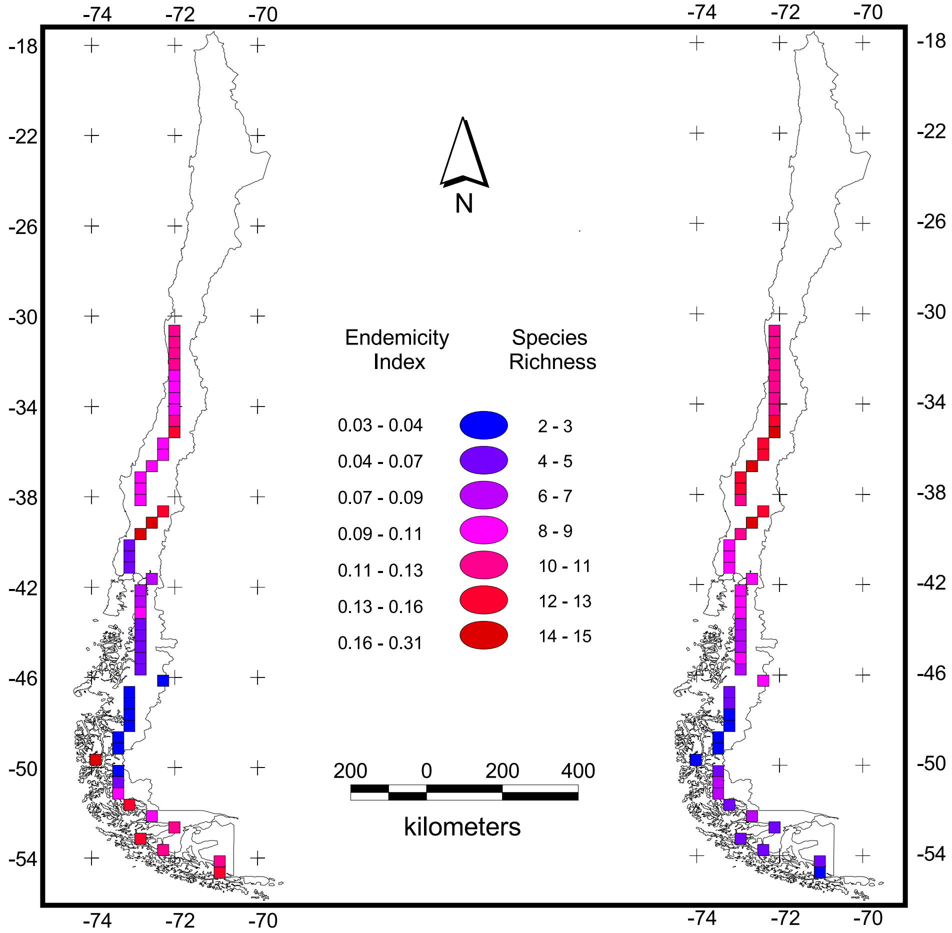

Figure 2. Spatial distribution of mammal species richness and endemicity (Ie) in Mediterranean and Temperate Chile. Maps of Chile are superimposed by a grid of 49 0.5° (lat/long) quadrats.

2005). In the case of endemicity, the best model included Elevation and Glaciation. In this case non-glaciated areas had a larger endemicity index than glaciated ones (Table 3).

The signed Mantel test results (Table 4) show a significant effect of Temperature and NDVI on richness and of Elevation and Glaciation in endemicity. It also reveals that there is a significant influence of spatial autocorrelation on richness. This was apparent in a significant effect of geographic distance and an increase in explained variability in richness in the two variable model when distance was included. Endemicity, however, was not affected by spatial autocorrelation.

Rarity and Life-history Traits

Without taking phylogenetic relatedness among species into account, univariate analyses show that latitudinal range and mean density are similarly influenced by

Table 2. Univariate analyses to assess the influence of six predictor variables on species richness (using Poisson regression) and endemicity (using linear regression) of small mammals assemblages in Mediterranean and Temperate Chile.

Predictor Variables	Regional richness		Endemicity Index		
	Deviance	AIC	Coefficient	*F* value	AIC
NDVI	52.03***	216.2	0.44	11.56**	-1.28
Elevation	10.23**	258	-0.57	22.55**	-9.71
Vegetation types	30.69***	237.5	0.25	3.16 n.s	6.3
Temperature	57.35***	210.9	0.45	12.04**	-1.68
Precipitation	15.98***	252.2	-0.35	6.71**	2.95
Glaciation	48.09***	220.14	-0.23	11.74**	-1.43

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

species attributes (Table 5). Latitudinal range and density were significantly and positively correlated with the number of vegetation types, such that specialists (i.e., species found in quadrants with few vegetation types) not only have narrower geographic ranges, but also occur at lower densities than do generalists (Fig. 5). The multivariate regression analysis gave results similar to the univariate analysis (Table 6). For density, the variables that entered the model were number of vegetation types (a measure of habitat breadth) and habits (terrestrial vs. fossorial). Similarly, the latitudinal range of species was best predicted by the number of vegetation types and by herbivory.

Phylogeny did not have a significant effect on density or geographic range (Table 6). When phylogenetic relatedness was accounted for, the results did not change, and the number of vegetation types remained as the only ecological trait significantly associated with latitudinal range and vegetation types and habits were the only traits related with density.

DISCUSSION

Richness, Endemicity and Environmental traits

In this work, we have documented patterns of species richness for small mammals inhabiting forested habitats in Chile. Species richness is highest between 35° and 40° S, followed by a decrease in richness until the tip of the continent. This non-linear pattern has also been reported in plants (Villagrán, 1995; Arroyo et al., 1996), birds (Cofré, 2004), and butterflies (Samaniego and Marquet, unpubl. data). Our results suggest that this pattern may be driven by ecological factors associated with energy input, as measured by NDVI and temperature. Similar results have been reported recently for the South American mammal fauna (Ruggiero and Kitzberger, 2004; Tognelli and Kelt, 2004) at a continental scale; these authors found that variables associated with productivity, such as actual evapotranspiration, NDVI, and solar radiation were the most important in affecting spatial changes in species richness for mammals. However,

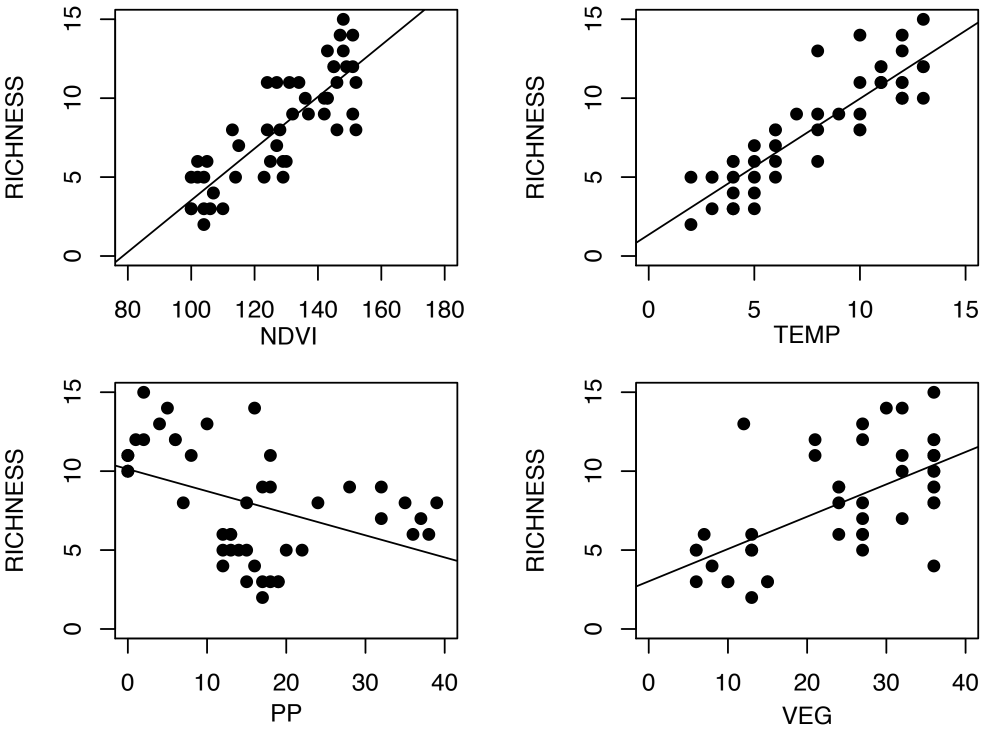

Figure 3. Mammal species richness in each 0.5° (lat/long) quadrat as a function of NDVI ($r_s = 0.81$, $p < 0.0001$); temperature ($r_s = 0.87$, $p < 0.0001$); annual mean daily precipitation, ($r_s = -0.54$, $p < 0.001$; and number of vegetation types ($r_s = 0.58$, $p < 0.001$).

we also found that glacial events may play a role in explaining richness patterns. Glaciation was the third most important determinant of richness in univariate analysis and strongly affected the spatial pattern of endemicity. It has been recently recognized that Pleistocene refuges and non-glaciated areas in the Nearctic and Palearctic can explain current biodiversity patterns as they have acted as important diversification centers (e.g., Mönkkönen and Viro, 1997; Baquero and Telleria, 2001; Hawkins and Porter, 2003). On the other hand, we also found a tendency for glaciated sites to exhibit lower endemicity indices than non-glaciated sites. This indicates that species with smaller ranges are not represented in most of the glaciated sites (see also Mönkkönen and Viro, 1997; Baquero and Telleria, 2001; Hawkins and Porter, 2003). According to Vuilleumier (1971), the main effect of Quaternary glaciations has been the reduction of species distribution in glaciated areas south of 45° S. Further analyses, however, are needed to substantiate the effect of glaciations and to separate them with others, such as a potential peninsular effect.

The lower regional richness observed between 45° and 52° S coincides with low endemism, given the over-representation of species with broad ranges from the Mediterranean area (e.g., *Abrothrix longipilis*, *A. olivaceus*) or other biomes (e.g., *Euneomys chinchilloides*, *Phyllotis xanthopygus*) (Murúa, 1996). We also observed a peak

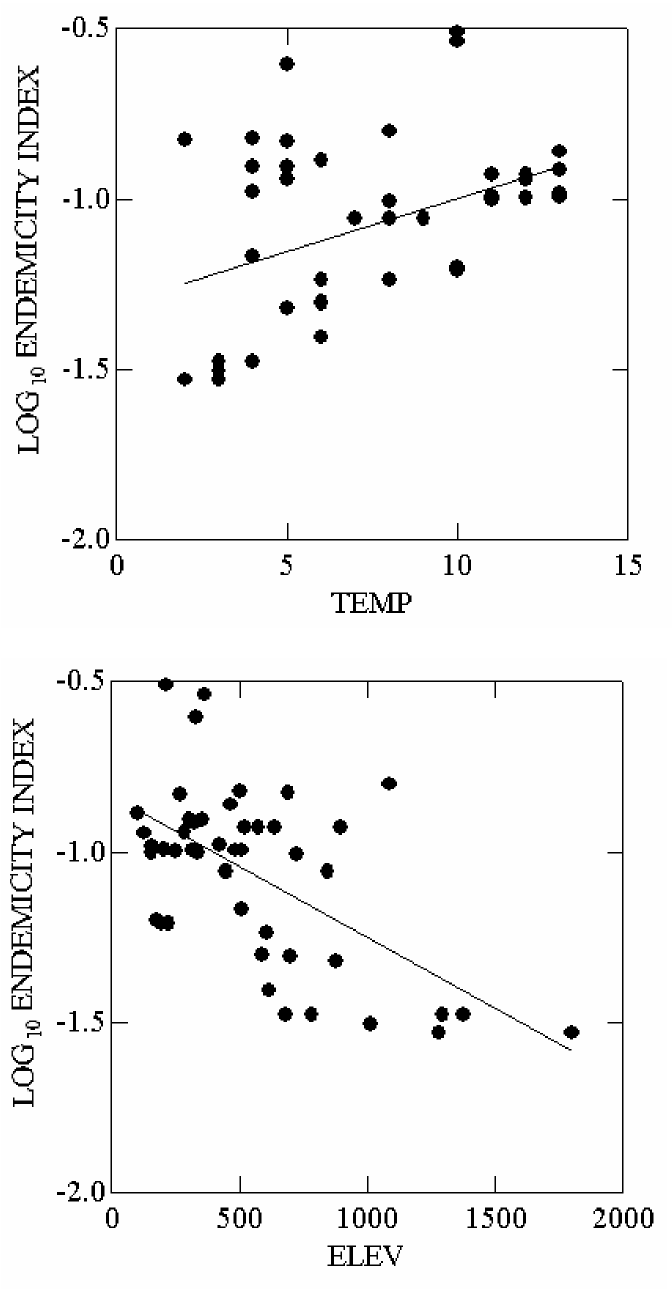

Figure 4. Mammal endemicity (I_e) as a function of temperature ($r_s = 0.34$, $p < 0.02$) and mean elevation ($r_s = -0.45$, $p < 0.001$).

Table 3. Best two variable model for species richness (based on Poisson regression) and endemicity (based on linear multiple regression) of small mammals assemblages in Mediterranean and Temperate Chile.

Richness				Endemicity			
Predictor Variables	Coefficient	Deviance	AIC	Predictor Variables	Coefficient	R^2	AIC
Temperature	1.31	57.35***	11.33	Elevation	-0.01***	0.36	-12.34
NDVI	0.17	1.55 n.s		Glaciation	-0.14*		

*** $p < 0.001$, * $p < 0.05$

Table 4. Results of multivariate Signed Mantel test including and not including spatial autocorrelation when testing for the influence of environmental variables on species richness and endemicity. Numbers are partial correlations.

	Richness		Endemicity	
Models with Environmental Variables	not including geographic distance	including geographic distance	not including geographic distance	including geographic distance
Temperature	12.75***	3.94**		
NDVI	9.06***	11.11***		
Distance		12.09***		
R^2	0.48	0.55		
Elevation			-14.16***	-14.12***
Glaciation			-7.93***	-7.98***
Distance				0.98 n.s.
R^2			0.24	0.20

** $p < 0.01$, *** $p < 0.001$

in endemism at the bottom of the latitudinal gradient due to species with restricted insular distributions (e.g., *Akodon lanosus*, *A. hershkovitzi*, *A. markhami*, and *Oligoryzomys magellanicus*). These species likely diversified in this area after it was colonized by ancestral taxa coming from more northern areas when Pleistocene ice fields started to retreat (e.g., Smith et al., 2001; Palma et al., 2005).

Biogeographic studies using unprojected latitudinal bands or degree-based quadrants are likely to be affected by area, as the area at different latitude differ due to the poleward convergence of longitudinal meridians (e.g., Lyons and Willig, 1999, Romdal et al., 2005). Area has no effect on richness in our study, probably because of the short latitudinal extent included in the analysis. This claim is based on the fact that none of all possible 2-variable models including area as a predictor had lower AIC value than the best model reported in Table 3. The same result has been observed when

Table 5. Results of univariate analyses (linear regression or one-way ANOVA) on the influence of eight species attributes either on the $\log_{10}$ density or the $\log_{10}$ latitudinal range of small mammal species from Mediterranean and Temperate Chile.

Variable	$\log_{10}$ Density		$\log_{10}$ Latitudinal range	
	Slope	*F* value	Slope	*F* value
Body size	-0.02	0.01	-0.25	2.09
Herbivory		0.51		0.66
Insectivory		0.003		0.11
Number of vegetation types	0.45	5.75*	0.61	18.17***
Activity		3.45		0.41
Habits		0.42		0.85
Sociability		0.21		0.05
Litter size	0.04	0.02	0.19	0.61

* $p < 0.05$, *** $p < 0.001$

analyzing all mammalian species in half-degree quadrants across Chile (Samaniego and Marquet, unpublished data.)

We have also shown a significant and positive effect of topographic heterogeneity on endemicity, as measured by mean difference in elevation. Such topographic heterogeneity may increase isolation between populations, and may foster population differentiation and speciation processes, thereby increasing the diversity of these areas, as suggested by Fuentes and Jaksic (1979) for lizards.

Rarity and Life-history Traits

At least 10 different hypotheses have been proposed to explain species rarity (see reviews by Kunin and Gaston, 1993; Gaston and Kunin, 1997; Gaston, 2003). We have found a strong relationship between latitudinal range and the number of vegetation types, or habitat breadth. We also find significant associations between density and number of vegetation types. Small mammals that only occur in a few habitats in Mediterranean or Temperate Chile have a significantly smaller latitudinal extent and a smaller population density than widespread mammals that occur in many habitats. This is in agreement with Brown's (1984, 1995) niche breadth hypothesis, which states that species with broad niches (e.g., habitat generalists) have higher abundance and larger geographic ranges than species with more restricted niches (e.g., specialists), although the mechanistic basis for this hypothesis might still be questionable, unless an independent measure of niche breadth is used. While a positive relationship between habitat breadth and geographic range has been found for many organisms including mammals (e.g., Jones, 1997; Eeley and Foley, 1999; Harcourt and Coppeto, 2002; see also Gaston, 2003), a correlation between habitat breadth and abundance has not often been reported (see Gaston et al., 1997 for review). However, our results

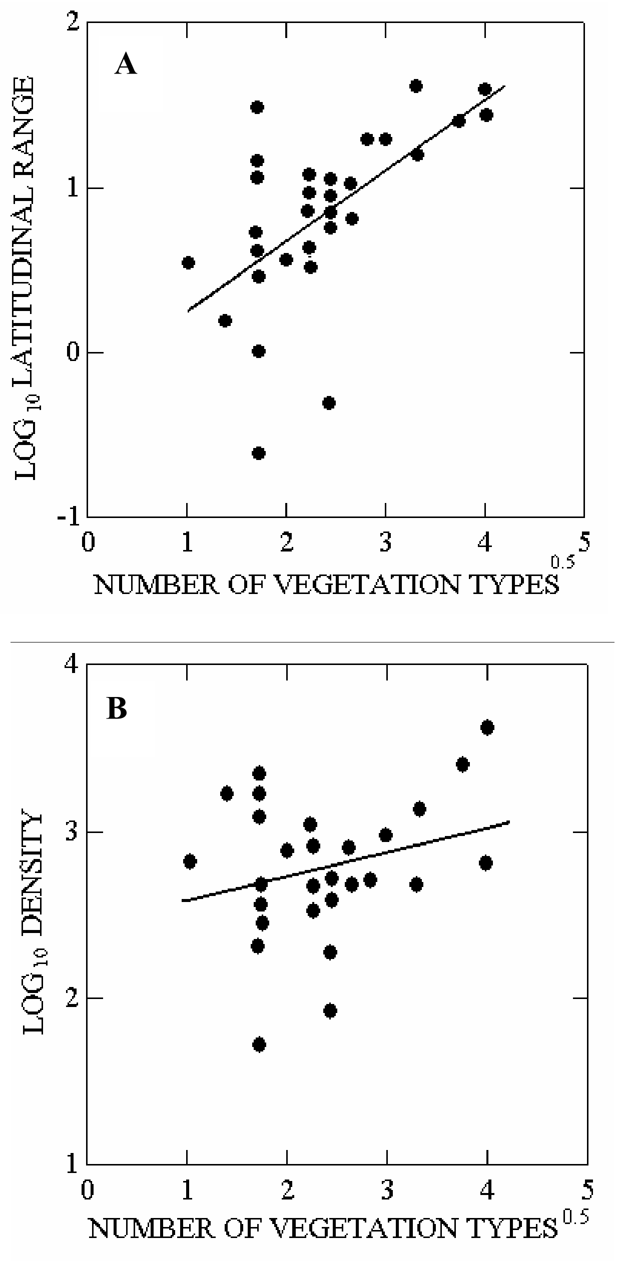

Figure 5. The relationship between number of vegetation types in 0.5° (lat/long) quadrants and latitudinal range (A) and population density (B).

Table 6. Results of multivariate Mantel test with and without consideration of phylogenetic distance, testing the influence of species attributes on $\log_{10}$ Density and $\log_{10}$ of latitudinal range. Numbers in table are *t*-values.

Species traits	$\log_{10}$ Density		$\log_{10}$ Latitudinal range	
	not including phylogenetic distance	including phylogenetic distance	not including phylogenetic distance	including phylogenetic distance
Phylogeny		0.21		-0.95
Number of Vegetation types	6.06**	6.01**	8.64***	8.63***
Habits	4.55**	4.54**		
R^2	0.13	0.13	0.14	0.14

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

should be interpreted with caution, since our analysis suffers from being restricted to "small mammals" which renders, for example, any correlation between body size and abundance or distribution difficult to find because of the reduced range of the size axis. Since other relationships can be similarly affected, further studies on the complete assemblage of Chilean mammals are necessary to assess the generality of these results.

Conservation Implications

Many studies have found no congruence between the number of rare species and overall richness for mammals (Ceballos and Brown, 1995; Ceballos et al., 1998; Baquero and Tellería, 2001) or other taxa (Prendergrast et al., 1993; Williams et al., 1996; Dobson et al., 1997; Kerr 1997; but see Arita et al., 1997). In contrast, we documented a positive correlation between richness and endemicity in small mammals of the Mediterranean and Temperate regions of Chile ($r = 0.628$, $p < 0.001$). This pattern emerges because the majority of the 14 species with the most restricted distributions in this region have their southern or northern distributional boundaries around 37° S. The transitional character of this area contributes to the emergence of this biodiversity pattern (Fig. 1b). For example, Reise and Venegas (1987) described an assemblage of 10 species – including 4 species with their northern distributional boundaries here: *Aconaemys fuscus*, *Ctenomys maulinus*, *Dromiciops gliroides*, and *Loxodontomys micropus* (= *Auliscomys micropus*) near Termas de Chillán (71° 25′ W, 36° 54′ S, 1,250 m). On the other hand, in coastal forests such as Nahuelbuta National Park (73° 07′ W, 37° 53′ S, 1,000 m) it is possible to find species from the Mediterranean as well as Temperate forest (e.g., *O. bridgesi* and *P. darwini* are from the Mediterranean area whereas *A. fuscus* and *D. gliroides* belong to the Temperate forest) (Jimenez et al., 1991; see also Fuentes and Jaksic 1979; Reise and Venegas, 1987; Medel et al., 1990; Murúa, 1996).

Species in different rarity categories (sensu Rabinowitz et al., 1986) require different conservation strategies (Arita et al., 1990). For example, specialized species with restricted distribution ranges that overlap species-rich areas (e.g., the genus *Aconaemys*, *Ctenomys maulinus*, *Loxodontomys pikumche*, *Octodon bridgesi*, and *Abrothrix sanborni*) are likely to benefit from a conservation strategy that targets species-rich regions. On the other hand, restricted and/or low abundance species whose geographic distribution do not overlap species-rich areas (such as *Octodon lunatus*, *Chinchilla lanigera*, *Chelemys megalonyx*, *Pearsonomys annectens*, *Octodon pacificus,* and *Rhyncholestes raphanurus*) will benefit most from a conservation strategy focusing on individual species. Thus, conservation strategies should remain flexible in the face of the diversity of biological attributes exhibited by taxa and habitats.

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LITERATURE CITED

Acevedo, D., and D. J. Currie
2003 Does climate determine broad-scale patterns of species richness? A test of the causal link by natural experiment. Global Ecology and Biogeography 12:461-473.

Akaike, H.
1973 Information theory as an extension of the maximum likelihood principle. Pp. 267-281 in 2nd International Symposium on Information Theory (Petrov, B. N., and F. Csaksi, eds.). Akademiai Kiado, Budapest, Hungary.

Amigo, J., and C. Ramírez
1998 A bioclimatic classification of Chile: woodland communities in the temperate zone. Plant Ecology 136:9–26.

Arita, H. T.
1993 Rarity in Neotropical bats: correlations with phylogeny, diet, and body mass. Ecological Applications 3:506-517

Arita, H. T., and F. Figueroa
1999 Geographic patterns of body-mass diversity in Mexican mammals. Oikos 85:310-319.

Arita, H. T., F. Figueroa, A. Frisch, P. Rodríguez, and K. Santos-Del-Prado
1997 Geographical range size and the conservation of Mexican mammals. Conservation Biology 11:92-100.

Arita, H. T., J. G. Robinson, and K. H. Redford
1990 Rarity in Neotropical forest mammals and its ecological correlates. Conservation Biology 4:181-192.

Armesto, J. J., Villagrán, C., and M. T. K. Arroyo (eds.)
1996 Ecología de los Bosques Nativos de Chile. Editorial Universitaria, Universidad de Chile, Santiago, Chile.

Arroyo M. T. K., L. Cavieres, A. Peñaloza, M. Riveros, and A. M. Faggi.
1996 Relaciones fitogeográficas y patrones regionales de riqueza de especies en la flora del bosque lluvioso templado de Sudamérica. Pp. 71-100 in Ecología de los Bosques Nativos de Chile (Armesto, J. J., C. Villagrán, and M. T. K. Arroyo, eds.). Editorial Universitaria, Universidad de Chile, Santiago, Chile.

Baquero R. A., and J. L. Tellería
2001 Species richness, rarity and endemicity of European mammals: a biogeographical approach. Biodiversity and Conservation 10:29–44.

Bevill, R. L., and S. M. Louda
1999 Comparisons of related rare and common species in the study of plant rarity. Conservation Biology 123:493-948.

Blackburn, T., and K. J. Gaston (eds.)
2003 Macroecology: Concepts and Consequences. Blackwell Publisher, Oxford, UK. 377 pp.

Böhning-Gaese, K., Halbe, B., Lemoine, N., and R. Oberrath
2000 Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds. Evolutionary Ecology Research 2:823-839.

Böhning-Gaese, K., and R. Oberrath
2001 Which factors influence the abundance and range size of central European birds? Avian Science 1:43-54.

Box, E. O., B. N., Holben, and V. Kalb
1989 Accuracy of the avhrr vegetation index as a predictor of biomass, primary productivity and net CO_2. Vegetatio 80:71–89.

Brown, J. H.
1984 On the relationship between abundance and distribution of species. American Naturalist 124:255–279

1995 Macroecology. University of Chicago Press, Chicago, Illinois, USA. 269 pp.

Cardillo, M., A. Purvis, W. Sechrest, J. L. Gittleman, J. Bielby, and G. M Mace
2004 Human population density and extinction risk in the world's carnivores. PLoS Biology 2:0909-0914 (online at http://biology.plosjournals.org/perlserv/?request=index-html&issn=1545-7885).

Ceballos, G., and J. H. Brown
1995 Global patterns of mammalian diversity, endemism, and endangerment. Conservation Biology 9:559-568.

Ceballos, G., P. Rodriguez, and R. A. Medellín
1998 Assessing conservation priorities in megadiverse Mexico: mammalian diversity, endemicity and endangerment. Ecological Application 8:8–17.

Cofré, H., and P. A. Marquet
1999 Conservation status, rarity and geographic priorities for conservation of Chilean mammals: An assessment. Biological Conservation 88:53–68.

Cofré, H. L.
2004 Diversidad de Aves en los Bosques del Centro y Sur de Chile: Una Aproximación Macroecológica. Ph.D. Thesis. P. Universidad Católica de Chile, Santiago, Chile.

Currie, D. J., and J. T. Fritz
1993 Global patterns of animal- and plant- species richness. Oikos 67:56–68.

Dalgaard P.
2002. Introductory Statistics with R. Springer-Verlag, New York, New York, USA. xv+267 pp.

Diamond, J. M.
1984 "Normal" extinctions of isolated populations. Pp. 191-246 in Extinctions (Nitecki, M. H., ed.). University of Chicago Press, Chicago, Illinois, USA.

Di Castri, F., and E. Hajek
1976 Bioclimatología de Chile. Pontificia Universidad Católica, Santiago, Chile. 128 pp.

Dobson, A. P., J. P. Rodríguez, W. M. Roberts, and D. S. Wilcove
1997 Geographic distribution of endangered species in the United States. Science 275:550-553.

Draper, N. R., and H. Smith
1998 Applied Regression Analysis. 3rd ed. Wiley, New York, USA. 706 pp.

Ebensperger, L., and H. Cofré
2001 On the evolution of group-living in the New World cursorial hystricognath rodents. Behavioral Ecology 12:227-236

Eeley, H. A. C., and R. A. Foley
1999 Species richness, species range size and ecological specialisation among African primates: geographical patterns and conservation implications. Biodiversity and Conservation 8:1033–1056.

Evans, K. L., P. H. Warren, and K. J. Gaston
2005 Species-energy relationships at the macroecological scale: a review of the mechanisms. Biological Reviews 80:1-25.

Felsenstein, J.
1985 Phylogenies and the comparative method. American Naturalist 125:1-15

Fraser, R. H.
1998 Vertebrate species richness at the mesoscale: relative roles of energy and heterogeneity. Global Ecology and Biogeography Letters 7:215–220.

Fuentes, E. R., and F. M. Jaksic
1979 Lizard and rodent: an explanation for their relative species diversity in Chile. Archivos de Biología y Medicina Experimental 12:179-190.

Gajardo, R.
1994 La Vegetación Natural de Chile. Clasificación y Distribución geográfica. Editorial Universitaria. Santiago, Chile. 165 pp.

Gaston, K. J.
1994 Rarity. Chapman and Hall, London, England. 205 pp.

2000 Global patterns in biodiversity. Nature 405:220-227.

2003 The Structure and Dynamics of Geographic Ranges. Oxford University Press, Oxford, England. 266 pp.

Gaston, K. J., T. M. Blackburn, and J. H. Lawton
1997 Interspecific abundance-range size relationships: An appraisal of mechanisms. Journal of Animal Ecology 66:579-601.

Gaston, K. J., and W. E. Kunin
1997 Rare-common differences: An overview. Pp. 12-29 in The Biology of Rarity: Causes and Consequences of Rare-Common Differences (Kunin, W. E., and K. J. Gaston, eds.). Chapman and Hall, London, England.

Gillespie, T. W.
2002 Latitudinal extent and natural history characteristics of birds in Nicaragua. Global Ecology and Biogeography 11:411-417.

Graham, M. H.
2003 Confronting multicollinearity in ecological multiple regression. Ecology 84:2809-2815.

Harcourt, A. H., S. A. Coppeto, and S. A. Parks
2002 Rarity, specialization and extinction in primates. Journal of Biogeography. 29:445-456.

Harvey, P. H., and M. D. Pagel
1991 The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford, England. 239 pp.

Hawkins, B. A.
2004 Summer vegetation, deglaciation and the anomalous bird diversity gradient in eastern North America. Global Ecology and Biogeography 13:321–325.

Hawkins, B. A., and E. E. Porter
2004 Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. Global Ecology and Biogeography 12:475-481

Hobbs, T. J.
1995 The use of NOAA-AVHRR NDVI data to assess herbage production in the arid rangelands of Central Australia. International Journal of Remote Sensing 16:1289–1302

Hubbell, S. P.
2001 A unified null theory of biogeography and relative species abundance. Monographs in Population Biology 32. Princeton University Press, Princeton, New Jersey, USA. 375 pp.

Hurlbert, A. H.
2004 Species-energy relationships and habitat complexity in bird communities. Ecology Letters 7:714–720.

Hurlbert, A. H., and J. P. Haskell
2003 The effect of energy and seasonality on avian species richness and community composition. American Naturalist 161:83–97.

Jaksic, F. M.
1997 Ecología de los Vertebrados de Chile. Ediciones Universidad Católica de Chile, Santiago, Chile. 262 pp.

Jetz, W., and C. Rahbek
2002 Geographic range size and determinants of avian species richness. Science 297:1548-1551.

Jiménez, J. E., P. Feisinger, and F. M. Jaksic
1992 Spatiotemporal patterns of an irruption and decline of small mammals in north-central Chile. Journal of Mammalogy 73:356-364.

Jiménez, J. E., P. A. Marquet, R. Medel, and F. M Jaksic
1991 Comparative ecology of Darwin's fox (*Pseudalopex fulvipes*) in mainland and island settings of southern Chile. Revista Chilena de Historia Natural 63:177-186.

Johnson, W. E., W. L. Franklin, and J. A. Iriarte
1990 The mammalian fauna of the northern Chilean Patagonia: a biogeographical dilemma. Mammalia 54:547-469.

Jones, C. B.
1997 Rarity in primates: implications for conservation. Mastozoología Neotropical 4:35-47.

Kaspari, M., S. O'Donnell and J. R. Kercher
2000 Energy, density, and constraints to species richness: Ant assemblages along a productivity gradient. American Naturalist 155:280–293.

Kelt, D. A.
1994 The natural history of small mammals from Aisén Region, southern Chile. Revista Chilena de Historia Natural 67:183–207.

Kelt, D. A., M. Taper, and P. L. Meserve
1994 Assessing the impact of competition on community assembly: a case study using small mammals. Ecology 76:1283-1296.

Kerr, J. T.
1997 Species richness, endemism, and the choice of areas for conservation. Conservation Biology 11:1094–1100

Kerr, J. T., and L. Packer
1997 Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. Nature 385:252-254

Kunin, W. E., and K. J. Gaston
1993 The biology of rarity: Patterns, causes, consequences. Trends in Ecology and Evolution 8:298-301.

Legendre, P., and L. Legendre,
1998 Numerical Ecology. 2nd ed. Elsevier, Amsterdam. 853 pp.

Legendre, P., F. J. Lapointe, and P. Casgrain
1994 Modelling brain evolution from behaviour: a permutational regression approach. Evolution 48:1487-1499.

Lemoine, N., and K. Böhning-Gaese
2003 Potential impact of global climate change on species richness of long-distance migrants. Conservation Biology 17:1-11.

Lyons, S. K., and M. R. Willig
1999 A hemispheric assessment of scale dependence in latitudinal gradients of species richness. Ecology 80:2483-2491.

Manly, B. F. J.
1986 Randomization and regression methods for testing for association with geographical, environmental, and biological distances between populations. Researches on Population Ecology 28:201-218.

Mann, G. F.
1978 Los Pequeños Mamíferos de Chile: Marsupiales, Quirópteros, Edentados y Roedores. Gayana (Zoología) 40:1-342.

Manne, L., and S. Pimm
2001 Beyond eight forms of rarity: Which species are threatened and which will be next? Animal Conservation 4:221-229.

Manne, L. L., T. M. Brooks, and S. L. Pimm
1999 Relative risk of extinction of passerine birds on continents and islands. Nature 399:258-261.

Mantel, N.
1967 The detection of disease clustering and a generalized regression approach. Cancer Research 27:209-220.

Marquet, P. A., M. Fernández, S. A. Navarrete, and C. Valdovinos.
2004 Diversity emerging: towards a deconstruction of biodiversity patterns. Pp. 191-209 in Frontiers of Biogeography: New directions in the Geography of Nature (Lomolino, M., and L. R. Heaney, eds). Sinauer Associates, Sunderland, Massachussetts, USA.

Medel, R. G., J. E. Jiménez, F. M., Jaksic, J. L. Yañez, and J. J. Armesto
1990 Discovery of a continental population of the rare Darwin's fox *Dusicyon fulvipes* (Martin, 1837) in Chile. Biological Conservation 51:71-77.

Mercer, J. H.
1983 Cenozoic glaciations in the Southern hemisphere. Annual Review of Earth and Planetary Science 11:99–132.

Meserve, P. L., and F. M. Jaksic

1991 Comparaciones de ensambles de vertebrados terrestres en pluviselvas templadas de Norte y Sudamerica. Revista Chilena de Historia Natural 64:511-536.

Meserve, P. L., D. A. Kelt, and D. R. Martínez

1991 Geographical ecology of small mammals in continental Chile Chico, South America. Journal of Biogeography 18:179-187

Mönkkönen, M., and P. Viro

1997 Taxonomic diversity of the terrestrial bird and mammal fauna in temperate and boreal biomes of the northern hemisphere. Journal of Biogeography 24:603–612.

Muñoz A., and J. Yañez

2000 Mamíferos de Chile. CEA Ediciones, Valdivia, Chile. 464 pp.

Murray, B. R., P. H. Thrall, A. M. Gill, and A. B. Nicotra

2002 How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. Austral Ecology 27:291-310.

Murúa, R.

1996 Comunidades de mamíferos del bosque templado de Chile. Pp. 113 – 134 in Ecología de los Bosques Nativos de Chile (Armesto, J. J., C. Villagrán, and M. K. Arroyo, eds.). Editoria Universitaria. Santiago, Chile.

Nychka, D.

2004 Fields: Tools for spatial data. R package version 2.0. Online at http://www.cgd.ucar.edu/stats/Software/Fields

Oberrath, R., and K. Böhning-Gaese

2001 Signed Mantel Test to cope with autocorrelation in comparative analyses. Journal of Applied Statistics 28:725-736.

2002 Phenological adaptation of ant-dispersed plants to seasonal variation in ant activity. Ecology 83:1412-1420.

Palma, R. E., E. Rivera-Milla, J. Salazar-Bravo, F. Torres-Pérez, U. F. J. Pardiñas, P. A. Marquet, A. E. Spotorno, A. P. Meynard, and T. L. Yates

2005 Phylogeography of *Oligoryzomys longicaudatus* (Rodentia: Sigmodontinae) in temperate South America. Journal of Mammalogy 86: 191-200.

Paruelo, J. M., E. G. Jobbágy, and O. E. Sala

2001 Current distribution of ecosystem functional types in temperate South America. Ecosystems 4:683-698.

Paruelo, J. M., E. G. Jobbágy, O. E. Sala, W. K. Laueroth, and I. C. Burke

1998 Functional and structure convergence of temperate grassland and shrubland ecosystems. Ecological Applications 8:194-206.

Pearson, O. P.
1983 Characteristics of a mammalian fauna from forest in Patagonia, southern Argentina. Journal of Mammalogy 64:476-492.

1984 Taxonomy and natural history of some fossorial rodents of Patagonia, southern Argentina. Journal of Zoology 202:225-237.

Pearson, O. P., and A. K. Pearson
1982 Ecology and biogeography of the southern rainforest of Argentina. Pp. 129–142 in Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, University of Pittsburgh, Special Publication Series 6. Pittsburgh, Pennsylvania, USA.

Pimm, S., H. Jones, and J. Diamond
1988 On risk of extinction. American Naturalist 132:757-785.

Prendergrast, J. R., R. M. Quinn, J. H. Lawton, B. C. Eversham, and D. W. Gibbons
1993 Rare species, the coincidence of diversity hotspots and conservation strategies. Nature 365:335-337.

Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace
2000 Predicting extinction risk in declining species. Proceedings of the Royal Society of London B 267:1947-1952

R Development Core Team
2005 R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Online at http://www.R-project.org.

Rabinowitz, D. S., S. Cains, and T. Dillon
1986 Seven forms of rarity and their frequency in the flora of the British Isles. Pp. 182-204 in Conservation Biology: The Science of Scarcity and Diversity (Soulé, M. E., ed.). Sinauer Associates, Sunderland, Massachusetts, USA.

Redford, K. H., and J. K Eisenberg
1992 Mammals of the Neotropics. Vol. 2: The Southern Cone of South America. University of Chicago Press, Chicago, Illinois, USA. 430 pp.

Reise, D., and W. Venegas
1987 Catalogue of records, localities, and biotopes for research work on small mammals in Chile and Argentina. Gayana (Zoologica) 51:103-130.

Ricklefs, R, and D. Schluter (eds.)
1993 Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press. Chicago, Illinois, USA. 414 pp.

Rodríguez, P., and H. T. Arita
2004 Beta diversity and latitude in North American mammals: Testing the hypothesis of covariation. Ecography 27:547-556.

Romdal, T. S., R. K. Colwell, and C. Rahbek
2005 The influence of band sum area, domain extent, and range sizes on the latitudinal mid-domain effect. Ecology 86:235-244.

Rosenzweig, M. L.
1995 Species Diversity in Space and Time. Cambridge University Press, Cambridge. USA, 458 pp.

Ruggiero, A. and T. Kitzberger
2004 Environmental correlates of mammal species richness in South America: effects of spatial structure, taxonomy and geographic range. Ecography 27:401-416.

Saavedra B., and J. A. Simonetti
2000 A northern and threatened population of *Irenomys tarsalis* (Mammalia: Rodentia) from Central Chile. Zeitschrift für Saugetierkunde 65:243-245.

2001 New records of *Dromiciops gliroides* (Microbiotheria: Microbiotheriidae) and *Geoxus valdivianus* (Rodentia: Muridae) in central Chile: their implications for biogeography and conservation. Mammalia 65:96-100.

2003 Holocene distribution of Octodontid rodents in central Chile. Revista Chilena de Historia Natural 76: 383-389.

Smith, M. F., D. A. Kelt, and J. L. Patton
2001 Testing models of diversification in mice in the *Abrothrix olivaceus*/*xanthorhinus* complex in Chile and Argentina. Molecular Ecology 10:397-405.

Smouse, P. E., J. C. Long, and R. R. Sokal
1986 Multiple regression and correlation extensions of the Mantel test of matrix correspondence. Systematic Zoology 35:627-632.

Spotorno, A. E., H. Cofré, G. Manríquez, Y. Vilina, P. A. Marquet, and L. I. Walker
1998 Una nueva especie de *Loxodontomys*, otro mamífero filotino en los Andes de Chile central. Revista Chilena de Historia Natural 71:359-373.

Spotorno, A. E., L. I. Walker, S. V. Flores, M. Yevenes, J. C. Marín, and C. Zuleta
2001 Evolución de los filotinos (Rodentia, Muridae) en los Andes del Sur. Revista Chilena de Historia Natural 74:151-166.

Taylor, C. M., and N. J. Gotelli
1994 The macroecology of *Cyprinella*: correlates of phylogeny, body size, and geographical range. American Naturalist 144:549-569

Tognelli, M. F., and D. A. Kelt
2004 Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. Ecography 27:427- 436.

Van Rensburg, B. J., S. L. Chown, and K. J. Gaston
2002 Species richness, environmental correlates, and spatial scale: A test using South African birds. American Naturalist 159:566-577.

Vázquez, L.-B., and K. J. Gaston
2004 Rarity, commonness, and patterns of species richness: The mammals of Mexico. Global Ecology and Biogeography 13:535-542.

Villagrán, C.
1995 Quaternary history of the Mediterranean vegetation of Chile. Pp 3–20 in Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia (Arroyo, M. K., P. H. Zedler, and M. D. Fox, eds.). Springer Verlag, Berlin, Germany. 455 pp.

Villagrán, C., P. Moreno, and R. Villa
1996 Antecedentes palinológicos acerca de la historia cuaternaria de los bosques chilenos. Pp 51–70 in Ecología de los Bosques Nativos de Chile (Armesto, J. J., C. Villagrán, and M. K. Arroyo, eds.). Editoria Universitaria, Santiago, Chile.

Vuilleumier, B. S.
1971 Pleistocene changes in the fauna and flora of South America. Science 173:771–780.

Whittaker, R. H., K. J. Willis, and R. Field
2001 Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography 28:453 - 470

Williams, P., D. Gibbons, C. Margules, A. Rebelo, C. Humpries, and R. Pressley
1996 A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. Conservation Biology 10:155-174.

Yañez, J., and A. Muñoz-Pedreroz
2000 Mamíferos vivientes de Chile. Mamíferos de Chile. Pp. 37-40 in Mamíferos de Chile (Muñoz-Pedreroz, A., and J. Yañez, eds.). Ediciones CEA, Valdivia, Chile.

Zar, J. H.
1999 Biostatistical Analysis. Fourth Edition, Prentice Hall, Upper Saddle River, New Jersey, USA. 929 pp.

THE BAT FAUNA OF COSTA RICA'S RESERVA NATURAL ABSOLUTA CABO BLANCO AND ITS IMPLICATIONS FOR BAT CONSERVATION

LA FAUNA DE MURCIÉLAGOS EN LA RESERVA NATURAL ABSOLUTA CABO BLANCO (COSTA RICA) Y SUS IMPLICACIONES EN LA CONSERVACIÓN DE LA QUIROPTEROFAUNA

Robert M. Timm and Deedra K. McClearn

ABSTRACT

Reserva Natural Absoluta Cabo Blanco, located at the southern tip of northwestern Costa Rica's Nicoya Peninsula, was established in 1963 and is the country's oldest nationally protected reserve. Because the climate of the Nicoya Peninsula is ideal for human habitation, the peninsula has been occupied for millennia and is a heavily impacted landscape. The region also is one of the most poorly studied in Central America in terms of biotic diversity. We initiated a multiyear survey of bats in the reserve and the adjacent Refugio de Vida Silvestre Cueva Los Murciélagos to quantify species diversity, abundances, habitat use, seasonality, and reproduction. By surveying bats during 5 rainy seasons and 4 dry seasons from July 1999 through February 2006, we address the following questions: Which species of bats are present in the area? Are the bat communities the same in 3 different habitats—coastal forest, inland forest, and limestone caves? Are the species diversity and abundances of bats in the rainy season similar to those in the dry season? Can we discern seasonal patterns of reproduction? Are the species diversity and abundances of bats at Cabo Blanco (a tropical moist forest in the Holdridge Life Zone classification) similar to those in the nearby tropical dry forest at Parque Nacional Palo Verde? What are the conservation implications of the bat assemblages found in this regenerating forest?

Using mist nets, searching for roosting bats, and an acoustical survey, 39 species of bats are documented in the area, including 5 emballonurids, 4 molossids, 1 mormoopid, 1 noctilionid, 21 phyllostomids, and 7 vespertilionids. The 2 most commonly captured bats, *Carollia perspicillata* and *Artibeus jamaicensis*, are abundant in both the inland and coastal forests and both are more abundant in the rainy season than in the dry season. Several species have clear habitat preferences, at least during the seasons in which we netted (*Glossophaga soricina* and *Uroderma bilobatum* along the coast and *Trachops cirrhosus* inland). The largest carnivores (*Noctilio leporinus*, *Chrotopterus auritus*, *Phyllostomus hastatus*, *Trachops cirrhosus*, and *Vampyrum spectrum*) are present, but the small and middle-sized predatory bats (*Micronycteris*, *Lophostoma*, and others)

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are poorly represented both in terms of diversity and abundance. We captured twice as many bats per hour of effort in the inland forest as we did in the coastal forest. The caves of Refugio de Vida Silvestre Cueva Los Murciélagos have 4 species of bats (*Balantiopteryx plicata, Saccopteryx bilineata, Desmodus rotundus*, and *Phyllostomus hastatus*) that are year-round residents.

Several species seem to be equally abundant in both seasons, including *Balantiopteryx plicata*, *Saccopteryx bilineata*, *Noctilio leporinus*, *Artibeus watsoni*, *Desmodus rotundus*, *Glossophaga soricina*, *Phyllostomus hastatus*, *Trachops cirrhosus*, *Lasiurus ega*, and *Myotis nigricans*. Our impression is that some species are more common during the rainy season than the dry season, but more data are needed to substantiate this assertion. Bats in the caves were equally abundant during each of our 8 cave surveys. *Desmodus rotundus* is the only species for which our data suggest year-round reproduction; we observed scrotal males, pregnant females, and juveniles during each of our visits to Cabo Blanco. Other species are present year-round but have seasonal reproductive activity. We captured *Artibeus watsoni* and *Carollia perspicillata* in both seasons but have seen pregnant females only during the rainy season.

Carollia perspicillata and *Artibeus jamaicensis* are the 2 most commonly captured bats at both Cabo Blanco and the nearby Parque Nacional Palo Verde. The species records and abundances of several other species differed between the sites, however. Species that are abundant at Palo Verde, but not yet recorded from Cabo Blanco, include *Pteronotus davyi*, *Pteronotus gymnonotus*, *Carollia subrufa*, *Centurio senex*, and *Natalus stramineus*. *Phyllostomus hastatus* is abundant at Cabo Blanco but not known from Palo Verde. Although both sites are relatively close together in the northern Pacific lowlands of Costa Rica, Cabo Blanco is substantially wetter, and the associated differences in vegetation may be driving bat distributional patterns.

We provide a number of new records and ecological information for bats on the Nicoya Peninsula and document that bat diversity and abundances can be substantial in regenerating forest. Several of the most commonly captured bat species are seed dispersers and may be critical to forest regeneration.

Key words: cave survey, Chiroptera, coexistence, community structure, feeding guilds, habitat fragmentation, Neotropics, regenerating forest, seasonality, species diversity.

RESUMEN

La Reserva Natural Absoluta Cabo Blanco, ubicada en el extremo sur de la península Nicoya de Costa Rica, se estableció en 1963 y es el área protegida más vieja del país. Dado a que el clima de la península Nicoya es ideal para la habitación humana y la producción de ganado, la península se ha habitado por miles de años y es una zona muy impactada en Centroamérica. Esta región también es una de las menos estudiadas en Centroamérica en cuanto a la diversidad biótica. Iniciamos un muestreo de murciélagos multianual dentro de la reserva y en el área adjunta, llamado el Refugio de Vida Silvestre Cueva Los Murciélagos, con el fin de determinar la diversidad de especies, abundancia, uso del hábitat, estacionalidad y reproducción. Después de haber hecho un muestreo a lo largo de 5 estaciones lluviosas y 4 estaciones secas desde julio 1999 hasta febrero 2006, investigamos las siguientes preguntas: ¿Cuáles especies de murciélagos están presentes dentro del área? ¿Existen diferencias en las comunidades de murciélagos

en 3 hábitats diferentes—bosque costero, bosque interno y cuevas calizas? ¿Existe una diferencia entre la estación seca y lluviosa en cuanto a la diversidad de especies y abundancia de murciélagos? ¿Hay patrones estacionales en cuanto a la reproducción? ¿Existe similitud en la diversidad y abundancia de murciélagos entre Cabo Blanco (un bosque húmedo tropical en la clasificación de Zonas de Vida Holdridge) y el vecino bosque seco tropical Parque Nacional Palo Verde? ¿Cuáles son las implicaciones a la conservación para los grupos de murciélagos que se encuentran en estos bosques en estado de regeneración?

Documentamos 39 especies de murciélagos en el área, incluyendo 5 especies de embalonúridos, 21 especies de filostómidos, 4 especies de molósidos, 1 mormoópido, 1 noctiliónido y 7 especies de vespertiliónidos. Las dos especies de murciélagos comúnmente capturadas, *Carollia perspicillata* y *Artibeus jamaicensis*, son abundantes tanto en bosques costeros como en bosques internos. Varias especies tienen preferencias a ciertos hábitats, por lo menos durante las estaciones de nuestras investigaciones (*Glossophaga soricina* y *Uroderma bilobatum* a lo largo de los bosques costeros y *Trachops cirrhosus* en los bosques internos). Los carnívoros más grandes (*Noctilio leporinus*, *Chrotopterus auritus*, *Phyllostomus hastatus*, *Trachops cirrhosus* y *Vampyrum spectrum*), están presentes, pero los murciélagos depredadores de tamaño pequeño y de tamaño mediano (*Micronycteris*, *Lophostoma* y otros) están pobremente representados. Capturamos dos veces más murciélagos por hora de esfuerzo en los bosques internos que en los bosques costeros. Las cuevas del Refugio de Vida Silvestre Cueva Los Murciélagos tienen 4 especies de murciélagos (*Balantiopteryx plicata*, *Saccopteryx bilineata*, *Desmodus rotundus* y *Phyllostomus hastatus*) que son residentes por todo el año.

Varias especies parecen ser igualmente abundantes en ambas temporadas, incluyendo *Balantiopteryx plicata*, *Saccopteryx bilineata*, *Noctilio leporinus*, *Artibeus watsoni*, *Desmodus rotundus*, *Glossophaga soricina*, *Phyllostomus hastatus*, *Trachops cirrhosus*, *Lasiurus ega* y *Myotis nigricans*. Nuestra impresión es que algunas especies son más comunes durante la época lluviosa que la época seca, pero se necesitan más datos para documentarlo. Los murciélagos en las cuevas fueron igualmente abundantes durante cada uno de los 8 muestreos de las cuevas. *Desmodus rotundus* es la única especie para que nuestros datos sugieron reproducción durante todo el año. Hemos observado machos reproductivos, hembras embarazadas y juveniles durante cada una de nuestras visitas a Cabo Blanco. Otras especies están presentes todo el año pero tienen una actividad reproductiva estacional. Capturamos *Artibeus watsoni* y *Carollia perspicillata* en ambas temporadas pero hemos registrado hembras embarazadas solamente durante la temporada lluviosa.

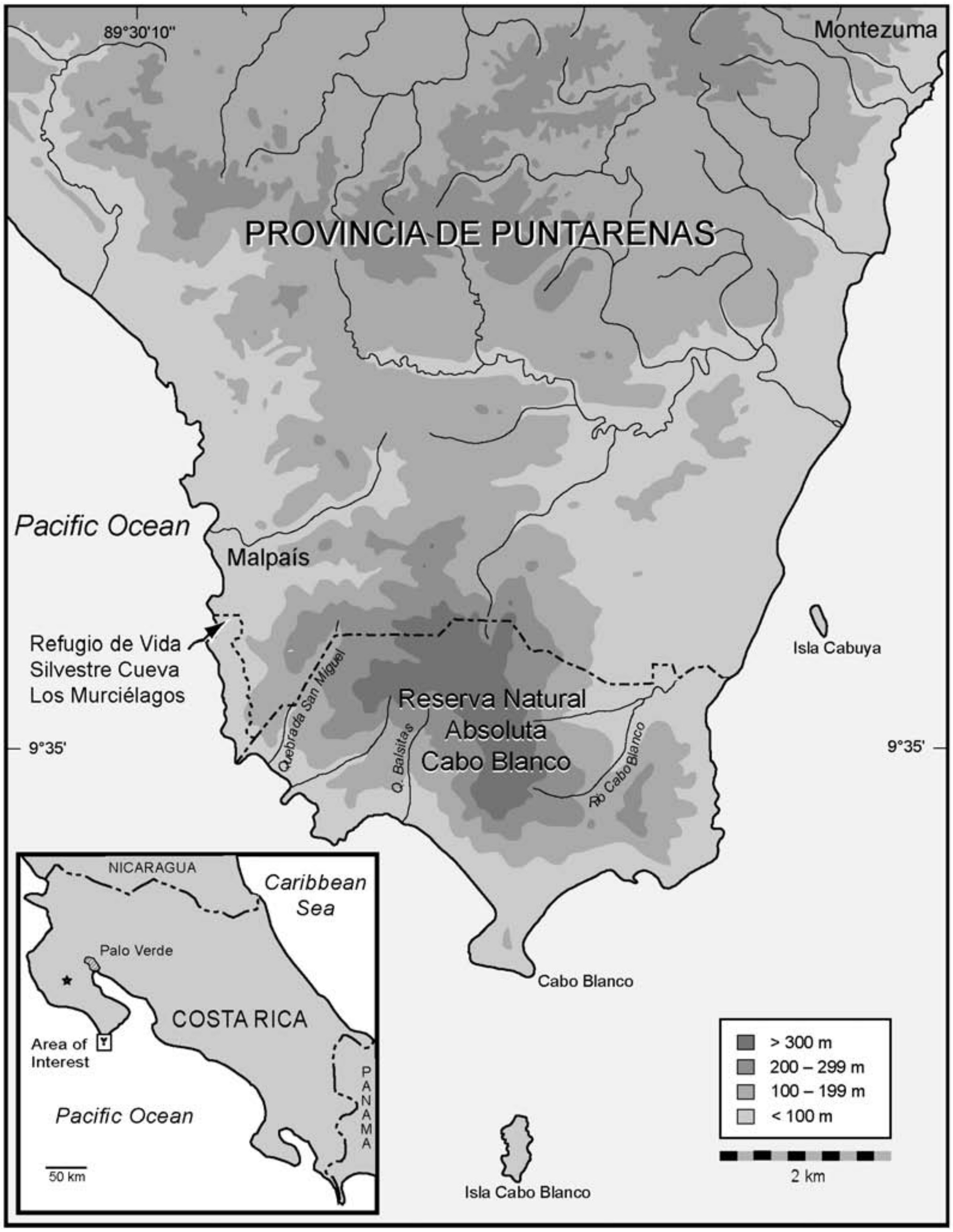
Carollia perspicillata y *Artibeus jamaicensis* son las 2 especies que se capturaron con más frecuencia en ambos Cabo Blanco y el vecino Parque Nacional Palo Verde. Sin embargo, los registros de especies y las abundancias de varias otras especies fueron diferentes entre los dos sitios. Las especies que son abundantes en Palo Verde pero aún no se registran en Cabo Blanco incluyen *Pteronotus davyi*, *Pteronotus gymnonotus*, *Carollia subrufa*, *Centurio senex* y *Natalus stramineus*. La especie *Phyllostomus hastatus* es abundante en Cabo Blanco pero no se registra en Palo Verde. A pesar de que los dos sitios están relativamente cerca uno del otro y en las tierras bajas del Pacífico norte de Costa Rica, Cabo Blanco es mucho más húmedo y las asociadas diferencias en la vegetación pueden ser responsables por dichos patrones de distribución de los murciélagos.

Proveemos nuevos registros e información ecológica para murciélagos en la península de Nicoya y documentamos que la diversidad y abundancia de los murciélagos pueden ser altas en bosques en proceso de regeneración. Varias de las especies de murciélagos capturadas más comúnmente son dispersores de semillas y por lo tanto pueden ser imprescindibles para la regeneración de los bosques.

Palabras clave: muestreo en cuevas, Chiroptera, coexistencia de especies, estructura comunitaria, gremios alimentarios, fragmentación de habitat, Neotropicó, bosque en recuperación, estacionalidad, diversidad de especies.

Costa Rica is one of the world's leading nations in establishing national parks and refuges, and currently more than 27% of the country's land surface is protected by government or private reserves. However, most of these reserves and wildlife refuges are relatively new, so the effects of former deforestation and land degradation are still evident even in well guarded areas. The oldest national reserve in Costa Rica is Reserva Natural Absoluta Cabo Blanco, at the extreme southern tip of the Nicoya Peninsula (Figs. 1, 2). This reserve was established in 1963, 7 years before the inception of Costa Rica's Servicio de Parques Nacionales, through the initiative and efforts of the Scandinavian emigrants Nicolas Wessberg and Karen Mogensen. They raised $30,000 in private funds to purchase the initial 1,172 ha. Later that year, the president of Costa Rica, Francisco Orlich Bolmarcich, declared the land a national reserve by executive decree. As an absolute reserve, no visitors were allowed, and no scientific investigations or photographs were permitted. The only official mandate was protection from the trio of threats—fire, timber harvesting, and poaching. Wessberg served as the reserve administrator without pay until he was murdered on the Osa Peninsula in 1975. In 1982, the reserve's original area was increased to include the first 1 km out from the shoreline, thus protecting 1,750 ha of ocean. Today, the reserve has expanded to cover 56,350 ha of marine area off Costa Rica's Pacific coast. The strict isolation of the reserve has eased in recent years, first with a government decree in 1988 opening the Cabuya (eastern) sector to the public and second with the opening of the San Miguel (western) sector to selected educational groups in 1999. Detailed overviews of the creation of

Figure 1 (facing page). Map of the southernmost tip of the Nicoya Peninsula showing the locations of Reserva Natural Absoluta Cabo Blanco and Refugio de Vida Silvestre Cueva Los Murciélagos in relation to the communities of Malpaís and Montezuma. Our netting along the coast was conducted between the Quebrada Balsitas and the unnamed stream immediately to the west. Our inland nets were set along the Quebrada San Miguel about a km from its mouth. The main building of the Estación Biológica San Miguel is located just east of the mouth of the Quebrada San Miguel. On the countrywide map, Parque Nacional Palo Verde (84 km to the north of Cabo Blanco) is indicated by cross hatchings and the community of Nicoya (near the base of the Peninsula) by the star. In 2005 the Ministerio del Ambiente y Energía (MINAE) acquired about a third of the private property that included Refugio de Vida Silvestre Cueva Los Murciélagos Reserva Natural Absoluta Cabo Blanco, including the bat caves and all land bordering the coast; the remainder of the property was acquired by a private landowner.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Río Cabo Blanco
Isla Cabuya
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9°35'
Cabo Blanco
Isla Cabo Blanco
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200 – 299 m
100 – 199 m
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Palo Verde
COSTA RICA
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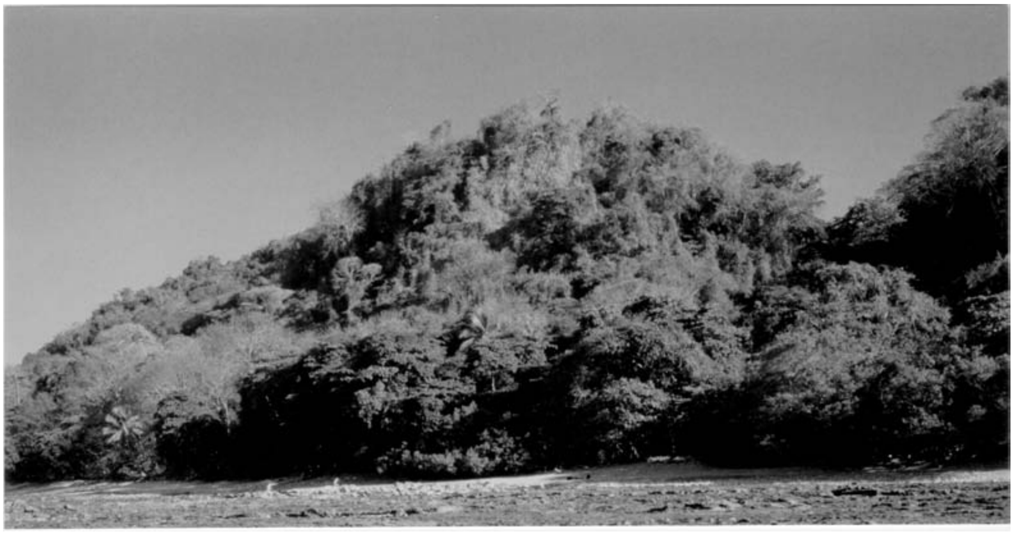

Figure 2. View of Reserva Absoluta Cabo Blanco taken from the Laguna San Miguel intertidal zone during the dry season of 2000. Note the rough terrain, the closed canopy of the 40-year-old secondary forest, and the scattering of leafless deciduous trees silhouetted against the sky.

Costa Rica's park service that emphasize the political and cultural history have been provided by Wallace (1992) and Evans (1999).

We have had the opportunity to survey bat distributions and abundances in the reserve in conjunction with our teaching efforts with the Organization for Tropical Studies over the past several years. Our goals herein are to document the recent history and the bat fauna of Reserva Natural Absoluta Cabo Blanco, focusing on the western sector around Estación Biológica San Miguel and the nearby Refugio de Vida Silvestre Cueva Los Murciélagos. We focused our survey on the following questions. What species are present in the area? Are bats equally abundant and diverse in 3 different habitats—the forest along the coast, inland forest, and limestone caves? Are the species diversity and abundances of bats in the rainy season similar to those in the dry season? Are there seasonal patterns in reproduction? Are the bat communities at Cabo Blanco and nearby but ecologically distinct Palo Verde similar?

Documentation of the bat fauna at the southern tip of the Nicoya Peninsula is valuable because this is one of the most poorly studied regions in Costa Rica, the region has been impacted by humans for several millennia, and our results have implications for bat conservation in Costa Rica as well as other areas in the Neotropics. Because the forest is regenerating and most species of mammals have received excellent protection for the past 4 decades, the forest and its wildlife species are in a state of rapid transition. Understanding how bats respond to conservation efforts will provide insights valuable to future conservation programs because bats play major roles as seed dispersers, pollinators, predators, and prey in the Neotropics.

METHODS

The information presented here comes from our survey studies and observations in and around Reserva Natural Absoluta Cabo Blanco, Puntarenas Province, Costa Rica. Our primary study sites are in the general vicinity of Estación Biológica San Miguel (9° 35' N, 85° 08' W) and the adjacent private reserve, Refugio de Vida Silvestre Cueva Los Murciélagos (9° 36' N, 85° 09' W) (Fig. 1). We have been working and teaching in the reserve regularly since 1999. For the bats, all linear measurements in the accounts that follow are in millimeters and weights are given in grams. Forearms (fa) were measured to the nearest 1 mm from the proximal extension of the radius–ulna (elbow) to the distal-most extension of the carpals (flexed wrist). Individuals categorized as adults are those with complete fusion of the epiphyses of metacarpals and phalanges. We recognize that some species of bats are more likely to be netted than others and that we are under-sampling the aerial insectivore community. Our characterizations of species as being abundant or uncommon refer to their presence as determined by our netting and survey techniques.

The focus of these accounts is the information we obtained between February 2000 and July 2003. The standard procedure in each netting session was to spend 1 night netting in the forest along the coast and 1 night in the forest inland (from sundown, ca. 1800 h, until after midnight). The coastal and inland sites are approximately 750 m apart, as the bat flies; the inland site is located on a ridge (ancient terrace) at ca. 70 m elevation. Occasionally, we would experience heavy rains after an hour or 2 of netting and would then resample that site for a second night. The number of nets used in specific locations was standardized across years, as was net placement. Depending on conditions (e.g., level of water in the stream over which we placed nets), we might add or delete one of the standard nets. We used more nets along the coast (30 or 42 m of net) than we did inland (18 or 24 m of net) because the inland ridge is considerably denser with vegetation than the coastal forest. Two of our standard net positions on the ridge were over a small stream, Quebrada San Miguel, and the third was across the trail approximately 20 m from the first stream crossing. We calculate our captures as bats per running meter of net per hour to standardize sampling, because we used a combination of 6- and 12-m mist nets at the sites. Data on capture rates and habitat preferences are from 4 rainy seasons (2000, 2001, 2002, and 2003) and 1 dry season (2001). Data from the rainy season 1999 and dry seasons of 2000, 2003, and 2006 are incorporated into the species accounts and inventory, but are not included in the analysis of habitat preferences because the sampling regime differed. In summary, we have netting data from 16 complete evenings, more than 12 partial evenings, 8 cave surveys, and numerous incidental observations over the 6-year period.

Bats were individually marked on a temporary basis with a black felt marker, and no recaptures in the same netting session are included. Data were analyzed using JMP and Minitab software. Habitat preferences are presented with and without Bonferroni corrections (Zar, 1996). For all of our analyses, we make the assumption that each capture is an independent event, in other words that bats are not captured in social groups and that we are not capturing the same individual from one year to the next. Additional netting was undertaken at selected sites, including several places over the Quebrada San Miguel, during both the rainy season and dry season.

Refugio de Vida Silvestre Cueva Los Murciélagos was a private reserve, adjacent to Reserva Natural Absoluta Cabo Blanco, and acted as a buffer area between the reserve and the community of Malpaís (Fig. 1). The property along the coast was obtained by Ministerio del Ambiente y Energía (MINAE) in 2005; it is thus protected albeit not part of Reserva Natural Absoluta Cabo Blanco. There are 3 caves on this property and another cave just to the north along the beach on private property. All 4 caves are formed from heavily eroded limestone that has been uplifted at an oblique angle. For the purposes of our surveys, we worked primarily in the 3 southernmost caves which were originally part of Refugio de Vida Silvestre Cueva Los Murciélagos. We numbered these cave 1 (the northernmost cave), cave 2 (the center cave), and cave 3 (the southernmost cave). Cave 1 is a simple, closed-end, relatively dark passageway with a small entrance. The cave was formed by water eroding the tectonically uplifted limestone. Because this cave lies only a few kilometers east of the subduction zone of the Cocos Plate, the limestone has been upthrust vertically at nearly a 90° angle to the ground level. This cave runs parallel (north–south) to the subduction zone. Cave 2 is a closed-end passage, with a small entrance that opens up into a large cavern within a few meters of the entrance. It also was formed by water eroding the uplifted limestone. This cave is not as dark as cave 1 and runs east–west. Cave 3 is a large open natural limestone arch with dark, closed-end side passages; most of the bats roosted in the dark side passages. The cave was formed by a combination of water eroding the limestone and the sloughing of massive limestone blocks from the ceiling. The cave on private property, cave 4, faces west toward the ocean and is considerably brighter than the other caves. Several areas of the ceiling are open allowing light throughout the cave. Caves 2, 3, and 4 lie perpendicular to the subduction zone. Caves 1–3 were censused visually 8 times over the 6 years and we attempted to disturb the bats as little as possible. At least 1 individual of each species of bat roosting in the caves was captured to confirm identifications. In our 8 surveys, we observed only a single bat that was not identified to species; it was a small phyllostomid that was roosting by itself. Before we entered the caves, we located roosting bats and identified those near the entrance to species. Then, as we entered the cave, 2 people were responsible for counting or estimating the number of bats present in deeper sections. We recorded temperature (to the nearest 0.1°C) using a Raytek long-range digital thermometer both throughout the caves and in the vicinity of roosting individuals or groups of bats and noted the approximate locations of all individuals.

Complementing the mist net and roost site surveys, we also incorporate the results of an acoustical survey. In late February 2005, Richard K. LaVal conducted a 4-night acoustical survey near the Estación Biológica San Miguel using the Anabat bat-detecting system (Titley Electronics, Ballina, New South Wales, Australia) to detect and identify ultrasonic signals from free-flying bats. Two nights of this survey were conducted in the vicinity of the field station buildings in a more open area than either of our netting surveys, and two nights were conducted along the Quebrada San Miguel. Both sites were relatively close (ca. 0.75 km) to our netting area along the coast.

Only 2 other mammalogists, Richard LaVal and Bernal Rodríguez, have worked at Cabo Blanco previously; both were there for just a few days. They provided us with a number of observations that we incorporate into the following species accounts. Reference specimens of selected species are deposited in the mammal collection of the Museo Nacional de Costa Rica (MNCR), San José and the University of Kansas Natural History Museum (KU), Lawrence, Kansas. Additional specimens from the region are deposited in the collections of the Museo Nacional de Costa Rica (MNCR), San José and the University of Michigan Museum of Zoology (UMMZ), Ann Arbor.

Selected species (i.e., *Diclidurus albus*, *Vampyrum spectrum*), not otherwise vouchered, are documented with photographs. Carcasses of 2 species of bats (*Desmodus rotundus* and *Phyllostomus hastatus*) located in the caves were saved as vouchers.

Genera are listed alphabetically within families and species alphabetically within genera. Recent phylogenetic treatments of the family Phyllostomidae (Wetterer et al., 2000; Jones et al., 2002; Baker et al., 2003; and references therein) document that the traditional classification of subfamilies and genera within the leaf-nosed bats needs to be reassessed. Recent overviews, keys, biogeography, and literature reviews of Costa Rican bats may be found in Reid (1997), Timm and LaVal (1998), Rodríguez-H. and Wilson (1999), Timm et al. (1999), LaVal and Rodríguez-H. (2002), and Wilson et al. (2002).

RESULTS

Site History and Description

Overview of Nicoya Peninsula. The Nicoya Peninsula is part of the Central American Pacific lowlands, much of which is classified as dry forest in the Holdridge Life Zone system (Holdridge, 1967; Holdridge et al., 1971; Herrera and Goméz, 1993). The main body of the peninsula is composed of underlying basalt and limestone (Tournon and Alvarado, 1997; Denyer and Kussmaul, 2000) with moderate relief (highest hill 1,000 m, average hills 600 m) (Bergoeing, 1998). Reserva Natural Absoluta Cabo Blanco, on the tip of the peninsula, consists of Pliocene and Pleistocene sedimentary deposits (Vásquez, 1983; Tournon and Alvarado, 1997). The mean annual temperature in the reserve is 28°C. The mean annual precipitation is 3,100–3,200 mm (higher than rainfall at the base of the peninsula), with a strong dry season from January through March—this qualifies the tip of the peninsula as tropical moist forest (Herrera, 1985; Lindquist, 2003; Lindquist and Carroll, 2004).

In order to understand the current status of the peninsular biota, a consideration of land use history is warranted. Most ecologists and archaeologists have abandoned the notion that Neotropical landscapes at the time of European contact were pristine or virgin wilderness little affected by human agency (Denevan, 1992; Bush and Colinvaux, 1994; Clark, 1996; Stahl, 1996; Kennedy and Horn, 1997). A treatment of land use history should therefore incorporate what is known of human/ecosystem interactions of the last few millennia. In the case of the Nicoya Peninsula, the available evidence indicates a long and complex history.

Culturally and with reference to archaeological study, the Nicoya Peninsula has been considered a part of lower or southern Central America (Linares, 1979; Fonseca Zamora, 1993), the southern end of Mesoamerica (Creamer, 1987; Sluyter, 1994), the southern frontier of Mesoamerica (Quesada López-Calleja, 1980), part of the Isthmo–Colombian Area (Snarskis, 2003), and/or a part of an Intermediate Area or buffer zone between Olmec and Mayan influences to the northwest and Incan influences to the southeast (Stone, 1977; Lange, 1984). Within Costa Rica, the peninsula is considered to be a component of the Greater Nicoya archaeological subarea (Lange, 1984), which is one of 3 major zones within Costa Rica (the others are the Diquís southern Pacific subarea and the Central Highlands/Atlantic Watershed subarea) (Stone, 1977; Snarskis, 1981; Quilter, 2004). Scattered evidence indicates human presence along the Pacific coast of Central America for the last 11,000 years (Cooke and Ranere, 1992).

Various authorities have written about the lives of the indigenous people of the Nicoya zone in the centuries before 1500. Collectively often referred to as the Chorotega, these people consisted of several different groups with distinct languages (including Pipil and Nicarao traders and settlers) (Fowler, 1985, 1991). Evidence exists for long and medium-distance trade, the former from Ecuador (Stone, 1977) and the latter along the Pacific coast in both directions and across the Golfo Nicoya between the mainland and the peninsula (Creamer, 1992). Based on interpretation of pottery remains, early (500 BC–600 AD) associations with people in the Central Highlands of Costa Rica seem to have waned by 1300 AD (Sheets et al., 1991). The best known archaeological site on the peninsula is Las Huacas, a large cemetery near the center of the peninsula (south of the town of Nicoya) that was excavated by the Swedish botanist Carl Hartman in the early 20th century (Hartman, 1907). He attempted to establish a stratigraphy of the remains in a desperate race against the looters that have plagued Costa Rican archaeological research for the last century (Lange, 1976; Skirboll, 1984). Las Huacas dates from the Early Polychrome Phase (= early Period V, 500–800 AD) and contains pottery, effigy grinding stones, and jade ornaments. The tradition of jade work on the Nicoya Peninsula evidently comes from Guatemala (Easby, 1968), but the source of the jade has not been definitively identified. A local (Nicoya) jade source has been postulated (Lange et al., 1981; Snarskis, 2003), but not located. A shift from jade to gold as a precious material occurred throughout Costa Rica around 500 AD, with metallurgy techniques introduced from Peru (Snarskis, 2003); the creative center of goldwork was in the Diquís rather than the Nicoya subarea (Bray, 1981). Clearly the people who lived in this region were influenced by both the well-studied Olmec/Maya and Inca civilizations by which they are bracketed geographically; nevertheless, one should not overlook the "uniquely innovative character" of the Greater Nicoya cultures (Abel–Vidor, 1981).

Several prominent archaeological investigations of the Nicoya area address population size, social organization, and diet of the indigenous people before and after contact with the Spanish invaders and settlers. First-hand descriptions by early European chroniclers also add to our knowledge. These sources, when pieced together, provide a revealing (albeit incomplete) narrative of the changes in natural resource use and availability over time. The Nicoya Peninsula (particularly at its base) is considered to have been moderately, but not highly populated for several thousand years prior to Spanish contact (Abel–Vidor, 1981). Trade and agricultural activities were concentrated along the shores of the Golfo Nicoya and the larger islands (especially Chira) within the gulf (Radell and Parsons, 1971). Social organization was in tribal groups rather than the chiefdom system associated with a distinct hierarchy of power, division of labor, and high population density (Creamer and Haas, 1985). Metates with evidence of corn-grinding wear (as opposed to ceremonial metates) have been found on the peninsula and date to the middle of Period IV (about 500 BC) (Snarskis, 1982), but other authorities push maize agriculture in the area as far back as 1800 BC (Hoopes, 1991). Maize and palm nut remains also are found in association with the jade-producing sites of 300 BC–500 AD (Snarskis, 2003), although the presence of wildlife bones at various peninsular locations throughout the centuries indicates a continued reliance on forest game (Kerbis, 1980). Household and hunting gardens (Linares, 1976) are known from other Central American areas and may have been in use here as well. Large scale clearing of forest probably did not occur, and building materials for houses and rafts would have been smaller diameter trees rather than the forest giants (L. Gómez, pers. comm.; but see Piperno and Pearsall (1998) for evidence of large scale deforestation around 9,000 BC at the Yeguada site in Panama).

Extensive use of shellfish (for food and for dye) and of fish from the gulf is indicated by large shell middens dating from 500 AD and also from the Middle Polychrome Phase (= late Period V, 800–1200 AD) (Kerbis, 1980; Snarskis, 2003). Curiously, however, exploitation of marine resources seems to have been intermittent (Moreau, 1984) and may have been associated with regional climate change (Messenger, 1991). Use of shellfish was "not characteristic" of the people living on the tip of the peninsula (Moreau, 1984), possibly because this zone had neither the nutrient-rich upwelling currents found further north along the coast (Hubbs and Rodden, 1964) nor the coastal mangrove forests that serve as shellfish hatcheries along the gulf coast.

One of the earliest Spanish chronicles of the post-contact era is that of Gonzalo Fernández de Oviedo y Valdés (simply Oviedo in most accounts), who traveled throughout the Peninsula in 1527, while his ship was being repaired on Isla Chira. He reported scattered plantings of cacao (see also Bergmann, 1969), many birds and large mammals, and 2 different types of corn planted by the local people, one of which was a dry season corn that matured in 40 days and provided sustenance while the rain-dependent corn was still growing (Oviedo, 1959 IV:423). He also commented on the varied diet (including deer, roasted toads, and fruit of forest trees) of the local people, the pearls gathered from the gulf, and the lustrous pottery of Chira (Oviedo, 1959 III:298–299).

The arrival of the Spanish to a particular New World location was accompanied by, and often preceded by, the arrival of Old World diseases (Lovell, 1992). Indigenous populations in the Nicoya area were greatly reduced by disease and the slave trade. A reduction in population of 90% is indicated for Nicaragua (including the Nicoya area) between 1500 and 1600 (Newson, 1982). The Spanish used the islands in the Golfo Nicoya to load slave ships with destinations in Panama and Peru. This trade led to the establishment of several shipbuilding sites in the region, with attendant mainland tree-cutting to supply wood (Radell and Parsons, 1971).

In the mid-16th century Nicoya (and the rest of Costa Rica) were parts of the Kingdom of Guatemala. It was common practice for Spanish citizens to buy government posts in order to profit from independent activities such as forced labor, smuggling, and control of trade routes (Patch, 1994). During this time, Costa Rica was not considered to have any prospects for income enhancement and the records indicate that no one ever offered to buy the post. Because the Costa Rica post (covering what is present-day central and eastern Costa Rica) was close to the isthmian crossing, and therefore strategically important, the Spanish crown was impelled to pay a salary to the holder of this position. The Nicoya post was marginally more profitable because of pearl fishing in the gulf, but there were not enough indigenous people in the area to sustain an encomienda economy (Patch, 1994).

Costa Rican government historical documents provide data on crops, livestock, and human populations for individual administrative units in the country. Large-scale cattle and mule ranches were concentrated along the northeastern (upper gulf side) of the Nicoya Peninsula during the 1600s (Molina and Palmer, 2000). In 1765, the Correximiento de Nicoya contained 1 small pueblo of about 50 Indian families "y pocas menos de gente Ladina, pobres," with the rest of the region consisting of haciendas for raising cattle, mules, and horses. Salaries were paid in silver, clothing, and cacao

(Fernández, 1976:125). In 1884, the Nicoya canton (distal half of the peninsula, including the town of Nicoya) produced some corn and sugarcane, a substantial amount of rice, and no coffee, wheat, or potatoes (Meléndez Chaverri, 1978:47–57). In 1904, this canton had a population of "10,750 habitantes dedicados a la agricultura, a la ganadería y a la pesca" (Noriega, 1924:161), many of whom lived in and around the town of Nicoya.

First-hand descriptions of the distal half of the Nicoya Peninsula by naturalists and travelers of the late 19th and early 20th centuries emphasize the hilly and forested nature of the terrain. In 1881, J. F. Bransford searched for a local source of the jade used in the numerous carvings found on the peninsula. He camped along the Río Nosara, west of the Las Huacas site, and said of his surroundings, "We were in the finest forest I had ever seen. Apparently not one of the magnificent trees in this valley had been cut since the conquest, except where for an acre or so in 2 places clearings had been made. The undergrowth was scanty, while high overhead there was a dense canopy supported by superb columns" (Bransford, 1884:815). The Swedish naturalist Carl Bovallius visited Nicoya in 1882 and wrote "la Península de Nicoya, ancha y montañosa…sus colinas recubiertas de bosques" (Zeledón Cartin, 1997:90). In 1905, the German naturalist Karl Sapper stated that the western and southwestern sides of the peninsular tip were characterized by "las selvas vírgenes," abundant game, and hunting trails through the forest and down to the coast (Zeledón, 1998:57). As recently as 1915, large parties of wealthy hunters from San José crossed the gulf and rented horses for the occasion, hunting deer (*Odocoileus virginianus*), the large, highly prized rodent the tepezcuintle or paca (*Cuniculus* (*Agouti*) *paca*), and fowl (L. Gómez, pers. comm.). Photographs from the time show forested backdrops to these expeditions.

The picture that emerges of land use on the Nicoya Peninsula in general can be summarized as follows: 1) moderate but fluctuating settlement sizes for several thousand years (before 1500), with exploitation of coastal and forest resources, clearings for agriculture, but probably no large scale deforestation, 2) depopulation, land abandonment and/or a shift of population centers, and the introduction of Old World crops and livestock during the 2 centuries following contact with the Spanish (Whitmore and Turner, 1992), 3) subsistence agriculture, some larger plantations, and livestock raising on the peninsula (Gundmundson, 1983), but with most of the backbone of the peninsula remaining forested for the next 250 years (based on first-hand accounts and aerial photographs taken in the 1940s) (see also Gómez, 1986), 4) higher populations and agricultural activities at the base of the peninsula (from the town of Nicoya north) in comparison to the tip of the peninsula, and 5) rapid deforestation throughout the peninsula during the late 1940s through to the present time.

Cabo Blanco Area. The area now encompassed within the Reserva Natural Absoluta Cabo Blanco has a history that is consistent with what is known of the rest of the peninsula. A special consideration of the topography and vegetation of particular sites within the reserve is warranted, however, because these details may help explain our results on the distribution and abundances of bat species.

Estación Biológica San Miguel is located in the San Miguel (western) sector of the reserve, 2 km south of the community of Malpaís, Costa Rica (Fig. 1). The main station building stands approximately 100 m from the high tide line and about 15 m east of the lower reach of the Quebrada San Miguel. The Quebrada San Miguel is a swiftly flowing stream with pools 2 m deep during the rainy season (May–November) (Fig.

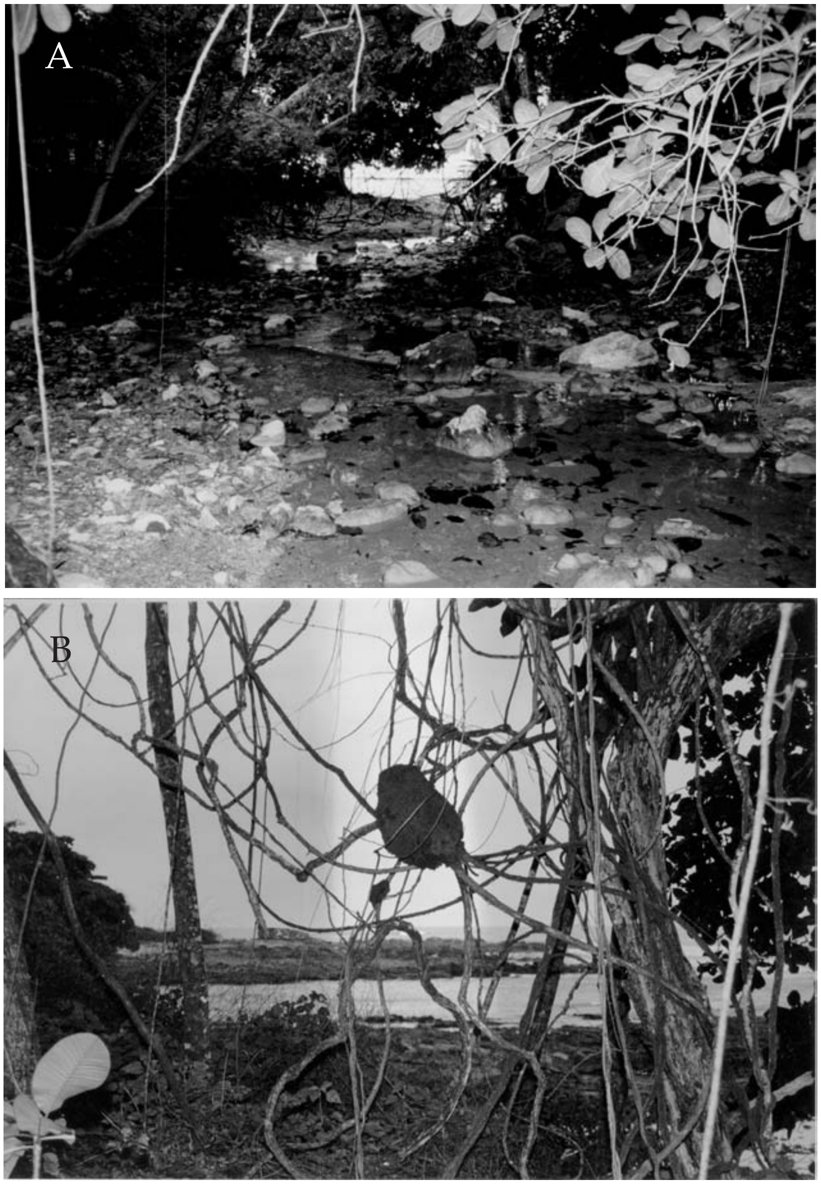

Figure 3. Photographs of 2 sampling sites. (A) Mouth of the Quebrada San Miguel during the rainy season of 2001. The view is from the footbridge next to the station, looking toward the Pacific Ocean. A furled mistnet is in the middle ground, stretched across the stream, in the location where we regularly catch *Noctilio leporinus*. Note the shallow water in the streambed. During the dry season this flow ceases entirely. (B) View of our coastal netting area from the trail where nets were set in the coastal forest (rainy season 2001). In the foreground is a tangle of lianas with a termite (*Nasutitermes*) nest and in the background is the Pacific Ocean looking south toward Isla Cabo Blanco. Photographs by Deedra McClearn.

3A). It dries up seasonally, leaving widely scattered, small and mid-sized pools in its upper reaches and a large pond of brackish water near the ocean. When the rains return, the force of the fresh water in the channel pushes aside the sand deposited by the high tide waves and reopens the way to the sea.

Our coastal forest nets were placed about 50 m from the high tide line, near and across a trail that runs from Quebrada San Miguel to Quebrada Balsitas to the southeast (Fig. 3B). The coastal strip is relatively flat, extends about 3 km in length, and varies in width from 50 to 150 m. Our standard netting positions were southeast of the intermediate, unnamed stream shown on the map. When the reserve was established, this coastal strip was planted in corn, except for a few patches of intact forest (D. Lieberman, pers. comm.). At present, the dominant vegetation along the shoreline includes the native liana *Adenocalymna inundatum* (Bignoniaceae), the fast-growing, native coastal shrub *Talipariti tiliaceus* (= *Hibiscus tiliaceus*; Malvaceae), the introduced beach almond *Terminalia catappa* (Combretaceae), and *Plumeria rubra* (Apocynaceae). A few meters inland, the 40 year old regenerating forest is composed of trees such as *Pachira* (= *Bombacopsis* or *Pochota*) *quinata* (Bombacaceae), *Calycophyllum candidissimum* (Rubiaceae), *Cordia collococca* (Boraginaceae), *Hyperbaena tonduzii* (Menispermaceae), *Lonchocarpus felipei* (Fabaceae), *Tabebuia rosea* (Bignoniaceae), *Pseudobombax septenatum* (Bombacaceae), *Sterculia apetala* (Sterculiaceae), and *Bactris major* (Arecaceae). Two of our coastal forest net sites are within a stand of royal palm *Attalea butyracea* (= *Scheelea rostrata*; Arecaceae). The soils here are very sandy and densely occupied by the burrow systems of the land crab *Gecarcinus quadratus* (Gecarcinidae). Hermit crabs (*Coenobita compressus*; Pagaridae) often are so abundant that their nocturnal scratching locomotion can easily be heard over the crash of the nearby surf.

Inland from the coastal strip, the land rises abruptly to a terrace of approximately 70 m elevation. Our inland forest nets were placed over the Quebrada San Miguel and a hiking trail that crosses the stream. Although this location is only a km from our coastal netting station, some of the site characteristics are distinctly different from those along the coast. The ocean cannot be heard from the inland forest netting site, and the density of land crab burrows is much reduced. Some of the tree species are the same as those found closer to the ocean, but inland there are also *Anacardium excelsum* (Anacardiaceae), *Licania arborea* (Chrysobalanaceae), *Manilkara chicle* (Sapotaceae), *Andira inermis* (Papilionaceae), *Brosimum alicastrum* (Moraceae), *Inga vera* (Mimosaceae), and *Luehea seemannii* (Tiliaceae). The understories of both coastal and inland forest have patches of *Piper tuberculatum* and *P. reticulatum* (Piperaceae). Lindquist (2003) and Camacho-Céspedes and Lindquist (in press) provide a broad overview of the trees found in the reserve including descriptions and relative abundances.

The limestone caves (described more fully in the Materials section) are situated in the Refugio de Vida Silvestre Cueva Los Murciélagos, within 200 m of the coast (Fig. 1). It is important to note that continuous forest connects all of the sites where we netted, observed, and handled the bats documented in this paper with the exception of 2 caves. Furthermore, the distances among the sites are within the nightly foraging ranges of most of the species described.

The Bat Fauna

For our results, we use 2 data sets, one of which is a subset of the other. The larger data set includes all of our netting records, cave observations, and incidental observations

Table 1. Bat species inventory for Cabo Blanco, Costa Rica. Total inventory = 39 species. Bats were caught in mist nets (in forest, along coast, or over Quebrada San Miguel), caught by hand (in the caves, in bat tents, and in the dining hall building), observed in limestone caves, observed and photographed in *Attalea* palms, or identified during an Anabat acoustical survey (by Richard K. LaVal, pers. comm.). Some of the forest nets were placed over the upper stretches of the Quebrada San Miguel and some over a hiking trail.

EMBALLONURIDAE

Balantiopteryx plicata (caves; acoustical survey)

Diclidurus albus (seen in *Attalea* along the coast, $N = 1$; acoustical survey)

Peropteryx macrotis (acoustical survey)

Saccopteryx bilineata (caves, flying near central building; acoustical survey)

Saccopteryx leptura (acoustical survey)

MOLOSSIDAE

Eumops (cf. *underwoodi* or *auripendulus*) (acoustical survey)

Molossus ater (acoustical survey)

Molossus molossus (acoustical survey)

Nyctinomops laticaudatus (acoustical survey)

MORMOOPIDAE

Pteronotus parnellii (over stream near mouth, $N = 1$)

NOCTILIONIDAE

Noctilio leporinus (over stream at mouth and over pool in forest; acoustical survey)

PHYLLOSTOMIDAE

Artibeus jamaicensis (coast, forest)

**Artibeus lituratus* (coast only, $N = 5$)

Artibeus phaeotis (coast only, $N = 1$)

**Artibeus watsoni* (coast, forest)

**Carollia castanea* (over stream in forest, $N = 2$)

Carollia perspicillata (coast, forest)

**Choeroniscus godmani* (coast only, $N = 3$)

**Chrotopterus auritus* (coast only, $N = 1$)

Table 1 (continued).

Desmodus rotundus (caves, coast, forest)
Glossophaga soricina (coast, forest)
**Glyphonycteris sylvestris* (forest only, *N* = 1)
Lonchophylla robusta (coast only, *N* = 1)
Lophostoma silvicolum (termite nest in Cabuya sector of Cabo Blanco)
**Micronycteris schmidtorum* (coast only, *N* = 1)
Phyllostomus hastatus (caves, forest)
Platyrrhinus helleri (coast, forest)
Sturnira lilium (coast, forest)
**Sturnira ludovici* (forest only, *N* = 1)
Trachops cirrhosus (forest only, *N* = 8)
Uroderma bilobatum (coast only & roosting under tents in Attalea, *N* = 10 netted)
Vampyrum spectrum (coast only, *N* = 1)

VESPERTILIONIDAE

Eptesicus furinalis (over stream in forest, *N* = 2)
Lasiurus blossevillii (acoustical survey)
Lasiurus ega (forest only, *N* = 5; acoustical survey)
**Myotis elegans* (acoustical survey)
Myotis nigrescens (in dining hall building, coast; acoustical survey)
**Myotis riparius* (forest only, *N* = 2; acoustical survey)
Rhogeessa tumida (coast, forest; acoustical survey)

*First records for Nicoya Peninsula. The determination of new records for the peninsula is based on a combination of criteria including netting records, personal observations, and available range maps.

from 1999 through 2006. The species inventory (Table 1) and the individual species accounts are based on these records. The second data set includes only the netting records from the coastal and inland forest sites during the 4 rainy seasons and 1 dry season for which our times and net placements were standardized. The analyses of netting effort, habitat comparisons, and sex ratios are based on this second data set.

Based on all of our records at Cabo Blanco, we document 39 species of bats belonging to 6 families from 6 years of data (1999–2006) at Reserva Natural Cabo Blanco and adjacent Refugio de Vida Silvestre Cueva Los Murciélagos (Table 1). Twenty-one of the 39 species are in the family Phyllostomidae. Twenty-seven species were captured in mist nets, 5 species of the family Emballonuridae are known from our cave surveys, direct observations, and Anatbat survey, and *Lophostoma silvicolum* from photographs provided by another investigator. Of the 27 species netted, 10 species are known from only 1 or 2 individuals. Species known from a singleton are: *Pteronotus parnellii*, *Artibeus phaeotis*, *Chrotopterus auritus*, *Lonchophylla robusta*, *Micronycteris schmidtorum*, *Sturnira ludovici*, and *Vampyrum spectrum*. Species known only from 2 individuals are: *Carollia castanea*, *Eptesicus furinalis*, and *Myotis riparius*.

In order to determine whether the rare bats were larger than the more commonly caught bats, we compared the masses of 8 of the 9 singleton individuals (excluding *D. albus*, which we never netted) with the mean mass from all the adult individuals of each of the 10 most commonly caught species (from the habitat comparison data set). There was no significant difference in body mass of the rare and the common bats (Mann–Whitney U-test, $U = 37$, $p = 0.82$).

We ran 1,282.75 m-hours of net in the coastal forest and 499.5 m-hours of net inland. The standardized netting sessions yielded 196 bats from 20 species. Our netting efforts along the coast produced a total of 109 bats with a mean of 0.085 bats per m-hour. Our efforts inland produced a total of 87 bats with a mean of 0.174 bats per m-hour (Table 2). Using a binomial test for the total bats/m h of netting in each habitat, the capture rates were significantly higher inland than along the coast ($p < 0.001$).

The most common bats captured in our inland–coast comparison were *Carollia perspicillata* ($N = 49$), *Artibeus jamaicensis* ($N = 43$), and *Glossophaga soricina* ($N = 20$). *C. perspicillata* accounted for 20% of the bats caught along the coast and 31% of the bats from the inland nets. *A. jamaicensis* accounted for 23% of the coast bats and 21% of the inland bats. There were no significant differences in site of capture for *C. perspicillata* or for *A. jamaicensis*, but *G. soricina* was more likely to be caught in the coastal forest

Table 2. Netting effort and number of bats captured per m-hour along the coast and inland for a 4-year period at Reserva Natural Absoluta Cabo Blanco on the Nicoya Peninsula of northwestern Costa Rica.

	Coast			Inland		
	hours	bats	bats per m-hour	hours	bats	bats per m-hour
July 2000	6.25	18	0.069	5.25	18	0.190
Feb. 2001[1]	4.25	6	0.034	3.50	13	0.155
July 2001	6.00	51	0.200	6.00	24	0.174
July 2002	7.50	18	0.080	5.50	25	0.189
July 2003	8.00	16	0.044	2.50	7	0.156
	Summaries					
Total # of m-hours of net	1,282.75			499.5		
Total # of bats	109			87		
Mean # of bats per m-hour	0.085			0.174*		

[1] dry season

*statistically significant difference in capture rates at the two sites using a binomial test (p < .001). We reject the null hypothesis that a captured bat is equally likely to be from a meterhour of netting effort in the inland forest as in the coastal forest.

Table 3. Habitat associations for the eight most commonly netted bats at Reserva Natural Absoluta Cabo Blanco.

Species	N	number caught along coast	number caught inland
Carollia perspicillata	49	22	27
Artibeus jamaicensis	43	25	18
Glossophaga soricina	20	19	1*
Artibeus watsoni	15	7	8
Desmodus rotundus	14	7	7
Rhogeessa tumida	12	4	8
Uroderma bilobatum	10	10	0*
Trachops cirrhosus	8	0	8**

Binomial tests for habitat comparisons $^{*}p < 0.001$, $^{**}p < 0.005$
The three indicated comparisons retain significance at an alpha level of 0.05 after a Bonferroni correction for 8 tests.

(19 of 20 captures, binomial test, $p < 0.001$) (Table 3). *Desmodus rotundus* ($N = 14$), *Artibeus watsoni* ($N = 15$), *Rhogeessa tumida* ($N = 12$), *Uroderma bilobatum* ($N = 10$), and *Trachops cirrhosus* ($N = 8$), also were netted in sufficient numbers to permit analysis of habitat associations—there was no significant difference in site of capture for the first 3 species, but *U. bilobatum* was netted only in the coastal forest (10 captures, binomial test, $p < 0.001$) and *T. cirrhosus* only inland (8 captures, binomial test, $p < 0.005$) (Table 3). Habitat associations for *G. soricina*, *U. bilobatum*, and *T. cirrhosus* retain their statistical significance when a Bonferroni correction for 8 tests is applied. Several other species were caught exclusively at 1 of the 2 sites, but sample sizes are not large enough to permit statistical analysis. *Artibeus lituratus* ($N = 5$) and *Choeroniscus godmani* ($N = 3$) were caught only along the coast and *Lasiurus ega* ($N = 5$) only inland.

The sex ratios indicate a predominance of males among our netted individuals. If we consider the collection of bats from species for which we have 10 or more individuals, we reject the null hypothesis of a balanced sex ratio (two-tailed Fisher's Exact test, $N = 142$, $p = 0.036$). For the 2 species with the most male-biased representation, we also reject the null hypothesis of equal numbers of males and females (binomial test for *Uroderma bilobatum*, $N = 10$, $p = 0.021$ and binomial test for *Artibeus jamaicensis*, $N = 32$, $p = 0.043$).

Species observed in the caves included *Balantiopteryx plicata*, *Saccopteryx bilineata*, *Desmodus rotundus*, and *Phyllostomus hastatus*, all of which are found in the caves year-round (see accounts below). The temperature ranges of all 3 caves are narrow, ranging from approximately 24.0°C near the floor to 26.8°C near the apices.

Sixteen species of bats—*Balantiopteryx plicata*, *Diclidurus albus*, *Peropteryx macrotis*, *Saccopteryx bilineata*, *Saccopteryx leptura*, *Noctilio leporinus*, *Lasiurus blossevillii*, *Lasiurus ega*, *Myotis elegans*, *Myotis nigricans*, *Myotis riparius*, *Rhogeessa tumida*, *Eumops* (cf *underwoodi* or *auripendulus*), *Molossus ater*, *Molossus molossus*, and *Nyctinomops laticaudatus*—were identified by Richard LaVal during his acoustical survey using the Anabat bat-detecting system (LaVal, pers. comm.). Of these, 8 species—*Peropteryx* *macrotis*, *Saccopteryx leptura*, *Lasiurus blossevillii*, *Myotis elegans*, *Eumops* sp., *Molossus ater*, *M. molossus*, and *Nyctinomops laticaudatus*—had not been identified previously with mist netting or our other survey methods. The most commonly recorded bat was *Saccopteryx leptura* followed by *S. bilineata*. This is the southernmost record for *Myotis elegans*.

The following section consists of species accounts for every bat that we recorded (excluding those known only from the acoustic survey) from Cabo Blanco. Each account includes a general species distribution, followed by our observations for Cabo Blanco. Information from the nearby Parque National Palo Verde is included as appropriate.

ORDER CHIROPTERA

Family Emballonuridae (Sac-winged Bats)

Balantiopteryx plicata
Gray Sac-winged Bat

The gray sac-winged bat, one of the few Central American bats that occurs primarily in dry forest, is found from western Mexico, along the Pacific basin of Central America, to the Guanacaste lowlands of northwestern Costa Rica, with an isolated population in western Colombia. This species can be very abundant locally, but has a discontinuous distribution.

Balantiopteryx plicata is common in the caves of Refugio de Vida Silvestre Cueva Los Murciélagos at the entrance of the reserve and almost certainly occurs throughout the reserve. We observed this sac-winged bat in 2 or 3 of the caves on each of our visits to the caves in both the rainy season and dry season. This species was observed in all 3 caves, although it was not present in all caves during each visit, suggesting that movement occurs among caves. When a cave was occupied, the numbers varied from 3 to an estimated 155–165 individuals (seen on 4 February 2001 roosting in cave 2). No seasonal or yearly trend is apparent in abundance patterns. On 8 February 2006, we surveyed another limestone cave on private property just to the north of our 3 study caves and located a colony of 150–160 *B. plicata*. It was the only species observed in the cave. *Balantiopteryx plicata* typically roosts near the entrance of caves in groups of 5–10. We have never observed this species roosting in inner, dark areas of caves. An adult female (fa = 43.1; MNCR 178) was collected on 22 April 1994 by Bernal Rodríguez from the caves Refugio de Vida Silvestre Cueva Los Murciélagos. We regularly observe the gray sac-winged bat roosting at Cueva del Tigre in Parque Nacional Palo Verde, during both the rainy and dry seasons.

Diclidurus albus
Northern Ghost Bat

The northern ghost bat is found from Nayarit, Mexico, to eastern Brazil. *Diclidurus albus* generally is considered a rare species throughout its range. Published records for Costa Rica document it as being widely distributed in lowlands, occurring from sea level to perhaps 1,300 m. Richard LaVal (pers. comm.) recently informed us that ghost bats occur at 2,500 m at San Gerardo de Dota. LaVal has recorded the vocalizations of this species using Anabat software several times in Costa Rica and suggests that it be considered as uncommon but not rare in the country.

We observed a single northern ghost bat at Estación Biológica San Miguel roosting under a frond of the palm *Attalea butyracea* on 4 February 2001. The bat was located ca. 750 m east of the field station roosting ca. 7 m off the ground and hanging from the center of the frond, which was parallel to the ground. This palm was in a grove of mature and immature *Attalea*. We searched this palm grove and others in the vicinity of Estación Biológica San Miguel on subsequent occasions but have never seen another ghost bat.

There is a specimen of *D. albus* in the Museo Nacional de Costa Rica (MNCR 1863) from Playa Montezuma, which is just northeast of the reserve (Rodríguez-H. and Wilson, 1999). We also have observed *D. albus* hanging from a palm frond near the Sirena Biological Station on the Osa Peninsula (Puntarenas Province) and 1 was found in a building at Parque Nacional Palo Verde (Guanacaste Province).

Our observation of *D. albus* at Cabo Blanco and the specimen from Playa Montezuma are the first records for the Nicoya Peninsula, and suggest that this species probably is distributed throughout the peninsula in low numbers.

Saccopteryx bilineata
Greater White-lined Bat

The greater white-lined bat is widespread and occurs from Colima, Mexico, to Brazil. *Saccopteryx bilineata* is common throughout lowland Costa Rica from sea level to 600 m and occurs in both the Pacific and Caribbean lowlands.

Saccopteryx bilineata roosts year-round in the caves of Refugio de Vida Silvestre Cueva Los Murciélagos. We found the greater white-lined bat to use all 3 caves, but it was never found in large numbers in any single cave. Generally, 3–5 *S. bilineata* are seen in each cave. The largest number of individuals observed was 13 on 21 February 2001, when we found 6 individuals in the center cave and 7 in the southernmost cave. *Saccopteryx bilineata* roosts near or at the entrance of caves where it is bright during the day. When both *S. bilineata* and *Balantiopteryx plicata* occur together, *S. bilineata* roosts somewhat interior to *B. plicata*. Both species were observed in all 3 caves, although not necessarily in each cave at each visit, suggesting that movement occurs among caves. *S. bilineata* was present in the largest of the caves (cave 3, the southernmost cave) every time we conducted our cave surveys. We also observed this species roosting along the sides of trees at Cabo Blanco; these colonies are found in dark, shady areas generally several m off the ground, and include 4–5 individuals. At Cabo Blanco, *S. bilineata* can be seen foraging in the clearings beginning a full hour before sunset and in the mornings as late as an hour after sunrise. After extremely heavy rains on the night of 4–5 July 2003, we observed *S. bilineata* foraging throughout the morning hours of 5 July.

Family Mormoopidae (Leaf-chinned Bats)

Pteronotus parnellii
Common Mustached Bat

The common mustached bat is known from Sonora, Mexico, to Brazil across a broad elevation range from sea level up to 3,000 m and in a wide array of habitats. *Pteronotus parnellii* is common and widely distributed in Costa Rican forests (Timm et al., 1989).

A single adult female (fa = 63, 21 g) *P. parnellii* captured at Cabo Blanco in early February 2000 at 2100 h evinced no sign of reproductive activity. The apparent rarity of mustached bats at Cabo Blanco (ca. 0.33% of our captures) is noteworthy given its abundance at others sites in the Pacific lowlands.

Family Noctilionidae (Bulldog or Fishing Bats)

Noctilio leporinus
Greater Bulldog Bat

The greater bulldog bat is known from Sinaloa and Veracruz, Mexico, to Argentina and throughout the Greater and Lesser Antilles. In Costa Rica, *Noctilio leporinus* is locally common along the coasts, estuaries, and lowland rivers where suitable calm water for fishing exists.

We netted *Noctilio leporinus* throughout the year at San Miguel. Bulldog bats fly conspicuously during both the rainy season and dry season at the mouth of Quebrada San Miguel, where the stream flows into the ocean. We capture the greater bulldog bat regularly (both rainy and dry seasons) near the mouth of the stream. During the rainy season, we have not captured fishing bats further upstream; however, in late dry season (11 April 2003) we captured a nonreproductive adult female over the largest of the pools that remained in the Quebrada San Miguel at 2130 h. Two adult females captured near the mouth of the stream on 2 February 2000 had enlarged teats, and 1 captured on 6 February 2006 was near term.

Family Phyllostomidae (Leaf-nosed Bats)

Artibeus jamaicensis
Jamaican Fruit-eating Bat

The Jamaican fruit-eating bat ranges from Sinaloa and Tamaulipas, Mexico, south through northern South America to Brazil and Paraguay. *Artibeus jamaicensis* is perhaps the most abundant bat at lower elevations throughout Costa Rica and Central America and occupies a wide array of habitats from sea level to at least 1,700 m.

Artibeus jamaicensis is abundant at Cabo Blanco. We captured 49 individuals at Cabo Blanco, including 29 males and 14 females during the rainy seasons (combined), when most of our captures occurred. Twenty were captured inland and 23 along the coast suggesting that this species is not restricted to a specific habitat. We netted this species throughout the evening hours from shortly after sunset until midnight. Forearms of adult females range from 54 to 60 ($\bar{x} = 51.8$, $N = 9$); forearms of adult males range from 55 to 69 ($\bar{x} = 62.0$, $N = 21$).

We never caught an obviously pregnant female, but 6 of the 7 females captured during July 2001 had an open, blood-infused vulva, suggesting that breeding was ongoing at that time. Fully scrotal males were netted in the dry season (early February 2000 and 4 February 2001) and during the rainy season (17 and 18 July 2000, 17 July 2001, 22 July 2002, and 2 July 2003). Volant juveniles were captured on 17 July 2001.

Artibeus lituratus
Big Fruit-eating Bat

The big fruit-eating bat ranges from Sinaloa, Mexico, through Central America to Argentina. *Artibeus lituratus* is widespread in Costa Rica (from sea level to perhaps 1,500 m) and often is locally abundant, but less so than *A. jamaicensis* at most sites.

We captured 5 *A. lituratus* at Cabo Blanco, all during the rainy season, and all in the coastal forest. On 17 July 2001, we caught a nonreproductive adult female (fa = 68) at 2215 h. On 18 July 2001, we caught an adult male (fa = 68) at 0010 h with enlarged testes. On 2–3 July 2003, we netted 3 male *A. lituratus*—a subadult male with small testes at 1935 h and 2 moderately scrotal adult males at 2015 h. These are the first records of *A. lituratus* for the Nicoya Peninsula.

Artibeus phaeotis
Pygmy Fruit-eating Bat

Pygmy fruit-eating bats occur from Sinaloa and Veracruz, Mexico, through Central America to Ecuador and Guyana. In Costa Rica, *Artibeus phaeotis* ranges from sea level to 1,200 m, but generally is more common at lower elevations and in wetter parts of the country; it may be uncommon or absent in drier areas.

A single adult male (KU 158312) *A. phaeotis* was netted in the coastal forest near Estación Biológica San Miguel on 18 July 1999 by McClearn and C. M. McCain.

Artibeus watsoni
Thomas's Fruit-eating Bat

Thomas's fruit-eating bat is found from Oaxaca and Veracruz, Mexico, through Central America to Colombia. In Costa Rica, *Artibeus watsoni* occurs from sea level to 1,500 m, but generally is more common at lower elevations and in wetter parts of the country and may be uncommon or absent in drier areas.

Our identification of the small *Artibeus* we captured at Cabo Blanco is based upon the size and shape of the talonid of the first upper molar (M1) and presence or absence of the minute last lower molar (m3). We consider the size and shape of the talonid on M1 the most definitive character for the identification of these 2 similar species. The M1 in *A. watsoni* has a small talonid, whereas in *A. phaeotis* the talonid is large and expanded lingually as illustrated in Timm (1985). The minute m3 is never present in *A. phaeotis*. In *A. watsoni* however, this character is variable; some individuals have this minute molar present on both mandibles, some have it present on 1 mandible and not the other, and some lack it entirely. With a single exception (see previous account), all small *Artibeus* that we examined at Cabo Blanco were clearly identified as *A. watsoni*.

Artibeus watsoni is abundant at Cabo Blanco in the dry seasons of 2000 and 2001 and the rainy season of 2001, but was uncommon during our other netting sessions. Eight were captured inland and 7 along the coast, suggesting that this species is not restricted to a specific habitat. Pregnant females and males with enlarged testes were found only during the dry season. Dry season captures included 7 individuals on 2–6 February 2000. One adult female (1840 h, fa = 39) was pregnant and 2 (2300 h, fa = 38; 0005 h, 37) had no obvious signs of reproductive activity. Two adult males (2309 h, fa = 36; fa = 37) had enlarged testes, 1 (0005 h, fa = 35) had intermediate sized testes, and 1

(2240 h, fa = 37) had small testes. Seven individuals were captured on 4 February 2001, including 2 pregnant females (1900 h, fa = 38; 2230 h, fa = 37), 1 adult female (2010 h, fa = 38) that was not obviously pregnant, 2 adult males (1930 h, fa = 36; 2200 h, fa = 36) with enlarged testes, and 2 subadult males (1850 h, fa = 34; 1930 h, fa = 36; 2050 h, fa = 36) with small testes.

Our few rainy season captures included a fully volant juvenile/subadult male (2215 h, fa = 38) with unfused epiphyses captured on 16 July 2001. On 17 July 2001, we captured 2 adult females (1850 h, fa = 39; 2040 h, fa = 38) that had open vaginal orifices, 1 subadult female (1850 h, fa = 34) that evidenced no sign of reproductive activity, and 1 subadult male (1850 h, fa = 34) with small testes. On 22 July 2002, a nonreproductive adult female (2005 h, fa = 38) was observed. On 4 July 2003, we captured 2 adult females (2015 h, 2145 h), neither of which showed signs of recent reproductive activity.

We located 3 tents of *A. watsoni* in *Sterculia apetala*. One tent was occupied by a single adult female *A. watsoni*. All tents were cut with the J-shaped pattern typical of tents made by *A. watsoni* (Timm, 1987). All were in young 3–4 m *S. apetala*, in leaves that hung parallel to the ground and ca. 2 m high. One plant had 2 tents and a second plant a few meters away had a single tent. Our search for tents of *A. watsoni* then and in all subsequent visits to Cabo Blanco failed to locate additional tents. This is the first record of *A. watsoni* using *S. apetala* for tent construction.

These are the first records of *A. watsoni* from the Nicoya Peninsula.

Carollia castanea
Chestnut Short-tailed Bat

Carollia castanea is found from Honduras to Bolivia. LaVal and Rodríguez-H. (2002) reported that in Costa Rica it is common in lowland wet areas on both sides of the continental divide but is rare in the dry Pacific lowlands. It is most common from sea level to 500 m, but has been captured as high as 1,350 m at Monteverde. In intact lowland wet forests, *C. castanea* is more abundant than its congeners, but it also occurs in second growth habitats.

We captured 2 adult *C. castanea* at Cabo Blanco. We captured an adult male on 11 April 2003 in a net set over an isolated spring-fed water hole in the streambed of the Quebrada San Miguel, and a second adult male (10 g; fa = 42) on 5 July 2003 in a net set over the Quebrada San Miguel while it was in full flow. These are the first records of *C. castanea* for the Nicoya Peninsula.

Carollia perspicillata
Seba's Short-tailed Bat

Seba's short-tailed bat is distributed from Puebla, Mexico, to Paraguay. It is an abundant species throughout Costa Rica and Central America and occurs in a wide array of habitats from sea level to at least 1,000 m.

We captured 54 *Carollia perspicillata* at Cabo Blanco. During our paired netting efforts, 27 were captured inland and 22 along the coast; additional individuals were netted in a variety of habitats. This species is the most abundant bat we captured during the rainy season, but is uncommon during the dry season. Forearms of adult females range from 41 to 45 ($\bar{x}$ = 42.4, N = 22); forearms of adult males range from

40 to 44 ($\bar{x}$ = 42.3, N = 17). We captured this species throughout the evening from shortly after sundown through our final netting for the evening, which generally was after midnight. *Carollia perspicillata* often was one of the earliest species captured each evening. Captures were most abundant from shortly after sundown and dropped off in the late evening.

Reproductive activity occurred in both the dry and rainy seasons. During the dry season, we have evidence for male reproductive activity—5 adult males, all of which were fully scrotal, on 2–6 February 2000 and a single adult male (fa = 40) with enlarged testes on 4 February 2001. Although males had large testes during the dry season, we never caught a female that was obviously pregnant or receptive. During the rainy season, we observed different states of reproductive activity in both males and females. On 17–20, July 2000 short-tailed bats, including a single adult male that was fully scrotal and 5 adult females, none of which was obviously pregnant, were captured. On 16–18 July 2001, we netted 6 adult males, 11 adult females, 3 juvenile males, and 1 juvenile female. Two of the males were fully scrotal, 2 of the females were pregnant, and 8 females had open vulvas. On 20–22 July 2002, we caught 9 males and 8 females; 4 of the males and 2 of the females were judged to be young adults. Of 2 males and 1 female captured on 4–5 July 2003, 1 male was fully scrotal, 1 male was moderately scrotal, and the female evidenced no sign of reproductive activity. An adult female (fa = 42.2; KU 158316) was collected near Estación Biológica San Miguel on 18 July 1999 by McClearn and McCain.

At Cabo Blanco we have not observed the similar appearing *C. subrufa*, a species that makes up a regular, albeit small, percentage of our captures at Palo Verde, nor have we observed *C. sowelli*, which may be abundant at higher elevations in Costa Rica.

Choeroniscus godmani
Godman's Whiskered Bat

Godman's whiskered bat is known from a poorly understood, discontinuous range from Sinaloa, Mexico, to Colombia, Venezuela, and Suriname. In Costa Rica, *Choeroniscus godmani* is found from sea level to 1,500 m, but is seldom encountered and little is known of its biology.

We captured this nectar-feeding bat on 3 occasions at Cabo Blanco, all along the coast and during the rainy season. A pregnant adult female (fa = 37.6) was captured on 17 July 2000 at 1830 h. Two females, which showed no recent reproductive activity, were captured on 22 July 2002, 1 adult (fa = 37) at 1830 h and 1 young adult (fa = 37) at 2145 h. These are the first records of *C. godmani* from the Nicoya Peninsula.

Chrotopterus auritus
Woolly False Vampire Bat

The woolly false vampire bat occurs from the southern Mexican states of Oaxaca and Veracruz through Central America to the Guianas, across northern and southern Brazil and eastern Peru, to northern Argentina. Although *Chrotopterus auritus* is widely distributed, few specimens of this species exist and little is known of its distribution and biology. As with all of the predaceous phyllostomids, this species generally is considered to be highly vulnerable to human disturbance.

We netted a single adult male *C. auritus* (fa = 84) in the coastal forest on 17 July 2001 at 2235 h. Although the woolly false vampire bat is a cave-roosting species, we have not observed it in Refugio de Vida Silvestre Cueva Los Murciélagos. The adult male is the first observation of the species on the Nicoya Peninsula and this record is especially noteworthy because forests in the reserve and throughout the Nicoya Peninsula have been heavily impacted by clearing for agriculture.

We regularly observe a small colony of *C. auritus* roosting in Cueva del Tigre in Parque Nacional Palo Verde during both the rainy season and dry season. These bats roost high in the cave, and the individuals cluster tightly together. We have found beetle elytra and cockroach (*Blaberus giganteus*) wings beneath these diurnal roosts.

Desmodus rotundus
Common Vampire Bat, Vampiro

The common vampire bat occurs from Sonora and Tamaulipas, Mexico, to Argentina. In Costa Rica, *Desmodus rotundus* is found from sea level to 2,700 m, and may be locally abundant, especially where there are cattle. However, vampires are uncommon or rare in larger blocks of intact forest where domesticated livestock are not present.

Desmodus rotundus is common at Cabo Blanco, and we captured this species during nearly every netting session. Twelve individuals were captured on the nights of 16–17 July 2001 in our nets in the reserve, although other netting efforts took smaller numbers. In the caves at Refugio de Vida Silvestre Cueva Los Murciélagos, we observed colonies of *D. rotundus* each time we visited, documenting that they are residents in the caves throughout the year. All 3 caves contained roosting colonies of vampires on most, but not all of our visits. The northernmost cave generally had the largest population, estimated at 20–25 individuals in February 2001 and 100 in July 2001, and was occupied each time we visited. Smaller numbers, ranging from just a few to 30, were found in the other 2 caves. Adult females with nonvolant young were observed in early and mid-February, mid-April, and early and mid-July in different years. Young vampires of different ages were seen with the adults during both the rainy season and dry season, documenting that reproduction occurs year-round. We attribute the seasonal and yearly differences in numbers of vampires in the caves to movement among the caves, and perhaps to movement to other caves in the region. The temperature ranges of roosting sites ranged from 25.4 to 26.2°C and vampires are found in dark areas, both in crevices and on flat expanses of walls.

The caves are located between the reserve and the community of Malpaís. We suspect that vampires here feed primarily on cattle from the adjacent farms, and we were told that vampires frequently do feed on cattle in the area. In the reserve, we netted *D. rotundus* early in the evening along the coast as they were heading towards the ocean. It is possible that these individuals feed on roosting sea birds on nearby Isla Cabo Blanco.

Within the reserve at Cabo Blanco, we captured an adult female (2250 h, fa = 62) in early February 2000 that was not obviously pregnant. On the nights of 16 and 17 July 2001, we captured 12 individuals including 11 adults and 1 juvenile. Adult females included 3 (1940 h, fa = 62; 2050 h, fa = 63; 2132 h, fa = 60) with an open blood-infused vulva and 1 (1930 h, fa = 59) that was not reproductively active. Adult males captured include 3 (1940 h, fa = 58; 2130 h, fa = 58; 2140 h, fa = 59) that were moderately scrotal and 2 (1940 h, fa = 58; 2314 h, fa = 58) that had small testes.

Glossophaga soricina
Common Long-tongued Bat

The common long-tongued bat is distributed from Sonora, Mexico, to northern Argentina. In Costa Rica, *Glossophaga soricina* occurs from sea level to 1,500 m. It is an abundant species throughout Central America, especially in disturbed habitats.

Glossophaga soricina is a common species at Cabo Blanco during the rainy season and along the coast; 19 of 20 *G. soricina* were caught along the coast. The ratio of 18 sexed animals was heavily biased toward males—14 adult males and 4 adult females. Our captures were distributed throughout the evening hours until 2330 h. Forearms of adult females ranged from 36 to 38 ($\bar{x}$ = 37.0, *N* = 4); forearms of adult males ranged from 35 to 38 ($\bar{x}$ = 36.3, *N* = 14).

Our evidence indicates that males may have enlarged testes during both the rainy and dry seasons, but we only captured pregnant females in the dry season. In early February 2000, 3 adult females were captured; 2 were pregnant (1910 h, 1935 h) and 1 not obviously pregnant (2000 h). On 3 February 2001, 1 scrotal adult male (1855 h) was captured. During the rainy season, when we had most of our *G. soricina* captures, scrotal males were observed but no female was obviously pregnant. On 17 July 2000, we captured 10 adults, 4 females and 6 males—none of the females (1910 h, 2305 h, 2325 h, 0014 h) were obviously pregnant, 5 males (1845 h, 1840 h, 1840 h, 1903 h, 2225 h) were fully scrotal and 1 (2100 h) had small testes. On 17 July 2001, we captured 1 adult female (1945 h) with no evidence of reproductive activity and 4 males, 2 fully scrotal adults (1850 h, 1915 h) and 1 juvenile male (1850 h) with small testes. On 4 July 2003, an adult male (1840 h) was captured with small testes.

A single specimen of *G. soricina* from nearby Tambor is in the collection at the University of Michigan (UMMZ 65096).

Glyphonycteris sylvestris
Tricolored Bat

The tricolored bat ranges from Nayarit and Veracruz, Mexico, south to Peru and southeastern Brazil, and is primarily a low elevation species (below 800 m). It is rare throughout this broad geographic range. We follow recent phylogenetic studies that refer this species to *Glyphonycteris* rather than *Micronycteris* (as it has been treated historically) because the traditionally recognized genus was paraphyletic (Wetterer et al., 2000). LaVal and Rodríguez-H. (2002) reported that this species is uncommon in the Guanacaste and northern Caribbean lowlands of Costa Rica. We caught a single adult male *G. sylvestris* (fa = 39) at 1900 h on 20 July 2002 in a net set across the Quebrada San Miguel in the inland forest at Estación Biológica San Miguel.

Lonchophylla robusta
Panama Long-tongued Bat

The Panama long-tongued bat is an uncommon species that occurs from southeastern Nicaragua to Peru and Venezuela. In Costa Rica, *Lonchophylla robusta* is known from only a few localities from sea level to 1,000–1,500 m (LaVal and Rodríguez-H., 2002).

We caught a single adult female *L. robusta* (fa = 39) at Cabo Blanco along the coast at 1840 on 16 July 2000. She was not obviously pregnant. This is the first record of this species for the Nicoya Peninsula.

Lophostoma silvicolum
White-throated Round-eared Bat

The white-throated round-eared bat is an uncommon species found in lowland forests from southern Honduras to Bolivia and northeastern Argentina. *Lophostoma silvicolum* has been observed in Costa Rica only a few times; it is known from both the Caribbean and Pacific lowlands at elevations below 500 m.

Two *L. silvicolum* were observed roosting in a cavity in an arboreal termite nest in the eastern sector of Reserva Natural Absoluta Cabo Blanco in July 2002. Alex Mordas observed and photographed the round-eared bats roosting in a cavity that ran along the length of the nest and perpendicular to the ground. Although the bats were not handled at the time, we are confident that they were *L. silvicolum* based on our study of the photographs. We identified the bat as *L. silvicolum* rather than *L. brasiliense* or *Tonatia saurophila* because of the very large, rounded ears that are joined at the base and haired at the inner edge; the overall gray coloration dorsally and the sharp contrast between the darker dorsal coloration and the white fur of the ventral neck region; the long, somewhat woolly fur; the pale stripe between the eyes; and the lightly haired face with a small noseleaf. We follow a recent molecular systematics revision of the genus *Tonatia* in treating the genus as paraphyletic with a distinct lineage referable to *Lophostoma*, which includes the species *L. brasiliense*, *L. carrikeri*, *L. evotis*, *L. schulzi*, and *L. silvicolum* (Lee et al., 2002).

Termites of the genus *Nasutitermes* (Isoptera: Termitidae) are moderately common at Cabo Blanco and make characteristic nests from 1 to several meters off the ground on the trunks of trees. During each of our visits to the western sector, we searched termite nests for excavated cavities and roosting bats, but with no success.

Three species of *Lophostoma* (*L. brasiliense*, *L. carrikeri*, and *T. silvicolum*) are known to use these large, waterproof termitaria as diurnal roosting sites (Kalko et al., 1999). *L. silvicolum* was expected to occur on the Nicoya Peninsula, although there are no previous records.

Micronycteris schmidtorum
Schmidt's Big-eared Bat

Schmidt's big-eared bat is found from southeastern Mexico through Central America to northeastern Brazil and Peru. *Micronycteris schmidtorum*, a rare and poorly known phyllostomine throughout its range, is known from Costa Rica by only a few specimens. The few captures of this species are all from the lowlands and include both the Pacific and Caribbean coasts.

An adult male (7.5 g; fa = 34.0; KU 158317) was collected in the coastal forest on 18 July 1999 by McClearn and McCain. This is the first record of *M. schmidtorum* from the Nicoya Peninsula.

Phyllostomus hastatus
Greater Spear-nosed Bat

The greater spear-nosed bat occurs from Belize and Honduras to Brazil and northern Argentina. *Phyllostomus hastatus* is the most abundant of the large, carnivorous bats in Central America and in Costa Rica is found from sea level to 1,000 m.

We found colonies of spear-nosed bats roosting in the southernmost cave (cave 3) at Refugio de Vida Silvestre Cueva Los Murciélagos on each of our 8 visits there, during both the rainy season and dry season. The colony size was estimated at > 70 individuals on 2 occasions (1 dry season and 1 rainy season) and at 35–40 on 2 occasions (rainy season). This is the darkest of the caves and has the largest, most topographically complex ceiling. It is the only cave to consistently have a colony of spear-nosed bats. The spear-nosed bats most frequently hung in extremely tight clusters from the ceiling where it was generally 4 m high or higher. The bats tended to roost in avons (a small eroded pocket in the ceiling of a cave) or other cavities in the ceiling. On some of our visits we also observed individuals roosting singly. A small colony of *P. hastatus* (5–10 individuals) was observed in cave 1 on 2 occasions.

We captured a single adult female in a net set in the inland forest on 20 July 2000. She was not obviously pregnant. On 23 July 2002, Timm watched an adult hanging from the ceiling of cave 3 capture and consume an adult *Polistes erythrocephalus* (Hymenoptera: Vespidae). The bat was hanging adjacent to an occupied wasp nest when first seen. The bat grabbed the wasp from the surface of the nest with its teeth and quickly chewed and consumed the insect.

A volant subadult male *Phyllostomus hastatus* (fa = 85, 84 g; MNCR 175) was collected at Cabo Blanco on 21 April 1994 by Bernal Rodríguez.

Platyrrhinus helleri
Heller's Broad-nosed Bat

Heller's broad-nosed bat occurs from Oaxaca and Veracruz, Mexico, to central Brazil. In Costa Rica, *Platyrrhinus helleri* is a lowland species found on both coasts from sea level to perhaps 1,500 m and generally is not an abundant species.

On 5 July 2003, we caught 4 adult *P. helleri*, 2 males and 2 females, in the inland forest in a net set over the Quebrada San Miguel. Neither of the females was obviously pregnant or showed any other evidence of recent reproductive activity. The males were not obviously scrotal. No other *P. helleri* were captured during our rainy season–dry season comparisons. On 11 April 2003 in the late dry season, we captured 15 adults in one-half hour in 2 nets set over isolated pools in the Quebrada San Miguel. This was the most abundant species we captured that evening. Richard LaVal informed us that he captured and released an adult female carrying a near-term embryo in late February 2005 in a net set over the Quebrada San Miguel near the field station. *Platyrrhinus helleri* was reported previously from Cabo Blanco by Rodríguez-H. and Wilson (1999) on the basis of a young adult female (fa = 38.4, 13 g; MNCR 169) collected on 19 April 1994.

Sturnira lilium
Yellow-shouldered Bat

The yellow-shouldered bat is known from Sonora and Tamaulipas, Mexico, to Argentina. *Sturnira lilium* is widespread through Costa Rica's lowlands and has been taken as high as 1,500 m. This species usually is more abundant in dry forest than in wet forest, and often is one of the most commonly captured species at a site. The similarity between this and related members of the genus (including at least 1 undescribed species; Timm unpubl.) from the southern Pacific region of Costa Rica makes accurate determination of species ranges problematic (Timm and Rodríguez, in prep.).

Over 3 rainy seasons, we captured 8 adult *S. lilium* at Cabo Blanco—4 inland and 4 along the coast. Our data suggest reproduction in early but not late July; since these records are not all from the same year, however, this pattern is merely suggestive. Two pregnant females were netted on 5 July 2003, 1 at 1833 h (fa = 37) and 1 at 1850 h (fa = 39), and a third female (fa = 37) at 1927 h had enlarged teats and was lactating. On 17 July 2001, an adult female (fa = 39) had an open pubic symphysis. Females with no apparent recent reproductive activity were caught on 17 July 2000 (fa = 37) at 1934 h and on 20 July at 1845 (fa = 37) and 2315 (fa = 41). On 18 July 2000 (fa = 39) at 1905 h, a nonscrotal adult male was captured over Quebrada San Miguel. An adult male *S. lilium* (MNCR 164) was collected at Cabo Blanco on 18 April 1994 by Bernal Rodríguez.

Sturnira ludovici
Highland Yellow-shouldered Bat

The highland yellow-shouldered bat is widely distributed from Sinaloa and Tamaulipas, Mexico, to Peru and Bolivia. This species occurs from sea level to high elevations in Costa Rica, but is most common at middle elevations.

We captured a single young adult male (fa = 39) *Sturnira ludovici* at Cabo Blanco on 20 July 2002 at 2110 h in the inland forest. This male had nearly fused wing epiphyses and sharp, unworn teeth. He did not have enlarged testes. This is the first record of *S. ludovici* for the Nicoya Peninsula.

Trachops cirrhosus
Fringe-lipped Bat

The fringe-lipped or frog-eating bat is found from Oaxaca and Veracruz, Mexico, to Brazil. *Trachops cirrhosus* is found throughout Costa Rica from sea level to 1,550 m.

At Cabo Blanco, we caught fringe-lipped bats regularly in nets set across the trail at our inland site and around isolated pools in Quebrada San Miguel during the dry season. We have never taken this species in nets across the stream during the rainy season when it was flowing or along the coast. A net set across a trail on the inland ridge captured *T. cirrhosus* each time we netted there during both the rainy season and dry season over the 4-year period. One pregnant adult female (fa = 59) was captured on 16 July 2001 at 1945 h. Two adult females handled on 18 July 2000 at 1850 h (fa = 58) and at 2210 h (fa = 61) and on 4 February 2001 at 1915 h (fa = 59) evidenced no obvious signs of reproductive activity. Three adult males captured included 1 that was fully scrotal on 18 July 2000 at 2050 h (fa = 59), 1 that was moderately scrotal on 16 July 2001 at 1945 h (fa = 57), and 1 with small testes on 4 February at 1915 h (fa = 58).

On 11 April 2003, we found a number of fringe-lipped bats actively circling over the Quebrada San Miguel beginning an hour after sunset. The streambed was dry except for isolated pools. When frogs (*Eleutherodactylus*) began calling well after sundown, the fringe-lipped bats became active, swooping back and forth in the region where the male frogs called.

Uroderma bilobatum
Common Tent-making Bat

The common tent-making bat is found from Oaxaca and Veracruz, Mexico, to Brazil. *Uroderma bilobatum* occurs in a wide array of habitats ranging from primary humid and dry forests to second-growth and pastureland. This is a common species in Costa Rica and is found from sea level to 1,200 m.

As the common name implies, *U. bilobatum* constructs roosts by modifying large leaves to form a tent for use as diurnal roosts and maternity sites. At Cabo Blanco, tents of *U. bilobatum* are abundant in the palm *Attalea butyracea* and were found in this palm during each of our visits. *Uroderma bilobatum* makes an elongate inverted V-shaped tent in *A. butyracea* by cutting the leaflets extending out from the midrib in a manner similar to that described for other species of pinnately compound-leafed palms (Timm, 1987; Timm and Lewis, 1991). This bat has a harem mating system with roosting groups including a single adult breeding male, a number of adult females, and their associated young. During each of the rainy seasons, we found several groups of *U. bilobatum* roosting under the tents and other individuals roosting singly. These clusters included lactating females with young and males with enlarged testes. During the dry season, we only observed *U. bilobatum* roosting singly and very few (1–3) bats were present under the tents in any year. We found tents of *U. bilobatum* only in *A. butyracea* at Cabo Blanco despite the wide array of plant species known to be used by this species for tents in other areas.

Based on tent surveys and netting data, both males and females are abundant at Cabo Blanco along the coast during the rainy season. Both sexes are far less abundant during the dry season. No tents were located away from the coast and we never netted this species away from the coast. Rainy season captures during our habitat surveys consisted of 6 adult males and 1 female. Of 2 adult males from 17 July 2000, 1 (1845 h, fa = 39) was fully scrotal and 1 (1945 h, fa = 43) was moderately scrotal. On 17 July 2001, we captured a single adult male (fa = 40) at 1915 h. On 22 July 2002, we captured 2 adult males (1830 h, fa = 46; 2105 h, fa = 42). On 5 July 2003 a moderately scrotal adult male was netted at 1945 h. The single female we netting was a nonreproductive adult on 5 July 2003 (fa = 42). Our dry season records include 3 adult males (1840 h, fa = 41; 1850 h, fa = 44 h; 2225 h, fa = 44), all with enlarged testes, and a single adult female (1850 h, fa = 43) that was not reproductively active on 3 February 2001.

Vampyrum spectrum
Great False Vampire Bat

The false vampire bat ranges from Veracruz, Mexico, to southwestern Brazil. In Central America, the species is found from sea level to at least 1,650 m (Reid, 1997). *Vampyrum spectrum* is a rare bat throughout its range and also is rare in Costa Rica, where it is known from only a few localities.

We captured a single young adult female *V. spectrum* (fa = 104) in the coastal forest at 0010 h on 17 July 2001. Her teats were minute and the vaginal orifice small and lacking pigment or other evidence of reproductive activity and we judged her to be nulliparous. This large predaceous bat flew into a net within 0.5 m of where we were extracting a distressed and vocalizing *Artibeus*. This is the first record of *V. spectrum* from the Nicoya Peninsula.

Family Vespertilionidae (Evening Bats)

Eptesicus furinalis
Argentine Brown Bat

The Argentine brown bat ranges from Jalisco and Tamaulipas, Mexico, south to Argentina. *Eptesicus furinalis* occurs in a wide range of environmental conditions from sea level to middle elevations, although it is not common in Costa Rica.

We captured 2 *E. furinalis* at Cabo Blanco; both were netted over the Quebrada San Miguel. An adult female (fa = 41) was caught in the inland forest on 18 July 2000 at 2005 h. She was not obviously pregnant. An adult male (7 g) was taken on 5 July 2003.

Lasiurus ega
Southern Yellow Bat

The southern yellow bat is found from southeastern Texas and adjacent Mexico to Argentina. This species has an enormous geographic range and occurs in a wide variety of habitats ranging from rainforest to xeric desert scrub. In Costa Rica, *Lasiurus ega* occurs from sea level to montane habitats, but it is not an abundant bat.

We observed *L. ega* on 5 separate occasions at Cabo Blanco during both the rainy season and dry season. Rainy season captures include an adult male (fa = 48) on 16 July 2001 at 2235 h and an adult female (fa = 48) on 20 July 2002 at 2045 h. During the dry season, we captured an adult female (fa = 48) in early February 2000 at 2020 h and another (fa = 42) in early February 2001. None of the females had evidence of recent reproductive activity, and none of the males had obviously enlarged testes. Most were netted over the Quebrada San Miguel. All were captured inland.

Richard LaVal (pers. comm.) informed us that he also has netted *L. ega* at Cabo Blanco. These are the first records of *L. ega* for the Nicoya Peninsula.

Myotis nigricens
Black Myotis

The black myotis is distributed from Tamaulipas, Mexico, to Argentina. It often is an abundant species roosting in buildings throughout Central America. In Costa Rica, *Myotis nigricans* is found from sea level to more than 3,000 m.

Individuals of *M. nigricens* regularly roost in the buildings of Estación Biológica San Miguel both in the rainy and dry seasons. We observed black myotis roosting only as single individuals, and in all cases an individual was seen tightly wedged in a small space between the ceiling planks or between the screens and the ceiling or walls. All bats were located close to the ceiling. *Myotis nigricens* is the only species of bat we saw roosting in the buildings at Cabo Blanco. This species was reported previously from Cabo Blanco by Rodríguez-H. and Wilson (1999) based upon an adult male (fa = 34.5, 3 g; MNCR 184) collected in the San Miguel Sector on 20 April 1994.

Myotis riparius
Riparian Myotis

The riparian myotis is known to occur from Honduras to Uruguay. It occupies a wide elevational range and wide array of habitats including both forested and savannah regions. In Costa Rica, *Myotis riparius* is known from sea level to at least 2,000 m (LaVal and Rodríguez-H., 2002).

We obtained *M. riparius* during both the rainy and dry seasons. An adult female (fa = 34) was captured on 18 July 2000 at 1835 h, and during the dry season, an adult female (fa = 33) was captured in early February 2000 at 2040 h. Neither female evinced sign of reproductive activity. These are the first records of *M. riparius* for the Nicoya Peninsula.

Rhogeessa tumida
Central American Yellow Bat

Rhogeessa tumida is the name applied previously to yellow bats occurring from eastern Mexico to northern South America; however, recent cytogenetic studies demonstrate that the genus is more speciose than previously believed and several biological species are represented in this broad geographic range. Genoways and Baker (1996) suggested that 10 species be recognized in the genus, with 2 (*R. tumida* and *R. io*) occurring in Costa Rica and Nicaragua. They considered the populations in Costa Rica's northwestern Pacific lowlands to be *R. tumida* and the species that occurs in the Caribbean lowlands and on the Osa Peninsula to be *R. io*, although they lacked specimens from those regions for cytogenetic studies. When studying specimens from Costa Rica, Timm and LaVal (1998) found *R. tumida* to be significantly smaller in size and lighter in color than *R. io*, and suggested that all *Rhogeessa* in the northwestern lowlands would be *R. tumida*. Based on forearm measurements, which range from 29 to 34 mm, and their lighter color, we assign the yellow bats of the southern Nicoya Peninsula to *R. tumida*. LaVal and Rodríguez-H. (2002) considered *R. tumida* to be an uncommon lowland species in the dry forests of Guanacaste, where it occurs up to 850 m. Timm et al. (1999) provided a more detailed review of the taxonomic history of Costa Rican *Rhogeessa*.

The yellow bat is encountered regularly at Cabo Blanco, especially in nets set over the Quebrada San Miguel, although not in high numbers. *Rhogeessa tumida* is one of the earliest bats caught in the evening. Eight were captured inland and 4 along the coast; in light of the fact that we had half the netting effort inland as along the coast, these observations suggest that this species is more abundant inland than along the coast. Most were captured in nets set over the stream. Adult females were captured on 18 July 2000 at 1855 h (fa = 29), 3 February 2001 at 1819 h (fa = 31), 16 July 2001 at 1813 h (fa = 30), 16 July 2001 at 1830 h (fa = 29), and 17 July 2001 at 2145 h (fa = 33). Adult males were captured on 18 July 2000 at 2145 h (fa = 34), 16 July 2001 at 1830 h (fa = 30), 20 July 2002 at 2305 h (fa = 30), 4 July 2003 at 1820 h (fa = 31), and 5 July 2003 at 1838 h (fa = 29). None of the females were obviously pregnant or had enlarged nipples. One male captured on 18 July had enlarged testes, and 1 captured on 5 July had moderately enlarged testes.

The only previous records of *R. tumida* from the Nicoya Peninsula are a single adult female (MNCR 183) collected at Cabo Blanco by Bernal Rodríguez and 2 specimens from Sámara (Guanacaste Province) reported by LaVal (1973).

DISCUSSION

For more than 4 decades, Reserva Natural Absoluta Cabo Blanco at the southern tip of the Nicoya Peninsula has been safeguarded from logging, hunting, and agricultural uses. Because human impact has been minimized here in recent years, wildlife has been protected and the forest is regenerating rapidly. Several mid-sized mammals that are uncommon in many areas of Central America are now common at Cabo Blanco. For example, white-faced capuchins (*Cebus capucinus*), tamandua anteaters (*Tamandua mexicana*), and white-nosed coatis (*Nasua narica*) are especially abundant in the reserve, and can be seen on a daily basis. Some poaching of game species does occur, however, as it does throughout the country, and we found the carcasses of 2 white-tailed deer (*Odocoileus virginianus*) that had been shot.

Our bat-netting efforts at Cabo Blanco over a 6-year period were designed as two-day field projects for graduate level tropical ecology courses run by the Organization for Tropical Studies. We present our observations in the species accounts above regarding reproduction and other aspects of natural history. Our data provide several first-capture records for the Nicoya Peninsula and have implications for forest and bat conservation as outlined below. Our capture data are heavily weighted toward the rainy season and our statements about seasonal patterns of bat abundance and reproduction must be considered preliminary. We make several statements regarding microhabitat differences of the bats at Cabo Blanco (in terms of how many bats are caught in a standard unit of netting effort and with regard to which bats are found where), but a more intensive study clearly is needed.

Diversity.—In 16 full evenings of netting, several partial evenings of netting, several cave surveys, targeted search and netting events, and an acoustical survey over 6 years, we identified 39 species of bats representing 6 families as occurring at Cabo Blanco. Phyllostomids accounted for 21 of the 39 species recorded. This dominance of phyllostomids is typical of Neotropical bat communities from Mexico to Paraguay with the total number of species depending on factors such as netting effort (Stevens et al., 2004; Stoner, 2005), size and heterogeneity of the sampling area (Moreno and Halffter, 2000; Gorresen and Willig, 2004), the variety of techniques used to capture bats (Voss and Emmons, 1996), and the latitude of the site (Stevens, 2004). Our survey efforts have not resulted in a complete bat inventory. We did achieve the 18 nights of netting that Moreno and Halffter (2000) considered adequate for identifying approximately 90% of the nettable bat species in a heterogeneous habitat in Mexico, but we are short of the 1,000 captures recommended by Bergallo et al. (2003) for a complete inventory. A concerted year-round bat community study using a variety of techniques would certainly increase the number of bats identified from this region of the Nicoya Peninsula. We expect that additional species of *Pteronotus* and molossids will be found in the reserve. Timm and W. Pineda (unpubl.) document that molossids are more common and widely distributed in Costa Rica's dry forest than had been previously believed. Of the species recorded, two-thirds (27 of 39) were captured in mist nets and one-third (N = 13) were detected only by other methods. Clearly mist nets are only one of the techniques that should be used in assessing the diversity of bats in the Neotropics.

Singletons.—Nine of the 27 (33.3%) species caught in mist-nets are known from only 1 individual and 3 others from only 2 captures. The rare species in the Cabo Blanco bat community are not larger in mass than the most common species. Although *Vampyrum spectrum* and *Chrotopterus auritus* (only 1 individual netted of each species) are the largest bats in the Neotropics, 3 other singletons were among the 4 smallest bats from the full assemblage, and 2 were mid-sized. This result agrees with a multi-site analysis of Neotropical bat communities (Arita, 1993), but goes against the general mammalian trend for large animals to have smaller population sizes.

Species known from a single individual in biodiversity inventories have several potential roles. Very low local abundance is a component of rarity and, as such, a possible criterion for identification of an endangered species (Arita, 1993). The addition of new rare species over time also could signal a shift in species' ranges and/or gradual climate change. Medellín et al. (2000) considered a large number of singletons in a bat inventory to be a sign of undisturbed forest. For hyperdiverse groups, the supply of singletons may be virtually limitless (i.e., lowland Neotropical ants—Longino and Colwell, 1997; Amazonian spiders—Silva and Coddington, 1996), but one would expect that with less diverse groups such as bats an increase in sampling effort would lead to a reduction in the number of species represented by a lone individual. It is interesting to note that after 56 nights of netting over 3 years at Parque Nacional Palo Verde, 17 of 47 (36%) species of bats were still known from only a single individual (Stoner and Timm, 2004).

Bat Inventories as an Indication of Habitat Disturbance.—The animalivorous bat fauna of Cabo Blanco is of particular interest in that the 3 largest carnivores in the Neotropics (*Chrotopterus auritus*, *Phyllostomus hastatus*, and *Vampyrum spectrum*) are present as are 2 other large predators, *Noctilio leporinus* and *Trachops cirrhosus*. Three of these species are abundant (*N. leporinus*, *P. hastatus*, and *T. cirrhosus*) and 2 are rare (*C. auritus* and *V. spectrum*; both known only by single captures). However, the small and middle-sized predatory bats are poorly represented. We have single observations of *Glyphonycteris sylvestris*, *Micronycteris schmidtorum*, and *Lophostoma silvicolum*), and other small and middle-sized species could be expected to occur in the region.

A number of authors propose using characteristics of a Neotropical bat community (or the phyllostomid subsection of the community) as correlates of the level of habitat disturbance. Indicators of minimal disturbance include the presence of phyllostomines (animalivorous bats) (Fenton et al., 1992; Timm, 1994; Patterson et al., 2003; Gorresen and Willig, 2004), the presence of more large than small fruit eaters (Schulze et al., 2000), and the proportion of rare species (Medellín et al., 2000). Indicators of considerable habitat disturbance include the dominance of 1 particular species (> 34% of total captures) (Medellín et al., 2000) and the prevalence of *Sturnira lilium* and *Carollia perspicillata* (Schulze et al., 2000) and *Desmodus rotundus* (Wilson et al., 1996). It is important to note that these studies were conducted in different sites widely scattered in the Neotropics (Costa Rica, Guatemala, Mexico, Paraguay, Peru) and the disturbed areas vary from forest fragments to cacao plantations to regenerating secondary forest. By these criteria, Reserva Natural Absoluta Cabo Blanco has characteristics of both a relatively undisturbed habitat and of a disturbed habitat. In the former category are: several species of phyllostomines, few *Sturnira lilium*, a substantial number of large frugivores (*Artibeus jamaicensis*), and several rare species. Possible indicators of habitat disturbance include large numbers of *Carollia perspicillata* and the moderate abundance of *Desmodus rotundus*. The dominance of *C. perspicillata* (31% of captures) in the coastal forest is an equivocal indicator.

Watt (1998), on the other hand, provided a critique of indirect measures to assess whether a forest is disturbed or not and suggested that research should focus on the type and severity of habitat disturbance rather than species-abundance models. He argued that direct ways of assessing forest disturbance such as visual evidence and local records of logging history are simpler, faster, more reliable, and free of assumptions about the impact of disturbance. Additionally, species-abundance models provide no quantitative measure of the degree of forest disturbance. By these criteria, we would consider the reserve a regenerating, non-fragmented landscape with pockets of old-growth forest.

Netting Effort.—We captured approximately twice as many bats per meter-hour of net inland (0.174 bats per m-hour of net) as we did along the coast (0.085 bats per m-hour of net). Most of these netting sessions were during the rainy season. We found that we caught so few bats along the coast during the dry season that we could not fashion a tenable field problem to keep students occupied. Our impressions that there were many fewer bats in the coastal forest during the dry season than during the rainy season therefore remain subjective. Dry season captures inland were extremely high when our nets were placed over isolated pools in the Quebrada San Miguel streambed. In the late dry season (April 2004), for example, we captured more than 50 bats in a 45-min period in 2 nets set over 1 large pool and a nearby small pool.

If we multiply our capture rates by 12 to evaluate capture rates in terms of captures per hour per 12 m net, we can compare our net success with values obtained by other workers. We caught approximately 1.02 bats per 12 m net-hour along the coast and 2.09 bats per 12 m net-hour in the inland forest. Elsewhere in Costa Rica, LaVal (2004a, 2004b) reported capture rates for wet forest at La Selva (1.05 bats per net-hour), 2 cloud forest habitats at Monteverde (0.94 in primary cloud forest, 1.65 in secondary cloud forest), and in dry forest at Santa Rosa (1.41 bats per 12 m net; from Fleming, 1988). Fenton et al. (1992) captured 0.2 to 2.2 bats per 12 m net per hour in various undisturbed forest habitats in Akumal, Mexico. Our capture rates in the inland forest are among the highest of all these rates. However, these comparisons should be taken only as approximations because a 12–m net will rarely, if ever, capture twice as many bats as a 6-m net, particularly if nets are set across narrow flyways.

Anabat Acoustical Survey.—In late February 2005 Richard K. LaVal conducted a 4-night acoustical survey near the Estación Biológica San Miguel using the Anabat bat-detecting system to detect and identify ultrasonic signals from free-flying bats. Based on their echolocation signatures, he identified the following 16 species of bats: *Balantiopteryx plicata*, *Diclidurus albus*, *Peropteryx macrotis*, *Saccopteryx bilineata*, *Saccopteryx leptura*, *Noctilio leporinus*, *Lasiurus blossevillii*, *Lasiurus ega*, *Myotis elegans*, *Myotis nigricans*, *Myotis riparius*, *Rhogeessa tumida*, *Eumops* (cf *underwoodi* or *auripendulus*), *Molossus* *ater*, *Molossus molossus*, and *Nyctinomops laticaudatus* (LaVal, pers. comm.). Of these, 8 species—*Peropteryx macrotis*, *Saccopteryx leptura*, *Lasiurus blossevillii*, *Myotis elegans*, *Eumops* sp., *Molossus ater*, *M. molossus*, and *Nyctinomops laticaudatus*—were not taken in mist nets by us on any other occasion. The most commonly recorded bat was *Saccopteryx leptura* followed by *S. bilineata*. This is the southernmost record for *Myotis elegans*.

Microhabitat Associations of Bats.—Habitat segregation exists even over the relatively short distance (less than 1 km) between our coastal and inland forest sites. *Glossophaga soricina* and *Uroderma bilobatum* were netted along the coast, whereas *Trachops cirrhosus* was netted only inland. Six species—*Artibeus jamaicensis*, *A. watsoni*, *Carollia perspicillata*, *Desmodus rotundus*, *Sturnira lilium*, and *Rhogeessa tumida*—were netted equally in both areas. We stress that our sampling efforts were not distributed over the year, but rather were focused almost exclusively in July and February, with 1 session in April. If the different species of bats are tracking food sources that are different or out of synchrony in the coastal and interior forests, we would be unable to resolve the issue of microhabitat associations until we have a better understanding of seasonal abundances of the various bat species.

We expect that additional netting will expand the number of species found in both habitats, especially for species represented by low numbers. For example, *Artibeus lituratus* and *Choeroniscus godmani* (known from the coast in small numbers) may well turn up in the forest and *Lasiurus ega* (known only from inland) also may use coastal habitat. The concentration of *Trachops cirrhosus* in the forest may be a true habitat choice, possibly based on the abundance of prey items (large insects and frogs) inland. *Uroderma bilobatum* roost in the young *Attalea* palms along the coast, and perhaps they restrict their foraging to this neighborhood during the July and February seasons of our netting efforts.

Seasonal Abundances of Bats.—We found some evidence of differences in seasonal abundance of species at Cabo Blanco. *Balantiopteryx plicata*, *Saccopteryx bilineata*, *Noctilio leporinus*, *Artibeus watsoni*, *Desmodus rotundus*, *Glossophaga soricina*, *Phyllostomus hastatus*, *Trachops cirrhosus*, *Lasiurus ega*, and *Myotis nigricans* seem to be equally abundant in both seasons. In contrast, *Artibeus jamaicensis*, *Carollia perspicillata*, *Sturnira lilium*, *Uroderma bilobatum*, and *Rhogeessa tumida* were abundant (or at least present) in the rainy season but uncommon during the dry season. No species was more abundant in the dry season than the rainy season.

Bats that utilize the caves (*Balantiopteryx plicata*, *Saccopteryx bilineata*, *Desmodus rotundus*, and *Phyllostomus hastatus*) were present in comparable population sizes during rainy and dry seasons. *Uroderma bilobatum* abandoned its roosting sites in the coastal *Attalea* palms during the dry season and we never saw more than 1 or 2 individuals during the dry seasons.

Do individuals of 1 or more species move out of the region during certain seasons? Seasonal migrations have long been known for north-temperate bats, as well as for birds and butterflies. Recently however, seasonal altitudinal migrations have been shown for Costa Rican birds (Stiles and Skutch, 1989), butterflies (Haber and Stevenson, 2004), and bats (Timm and LaVal, 2000; Stoner, 2001; LaVal, 2004a, Stoner and Timm, 2004). In recent years, it has become apparent that bats in Costa Rica (and presumably elsewhere in Central America) move considerable distances, probably in response to seasonal variation in food resources and, at times, probably because of inclement weather. Timm and LaVal (2000) documented that several species of middle- and high-elevation species show strong seasonal variation in abundance that they interpreted as migrations into and out of the area. They suggested that these bats were tracking seasonal increases and decreases in abundance of preferred foods (also see LaVal, 2004a, 2004b). With additional capture data we hope to evaluate the relative abundance of males and female in both the rainy season and dry season.

Food Availability for Bats.—A number of species in the pantropical family Moraceae are found at Cabo Blanco; the best known members are the figs. The diversity and abundance of figs found here provide an especially rich food source for bats and other mammals. At least 6 species of figs in the genus *Ficus* occur in the Reserve. Other species of free-standing trees in the Moraceae that produce fruits eaten by bats at Cabo Blanco include *Brosimum alicastrum*, *B. costaricanum*, *Clarisia biflora*, *Pseudolmedia spuria*, and *Trophis racemosa*. *Brosimum alicastrum* and *Trophis racemosa* are the 2 most abundant species of Moraceae found throughout the reserve. *Brosimum alicastrum* and *B. costaricanum* can produce massive fruit crops (Camacho-Céspedes and Lindquist in press). *Artibeus jamaicensis*, a fig specialist, was one of the most abundant bats at Cabo Blanco. We captured it both during the rainy and dry seasons, but it was more abundant in the rainy season. Interestingly, *Artibeus lituratus*, another fig specialist, was an uncommon bat at Cabo Blanco.

Species of the understory shrub *Piper* comprise an essential food source for bats of the genera *Carollia* and *Sturnira*. At Cabo Blanco, *Piper* grows abundantly away from the maritime influence and is most abundant along streams. Two species of *Piper*, *P. reticulatum* and *P. tuberculatum*, are known from the reserve, with *P. reticulatum* common and producing flowers and fruit throughout the year (Camacho-Céspedes and Lindquist in press). With the exception of *Glossophaga soricina*, the nectar-feeding bats of the subfamily Glossophaginae are not well represented at Cabo Blanco either in terms of species diversity or abundance. *Pachira quinata*, a common canopy tree throughout the reserve, is fed upon and flowers pollinated by nectar bats, presumably *G. soricina*, but this remains unstudied. The seasonal variation in abundance of food and water likely are critical to a number of bat species, but the details remain untested at Cabo Blanco. At Cabo Blanco, the nectar feeding bat community is not as diverse as at other sites in Costa Rica such as La Selva, Monteverde, and Palo Verde.

Comparison with Palo Verde, a Dry Forest Site.—In comparing the species diversity and abundances of bats at Cabo Blanco to those seen at Costa Rica's Parque Nacional Palo Verde, we find both similarities and differences. Palo Verde is located in tropical dry forest of the Guanacaste lowlands ca. 84 km north of Cabo Blanco, and is considerably drier than Cabo Blanco; Timm has been working there since 1974 (see Stoner and Timm, 2004; Timm, unpubl.). Both sites have species that either are not present at the other site or are found there in quite different abundances. Interestingly, both the similarities and differences in the bat faunas between the sites represent most of the major feeding niches. Species that are found in similar relative abundances at both sites include *Balantiopteryx plicata*, *Saccopteryx bilineata*, *Artibeus jamaicensis*, *Artibeus watsoni*, *Carollia perspicillata*, *Chrotopterus auritus*, *Desmodus rotundus*, *Sturnira lilium*, *Trachops cirrhosus*, *Uroderma bilobatum*, *Vampyrum spectrum*, and *Rhogeessa tumida*. One species, *Phyllostomus hastatus*, is common at Cabo Blanco, but not yet recorded at Palo

Verde despite extensive netting and cave surveys there over several years. The other large predaceous bats (*C. auritus*, *T. cirrhosus*, and *V. spectrum*) are seen in similar abundances at the two sites. *Glyphonycteris sylvestris* and *Lophostoma silvicolum*, which are rare at Cabo Blanco, have yet to be recorded at Palo Verde. In contrast, Palo Verde has a richer fauna of the small and mid-sized phyllostomines than is seen at Cabo Blanco.

Species that are found in moderate abundance at Palo Verde, but not yet recorded from Cabo Blanco, include *Pteronotus davyi*, *P. gymnonotus*, *Carollia subrufa*, *Centurio senex*, *Micronycteris minuta*, and *Natalus stramineus*. Species that are relatively common at Palo Verde but rare at Cabo Blanco include *Pteronotus parnellii* and *Artibeus lituratus*. Species that are rare at both sites include *Diclidurus albus*, *Carollia castanea*, and *Myotis riparius*.

Artibeus jamaicensis is an abundant species at Cabo Blanco, comprising 25% of our captures, and also is abundant at Palo Verde, where it constitutes 13.9% of captures (Stoner and Timm, 2004). Similarly, *Carollia perspicillata* comprises 27% of our captures at Cabo Blanco and roughly 10% of our captures at Palo Verde. Stoner and Timm (2004) found *S. lilium* to be one of the most abundant species of bats at Palo Verde; however, we observed this species at Cabo Blanco only during the rainy season, and it clearly was not as abundant there as it is at Palo Verde. *Pteronotus parnellii* was fairly common at Palo Verde and captured there regularly both in the rainy and dry seasons; in contrast, we caught a single adult female at Cabo Blanco in the dry season. Additionally, nets set over water at Cabo Blanco late in the dry season catch large numbers of bats very quickly, which also is our experience at Palo Verde.

In the caves of Refugio de Vida Silvestre Cueva Los Murciélagos, we regularly observed *Balantiopteryx plicata*, *Saccopteryx bilineata*, *Desmodus rotundus*, and *Phyllostomus hastatus* during both the rainy and dry seasons. In the Cueva del Tigre complex at Palo Verde, we also observed *B. plicata*, *S. bilineata*, and *D. rotundus*, roosting both in the rainy and dry seasons; however, we have never observed *P. hastatus* there. The large phyllostomine roosting in the caves there was *Chrotopterus auritus*, which was found year-round; it has not been seen roosting in any of the caves at Refugio de Vida Silvestre Cueva Los Murciélagos.

In tropical dry forest and moist forest, ground level nets are very effective at sampling bat diversity, especially when nets are placed over water in the dry season. Canopy level netting, which has proven successful elsewhere in the tropics, may not be as effective in these forests in detecting additional species because of the low canopy height. There is no doubt that additional survey techniques such as acoustical surveys with electronic bat detectors to detect and identify ultrasonic signals from bats will increase the number of species known from Cabo Blanco. Additional netting will increase the species list, but we do not predict that this increased effort will make the species inventory congruent with that of Palo Verde.

Conservation.—Bats were extremely abundant at Cabo Blanco, especially species of nectarivorous and frugivorous phyllostomids. Critical to regeneration of tropical forests is the ability of seeds to move from the parent plant to new areas. LaVal (2004a) reported that bats disperse more seeds than do birds, that pioneer species of plants are especially well represented in bat-dispersed seeds, and that these seeds are dispersed primarily to disturbed areas. Bats, because of their high mobility, can disperse large numbers of seeds for considerable distances. Bats at Cabo Blanco face large fluctuations in the availability of food resources during the year, and may well be tracking the abundance of preferred foods.

In summary, the bat fauna in and around 40-year-old regenerating forest of Costa Rica's Reserva Natural Absoluta Cabo Blanco is diverse and many species, especially those that are the primary dispersers of seeds, are extremely abundant. The largest carnivores are present, but the small and middle-sized predators are poorly represented. Several species have clear habitat preferences and seasonal differences occur in abundance and reproductive patterns. Finally, the species composition and abundances differ somewhat from the relatively close, dry forest site, Palo Verde. Because of their high mobility, perhaps bats, more than most other mammals, follow the prophecy (slightly corrupted) from the 1989 movie *Field of Dreams*: if you preserve it … they will come.

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LITERATURE CITED

Abel–Vidor, S.
1981 Ethnohistorical approaches to the archaeology of Greater Nicoya. Pp. 85–92 in Between Continents/Between Seas: Precolumbian Art of Costa Rica (Benson, E. P., ed.). Harry N. Abrams, Inc., New York, New York, USA. 240 pp.

Arita, H. T.
1993 Rarity in Neotropical bats: correlations with phylogeny, diet, and body mass. Ecological Applications 3:506–517.

Baker, R. J., S. R. Hoofer, C. A. Porter, and R. A. Van Den Bussche
2003 Diversification among New World leaf-nosed bats: an evolutionary hypothesis and classification inferred from digenomic congruence of DNA sequence. Occasional Papers, Museum of Texas Tech University 230:i + 1–32.

Bergallo, H. G., C. E. L. Esbérard, M A. R. Mello, V. Lins, R. Mangolin, G. G. S. Melo, and M. Baptista
2003 Bat species richness in Atlantic forest: what is the minimum sampling effort? Biotropica 35:278–288.

Bergmann, J. F.
1969 The distribution of cacao cultivation in Pre-Columbian America. Annals of the Association of American Geographers 59:85–96.

Bergoeing, J. P.
1998 Geomorfología de Costa Rica. Instituto Geográfico Nacional, San José, Costa Rica. 409 pp.

Bransford, J. F.
1884 Report on explorations in Central America, in 1881. Annual Report of the Board of Regents of the Smithsonian Institution for the year 1882:803–825.

Bray, W.
1981 Gold work. Pp. 153–166 in Between Continents/Between Seas: Precolumbian Art of Costa Rica (Benson, E. P., ed.). Harry N. Abrams, Inc., New York, New York, USA. 240 pp.

Bush, M. B., and P. A. Colinvaux
1994 Tropical forest disturbance: paleoecological records from Darien, Panama. Ecology 75:1761–1768.

Camacho-Céspedes, F., and E. S. Lindquist; V. Knight, illustrator
In press Árboles Comunes de la Reserva Natural Absoluta Cabo Blanco, Costa Rica. Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica.

Clark, D. B.
1996 Abolishing virginity. Journal of Tropical Ecology 12:735–739.

Cooke, R., and A. J. Ranere
1992 Prehistoric human adaptations to the seasonally dry forests of Panama. World Archaeology 24:114–133.

Creamer, W.
1987 Mesoamerica as a concept: an archaeological view from Central America. Latin American Research Review 22:35–62.

1992 Regional exchange along the Pacific coast of Costa Rica during the Late Polychrome period, A.C. 1200–1550. Journal of Field Archaeology 19:1–16.

Creamer, W., and J. Haas
1985 Tribe versus chiefdom in lower Central America. American Antiquity 50:738–754.

Denevan, W. M.
1992 The pristine myth: the landscape of the Americas in 1492. Annals of the Association of American Geographers 82:369–385.

Denyer, P., and S. Kussmaul
2000 Geología de Costa Rica. Editorial Tecnológica de Costa Rica, San José, Costa Rica. 515 pp.

Easby, E. K.
1968 Pre-Columbian jade from Costa Rica. André Emmerich, Inc., New York, New York, USA. 103 pp.

Evans, S.
1999 The Green Republic: A Conservation History of Costa Rica. University of Texas Press, Austin, Texas, USA. 317 pp.

Fenton, M. B., L. Acharya, D. Audet, M. B. C. Hickey, C. Merriman, M. K. Obrist, D. M. Syme, and B. Adkins
1992 Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. Biotropica 24:440–446.

Fernández, L.
1976 Asentamientos, hacienda y gobierno. Volumen III. Colección de documentos para la historia de Costa Rica. Editorial Costa Rica, San José, Costa Rica. 413 pp.

Fleming, T. H.
1988 The Short-tailed Fruit Bat: A Study in Plant-Animal Interactions. The University of Chicago Press, Chicago, Illinois, USA. 365 pp.

Fonseca Zamora, O. M.
1993 Art, ideology, and totality: representational art of Costa Rica's central region in the Late Period (A.D. 800–1500). Pp. 103–140 in Reinterpreting Prehistory of Central America (Graham, M. M., ed.). University of Colorado Press, Niwot, Colorado, USA. 336 pp.

Fowler, W. R., Jr.
1985 Ethnohistoric sources on the Pipil–Nicarao of Central America: a critical analysis. Ethnohistory 32:37–62.

1991 The formation of complex society among the Nahua group of southeastern Mesoamerica: a comparison of two approaches. Pp. 193–213 in The formation of complex society in southeastern Mesoamerica (Fowler, W. R., Jr., ed.). CRC Press, Boca Raton, Florida, USA. 286 pp.

Genoways, H. H., and R. J. Baker
1996 A new species of the genus *Rhogeessa*, with comments on geographic distribution and speciation in the genus. Pp. 83–87 in Contributions in Mammalogy: A Memorial Volume Honoring Dr. J. Knox Jones, Jr. (Genoways, H. H., and R. J. Baker, eds.). Museum of Texas Tech University, Lubbock, Texas, USA., il + 315 pp.

Gómez, L. D.
1986 Vegetación de Costa Rica: apuntes para una biogeografía Costarricensie. Pp. 1–327 + 9 maps in Vegetación y Clima de Costa Rica, vol. 1 (Gómez, L. D., ed.). Editorial Universidad Estatal a Distancia, San José, Costa Rica. 256 pp.

Gorresen, P. M., and M. R. Willig
2004 Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. Journal of Mammalogy 85:688–697.

Gudmundson, L.
1983 Hacendados, Políticos y Precaristas: La Ganadería y el Latifundismo Guanacasteco 1800–1950. Editorial Costa Rica, San José, Costa Rica. 256 pp.

Haber, W. A., and R. D. Stevenson
2004 Diversity, migration, and conservation of butterflies in northern Costa Rica. Pp. 99–114 in Biodiversity Conservation in Costa Rica: Learning the Lessons in a Seasonal Dry Forest (Frankie, G. W., A. Mata, and S. B. Vinson, eds.). University of California Press, Berkeley, California, USA. 341 pp.

Hartman, C. V.
1907 Archaeological researches on the Pacific Coast of Costa Rica. Memoirs of the Carnegie Museum 3(1):iii + 1–188.

Herrera, W.
1985 Clima de Costa Rica. Pp. 1–118 + 9 maps in Vegetación y Clima de Costa Rica, vol. 2 (Gómez, L. D., ed.). Editorial Universidad Estatal a Distancia, San José, Costa Rica.

Herrera Sota, W., and L. D. Gómez Pignataro
1993 Mapa de Unidades Bióticas de Costa Rica. Escala 1:685000. INCAFO, San José, Costa Rica.

Holdridge, L. R.
1967 Life Zone Ecology. Tropical Science Center, San José, Costa Rica. 206 pp.

Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, and J. A. Tosi, Jr.
1971 Forest Environments in Tropical Life Zones: A Pilot Study. Peramon Press, New York, New York, USA. 747 pp.

Hoopes, J. W.
1991 The Isthmian alternative: reconstructing patterns of social organization in Formative Costa Rica. Pp. 171–192 in The formation of Complex Society in Southeastern Mesoamerica (Fowler, W. R., Jr., ed.). CRC Press, Boca Raton, Florida, USA. 286 pp.

Hubbs, C. L., and G. I. Roden
1964 Oceanography and marine life along the Pacific coast. Pp. 143–186 in Handbook of Middle American Indians. Volume I. Natural Environment and Early Cultures (West, R. C., eds.). University of Texas Press, Austin, Texas, USA. 570 pp.

Jones, K. E., A. Purvis, A. MacLarnon, O. R. P. Bininda-Emonds, and N. B. Simmons
2002 A phylogenetic supertree of the bats (Mammalia: Chiroptera). Biological Review 77:223–259.

Kalko, E. K. V., D. Friemel, C. O. Handley, Jr., and H.-U. Schnitzler
1999 Roosting and foraging behavior of two Neotropical gleaning bats, *Tonatia silvicola* and *Trachops cirrhosus* (Phyllostomidae). Biotropica 31:344–353.

Kennedy, L. M., and S. P. Horn
1997 Prehistoric maize cultivation at the La Selva Biological Station, Costa Rica. Biotropica 29:368–370.

Kerbis, J.
1980 The analysis of faunal remains from the Vidor Site. Vínculos 6:125–140.

Lange, F. W.
1976 Costa Rica and the "subsistence archaeologist." Current Anthropology 17:305–307.

1984 The Greater Nicoya Archaeological Subarea. Pp. 165–194 in The Archaeology of Lower Central America (Lange, F. W., and D. Z. Stone, eds.). University of New Mexico Press, Albuquerque, New Mexico, USA. 476 pp.

Lange, F. W., R. L. Bishop, and L. van Zelst
1981 Perspectives on Costa Rican jade: compositional analyses and cultural implications. Pp. 167–175 in Between Continents/Between Seas: Precolumbian Art of Costa Rica (Benson E. P., ed.). Harry N. Abrams, Inc., New York, New York, USA. 240 pp.

LaVal, R. K.
1973 Systematics of the genus *Rhogeessa* (Chiroptera: Vespertilionidae). Occasional Papers, Museum of Natural History, University of Kansas 19:1–47.

2004a An ultrasonically silent night: the tropical dry forest without bats. Pp. 160–176 in Biodiversity Conservation in Costa Rica: Learning the Lessons in a Seasonal Dry Forest (Frankie, G. W., A. Mata, and S. B. Vinson, eds.). University of California Press, Berkeley, California, USA. 341 pp.

2004b Impact of global warming and locally changing climate on tropical cloud forest bats. Journal of Mammalogy 85:237–244.

LaVal, R. K., and B. Rodríguez-H.
2002 Murciélagos de Costa Rica: Bats. Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica. 320 pp.

Lee, T. E., Jr., S. R. Hoofer, and R. A. Van Den Bussche
2002 Molecular phylogenetics and taxonomic revision of the genus *Tonatia* (Chiroptera: Phyllostomidae). Journal of Mammalogy 83:49–57.

Linares, O. F.
1976 "Garden hunting" in the American tropics. Human Ecology 4:331–349.

1979 What is lower Central American archaeology? Annual Review of Anthropology 8:21–43.

Lindquist, E. S.
2003 Patterns of Coastal Forest Composition, Structure, and Recruitment, Costa Rica: Functions of an Environmental Gradient, Seed Rain Distribution, and Crab Predation Pressure. Ph.D. Dissertation, University of Georgia, Athens, Georgria, USA. 188 pp.

Lindquist, E. S., and C. R. Carroll
2004 Differential seed and seedling predation by crabs: impacts on tropical coastal forest composition. Oecologia 141:661–671.

Longino, J. T., and R. K. Colwell
1997 Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. Ecological Applications 7:1263–1277.

Lovell, W. G.
1992 "Heavy shadows and black night": disease and depopulation in colonial Spanish America. Annals of the Association of American Geographers 82:426–443.

Medellín, R. A., M. Equihua, and M. A. Amin
2000 Bat diversity and abundance as indicators of disturbance in Neotropical rainforests. Conservation Biology 14:1666–1675.

Meléndez Chaverri, C.
1978 Documentos Fundamentales del Siglo XIX. Editorial Costa Rica, San José, Costa Rica. 507 pp.

Messenger, L. C., Jr.
1991 Climatic settings and prehistoric social complexity: the Central American isthmus. Pp. 237–275 in The Formation of Complex Society in Southeastern Mesoamerica (Fowler, W. R., Jr., ed.). CRC Press, Boca Raton, Florida, USA. 286 pp.

Molina, I., and S. Palmer
2000 The History of Costa Rica. Editorial de la Universidad de Costa Rica, San José, Costa Rica. 174 pp.

Moreau, J.-F.
1984 Subsistance changes on the coast of the Greater Nicoya Region. Pp. 129–141 in Inter-regional Ties in Costa Rican Prehistory (Skirboll, E., and W. Creamer, eds.). BAR, International Series, Oxford, England 226:1–276.

Moreno, C. E., and G. Halffter
2000 Assessing the completeness of bat biodiversity inventories using species accumulation curves. Journal of Applied Ecology 37:149–158.

Newson, L.
1982 The depopulation of Nicaragua in the sixteenth century. Journal of Latin American Studies 14:253–286.

Noriega, F. F.
1924 Diccionario Geográfico de Costa Rica. Imprenta Nacional, San José, Costa Rica. 274 pp.

Oviedo y Valdés, G. F. de
1959 Historia General y Natural de las Indias. Volumes I–V. Atlas, Madrid, Spain.

Patch, R. W.
1994 Imperial politics and local economy in colonial Central America 1670–1770. Past and Present 143:77–107.

Patterson, B. D., M. R. Willig, and R. D. Stevens
2003 Tropic strategies, niche partitioning, and patterns of ecological organization. Pp. 536–579 in Bat Ecology (Kunz, T. H., and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois, USA. 779 pp.

Piperno, D. R., and D. M. Pearsall
1998 The Origins of Agriculture in the Lowland Neotropics. Academic Press, London. 400 pp.

Quesada López-Calleja, R.
1980 Costa Rica: La Frontera Sur de Mesoamérica. 2nd ed., Instituto Costarricense de Turismo, Madrid, Spain. 288 pp.

Quilter, J.
2004 Cobble Circles and Standing Stones. University of Iowa Press, Iowa City, Iowa, USA. 218 pp.

Radell, D. R., and J. J. Parsons
1971 Realejo: a forgotten colonial port and shipbuilding center in Nicaragua. Hispanic American Historical Review 51:295–312.

Reid, F. A.
1997 A Field Guide to the Mammals of Central America & Southeast Mexico. Oxford University Press, New York, New York, USA. 334 pp.

Rodríguez-H., B., and D. E. Wilson
1999 Lista y distribución de las especies de murciélagos de Costa Rica. Occasional Papers in Conservation Biology, Conservation International 5:1–34.

Schulze, M. D., N. E. Seavy, and D. F. Whitacre
2000 A comparison of the phyllostomid bat assemblages in undisturbed Neotropical forest and in forest fragments of a slash-and-burn farming mosaic in Petén, Guatemala. Biotropica 32:174–184.

Sheets, P, J. Hoopes, W. Melson, B. McKee, T. Sever, M. Mueller, M. Chenault, and J. Bradley
1991 Prehistory and volcanism in the Arenal area, Costa Rica. Journal of Field Archaeology 18:445–465.

Silva, D., and J. A. Coddington
1996 Spiders of Pakitza (Madre de Dios, Peru): species richness and notes on community structure. Pp. 253–311 in Manu: The Biodiversity of Southeastern Peru (Wilson, D. E., and A. Sandoval, eds.). Smithsonian Institution Press, Washington, D.C., USA. 679 pp.

Skirboll, E.
1984 Carl Hartman and the beginning of scientific archaeology in Costa Rica. Pp. 1–13 in Inter-regional Ties in Costa Rican Prehistory (Skirboll, E., and W. Creamer, eds.). BAR, International Series, Oxford, England 226:1–276.

Sluyter, A.
1994 Intensive wetland agriculture in Mesoamerica: space, time, and form. Annuals of the Association of American Geographers 84:557–584.

Snarskis, M. J.
1981 The archaeology of Costa Rica. Pp. 15–84 in Between Continents/ Between Seas: Precolumbian Art of Costa Rica (Benson, E. P., ed.). Harry N. Abrams, Inc., New York, New York, USA. 240 pp.

1982 La cerámica precolombina en Costa Rica. Instituto Nacional de Seguros, San José, Costa Rica. 136 pp.

2003 From jade to gold in Costa Rica: how, why, and when. Pp. 159–204 in Gold and Power in Ancient Costa Rica, Panama, and Colombia (Quilter, J., and J. W. Hoopes, eds.). Dumbarton Oaks, Washington, D.C., USA. 429 pp.

Stahl, P. W.
1996 Holocene biodiversity: an archaeological perspective from the Americas. Annual Review of Anthropology 25:105–126.

Stevens, R. D.
2004 Untangling latitudinal richness gradients at higher taxonomic levels: familial perspectives on the diversity of New World bat communities. Journal of Biogeography 31:665–674.

Stevens, R. D., M. R. Willig, and I. Gamarra de Fox
2004 Comparative community ecology of bats from eastern Paraguay: taxonomic, ecological, and biogeographic perspectives. Journal of Mammalogy 85:698–707.

Stiles, F. G., and A. F. Skutch
1989 A Guide to the Birds of Costa Rica. Cornell University Press, Ithaca, New York, New York, USA. 511 pp.

Stone, D.
1977 Pre-Columbian Man in Costa Rica. Peabody Museum Press, Cambridge, Massachusetts, USA. 238 pp.

Stoner, K. E.
2001 Differential habitat use and reproductive patterns of frugivorous bats in tropical dry forest of northwestern Costa Rica. Canadian Journal of Zoology 79:1626–1633.

Stoner, K. E., and R. M. Timm
2004 Tropical dry-forest mammals of Palo Verde: ecology and conservation in a changing landscape. Pp. 48–66 in Biodiversity Conservation in Costa Rica: Learning the Lessons in a Seasonal Dry Forest (Frankie, G. W., A. Mata, and S. B. Vinson, eds.). University of California Press, Berkeley, California, USA. 341 pp.

Timm, R. M.
1985 *Artibeus phaeotis*. Mammalian Species 235:1–6.

1987 Tent construction by bats of the genera *Artibeus* and *Uroderma.* Pp. 187–212 in Studies in Neotropical Mammalogy: Essays in Honor of Philip Hershkovitz (Patterson, B. D., and R. M. Timm, eds.). Fieldiana: Zoology, new series 39.

1994 The mammal fauna. Pp. 229–237 & 394–398 in La Selva: Ecology and Natural History of a Neotropical Rain Forest (McDade, L. A., K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, eds.). University of Chicago Press, Chicago, Illinois, USA. 486 pp.

Timm, R. M., and R. K. LaVal
1998 A field key to the bats of Costa Rica. Occasional Publication Series, Center Latin American Studies, University of Kansas 22:1–30.

2000 Mammals. Pp. 223–244 & 553–560 in Monteverde: Ecology and Conservation of a Tropical Cloud Forest (Nadkarni, N. M., and N. T. Wheelwright, eds.). Oxford University Press, New York, New York, USA. 573 pp.

Timm, R. M., R. K. LaVal, and B. Rodríguez-H.
1999 Clave de campo para los murciélagos de Costa Rica. Brenesia 52:1–32.

Timm, R. M., and S. E. Lewis
1991 Tent construction and use by *Uroderma bilobatum* in coconut palms (*Cocos nucifera*) in Costa Rica. Pp. 251–260 in Contributions to Mammalogy in Honor of Karl F. Koopman (Griffiths, T. A., and D. Klingener, eds.). Bulletin of the American Museum of Natural History 206:1–432.

Timm, R. M., D. E. Wilson, B. L. Clauson, R. K. LaVal, and C. S. Vaughan
1989 Mammals of the La Selva–Braulio Carrillo Complex, Costa Rica. North American Fauna 75:1–162.

Tournon, J., and G. E. Alvarado Induni
1997 Mapa Geológico de Costa Rica. Editorial Tecnológica de Costa Rica. Cartago, Costa Rica. 79 pages + map.

Vásquez M., A.
1983 Soils. Pp. 63–65 in Costa Rican Natural History (Janzen, D. H., ed.). University of Chicago Press, Chicago, Illinois, USA. 816 pp.

Voss, R. S., and L. H. Emmons
1996 Mammalian diversity in Neotropical lowland rainforests: a preliminary assessment. Bulletin of the American Museum of Natural History 230:1–115.

Wallace, D. R.
1992 The Quetzal and the Macaw: The Story of Costa Rica's National Parks. Sierra Club Books, San Francisco, California, USA. 222 pp.

Watt, A. D.
1998 Measuring disturbance in tropical forests: a critique of the use of species-abundance models and indicator measures in general. Journal of Applied Ecology 35:467–469.

Wetterer, A. L., M. V. Rockman, and N. B. Simmons
2000 Phylogeny of phyllostomid bats (Mammalia: Chiroptera): data from diverse morphological systems, sex chromosomes, and restriction sites. Bulletin of the American Museum of Natural History 248:1–200.

Whitmore, T. M., and B. L. Turner II
1992 Landscapes of cultivation in Mesoamerica on the eve of the conquest. Annals of the Association of American Geographers 82:402–425.

Wilson, D. E., C. F. Ascorra, and S. Solari T.
1996 Bats as indicators of habitat disturbance. Pp. 613–625 in Manu: The Biodiversity of Southeastern Peru (Wilson, D. E., and A. Sandoval, eds.). Smithsonian Institution Press, Washington, D.C., USA. 679 pp.

Wilson, D. E., R. M. Timm, and F. A. Chinchilla
2002 Mamíferos de Costa Rica. Pp. 227–253 in Diversidad y Conservación de los Mamíferos Neotropicales (Ceballos, G., and J. A. Simonetti, eds.). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad y Universidad Nacional Autónoma de México, México, D.F. 582 pp.

Zar, J. H.
1996 Biostatistical Analysis. Prentice Hall, Inc., Upper Saddle River, New Jersey, USA. 662 pp. + appendices.

Zeledón Cartín, E.
1997 Viajes por la República de Costa Rica. I. Oersted–Belly–Bovallius. Ministerio de Cultura, Juventud y Deportes, San José, Costa Rica.

1998 Viajes por la República de Costa Rica. III. Seebach–Sapper. Ministerio de Cultura, Juventud y Deportes, San José, Costa Rica.

HOW WELL DO PROTECTED AREAS REPRESENT THE TERRESTRIAL MAMMAL FAUNA OF SOUTH AMERICA?

¿CÚAN BIEN REPRESENTADA ESTÁ LA MASTOFAUNA SUDAMERICANA EN LAS ÁREAS PROTEGIDAS EXISTENTES?

Marcelo F. Tognelli

ABSTRACT

Long-term conservation of species requires the establishment of a network of protected areas. In the past, these have been established on an opportunistic basis without considering how many and which taxa were protected. I assessed the effectiveness of protected areas to adequately represent the diversity of terrestrial mammal species, as well as threatened and restricted-range species, in South America. Protected areas were analyzed hierarchically as (a) all protected areas, and (b) only IUCN-coded (categories I-VI) areas. The proportion of species represented in grid cells covered by protected areas was compared against randomly selected sets of cells. Significant gaps exist in the coverage of all species, as well as both threatened and restricted-range species. In most cases, IUCN reserves are more efficient, protecting approximately the same percentage of species as all protected areas, but using fewer cells. Major gaps in protected area coverage are in eastern Brazil, particularly the Atlantic Forests, the high Andes of Peru, Ecuador, and Colombia, and the southern Yungas.

Key words: Conservation, terrestrial mammals, South America, protected areas, GAP analysis

RESUMEN

La conservación a largo plazo de las especies requiere del establecimiento de una red de áreas protegidas. En el pasado, éstas han sido establecidas en forma oportunística sin considerar cuántos y cuáles taxa eran protegidos. En este estudio, evalúo la efectividad de las áreas protegidas para representar la diversidad de las especies de mamíferos terrestres sudamericanos, así como también de los mamíferos en peligro y de distribución geográfica restringida. Las áreas protegidas fueron analizadas de manera jerárquica como (a) todas las áreas protegidas, y (b) sólo aquellas clasificadas por IUCN (categorías I-VI). La proporción de especies representadas en celdas consideradas

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cubierta por áreas protegidas fue comparada con un set de celdas seleccionadas al azar. Los resultados muestran que existen vacíos significativos en la cobertura del total de las especies, así como también de las especies en peligro y de distribución restringida. En la mayoría de los casos, las reservas categorizadas por IUCN son más eficientes que todas las áreas protegidas, protegiendo aproximadamente el mismo porcentaje de especies pero en menor cantidad de celdas. Los vacíos más importantes de la cobertura de áreas protegidas se encuentran en el este de Brasil, principalmente en la Mata Atlántica, las partes altas de los Andes de Perú, Ecuador y Colombia, y la porción sur de las Yungas.

Palabras claves: Conservación, mamíferos terrestres, América del Sur, áreas protegidas, análisis de vacancia

INTRODUCTION

One of the major challenges faced by conservation biologists is the preservation of species *in situ*. Because of limited resources and conflict with other land uses, such as agriculture and development, allocation of land for conservation purposes requires a complex suite of management strategies (Margules and Pressey, 2000). One such management strategy is the establishment of a network of protected areas for the long-term conservation of species. However, most existing systems of protected areas were not chosen to meet specific biodiversity objectives. Historically, protected areas have been established opportunistically, assigning land with low potential for economic and political conflict, or high potential for tourism and recreation, which usually do not adequately represent overall biodiversity (Pressey et al., 1993; Pressey and Tully, 1994; Rodrigues et al., 1999; Margules and Pressey, 2000).

The performance of existing protected areas in representing biodiversity has been assessed in different geographic regions, and at different spatial scales, from regional to continental (Rebelo and Siegfried, 1992; Castro Parga et al., 1996; Pressey et al., 1996; Williams et al., 1996; Fjeldså and Rahbek, 1997; Araújo, 1999; Rodrigues et al., 1999; Wessels et al., 2000; Eeley et al., 2001; Fjeldså et al., 2004). These are basically gap analyses (Jennings, 2000) that are performed by overlaying maps of the distribution of biological attributes (e.g., species) over a map of the protected area system, and identifying those attributes that are not represented within the reserve network. Usually, the units of analysis employed are grid cells in which the biological attributes are considered as binary variables (either present or absent). In most studies, a grid cell is considered as already protected when a certain percentage of its area overlaps an existing protected area (e.g., >33% in Fjeldså and Rahbek (1997), >50% in Williams et al. (1996)). Most of these studies have concluded that existing networks of protected areas do not adequately conserve overall diversity. Additionally, some authors have tested the sensitivity of using different cut-offs criteria for determining protected grid cells (Araújo, 2004; Fjeldså et al., 2004).

South America is one of the richest continents biologically (Fjeldså and Rahbek, 1998). Approximately 20% of the world’s terrestrial mammals live there, with a high percentage of endemic species (Eisenberg and Redford, 1999). Mammal population losses have been high, however, primarily due to anthropogenic disturbances and unsustainable land uses (Ceballos and Ehrlich, 2002). As human-induced changes accelerate rapidly, it is crucial to evaluate how conservation efforts might be made more efficient. A first major step towards this goal is to assess whether the existing system of protected areas is adequate to conserve terrestrial mammal species in South America, and identify where the major gaps are located in order to better allocate resources. Although continent-wide gap analyses have been performed for South American birds (Fjeldså and Rahbek, 1997, 1998), no study has yet assessed the performance of existing protected areas in representing terrestrial mammal diversity. This study is a preliminary assessment, at a relatively coarse scale, of the effectiveness of protected areas to conserve overall terrestrial mammal diversity, as well as threatened and restricted-range mammal species in South America. Specifically, this study evaluates the extent to which IUCN-coded and all protected areas across South America cover the distribution of all terrestrial mammals, and of threatened and restricted-range species.

MATERIALS AND METHODS

Information on the distribution of terrestrial non-volant mammals of South America was compiled from the published literature (see list of reference sources in Tognelli (2005), updated with Patterson et al. (2003)). Exotic species were excluded from the data set. The presence/absence of 820 species was recorded on grid cells of 100 km x 100 km (approximately equivalent to 1 geographic degree at the equator) covering the South American continent. Only cells that were occupied by ≥2500 km^2 of continental land (e.g., ≥25% of grid area) were entered in the analysis, yielding a total of 1829 cells for the South American continent. A species was counted as present in a cell only if its geographic range overlapped ≥ 2500 km^2. Species with very small geographic ranges (< 10000 km^2) were allocated to a cell when ≥ 25% of their distribution overlapped that cell. Although these maps comprise merely "best estimates" for the ranges of many of these species, the urgency of systematic conservation planning in South America is too great to wait until better data becomes available.

The mammal database was subdivided into 3 groups. The first group contained all species in the dataset. The second group contained all species listed by IUCN (2002) as vulnerable, endangered, and critically endangered. This group is hereafter referred to as threatened species, and comprises 115 species. Finally, the third group contained the 25% most geographically rare species (the rare quartile of Gaston (1994)), and is referred to as restricted-range species, comprising 203 species. Species in this group were present in from 1 to 5 grid cells.

Protected area data were obtained from the World Database of Protected Areas (WDPA, 2004) developed by the World Conservation Monitoring Centre (UNEP-WCMC). This is the most current and comprehensive database for all protected areas available, and was subdivided into 2 subsets. The first included protected areas that are classified in any of the IUCN management categories (I-VI), referred to as IUCN reserves (Fig. 1A). Some protected areas in this subset had no polygon layers and were represented only by a point record with their associated area. These point records were converted to circular shapes (centered in their geographic coordinates) and merged with the layer containing polygons. The second subset consisted of all protected areas, including both IUCN-coded reserves and all other reserves that have not been coded by IUCN (Fig. 1A). The latter is referred to as all protected areas.

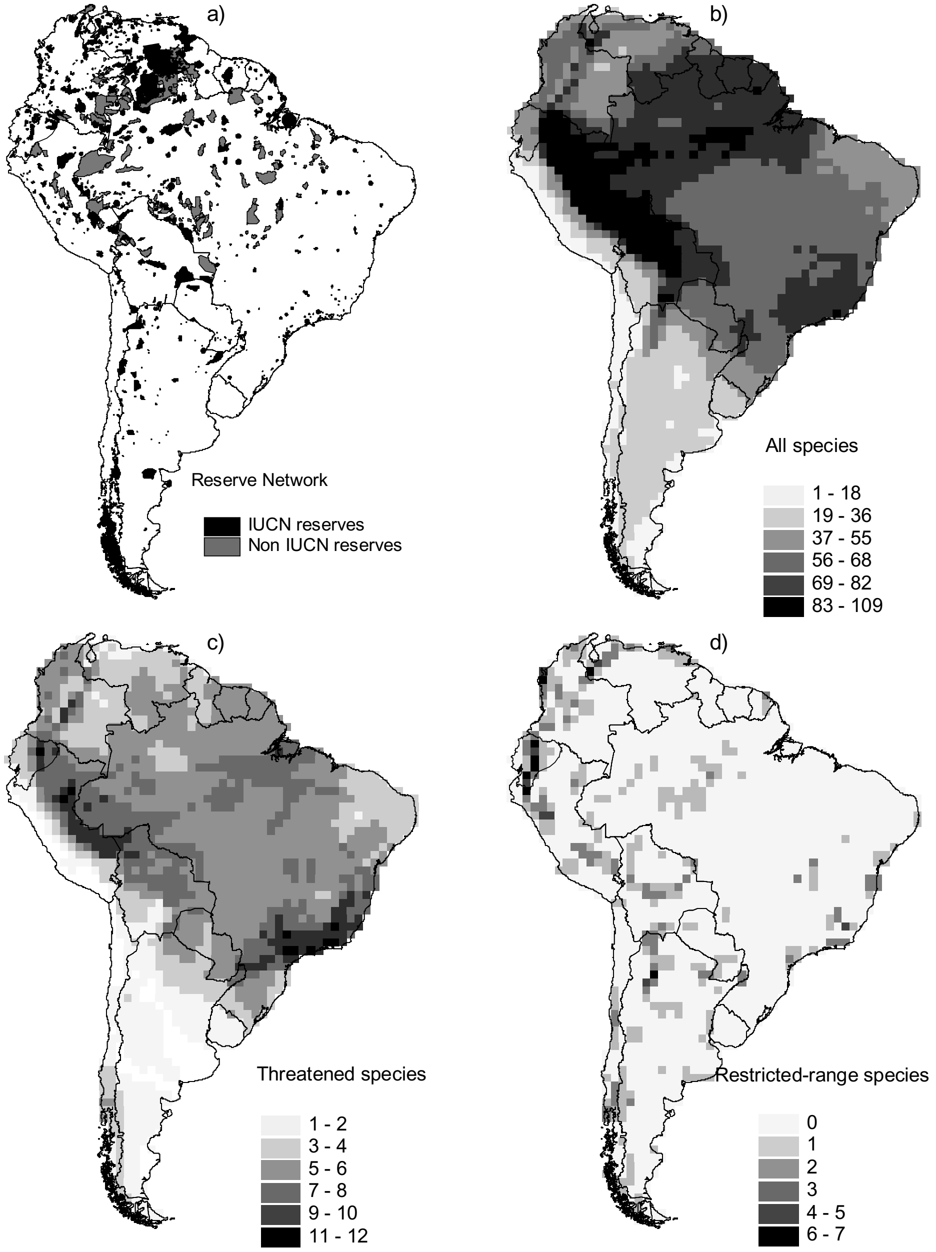

Figure 1. Distribution of protected areas in South America (a) from WDPA (2004): IUCN reserves (black) and non IUCN reserves (gray), and patterns of species richness of all species (b), threatened species (c), and restricted-range species (d) of South American terrestrial mammals.

The percentage of protected areas present in each 100 km x100 km grid cell was calculated by superimposing polygons of protected areas onto a grid covering South America. Four different thresholds (>10%, >25%, >33%, and >50% of area under protection) were set arbitrarily to determine whether a cell was considered “covered” or not. Species whose distributions overlapped with covered cells were considered protected. Protected areas that overlapped less than the cut-off criteria with a grid cell were not considered in the analysis.

The effectiveness of protected areas at representing each mammal group was tested by comparing the results for each group, for each cut-off criterion, and for each subset of reserve systems with 1000 randomly selected sets of equal number of grid cells. Following previous studies (Williams et al., 2000a, 2000b; Lund and Rahbek, 2002), for a reserve network to be regarded effective, its performance in representing the species in each mammal group must be better than the upper 95% confidence limit achieved by randomly selected cells. The performance of the sets of “covered” grid cells was plotted along with those of random sets, and along with a near-minimum solution derived using complementarity, and designed to conserve at least 1 population of each species of each mammal group.

Complementary analyses were performed with ResNet and Surrogacy software (Aggarwal et al., 2000; Garson and Sarkar, 2001). These programs use similar algorithms, with 2 separate processes: initialization and iteration. Initialization is the determination of the first grid cell to select given a set of selection criteria, whereas iteration is the process of selecting subsequent grid cells; the latter is repeated until a quitting rule is attained (e.g., until all focal species have been selected at least 1 time). In the initialization process, there is a choice between selecting a site based either on the richness or the rarity of species found there, whereas in the iterative step rarity is emphasized and complementarity is employed only in the case of ties. When using rarity, the planning units (i.e. grid cells) are ranked according to whether they contain the rarest species, the next rarest species, and so on, iteratively. However, when using complementarity, the planning units are ordered on the basis of the number of species which have not met the targeted representation. All analyses in this study were initialized using rarity. A detailed description of the algorithm used by these programs can be found in Aggarwal et al. (2000), Sarakinos et al. (2001), and Sarkar et al. (2002).

To exemplify this process, a single analysis was performed for the IUCN reserves dataset with a cut-off criterion of 33%. For those species not already covered in this dataset, the number of extra cells needed to conserve at least 1 population of each species was determined. Additionally, I used a measure of irreplaceability (the likelihood that a given site will need to be protected to ensure achievement of a set of regional conservation targets; Ferrier et al., 2000) to assess the conservation value of each cell. To do this, for all species of each target group (all species, threatened species, and restricted-range species) not already covered in the focal dataset, the reserve selection algorithm was run 100 times. The level of irreplaceability then was determined by the number of times a particular cell was selected. For example, a cell that was selected 100 times was considered completely irreplaceable. On the other hand, other cells were not selected all times and had alternative cells that would reach the same target representation if selected. These cells were considered flexible cells. Flexibility is the ability to incorporate all possible solutions in the reserve selection process (Rodrigues et al., 2000). These analyses were performed with Marxan (Ball and Possingham, 2000).

RESULTS

The richest areas of non-volant terrestrial mammals in South America are the Eastern Versant of the Andes of Bolivia, Peru, Ecuador, and Colombia, followed by the Amazon Basin, and the Atlantic Coastal Rain Forests (Fig. 1B). The number of threatened species is greatest in the Atlantic Coastal Rain Forests, the Eastern Versant of the Andes of Peru, and the Moist Forests of Northern Brazil (Fig. 1C). The highest concentration of restricted-range species is in areas above 500 m of elevation, extending along the Andes of Venezuela south to the southern part of the Yungas (Fig. 1D).

As expected, the near-minimum solutions for each target group are much more efficient than both IUCN reserves, and all protected area networks (Fig. 2 A-C). Grid cells "covered" by IUCN reserves using different percentage cut-off criteria varied from 70 (>50% covered) to 344 (>10% covered). When all species in the dataset were considered, none of the IUCN reserves networks are more effective than the 95% upper confidence limit of randomly selected cells (Fig. 2A), although the effectiveness of the reserve network defined by the percentage of area covered of >10% (circles in Fig. 2) is roughly equal to those of random cells. The pattern of coverage of IUCN reserves for threatened species is very similar (Fig. 2B); all observed values did not perform significantly better than randomly drawn cells. However, for restricted-range species, the IUCN reserves that overlapped >10%, >25%, and >33% performed better than equal numbers of randomly selected cells (Fig. 2C).

The number of grid cells "covered" by all protected areas (IUCN-coded plus non IUCN-coded) ranged from 148 (>50% covered) to 524 grid cells (>10% covered). For all target groups (all species, threatened species, and restricted-range species), the performance of all protected areas in representing each target group was less effective than randomly selected cells (Fig 2A-C), with the exception of restricted-range species using a cut-off criterion of >10% and >25%, where the performance is slightly better (Fig 2C). Remarkably, in all cases and for all mammal groups, IUCN reserves are more efficient (i.e., they protect approximately the same or higher percentages of target groups but with fewer grid cells) than when all protected areas are included (Fig. 2A-C).

At the 33% threshold of IUCN reserves, conservation gaps (number of species not protected by reserves) of all species of terrestrial mammals are located in the Atlantic Coastal Forests of Brazil, the southeastern portion of the Cerrado, part of the Caatinga, the Montane Forests of Ecuador and southern Colombia, and the Peruvian Yungas (Fig. 3A). Conservation gaps for threatened species are concentrated primarily in the Atlantic Coastal Forests of Brazil (Fig. 3B), whereas for restricted-range species major gaps in conservation are located in the Andean Montane Forests of Ecuador and Colombia, the Central Andean Wet Puna of Argentina, and the Southern Andean Yungas of Argentina (Fig. 3C). In addition to the grid cells considered "covered" by IUCN reserves at the 33% threshold, 115 cells are needed in order to protect all species at least once (Fig. 4), while 35 and 100 are needed to protect all threatened and restricted-range species, respectively. Of the 115 additional cells necessary to protect all species, 61 are considered irreplaceable (they were selected 100 times out of 100 iterations), and the remaining 54 are flexible cells (they were selected between 1 and 99 times out of 100 iterations; Fig. 4).

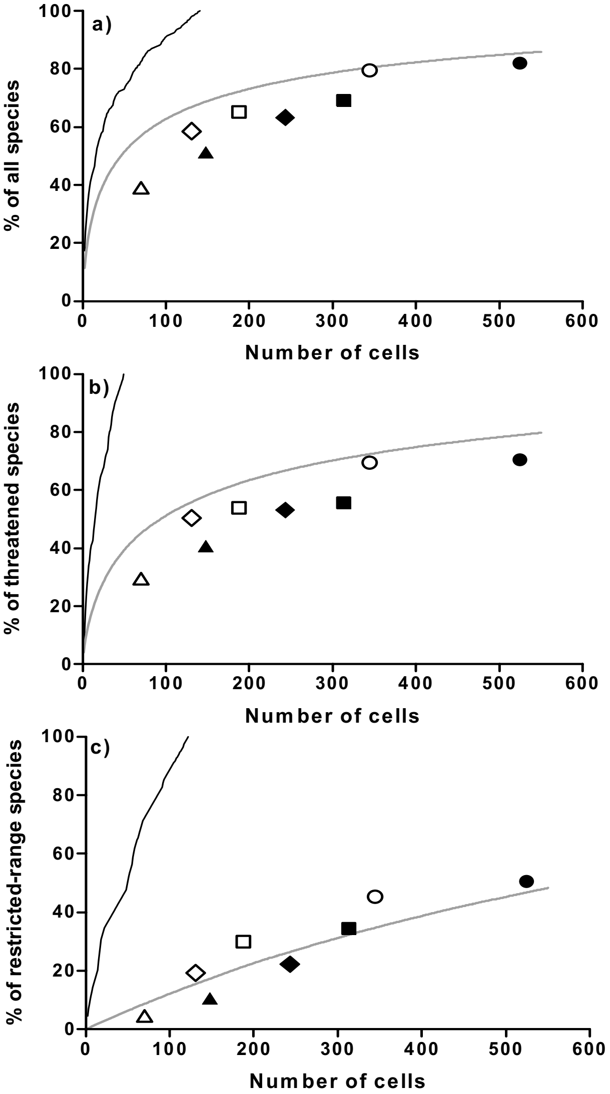

Figure 2. Effectiveness of IUCN reserves (open symbols) and all protected areas (solid symbols) in representing all species (a), threatened species (b), and restricted-range species of mammals (c) relative to the 95% upper confidence limit of randomly selection of sites (gray line), and the near-minimum solution for each target group (black line). Circles, squares, diamonds, and triangles represent >10%, >25%, >33%, and >50% of a grid cell covered by a reserve, respectively.

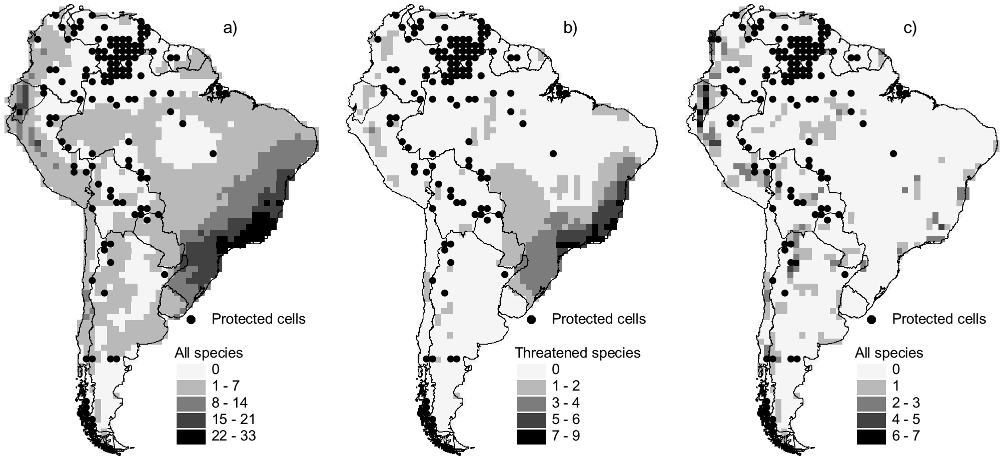

Figure 3. Gaps in species richness of all mammal species (a), threatened species (b), and restricted-range species not covered by IUCN reserves. Dots represent "covered" grid cells where at least 33% of a grid cell is protected by an IUCN reserve.

DISCUSSION

This study suggests that significant gaps exist in the protected area network in South America. Neither IUCN reserves nor all protected areas adequately preserve all terrestrial and threatened mammal species. In most cases, the existing protected area network is not more effective than randomly selected cells. However, IUCN reserves do perform better at protecting restricted-range species than randomly selected cells (in 3 of the 4 cut-off criteria). Nevertheless, the percentage of restricted-range species represented by IUCN reserves using a more liberal cut-off criterion (>10% of a grid cell covered) protects only 45% of species. This is a very low representation considering that all of these species occur only in a few cells and are prone to becoming endangered in the near future (Rabinowitz et al., 1986; Arita et al., 1990).

When all reserves are considered (i.e., IUCN-coded and all other reserves), the representation gaps are even worse. In only 2 cases do all protected areas perform slightly better than randomly selected cells. Compared to IUCN reserves, very little is gained in terms of percentage of species covered, when all protected areas are included. However, it is highly probable that there is a lot of redundancy in the coverage of species when all protected areas are considered. This can be inferred from the figures showing patterns of distribution of protected areas, species richness, and richness of unrepresented species (Figs. 1 and 3). Most protected areas are located in the Amazon Basin and the eastern Andean foothills where most of the species occur. However, there are hotspots of threatened species in the Atlantic Coastal Forests of Brazil, and hotspots of restricted-range species along the high Andes which have very low reserve coverage (Figs. 1 and 3), and are therefore identified as conservation gaps.

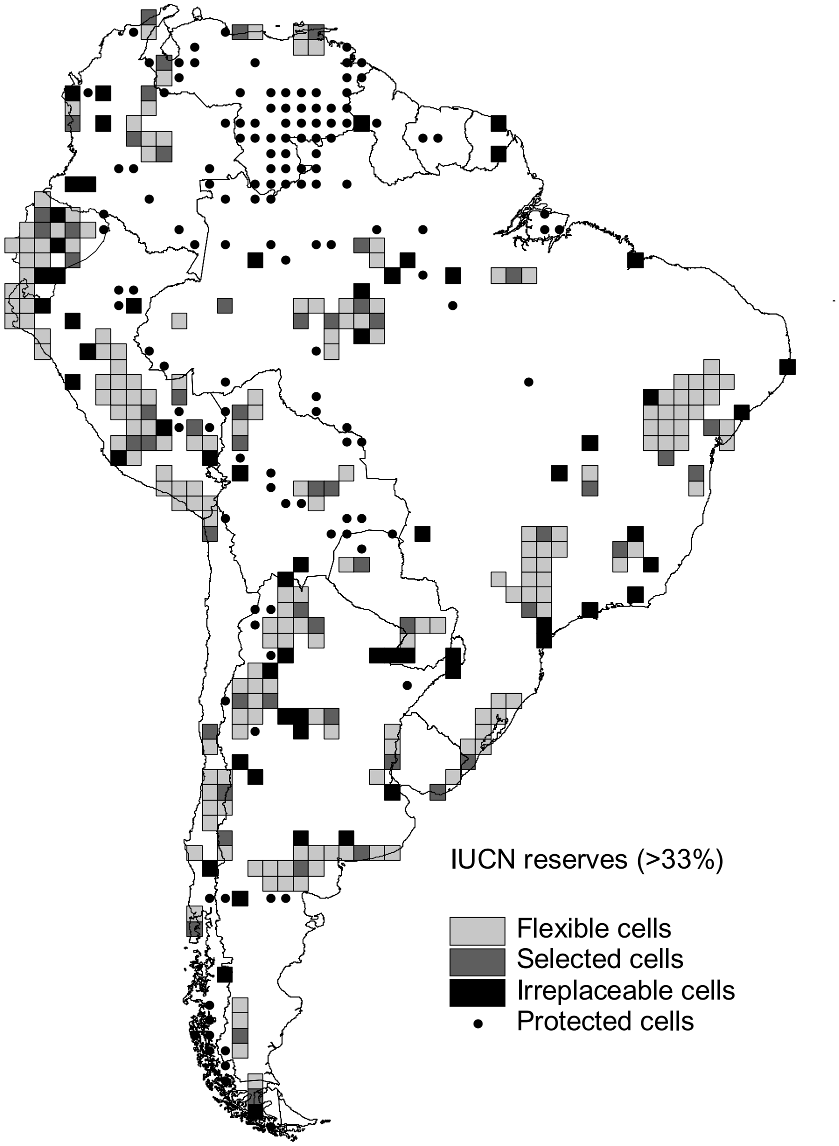

Figure 4. Additional cells needed to complement existing IUCN reserves to conserve at least 1 population of all species of terrestrial mammals in South America. Black dots represent IUCN reserves where at least 33% of a grid cell is covered. Black cells are irreplaceable cells. Cells with grades of gray are flexible cells and selected cells using complementarity analysis (see text for details).

Patterns of species richness of terrestrial mammals are similar to those of South American birds, with the greatest concentration of species in the eastern slope of the Andes, the Amazon Basin, and the Atlantic Coastal Forests of Brazil (Fjeldså and

Rahbek, 1998; Rahbek and Graves, 2001). Moreover, the distribution of irreplaceable cells selected to represent 913 species of birds (Fjeldså and Rahbek, 1998) is similar to the distribution of irreplaceable cells highlighted in this study. As with terrestrial mammals, most irreplaceable cells selected to protect bird species are concentrated on the western side of the Andes of Colombia, Ecuador, and Peru, and on the Atlantic Coastal Forests of Brazil (Fjeldså and Rahbek, 1998). In contrast, terrestrial mammals require a few more irreplaceable cells in the Amazon basin, and in central and northern Argentina (Fig. 4). It is reassuring, however, to see that, at least in some areas, there is an overlap in irreplaceable cells and that protecting terrestrial mammals might lead to the protection of restricted-range bird species, and vice-versa. Nonetheless, a major analysis likely is needed, incorporating as many taxa as possible, to develop a conservation blueprint for South America as has been done for Africa (Brooks et al., 2001).

There are some caveats to the matching of species with reserves using coarse grid-cell data (Rodrigues et al., 1999; Araújo, 2004). First, many species might receive some limited protection in grid cells that are not considered covered because the reserves occurring there do not reach the percentage cut-off criterion (Williams et al., 1996). An example in this study is the case of small protected areas in eastern Brazil and the high Andes of Peru, Ecuador, and Colombia. Indeed, for IUCN reserves and using a >33% threshold (Fig. 4), 60 of the 115 cells needed to conserve at least 1 population of all species already have some limited reserve coverage. However, the average percentage of grid cell coverage by protected areas in these 60 cells is less than 6%.

The second caveat is related to this point. What is a good threshold criteria for considering a cell protected? Ten percent of a grid cell of 10000 km^2 is 100000 ha, which is a relatively large reserve for many small to medium-size mammal species. Therefore, not taking into account protected areas that do not reach the 10% cut-off criterion implies discarding reserves that might have some conservation impact. On the other hand, however, setting a liberal threshold of ≤10% increases the likelihood of introducing commission errors, which occur when a species is considered covered when, in fact, it is not (Rodrigues et al., 2003). In this particular case, the distribution range of a certain species could overlap with a grid cell in the remaining 90% not covered by the protected area, and still be considered as protected. A recent analysis (Araújo, 2004) argues for sensitivity analyses to guide decisions, and reduce uncertainty, for setting threshold criteria of percentage of a grid cell covered by a protected area when assessing effectiveness of existing reserve networks. Assigning reserves to grid cells using different cut-off criteria is one way to reduce uncertainty in the results (Araújo, 2004). In this particular study, the real coverage of the South American continent by IUCN protected areas is approximately 7.5%, representing 137 cells. Thus, if we want to match this number of cells, the threshold criterion of percentage of a grid cell covered by a protected area should be 32% (136 cells), which is very close to the 33% used in this study as a particular case (Fig. 4). The real percentage covered by all protected areas in South America is almost 12.5%, representing 228 cells. Matching this number of grid cells with a percentage cut-off criterion results in a threshold of 36% of protected area overlap with a grid cell.

Finally, I did not take socio-economic factors (i.e., population density, development, agriculture, etc.) into account, and conflicts may arise between conservation and anthropogenic factors in some of the cells selected in this exercise. Addition of socio-economic factors could certainly alter the selection of cells and lead to an increase in the number of cells needed to conserve at least 1 population of each species (Fjeldså and Rahbek, 1998; Luck et al., 2004).

The approach presented here underscores and exposes some of the broader patterns of conservation gaps of South American terrestrial mammals. Further investigations at finer resolutions, and detailed assessments of species present in protected areas, including other taxonomic groups, are needed to improve upon this study. Additional data would allow a more precise assessment of the gaps in species representation, and would guide management decisions and conservation strategies at finer scales. A systematic conservation planning approach (Margules and Pressey, 2000), taking into account socio-economic and other variables, besides and in addition to biodiversity, should guide the establishment of new conservation areas in South America, as an alternative to older *ad hoc* methodology.

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LITERATURE CITED

Aggarwal, A., J. Garson, C. R. Margules, A. O. Nicholls, and S. Sarkar
2000 ResNet Manual. University of Texas, Austin, Texas, USA.

Araújo, M. B.
1999 Distribution patterns of biodiversity and the design of a representative reserve network in Portugal. Diversity and Distributions 5:151-163.

2004 Matching species with reserves - uncertainties form using data at different resolutions. Biological Conservation 118:533-538.

Arita, H. T., J. G. Robinson, and K. H. Redford
1990 Rarity in the Neotropical forest mammals and its ecological correlates. Conservation Biology 4:181-192.

Ball, I., and H. Possingham
2000 MARXAN (Marine Reserve Design using Spatially Explicit Annealing) Version 1.8.2. The University of Queensland, Australia.

Brooks, T., A. Balmford, N. Burgess, J. Fjeldså, L.A. Hansen, J. Moore, C. Rahbek, and P. Williams
2001 Toward a blueprint for conservation in Africa. BioScience 51:613-624.

Castro Parga, I., J. C. M. Saiz, C. J. Humphries, and P. H. Williams
1996 Strengthening the natural and national park system of Iberia to conserve vascular plants. Botanical Journal of the Linnean Society 121:189-206.

Ceballos, G., and P. R. Ehrlich
2002 Mammal population losses and the extinction crisis. Science 296:904-907.

Eeley, H. A. C., M. J. Lawes, and B. Reyers
2001 Priority areas for the conservation of subtropical indigenous forest in southern Africa: a case study from KwaZulu-Natal. Biodiversity and Conservation 10:1221-1246.

Eisenberg, J. F., and K. H. Redford
1999 Mammals of the Neotropics. The Central Neotropics: Ecuador, Peru, Bolivia, Brazil. University of Chicago Press, Chicago, Illinois, USA. 610 pp.

Ferrier, S., R. L. Pressey, and T. W. Barrett
2000 A new predictor of the irreplaceability of areas for achieving a conservation goal, its application to real-world planning, and a research agenda for further refinement. Biological Conservation 93:303-325.

Fjeldså, J., N. D. Burgess, S. Blyth, and H. M. de Klerk
2004 Where are the major gaps in the reserve network for Africa´s mammals? Oryx 38:17-25.

Fjeldså J., and C. Rahbek
1997 Species richness and endemism in South American birds: Implications for the design of networks of nature reserves. Pp. 466-482 in Tropical forests remnants:ecology, management and conservation of fragmented communities (Laurance, W. F., and R. O. Bierregaard, eds.). University of Chicago Press, Chicago, Illinois, USA.

1998 Continent-wide conservation priorities and diversification processes. Pp. 139-160 in Conservation in a changing world (Mace, G., A. Balmford, and J. R. Ginsberg, eds.). Cambridge University Press, Cambridge, UK.

Garson, J., and S. Sarkar
2001 Surrogacy Manual, version 1.1. University of Texas, Austin, Texas, USA.

Gaston, K. J.
1994 Rarity. Chapman and Hall Ltd., London, UK. 205 pp.

IUCN 2002
2002 IUCN Red List of Threatened Species. www.iucn.org.

Jennings, M. D.
2000 Gap analysis: concepts, methods, and recent results. Landscape Ecology 15:5-20.

Luck, G. W., T. H. Rickets, G. C. Daily, and M. Imhoff
2004 Alleviating spatial conflict between people and biodiversity. Proceedings of the National Academy of Sciences (USA) 101:182-186.

Lund, M. P., and C. Rahbek
2002 Cross-taxon congruence in complementarity and conservation of temperate biodiversity. Animal Conservation 5:163-171.

Margules, C. R., and R. L. Pressey
2000 Systematic conservation planning. Nature 405:243-253.

Patterson, B. D., G. Ceballos, W. Sechrest, M. F. Tognelli, T. Brooks, L. Luna, P. Ortega, I. Salazar, and B. E. Young
2003 Digital distribution maps of the mammals of the western hemisphere, version 1.0. NatureServe, Arlington, Virginia, USA.

Pressey, R. L., C. J. Humphries, C. R. Margules, R. I. Vane-Wright, and P. H. Williams
1993 Beyond opportunism: key principles for systematic reserve selection. Trends in Ecology and Evolution 8:124-128.

Pressey, R. L., H. P. Possingham, and C. R. Margules
1996 Optimality in reserve selection algorithms: when does it matter and how much? Biological Conservation 76:259-267.

Pressey, R. L., and S. L. Tully
1994 The cost of ad hoc reservation - a case-study in western new-south-wales. Australian Journal of Ecology 19:375-384.

Rabinowitz, D., S. Cairns, and T. Dillon
1986 Seven forms of rarity and their frequency in the flora of the British Isles. Pp. 182-204 in Conservation Biology: The Science of Scarcity and Diversity (Soulé, M. E., ed.). Sinauer, Sunderland, Massachusetts, USA.

Rahbek, C., and G.R. Graves
2001 Multiscale assessment of patterns of avian species richness. Proceedings of the National Academy of Sciences (USA) 98:4534-4539.

Rebelo, A. G., and W. R. Siegfried
1992 Where should nature-reserves be located in the cape floristic region, South Africa? Models for the spatial configuration of a reserve network aimed at maximizing the protection of floral diversity. Conservation Biology 6:243-252.

Rodrigues, A. S., J. O. Cerdeira, and K. J. Gaston
2000 Flexibility, efficiency, and accountability: adapting reserve selection algorithms to more complex conservation problems. Ecography 23:565-574.

Rodrigues, A. S. L., S. J. Andelman, M. I. Bakarr, L. Boitani, T. M. Brooks, R. M. Cowling, L. D. C. Fishpool, G. A. B. da Fonseca, K. J. Gaston, M. Hoffman, J. Long, P. A. Marquet, J. D. Pilgrim, R. L. Pressey, J. Schipper, W. Sechrest, S. N. Stuart, L. G. Underhill, R. W. Waller, M. E. J. Watts, and X. Yan
2003 Global Gap Analysis: towards a representative network of protected areas. Advances in Applied Biodiversity Science 5. Conservation International, Washington D.C., USA. 100 pp.

Rodrigues, A. S. L., R. Tratt, B. D. Wheeler, and K. J. Gaston
1999 The performance of existing networks of conservation areas in representing biodiversity. Proceedings of the Royal Society of London Series B Biological Sciences 266:1453-1460.

Sarakinos, H., A. O. Nicholls, A. Tubert, A. Aggarwal, C. R. Margules, and S. Sarkar
2001 Area prioritization for biodiversity conservation in Quebec on the basis of species distributions: a preliminary analysis. Biodiversity and Conservation 10:1419-1472.

Sarkar, S., A. Aggarwal, J. Garson, C. R. Margules, and J. Zeidler
2002 Place prioritization for biodiversity content. Journal of Biosciences 27:339-346.

Tognelli, M. F.
2005 Assessing the utility of indicator groups for the conservation of South American terrestrial mammals. Biological Conservation 121:409-417.

Wessels, K. J., B. Reyers, and A. S. Van Jaarsveld
2000 Incorporating land cover information into regional biodiversity assessments in South Africa. Animal Conservation 3:67-79.

WDPA (World Database on Protected Areas)
2004 IUCN-WCPA/UNEP-WCMC, Washington D.C., USA.

Williams, P., D. Gibbons, C. Margules, A. Rebelo, C. Humphries, and R. Pressey
1996 A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. Conservation Biology 10:155-174.

Williams P. H., N. Burgess, and C. Rahbek
2000a Assessing large ‘flagship species’ for representing the diversity of sub-Saharan mammals. Pp. 85-99 in Priorities for the Conservation of Mammalian Diversity: Has the Panda had its Day? (Entwistle, A., and N. Dunston, eds.). Cambridge University Press, Cambridge, UK.

2000b Flagship species, ecological complementarity and conserving the diversity of mammals and birds in sub-Saharan Africa. Animal Conservation 3:249-260.

DOMESTICATION OF GUINEA PIGS FROM A SOUTHERN PERU-NORTHERN CHILE WILD SPECIES AND THEIR MIDDLE PRE-COLUMBIAN MUMMIES

DOMESTICACIÓN DEL CUY A PARTIR DE POBLACIONES ORIGINARIAS DEL SUR DEL PERÚ Y NORTE DE CHILE, CON LA DESCRIPCIÓN DE SUS MOMIAS PRECOLOMBINAS

Angel E. Spotorno, Germán Manríquez, Andrea Fernández L.,
Juan Carlos Marín, Fermín González, and Jane Wheeler

ABSTRACT

To investigate the origins and domestication of guinea pigs, or cuyes (*Cavia porcellus*), we re-analyzed 12S rRNA (759 bp) and cytochrome *b* gene (1140 bp) sequence data from relevant species and breeds. Seventeen pre-Columbian mummified cuyes from southern Peru and northern Chile sites are described and compared with both domesticated (living Andean creole and European breeds) and wild species. All molecular analyses point to the western *C. tschudii* rather than to the eastern *C. aperea* as the ancestral wild species. Domesticated Andean and European cuyes were different both in biochemical and morphological analysis ; both breeds exhibited a lower neurocranium than that of *C. tschudii*. Principal component analysis of skeletal measurements showed that most of the mummies anayzed were juveniles, but at least 2 appeared to be adults when compared with wild and Andean cuyes. The degree of domestication in these mummies was evaluated under the criteria of the "domestication syndrome": their size, hair color and design polymorphisms, and lower skulls demonstrated that they were fully domesticated in southern Perú-northern Chile more than 500 years before the arrival of Spaniards to the Americas; this was the first or major step in the process of cuy domestication. The second stage was the European one, under a different selection regime acting for another 500 years. The third stage is ongoing, with heavy selection for size and meat volume.

Key words: Andes, Caviidae, Chile, Perú, 12S, cytochrome *b*, skull, domestication syndrome, guinea pig

RESUMEN

Para investigar los orígenes y la domesticación de los cobayos o cuyes (*Cavia porcellus*), hemos re-analizado los datos de secuencias para 12S rRNA (759 pares de bases) y del

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Pp. 367-388 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

gen para citocromo *b* (1140 pares de bases) en especies y cepas relevantes. Se describen 17 cuyes precolombinos momificados del sur del Perú y norte de Chile, los que son comparados con domesticados (cepas criollas andinas y europea) así como con especies silvestres. Todos los análisis moleculares indican que la especie ancestral es *C. tschudii* de los Andes Occidentales más que la oriental *C. aperea*. Los cuyes domésticos de los Andes y de Europa resultaron diferentes tanto en los análisis bioquímicos como morfológicos; ambas cepas mostraron neurocráneos más bajos que aquéllos de *C. tschudii*. El análisis de componentes principales de medidas esqueléticas mostró que la mayoría de las momias analizadas eran juveniles, pero al menos 2 aparecieron como adultos cuando se los comparó con los cuyes silvestres y andinos. El grado de domesticación de estas momias fue evaluado según los criterios del "síndrome de domesticación": sus tamaños, color de pelaje y polimorfismos de diseño mostraron que ellos ya estaban completamente domesticados en el sur del Perú y norte de Chile más de 500 años antes de la llegada de los españoles a las Américas; ésta fue la primera o principal etapa en el proceso de domesticación del cuy. La segunda etapa fue la europea, bajo un régimen diferente de selección actuando durante otros 500 años. La tercera etapa es la actual, con fuerte selección para tamaño y volumen de carne.

Palabras claves: los Andes, Caviidae, Chile, Perú, 12S, citocromo *b*, craneo, sindrome de domesticación, cuy

INTRODUCTION

Cuyes, cavies, or "guinea pigs" (*Cavia porcellus* (Linnaeus 1758)) are small mammals of South American origin (Wagner and Manning, 1976), still kept today as "criollos" (Chauca, 1997) by the native peoples of the Andes for food and cultural practices (Morales, 1994). They are also well known as domestic pets and laboratory models utilized worldwide since their introduction to Europe in the XVI Century from undocumented sources (Woods, 1993). Along with llama and alpaca, the cuy is one of only 3 mammal species to have been domesticated in the Americas, probably within the single domestication center of the New World: the Central Andes (Wing, 1986). By the time the Spaniards arrived in the Americas, cuyes were fully domesticated (Clutton-Brock, 1999), but very few details of the early process of domestication are known.

Despite the extensive knowledge accumulated on the biology (Cooper and Schiller, 1975; Wagner and Manning, 1976) of the European breed, *C. porcellus*, there are many controversies about its precise geographic origins (Clutton-Brock, 1999), phylogenetic relationships (Weir, 1974), and even its conspecificity with 1 of the 5 presently recognized wild species of the genus *Cavia* living in South America (Woods, 1993). For instance, *C. porcellus* was included within *C. aperea* (Eisenberg and Redford, 1999), and some recent authors still name cuyes as *Cavia aperea* f. *porcellus* (Sachser, 1998; Kunzl and Sachser, 2000; Trillmich et al., 2003); such taxonomic ascription was based on morphological studies (Huckinghaus, 1961, but see Cabrera (1953) for an alternative view) and the important fact that fertile hybrids were produced from *C. aperea* x *C. porcellus* crosses (Pictet and Ferrero, 1951; Rood, 1972). However, fertile hybrids also were produced by crossing *C. porcellus* with *C. tschudii* collected in Cusco, Peru (Castle, 1916). By contrast, crosses of domestic cuyes with a third living species, *C. fulgida* from Brazil, gave infertile males (Detlefsen, 1914). Therefore, and considering that most agree that species are closed genetic systems in nature (Harrison, 2002), the 2 most probable living candidates for the ancestral species of domestic cuyes are the eastern *C. aperea*, now ranging from Colombia through Argentina (Eisenberg and Redford, 1999), and the western *C. tschudii,* from southern Peru and northern Chile (Eisenberg and Redford, 1999). Given the disjunct geographic distribution of these 2 species, the determination of the ancestral species would be a clue of the whereabouts of the original area of domestication (Weir, 1974).

The most promising solution to the question of guinea pig origins involves the application of modern molecular techniques (Hillis et al., 1996). Although Rowe & Honeycutt (2002) have recently reassessed the work of Nedbal (1994), adding 2 nuclear sequences to the original work with 12S plus morphological and ecological correlates, neither study examined the *C. aperea* and *C. tschudii* sequences simultaneously. In the present study we reexamine 12S sequence data to compare results with those based on the complete cytochrome *b* gene sequences of *Cavia* species (Spotorno et al., 2004) and address the question of cuy origins.

Direct evidence about the domestication process is preserved in numerous naturally mummified cuyes of different periods recovered from many Andean archeological sites (Fig. 1). Sacrificial cuyes were included as religious offerings in human tombs or house settlements (Gade, 1967; Sandweiss and Wing, 1997); many anatomical features are preserved in these burials due to the extreme aridity in these areas. In general, these cuyes have been studied more as cultural objects than as complex biological entities (Archetti, 1997). Herein, we describe and analyze 16 cavy mummies recently excavated from southern Peru at the El Yaral site (Rofes, 1998; Rofes and Wheeler, 2003), as well as a single cuy mummy found in a northern Chile site, Punta Pichalo, Pisagua, excavated early in the 20th century by the German archeologist M. Uhle (Uhle, 1917). These 2 sites are located within the present geographic distribution of the extant *C. tschudii* (Eisenberg and Redford, 1999).

The purposes of the present paper are: (1) to re-analyze 12S molecular data relevant to the origin and divergence of the domestic guinea pigs, (2) to document and analyze 17 pre-Columbian mummified cuyes from southern Peru and northern Chile sites, (3) to evaluate whether such pre-Hispanic cuyes were fully domesticated, by comparing them with actual Andean breeds and wild species, and (4) to suggest a plausible scheme describing the processes which occurred during the domestication of cuyes.

MATERIAL AND METHODS

*Specimens***.** Wild and domestic animals or archeological samples were obtained in the field from rural houses or from museum collections. Skulls and skins, whenever available, were prepared as voucher specimens; most were deposited in the collection of the Laboratorio de Genómica Evolutiva, Instituto de Ciencias Biomédicas, Facultad de Medicina, Universidad de Chile, Santiago, Chile (acronym LCM). Taxonomy follows Woods (1993). Original localities of examined specimens, and sources (collection numbers) are in Appendix 1. GenBank accession numbers of sequences are listed below.

We studied X-rays of 16 mummies from El Yaral site (Valley of Moquegua, southern Peru), specifically collected at the locality named M8. These animals were

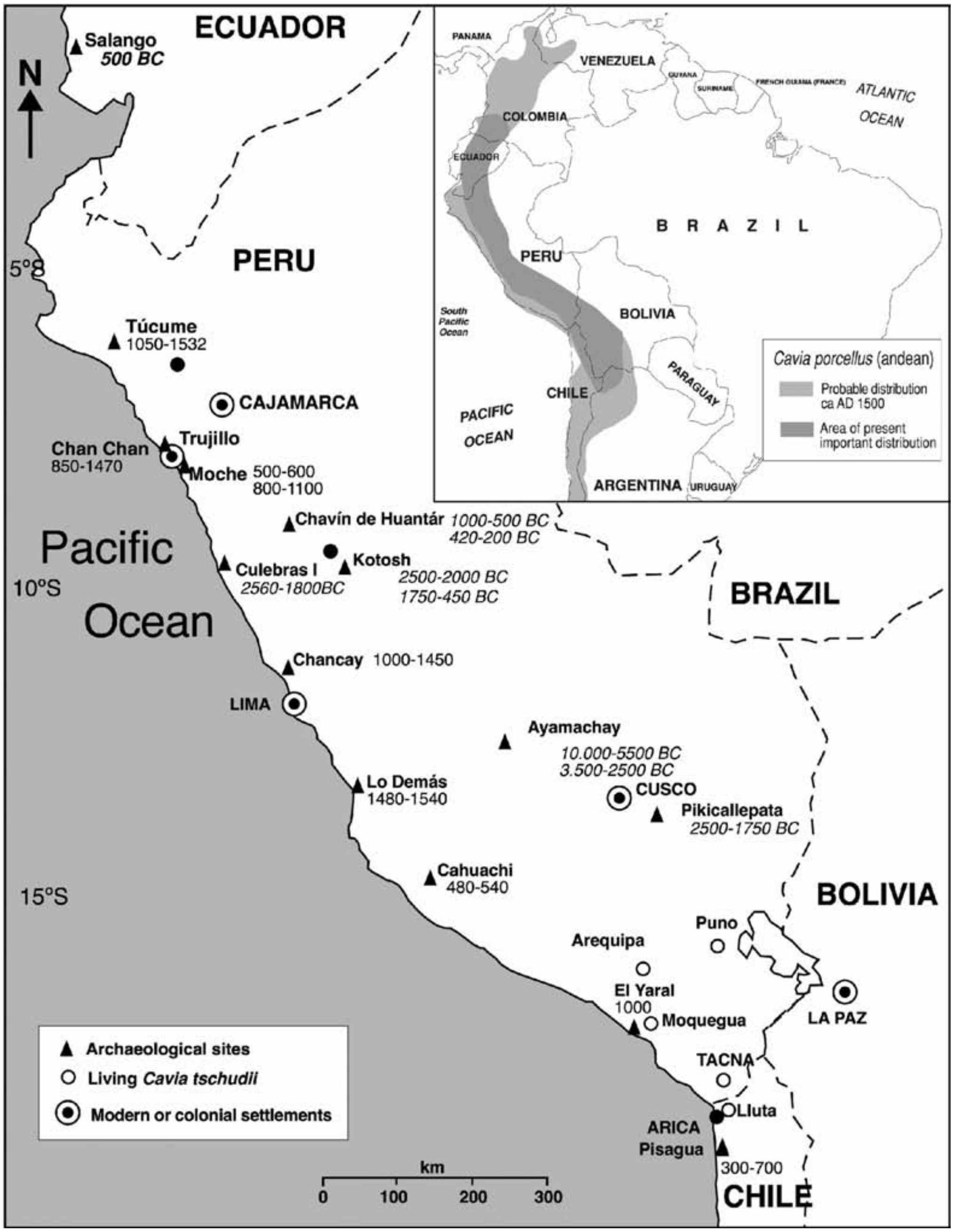

Figure 1. Map of archeological sites with guinea pig remains (modified from Sandweiss and Wing, 1997). Approximate B.P. dates are shown; B.C. dates are in italics. Modern or colonial settlements are included. Some localities of wild Cavia tschudii also shown. Inset: Historical and present distribution of domestic cuyes (Andean breed) in South America (modified from Gade 1967).

chosen from approximately 70 naturally desiccated guinea pigs, sacrificed and buried beneath 3 habitation structures of a Chiribaya occupation (Rofes, 1998). This material has been ascribed to the "Intermedio Tardío Peruano", 1000 A.D. (Rofes, 1998; Rofes and Wheeler, 2003) . Twenty-three naturally mummified llamas and alpacas were also recovered from the same site (Wheeler et al., 1998), as were their parasites (Leguia and Casas, 1998).

The other mummy we studied was from Punta Pichalo, Pisagua, Chile; it belonged to the Max Uhle Collection, now deposited at the Museo Nacional de Historia Natural in Santiago, Chile. It carried a label with the inscription "2.532 M.N.H.N. Caja 133. Cuerpo disecado de roedor cui?. CEMENTERIO "C" arriba. PISAGUA (PTA. PICHALO) REG. TARAPACA."; at the reverse is written "Colecc. Max Uhle. 1913". It was originally found together with many cultural objects, all listed in Cocilovo (1994). The C cemetery, or Pisagua C, was originally ascribed to the Tiwanaku Period, 400-700 AD (Uhle, 1919), although it was recently extended to encompass 300-700 AD (Cocilovo, 1994). This specimen had received only cursory cataloguing (Uhle, 1919).

Molecular Analysis. We used the following mitochondrial 12S rRNA gene sequences retrieved from GenBank: *Dolichotis patagonum* AF433939, *Dolichotis salinicola* AF433918 and AF433919, *Galea musteloides* AF433910 and 433911, *Galea spixii* AF433934, *Microcavia australis* AF433914 and AF433915, *Cavia aperea* AF433908, *Cavia porcellus* AF433909 (see Rowe and Honeycutt, 2002), and *Cavia tschudii* AY012121 (see Murphy et al., 2001), and *Cavia guianae* U12449 (see Nedbal et al., 1994). Sequences were aligned using Clustal V (Higgins et al., 1992) and proofed by hand, resulting in a total of 895 characters. Following previous analysis on this particular gene (Rowe and Honeycutt, 2002), 136 ambiguous base pairs (sites 57-62, 75-85, 115-121, 161-166, 217-231, 289-293, 299-303, 314-326, 367-382, 477-481, 653-660, 739-746, 751-760, 776-781, 881-895) were removed, leaving 759 bp for phylogenetic analysis. Maximum-parsimony (MP) analyses were conducted using PAUP*4.0b8a (Swofford, 2002). The branch-and-bound option was used to identify the most parsimonious tree(s). Heuristic bootstrap analysis with 1,000 replicates were run, and Bremer decay indexes (SI) were calculated using AutoDecay 4.0 (Eriksonn, 1999) to estimate branch support.

Maximum likelihood (ML) analyses also were implemented in PAUP* 4.0b8a (Swofford, 2002), with gaps excluded. The HKY+G model generated significantly better likelihood scores using MODELTEST (Posada and Crandall 1998); therefore this model was chosen to perform heuristic searches with the tree-bisection-reconnection (TBR) branch swapping, and bootstrap analysis.

Morphological Descriptions. We have followed the standard nomenclature and anatomical descriptions extensively treated elsewhere for *C. porcellus* (Cooper and Schiller, 1975).

Geometric Morphometrics Analysis of Skull Shape Variation. Twenty landmarks were defined along the *Cavia* skull, chosen to recover most of its morphology. The coordinates for each specimen were registered through the program TPSDIG (Rohlf, 1998). Mean configuration for individuals in a sample was obtained by the technique of generalized adjustments of minimum squares (Rohlf and Slice, 1990), minimizing the differences due to scale, translation and rotation between specimens. Such mean configurations were used to estimate the affine and non-affine (partial warps) components of shape.

Variation in their mean positions through the different samples (*C. tschudii* $N = 16$, *C. porcellus* Andean breed $N = 13$, and *C. porcellus* European breed $N = 14$; original localities and museum collection numbers in Appendix 1) were analyzed by means of the Thin Plate Spline technique (relative warp analysis), available through the computer programs TPSPLINE and TPSRW (Rohlf and Slice, 1990).

Skeletal Measurements and Principal Component Analysis. Whole specimens were photographed under x-ray machines at natural size, extending their legs if possible, or taking photographs from various angles. Negatives were scanned to digital form, and measurements from images were taken through the NIH Image v. 1.61 computer program (Rasband and Bright, 1995). We performed principal components analysis on a variance-covariance matrix, with the program NTSYS-pc v 2.1a (Rohlf, 1995). To estimate standard errors for the principal components, a jackknife resampling procedure was applied using the program JACKknifed Interactive Eigenanalysis v. 1.2 (Cavalcanti, 2001).

RESULTS

Molecular Analysis of 12S Gene Sequences from Domestic and Wild Cavies

Maximum-parsimony (MP) analysis of the 759 bp matrix detected 175 parsimony-informative characters and generated a single parsimonious tree of 320 steps. This tree (Fig. 2) had a Consistency Index (CI) of 0.75, and a Recalculated Index (RC) of 0.56. Bootstrap and Support Index values (Fig. 2) gave strong support to all branches except that of the *C. porcellus* -*C. tschudii* branch, which received a support of 85% bootstrap

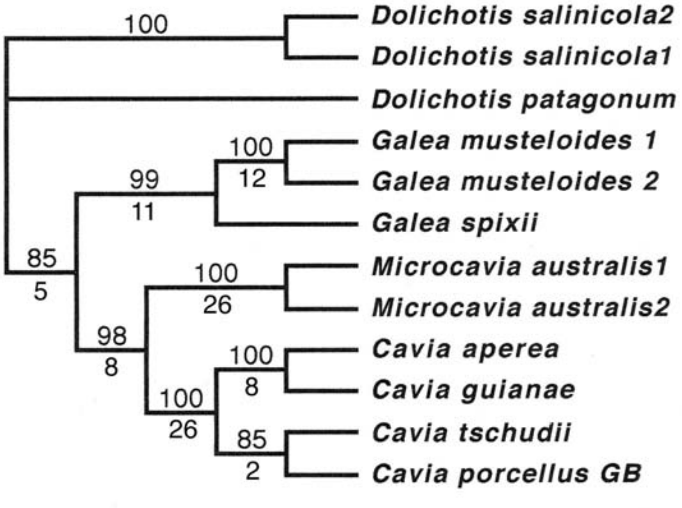

Figure 2. Maximum parsimony tree based on published 12S rRNA sequences (see Material and Methods). Bootstrap values above branches, Bremer Support Index values below them.

and a SI of 2. This branch was based on a single substitution at site 67, in contrast with the 6 substitutions shared by *C. aperea* and *C. guianae*. Given the contrasting hypothesis about the relationships of domestic cuyes, we force *C. aperea* to join *C. porcellus*; this alternative tree had 16 additional steps, a CI = 0.71, and a RC = 0.50, with no substitutions defining this hypothetical branch (Kishino-Hasegawa test as implemented in PAUP; $p < 0.0001$).

Maximum-likelihood analysis produced a tree identical to the most parsimonious one, with a –ln L of 2559.35. All bootstrap values (500 replicates) were also high except that of the *C. porcellus* -*C. tschudii* branch, which received only a 65% support. Forcing *C. aperea* to be the sister branch of *C. porcellus* produced a significantly less likely topology (-ln L = 2648.49; Kishino-Hasegawa test; $p < 0.001$).

Geometric Morphometry of Skull Modified by Domestication

The deformation in the grids recovering the shape changes in the skulls of the Andean and European breeds of *C. porcellus* compared with those of wild *C. tschudii* exhibited significant differences in the affine and non affine components (not shown). Most of the non-affine variations affected the neurocranial region (Fig. 3c), with a contraction of the braincase at the landmarks associated with the coronal, sagittal, and parietal sutures (landmarks 5 and 6 in Fig. 3), and with the most posterior point at the nuchal crest (landmark 7). When the skulls of both breeds of *C. porcellus* were compared, slight differences in the orbit, maxillary, bullae, and paracondylar process sizes and shapes were evident (left of Fig. 3), but they were not significant by the methods and landmarks used here.

Cavy Mummies from Southern Peru-northern Chile

Cavies from El Yaral, southern Peru

From this site we obtained a series of well-preserved bodies, all with their heads removed and placed above or beneath each individual (Plate I). In 7 bodies whose vertebral columns were observed under the X-rays, most if not all cervical vertebrae were twisted or bent, a clear indication of the killing method used. No visible tails were externally observed, but several internal caudal vertebrae usually were visible in the radiographs. Specimen M8-8254 showed a rounded mass 5 mm in diameter inside the mouth (Plate Ic); also, specimen 7364 showed an elongated mass 9 mm long in the same place (Plate Id). Four and 3 digits were usually seen in the manus and pes, respectively. Substantial portions of intestines and most internal organs were evident on the X rays (Plate Ib). Skin colors were variable, from uniform brown to chestnut, dark brown, and orange piebald (Table 1).

Most specimens appeared to be juveniles, judging from the measurements of their skulls and long bones when compared with those of wild *C. tschudii* and *C. porcellus* adults (Table 1). In fact, most mummies obtained negative values along the first axis in the principal component analysis (Fig. 4). This particular axis explained 80.4% of the total variance, and had correlations of 0.61 with the diastema length (Table 2), and then of 0.39 with humerus lengths (Table 2). Nevertheless, at least 2 of these mummies (7230 and 3026) were larger than some wild *C. tschudii* and *C. porcellus* adults included for comparison; for instance, wild specimen 3080 was a mature male with differentiated

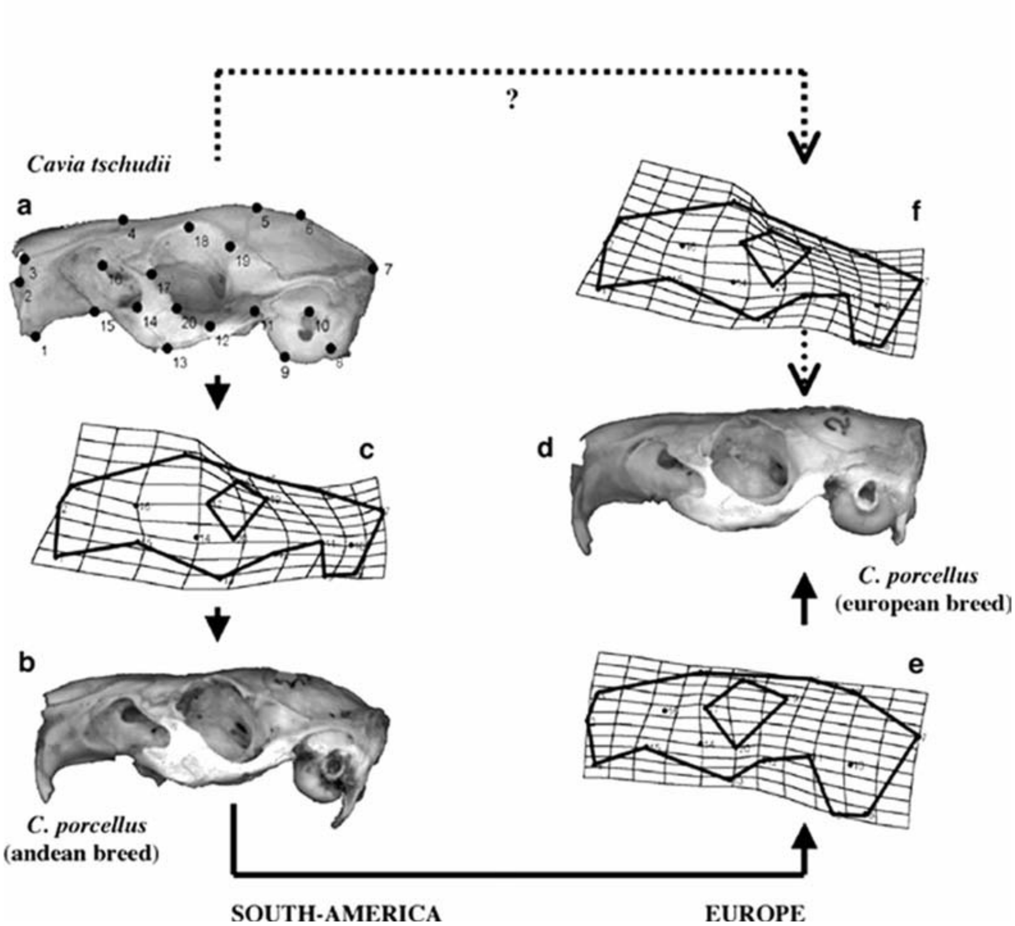

Figure 3. Geometric morphometry analysis of guinea-pig skull shape variation through domestication. A. Lateral view of a *Cavia tschudii* skull, with 20 defined landmarks chosen to describe its basic morphology. B. Lateral view of an Andean *C. porcellus* skull. C. Transformed cartesian grid obtained when the 20 landmarks of Andean *C. porcellus* were superimposed with the homologous landmarks from *C. tschudii*. D. Lateral view of an European *C. porcellus* skull. E. Transformed cartesian grid obtained when the 20 landmarks of European *C. porcellus* were superimposed with the homologous landmarks from Andean *C. porcellus*. F. Transformed cartesian grid obtained when the 20 landmarks of European *C. porcellus* were superimposed with the homologous landmarks from wild *C. tschudii*. Solid arrow shows the most plausible direction of skull shape variation associated with the *Cavia* domestication process. A less probable transition from *C. tschudii* to the European breed is also shown (dotted line).

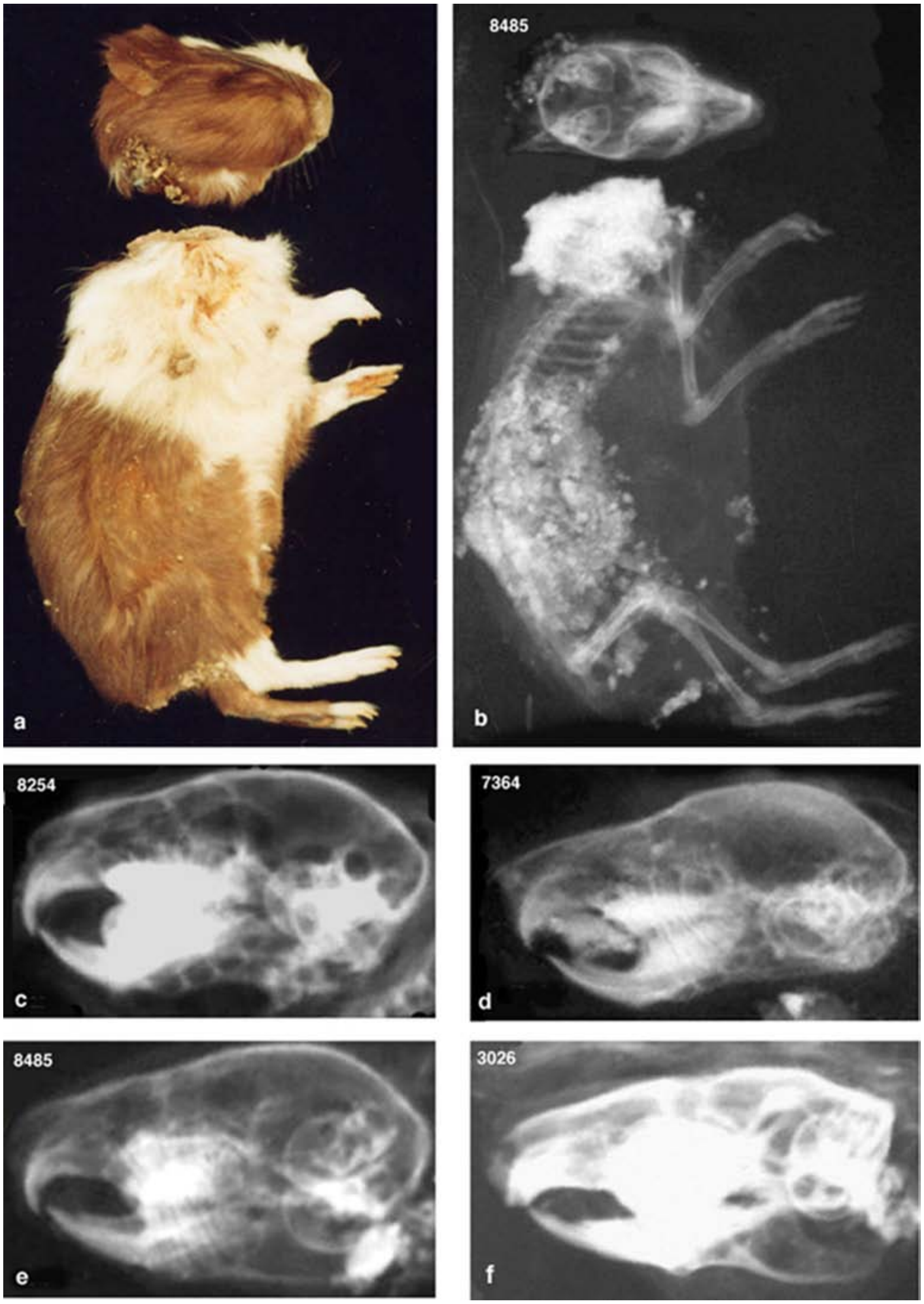

Plate I. Guinea pig mummies from El Yaral, Moquegua, Peru. a) external and b) X-ray of young specimen M8 8485 (see Table 1). c) d) and e) Young specimens. f) Adult M8 3026.

Table 1. Measurements (in grams and millimeters) and skin color of naturally desiccated cuy mummies from the sites of Punta Pichalo, Pisagua (northern Chile, MHN) and El Yaral (southern Peru, site M8, material kept by J. Wheeler), of contemporary domestic cuyes, and wild guinea pigs (LCM). GL = Greatest length. Measurements judged to be underestimations (i.e., dry weights) are in square brackets.

Specimen (together with)	Weight gr	Skull GL	Humerus GL	Femur GL	Molar Row	Diastema	Tibia GL	Dorsum Color	Venter Color	Foot Color	Face Color
MHN 2532	38	54	36	39	16	13	37	gray	yellow	gray	black line
M8-3026	-	65	40	47	18	15	44				
M8-7230	[95.5]	55	34	39	19	12	41	brown	brown	white	brown
M8-7364	-	42	[20]	[24]	12	9	29	orange	orange	white	white
M8-7453	-	-	-	-	-	-	-	brown	brown	brown	white
M8-8033	[80.3]	63	-	-	15	14	-	brown	brown	brown	brown
M8-8085	-	45	[20]	[30]	-	6	[28]	chestnut	chestnut	chestnut	white
M8-8254	-	42	25	29	12	9	30	brown	white	brown	brown
M8-8262	[56.1]	-	-	-	-	-	-	orange	white	white	orange
M8-8263	[31.5]	43	26	29	14	5	30	brown	white	brown	brown
M8-8264	-	50	32	35	13	10	37				
M8-8396 (R236)	[36.8]	44	30	34	13	8	36	orange	orange	white	orange
M8 8485	-	41	25	28	11	10	30	brown	white	white	brown
M8-8849 (R267)	-	43	28	30	12	11	32	chestnut	white	white	brown
M8-8849-2	-	46	29	32	13	10	32				
M8-2208 (Yaral 62)								brown	brown	brown	brown
M8-R193 (Yaral 64, 316)								brown	brown	white	brown

Table 1 (continued).

Cavia porcellus (Andean breed, Arica, Chile)											
LCM 3137	743	59	36	45	12	11	46	black			
LCM 3135	823	69	41	45	17	18	46	gray			
LCM 3136	-	68	41	47	16	17	47	brown			
LCM 3138	858	68	41	49	18	13	48	white			black
Cavia tschudii (Lluta, 30 km west of Arica, Chile)											
LCM 3081	300	61	45	42	14	13	50	gray agouti			
LCM 3080	306	56	36	39	11	12	42	gray agouti			
LCM 3110	233	57	43	44	13	12	45	gray agouti			

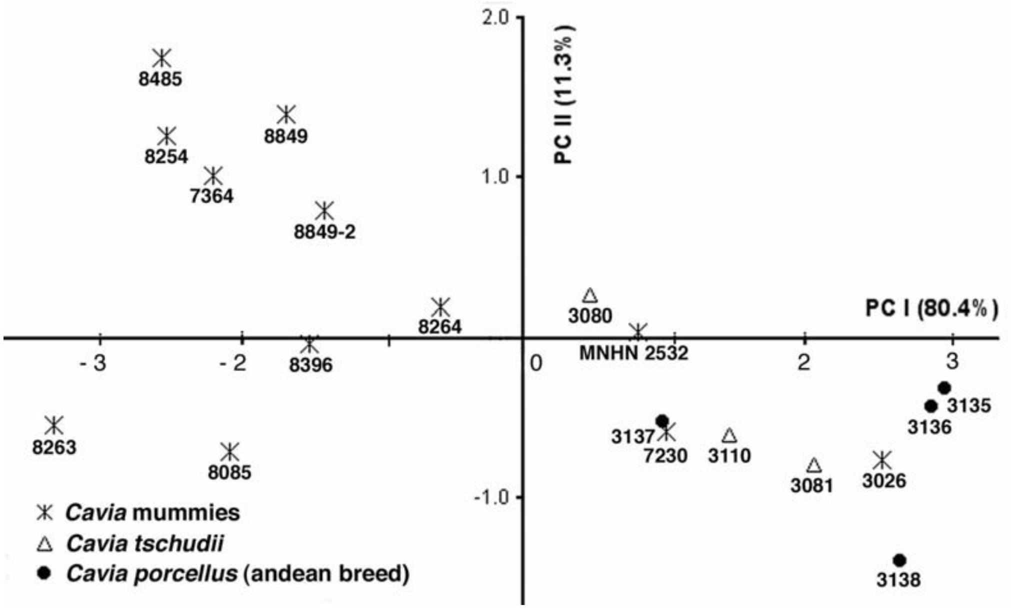

Figure 4. Principal Component Analysis of skeletal measurements from domestic cuyes (Andean breed), mummies and wild guinea pigs (from data in Table 1). Numbers designate collection number of specimens. Percentages are percent of total variance explained by each axis.

Table 2. Coefficients of each morphological variable on the first 3 PC axes (eigenvalues in parenthesis).

	Axis1 (0.0413)	Axis 2 (0.0058)	Axis 3 (0.0033)
Skull	0.3832	-0.2021	-0.0157
Humerus	0.3928	-0.2832	-0.2594
Femur	0.3664	-0.2811	-0.1213
Molar row	0.2339	-0.3127	0.8995
Diastema	0.6138	0.7785	0.0933
Tibia	0.3648	-0.3099	-0.3161

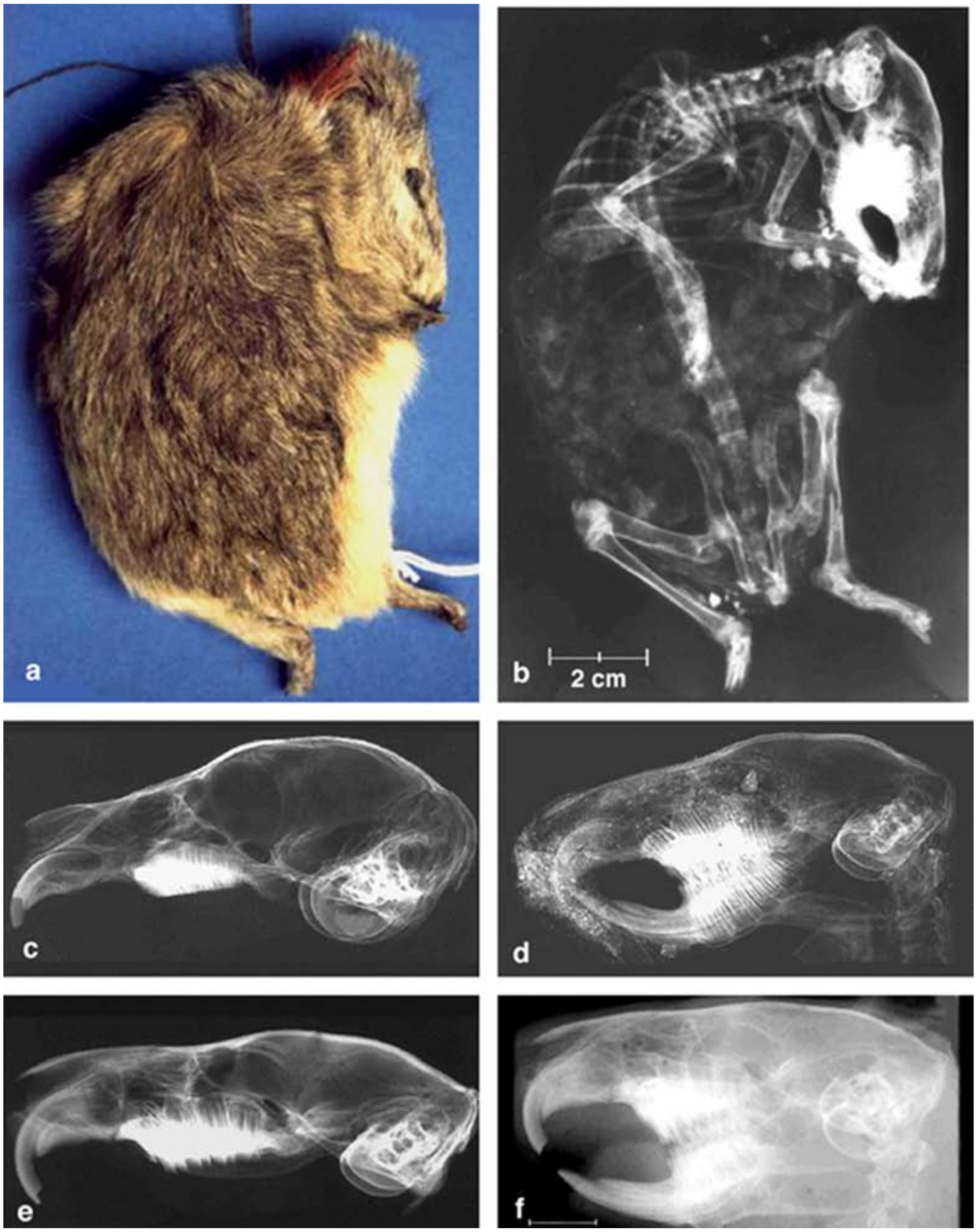

Plate II. Guinea pig mummy MNHN 2532 from Punta Pichalo, Pisagua. Chile and domestic and wild cavies. a) Mummy external dorsal view. Flamingo red feather at the neck tied with camelid brown thread (terminals above). b) X-ray. Intestine portions (arrows). c) Wild *Cavia tschudii* LCM 205, skull X-ray . d) Mummy skull X-ray. e) *Cavia porcellus*, Andean breed skull from Arica, Chile; 91 days age. f) *Cavia porcellus*, laboratory breed skull.

sperms within an 18 x 16 mm testes.

Cavy from Punta Pichalo, Pisagua, Chile

This specimen is a very well-preserved body with the full skeleton intact (Plate II). It had a brown thread tied around the neck, probably made of llama or alpaca wool, with a red feather that was identified as belonging to a flamingo (Plate IIa). The body exhibited no externally visible tail, but at least 4 distal caudal vertebrae were clearly revealed in the radiographs, probably Ca4 through Ca7 (Cooper and Schiller, 1975). Skull morphology confirmed that it belonged to a member of the genus *Cavia* (Eisenberg and Redford, 1999). Four digits in the right manus and 3 digits at the right pes were observed, and the corresponding phalanges observed on the X-ray plate (Plate IIb). A few portions of the intestines were still visible, but other internal organs clearly have been removed, probably through the perigenital area, which showed some visible cuts.

The skin color was uniformly gray brown with a yellowish belly, but a remarkable black frontal line 3 mm wide crossed from above the eyes to the nose and mouth. A small black line ran parallel to the frontal line from the internal border of the right eye towards the mouth (Plate IIa), but was less apparent on the left side. The body size of this mummy appeared to be similar to mature wild and domestic guinea pigs (Fig. 4). Its diastema, molar row and femur lengths were similar or higher than those of the wild guinea pig 3081 or the domestic Andean breed 3137 (Table 1).

DISCUSSION

The domestication of guinea pigs in South America has a long history of more than 4 and possibly 7 millennia (Wing, 1986). The process and its steps can be revealed by comparing the biological characteristics from 4 sets of animals: the wild species, the 2 living domestic breeds (Andean and European), and preserved remains from different periods in this process in the Andes. To our knowledge, our study is the first to consider these 4 groups simultaneously. In fact, our data clarify 3 particular issues about the process of cuy domestication: 1. the controversial origins from a wild species, 2. the diversification of living domestic cuyes; and 3. the biological characteristics of some antique mummies when compared with wild and domestic cuyes to evaluate their degree of domestication.

The most closely related wild species of domestic *C. porcellus* clearly seems to be *C. tschudii* rather than *C. aperea*, according to all available molecular data. The present re-analysis of molecular data on published 12S sequences, although weak in supporting the grouping of single specimens of *C. porcellus* with *C. tschudii* (Fig. 2), detected a single substitution exclusive to such a branch. More importantly, the alternative hypothesis of grouping *C. porcellus* with *C. aperea* was clearly rejected by both parsimony and maximum-likelihood methods. These results are consistent with those recently obtained from the analysis of complete cytochrome *b* gene sequences (Spotorno et al., 2004), where all maximum parsimony and likelihood analyses grouped *C. porcellus* with *C. tschudii* rather than with *C. aperea*. This topology also appeared in the cladistic analysis of corresponding amino acids, being supported by 3 amino acid substitutions and a 96% bootstrap (Fig. 5). When the *C. aperea* branch was forced to join *C. porcellus*, the

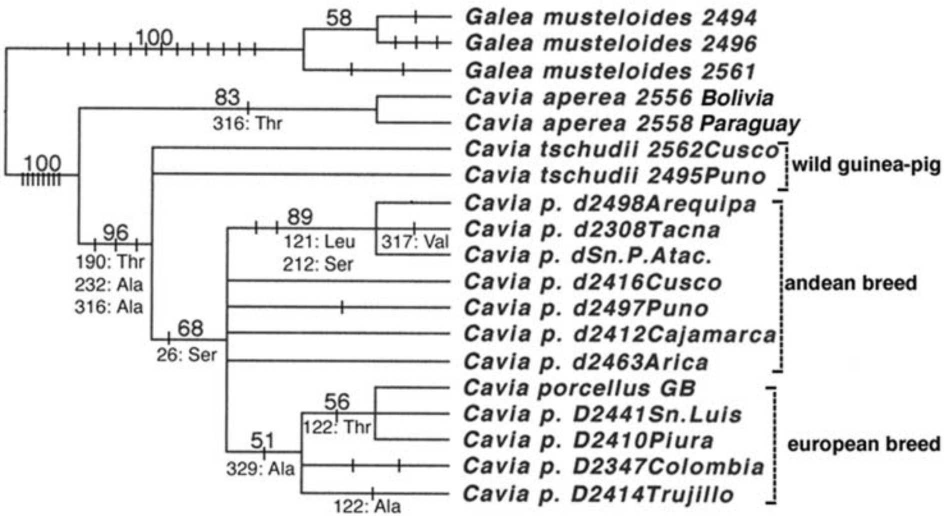

Figure 5. Consensus MP tree based on the inferred 380 amino acids of cytochrome *b* gene (51 were informative). Tree length = 779 steps. CI = 0.802 and RC = 0.72. Characters were ordered according to the outgroup. Bootstrap values (1000 replicates; >50%) over each branch. Site number below, followed by the exclusively shared amino acid substitution. Modified from Spotorno et al. (2004).

resulting trees were consistently longer, less likely, and with fewer defining characters than the best tree. If there is a living sister species to *C. porcellus*, molecular data point to the western *C. tschudii* (Eisenberg and Redford, 1999).

Based on all available data therefore, the most probable original region of cuy domestication was southern Peru and northern Chile. Concordantly, the oldest archeological site with cuy remnants is Ayamachay, in central southern Peru (Fig. 1). However, a similarly old site is located farther north, at Tequendama, near Bogotá, Colombia (Sandweiss and Wing, 1997). Examination of these remnants may provide further resolution.

The diversification of living domestic cuyes has not been studied in detail. The existence of morphological differences in at least 2 different lineages, the Andean (called "criollos" in Perú (Chauca, 1997)) and the European breeds are evident in our geometric morphometry comparisons of skull shapes (Fig. 4). Such differences were clearly documented also with cytochrome *b* gene sequences and their correspondent amino acids, where 5 European specimens clustered in a branch defined by an exclusive alanine at site 329 (Fig. 5), and supported by a 84% bootstrap in the more reliable maximum likelihood analysis of original DNA sequences (Spotorno et al., 2004). By contrast, the 7 Andean specimens studied did not cluster in a single group, although a distinct southern Perú/northern Chile lineage emerged in all analyses; it had 2 exclusive amino acid substitutions (Fig. 5) and was supported by a 99% bootstrap in maximum likelihood analyses. Thus, these data show that the Andean lineage is diverse, most probably the actual descendants of pre-Columbian lineages, and clearly distinct from the European breed. Further morphological and molecular studies of worldwide samples might detect other lineages of *C. porcellus*, in particular the old pre-Columbian lineages still raised in many rural houses throughout the Andes. Unfortunately, the commercial dissemination of improved cuyes (Chauca, 1997) and the actual urbanization and acculturation processes acting on Andean indigenous peoples (Archetti, 1997) are increasing the mixing and loss of many of these ancient genomes.

The process towards the domestication of a mammal species appears to follow a universal pattern, producing the so-called "domestication syndrome" (Thorpe and Smartt, 1995). It is characterized by increase in body size and fertility, pelage polymorphisms, changes in the color and size of eyes, ears, and face, reduction of brain size and dentition, redistribution of body fat, and behavioral changes, among others. In the case of cuyes, the rather numerous well-preserved mummies provide the intermediate material linking the wild species to the living domestics. Now that the ancestral wild species is known, a better evaluation of the degree of domestication degree in such mummies can be performed.

Although the mummies from El Yaral and Pisagua studied here belong to a rather late pre-Columbian period (Fig. 1), they seem to be fully domesticated, according to some of the above criteria. At least 2 of them (3026 and 3137) have similar or larger sizes than mature wild *C. tschudii* and Andean *C. porcellus* (Fig. 4); the Pisagua mummy is also similar in size to adult wild *C. tschudii*. Moreover, most of them show skins with evident color polymorphisms (El Yaral, Table 1 and Plate Ia) or particular hair designs (Pisagua, Plate IIa). Finally, most of them seem to have reduced brains, judging from the low neurocranial heights of their skulls (Plates I and II), with the exception of juveniles such as 8254, 7364, and 8485 (Plate Ic, d and e, and Table 1).

Domestication traits in pre-Columbian cavies have rarely been reported. The coat color of 5 mummified young guinea pigs from Lo Demás (Fig. 1) is said to be varied (Sandweiss and Wing, 1997). Three cavies from a pre-Columbia site at Ancón, Perú "had quantities of adhering white and/or pure brown hairs" (Gilmore, 1950). The predominance of juvenile mummies usually precludes an easy detection of size increase. Nevertheless, the traits of El Yaral and Pisagua mummies described above demonstrate that guinea pigs were already domesticated between AD 300 and 1000, well before the Spaniards arrived to the Americas in the XVI century.

The domestication of guinea pigs might be briefly described as a 3-step process. The major or first domestication, from the wild species to the fully domestic pre-Columbian cuy, occurred in the western Andes. The local indigenous peoples produced there a larger, heavier, polymorphic, and smaller brained (Fig. 3c) animal than its wild ancestor. They continued to breed the Andean (or "criollo") breed or breeds for another 500 years. A second stage involved Europeans, who took a small sample from the Andean breed, and transformed it into the worldwide laboratory/pet guinea pig through a new selection regime. They produced a larger, heavier, more polymorphic, more prolific (Kunz, 2003), and smaller brained (Huckinghaus, 1961) animal than its Andean domestic ancestor. The European breed should also have less genetic diversity than its direct Andean ancestors, considering its historically documented origins (Wagner and Manning, 1976) and its molecular identity (Fig. 5). Finally, a third and more recent stage involved a modern selection regime (Chauca, 1997) to obtain a large, heavy, and prolific "improved" animal for meat production, extensively used by local restaurants along Central and South America (Morales, 1995).

About 50 years ago, in his splendid revisionary work, Gilmore (1950:460) concluded: "Hence, the rarity of the domesticated cavy in Peruvian archaeology is a mystery and a paradox, and may be considered weighty evidence against the theory that the cavy was domesticated in the Peruvian area. However, the morphologic and genetic evidence points to the Andean Highland area, or its immediate environs, as the home of the domesticated cavy." Using new material and data, we have provided further support for an Andean origin of domestication, with *C. tschudii* being the likely ancestral form. The results presented herein appear to resolve this paradox. Nevertheless, much more work remains to be done on the biology and evolution of this gracile and useful mammal.

ACKNOWLEDGEMENTS

This project was inspired following the ancient trail opened by some of the ancestors of the first author (AS), a path also walked by a young O. P. Pearson studying wiskachas (*Lagidium*) and achakus (rodents) in southern Peru and northern Chile. Our work was supported by a Fondo Nacional de Ciencia y Tecnología grant (FONDECYT 1011052, Chile, to AS). We thank S. Quevedo, of the Museo Nacional de Historia Natural, Santiago, Chile, for access to the Punta Pichalo mummy, the Servicio Agrícola y Ganadero, Chile (permit 2273-August 1997), the Corporación Nacional Forestal, and the Ministerio de Agricultura, Chile for granting other collection permits, to Dr. D. Díaz Coahila, Facultad de Medicina Veterinaria, Universidad Nacional Mayor de San Marcos, Lima, for X-raying the El Yaral mummies, to Lic. H. Ceballos, for access to tissues and skull photographs, to Dr. M. Kuntz and J. Oyarce for their technical assistance in the collection and care of animals, and to 3 external reviewers and the editors of this volume for their excellent assistance.

APPENDIX 1: COLLECTION LOCALITIES

Collection localities of specimens examined for geometric morphometry (names follow Woods (1993); collection and number in parenthesis; acronym LCM = Laboratorio de Citogenetica de Mamiferos, Universidad de Chile, Santiago, Chile; MHN = Museo de Historia Natural, Santiago, Chile; HZEGA = Horacio Zeballos personal collection, MUSA = Museo de Historia Natural de la Universidad Nacional de San Agustín de Arequipa, Peru.) were as follows:

Cavia tschudii. CHILE: Lluta, I Región (LCM2567, MHN371, MHN372, MHN377). PERU: Islay, Arequipa (HZEGA2, HZEGA3); Sabandia, Arequipa (MUSA104); Socabaya, Arequipa (MUSA203); Majes, Arequipa (MUSA214, MUSA217); Chiguata, Arequipa (MUSA221, MUSA237, MUSA93); Islay, Arequipa (MUSA678); Sachaca, Arequipa (MUSA88); El Cural, Arequipa (MUSA98).

Cavia porcellus. Andean creole breed. CHILE: Arica, Agromarket (LCM2477, LCM2479, LCM2489, LCM2490, LCM2506, LCM2515, LCM2524, LCM2526). PERU: Apacheta, Arequipa (MUSA100, MUSA101, MUSA219); Majes, Arequipa (MUSA215), El Cural, Arequipa (MUSA99).

Cavia porcellus European laboratory breed. CHILE: Pirbright breed, Instituto de Salud

Pública, Santiago (LCM2510,LCM2514, LCM2516, LCM2517, LCM2525, LCM2530, LCM2532, LCM2534, LCM2535, LCM2553); Criadero Lampa, Santiago (LCM293, LCM295); Criadero Florida, Santiago (LCM544). COLOMBIA: Palmira market (LCM2347).

LITERATURE CITED

Archetti, E.
1997 Guinea Pigs: Food, Symbol and Conflicts of Knowledge in Ecuador (Global Issues). Berg Publications Ltd., New York, New York, USA. 256 pp.

Cabrera, A.
1953 Los roedores argentinos de la familia Cavidae. Ministerio de Educación, Facultad de Agronomía y Veterinaria, Universidad de Buenos Aires. Publicación 6:1-93.

Castle, W. E.
1916 An expedition to the home of the guinea-pig and some breeding experiments with material there obtained. Carnegie Institution of Washington Publication 241:1-55.

Cavalcanti, M. J.
2001 JACKknifed Interactive Eigenanalysis v. 1.2. Program from Setor de Paleovertebrados, Departamento de Geologia e Paleontologia, Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brasil.

Chauca, L.
1997 Producción de cuyes (*Cavia porcellus*). FAO, Roma, Italia. 77 pp.

Clutton-Brock, J.
1999 A Natural History of Domesticated Mammals. Cambridge University Press, London, UK. 238 pp.

Cocilovo, J. A.
1994 Biología de la Población Prehistórica de Pisagua. Doctoral Thesis. Universidad de Córdoba, Argentina, Córdoba. 251 pp.

Cooper, G., and A. L. Schiller
1975 Anatomy of the Guinea Pig. Harvard University Press, Cambridge, Massachusetts, USA. 417 pp.

Detlefsen, J. A.
1914 Genetic studies on a cavy species cross. Carnegie Institution of Washington Publication 205:1-134.

Eisenberg, J. F., and K. H. Redford
1999 Mammals of the Neotropics: The Central Neotropics. The University of Chicago Press, Chicago, Illinois, USA. 609 pp.

Eriksonn, T.
1999 AutoDecay ver. 4.0 (program distributed by the author). Bergius Foundation, Royal Swedish Academy of Sciences, Stockholm, Sweden.

Gade, D. W.
1967 The guinea-pig in andean folk culture. Geographical Review 57:213-224.

Gilmore, R. M.
1950 Fauna and Ethnozoology of South America. Pp. 345-464 in Handbook of South American Indians. Volume 6 (Steward. J. H., ed.). Bureau of American Ethnology Bulletin, Smithsonian Institution., Washington, D.C., USA.

Harrison, R. G.
2002 Species concepts. Pp. 1078-1083 in Encyclopedia of Evolution (Pagel, M., ed.). Oxford University Press, New York, New York, USA.

Higgins, D. G., A. J. Bleasby, and R. Fuchs
1992 CLUSTAL V: improved software for multiple sequence alignment. Cabios 8:189-191.

Hillis, D., C. Moritz, and B. Mable
1996 Molecular Systematics. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA. 1016 pp.

Huckinghaus, F.
1961 Vergleichende Untersuchungen uber die Formenmannigfaltigkeit der Unterfamilie der Caviinae Murray 1886. Zeitschrift fur Wissenschaftliche Zoologie 166:1-98.

Kunz, M. L.
2003 Estudio Comparado de Variables Corporales y Tamaño de Camada en Cuyes (Ca*via porcellus*) Amerindios (Arica) y de Laboratorio desde el Nacimiento hasta los Cuatro Meses de Edad. Tesis Médico Veterinario. Universidad de Chile, Santiago, Chile. 89 pp.

Kunzl, C., and N. Sachser
2000 Behavioural and endocrinological changes during the process of domestication in guinea pigs. Archiv Fur Tierzucht-Archives of Animal Breeding 43:153-158.

Leguia, G., and E. Casas

1998 Especies de parásitos gastrointestinales, tisulares y ecto parásitos en camélidos precolombinos. P. 55 in Abstracts of the III Congreso Mundial de Estudios sobre momias, Arica, Chile.

Morales, E.

1994 The guinea pig in the Andean economy: From household animal to market commodity. Latin American Research Review 29:129-142.

1995 The Guinea Pig. Healing, Food, and Ritual in the Andes. The University of Arizona Press, Tucson, Arizona, USA. 177 pp.

Murphy, W. J., E. Eizirik, W. E. Johnson, Y. P. Zhang, O. A. Ryder, and S. J. O'Brien

2001 Molecular phylogenetics and the origins of placental mammals. Nature 409:614-618.

Nedbal, M., M. Allard, and R. Honeycutt

1994 Molecular systematics of Hystricognath rodents: Evidence from the mitochondrial 12 S rRNA gene. Molecular Phylogenetics and Evolution. 3:206-220.

Pictet, A., and A. Ferrero

1951 La descendance d'un croisement interspecifique de cobayes (*Cavia aperea* D'Az x *Cavia cobaya* Marc) analysee durant 25 annees. Genetica 25:357-515.

Posada, D. and K. A. Crandall

1998 Modeltest: testing the model of DNA sustitution. Bioinformatics 14:817-818.

Rasband, W., and D. S. Bright

1995 NIH Image: a public domain image processing program for the Macintosh. Microbeam Analysis Society Journal 4:137-149.

Rofes, J.

1998 Momias de cuyes en el Yaral. Pp. 55-56 in Abstracts of the III Congreso Mundial de Estudios sobre momias, Arica, Chile.

Rofes, J., and J. C. Wheeler

2003 Sacrificio de cuyes en los Andes: El caso de El Yaral y una revisión biológica, etnográfica y arqueológica de la especie *Cavia porcellus*. Archaeofauna 12:29-45

Rohlf, F. J.

1995 NTSYS-pc, version 2.10a. Applied Biostatistics Inc., New York, New York, USA.

1998 TPSDIG. Department of Ecology and Evolution, SUNY at Stony Brook, New York, USA.

Rohlf, F. J., and D. Slice
1990 Extensions of the Procrustes method for the optimal superimposition of landmarks. Systematic Zoology 39:40-59.

Rood, J.
1972 Ecological and behavioural comparations of three genera of Argentine cavies. Animal Behaviour Monographs 5:1-83.

Rowe, D. L., and R. L. Honeycutt
2002 Phylogenetic relationships, ecological correlates, and molecular evolution within the Cavioidea (Mammalia, Rodentia). Molecular Biology and Evolution 19:263-277.

Sachser, N.
1998 Of domestic and wild guinea pigs: studies in sociophysiology, domestication, and social evolution. Naturwissenschaften 85:307-317.

Sandweiss, D. H., and E. S. Wing
1997 Ritual rodents: the guinea pigs of Chincha, Peru. Journal of Field Archaeology 24:47-58.

Spotorno, A. E., J. P. Valladares, J. C. Marin, and H. Zeballos.
2004 Molecular diversity among domestic guinea-pigs (*Cavia porcellus*) and their close phylogenetic relationship with an Andean wild species, *C. tschudii*. Revista Chilena de Historia Natural 77:243-250.

Swofford, D. L.
2002 PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), 4.0bv.10. Sinauer Associates, Sunderland, Massachusetts, USA.

Thorpe, J. P., and J. Smartt
1995 Genetic diversity as a component of biodiversity. Pp. 57-87 in Global Biodiversity Assessment (Watson, R. T., and V. H. Heywood, eds.). Cambridge University Press, New York, New York, USA.

Trillmich, F., M. Bieneck, E. Geissler, and H. J. Bischof
2003 Ontogeny of running performance in the wild guinea pig (*Cavia aperea*). Mammalian Biology 68:214-223.

Uhle, M.
1917 Los aborígenes de Arica. Publicaciones del Museo de Etnología y Antropología de Chile 1:151-176.

1919 Fundamentos étnicos de la región de Arica y Tacna. Bolectín de la Sociedad Ecuatoriana de Estudios de Historia Americana 2:1-37.

Wagner, J. E., and P. J. Manning
1976 The Biology of the Guinea Pig. Academic Press, New York, New York, USA. 317 pp.

Weir, B. J.
1974 Notes on the origin of the domestic guinea-pig. Pp. 437-446 in Symposia of the Zoological Society of London (Rowlands, I. W., and B. J. Weir, eds.). Academic Press, London, UK.

Wheeler, J. C., A. J. F. Russel, and H. Redden
1998 Preconquest llama and alpaca breeding as reconstructed from the El Yaral mummies. Pp. 56-57 in Abstracts of the III Congreso Mundial de Estudios sobre momias, Arica, Chile.

Wing, E.
1986 Domestication of Andean mammals. Pp. 246-264 in High Altitude Tropical Biogeography (Vuilleumier, F., and M. Monasterio, eds.). Oxford University Press, New York, New York, USA.

Woods, C.
1993 Suborder Hystricognathi. Pages 771-806 in Mammal Species of the World: A Taxonomic and Geographic Reference. Second ed. (Wilson, D. E., and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C., USA.

PART 2: SYSTEMATICS, TAXONOMY, EVOLUTION

Oliver Pearson's earliest published papers were taxon descriptions, but it was perhaps not until the publication of his 1958 revision of the Leaf-eared mice (*Phyllotis*) that even he would have regarded himself as a card-carrying systematist. From that landmark study to his most recent papers, Paynie continued as one of the major figures illuminating the evolutionary and taxonomic history of South American mammals, tackling some of the most vexing groups where his own perceptive eye in the museum and keen observations of animals in nature created clarity from chaos.

There are many notable elements in the chapters that form this section of our tribute to Paynie, but 2 stand out in particular. First and foremost, Paynie dedicated his professional life to scholarly development in the countries where he worked, and he would be exceedingly pleased to see the large number of contributions authored by Latin American scholars. Second, it is not an artifact that many of the rodent groups, or conceptual areas, upon which Paynie focused his own attention are subjects of papers included herein. Not surprisingly, *Phyllotis* figures prominently, including the description of a new species (Jayat et al.), new and novel cytogenetic comparisons (Walker and Flores), and a molecular phylogenetic analysis (Steppan et al.). Other contributions address systematic issues in additional taxa central to Pearson's own scholarly work, such as Smith and Patton's phylogenetic analysis of grass mice of the genus *Akodon*; Palma et alias' review of the Long-tailed pygmy rice rat, *Oligoryzomys longicaudatus*; Tomasco and Lessa's analysis of a namesake, Pearson's tuco-tuco, *Ctenomys pearsoni*; and both Gallardo et alias' and Vassallo and Mora's examination of octodontids more generally. Although Pearson did not directly work on phyllostomid bats of the genus *Micronycteris* (Fonseca et al.) or the sigmodontine rodent genus *Thomasomys* (Salazar-Bravo and Yates), the MVZ collections contain many specimens of each that he collected, and puzzled over. And, his earliest work centered on neotomine and peromyscine rodents illuminated by the molecular study of Reeder and Bradley. As a systematic scholar, Pearson recognized the importance of the geographic precision of type localities, which is an area treated by Pardiñas et al. in their contribution. And, he thought not only about taxa per se but also species assemblages, both from an ecological as well as a biogeographic perspective, areas treated geographically by Díaz and Barquez and taxonomically, for marsupials, by Flores et al. Finally, since Pearson was the first to articulate the biological commonalities of subterranean rodent lineages worldwide (Pearson, 1959 [1960]), it is only fitting that this section include an ecological and phylogenetic analysis of one such group, the mole rats of the Middle East (Polyakov et al.).

LITERATURE CITED

Pearson, O. P.
1959 [1960] Biology of the subterranean rodents, *Ctenomys*, in Peru. Memorias del Museo de Historia Natural 'Javier Prado' 9:1-56.

RESOLUTION OF SOME PROBLEMATIC TYPE LOCALITIES FOR SIGMODONTINE RODENTS (CRICETIDAE, SIGMODONTINAE)

RESOLUCIÓN DE ALGUNOS PROBLEMAS RELATIVOS A LOCALIDADES TÍPICAS DE ROEDORES SIGMODONTINOS (CRICETIDAE, SIGMODONTINAE)

Ulyses F. J. Pardiñas, Pablo Teta, Guillermo D'Elía,
Sebastián Cirignoli, and Pablo E. Ortiz

ABSTRACT

Herein we comment on the location of 8 Argentinean type localities for 22 sigmodontine taxa (Cricetidae: Sigmodontinae). This study is based on information gathered from original publications, labels of type specimens, field catalogs and notes housed in museums, and historical records and maps. These localities (arranged in order of increasing latitude) are: Higuerilla (Province of Jujuy), Caraguatay and río Paranay (Province of Misiones), río de Oro (Province of Chaco), Otro Cerro (Province of Catamarca), "Norte de Entre Ríos" (Province of Entre Ríos), Isla Ella (Province of Buenos Aires), Neuquén, río Limay (Province of Neuquén), and Valle del Lago Blanco or Valle/Región Koslowsky (Province of Chubut). We clarify the geographic location, provide current names, and/or restrict these type localities. Finally, we also pose comments on the taxonomic significance of these actions.

Key words: Argentina, Sigmodontinae, type localities, taxonomy

RESUMEN

Sobre la base de una revisión de las fuentes originales, etiquetas de los holotipos, notas de museos y catálogos, reseñas históricas y consulta cartográfica, se discute la ubicación de 8 localidades típicas argentinas de roedores sigmodontinos (Cricetidae: Sigmodontinae). Estas localidades (ordenadas por latitud creciente) son: Higuerilla (Provincia de Jujuy), Caraguatay y río Paranay (Provincia de Misiones), río de Oro (Provincia del Chaco), Otro Cerro (Provincia de Catamarca), "Norte de Entre Ríos" (Provincia de Entre Ríos), Isla Ella (Provincia de Buenos Aires), Neuquén, río Limay (Provincia del Neuquén) y Valle del Lago Blanco o Valle/Región Koslowsky (Provincia del Chubut). En todos los casos se comentan las implicaciones taxonómicas y principales problemáticas relacionadas.

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Palabras clave: Argentina, Sigmodontinae, localidades tipo, taxonomía

INTRODUCTION

According to the International Code of Zoological Nomenclature (ICZN, 1999) the geographical place of capture or collection of the name-bearing type of a nominal species or subspecies is the type locality of the taxon in question. Often, when attempting to resolve taxonomic problems, it is of vital importance to collect additional specimens (topotypes) at a particular type locality. Whatever the reasons this material is needed, these specimens must be collected at the type locality of the taxa in question. As such, the value of knowing the exact place of collection of what later become type specimens is clear for all those interested in taxonomy.

Approximately 129 named taxa, either species or subspecies, have been based on sigmodontine rodents (Cricetidae, Sigmodontinae) collected in Argentina. These specimens were collected at 90 localities (Fig. 1). The distribution of these type localities is highly asymmetrical, with most concentrated in those provinces extensively surveyed during the early 19th and late 20th centuries. Buenos Aires Province contains the maximum number of sigmodontine type localities (16), followed by Tucumán Province (10), and Jujuy Province (8), while several provinces (e.g., Santiago del Estero, Santa Fe) have none. At least 3 periods of taxonomic descriptions can be recognized in the history of the study of Argentine sigmodontine rodents (Fig. 2). The first, early in the 19th century, involved the pioneer work of Azara, Darwin, and Waterhouse. The second and most prolific period, from 1890 to 1930, had as main protagonists Emilio Budin in the field and Oldfield Thomas at the British Museum of Natural History. Finally, a third period, beginning around 1970, included the work of several contemporary mammalogists (e.g., Massoia, Contreras, Mares, and Braun). This third period is characterized by the fact that, in general, collectors and describers are the same person.

Unfortunately, several Argentine sigmodontine type localities are difficult or impossible to locate. This situation, which evidently hampers several taxonomic studies, is due to a large array of problems ranging from an original definition involving vast or ambiguously defined areas (e.g., many of the Waterhouse references), to the use of names never recorded in maps (e.g., Higuerilla), and to the changing of some geographic names (e.g., Bonifacio = Laguna Alsina). These problems are rooted in several sources, most notably: a) lack of maps or detailed maps at the time of collection; b) large temporal gaps between the collection of specimens and their description, which led to the publication of incorrect, misinterpreted, or ambiguous references; c) changes or restrictions of several type localities proposed by authorities unfamiliar with the geography of the country and/or based on misinterpretations of the original or alternative information sources.

Concern about these problematic type localities was manifested as early as the first decades of the last century when Thomas (1919c, 1920) discussed the location and the real existence of some of them. Later, comments in relation to these issues were posed mainly as isolated notes in taxonomic or biogeographic contributions (e.g., Pearson, 1958; Hershkovitz, 1962; Massoia and Fornes, 1964; Myers et al., 1990; Pardiñas, 1996; Pardiñas and Galliari, 1998; Díaz, 1999). However, 3 studies directly focused on these problematic type localities. First, Pearson and Lagiglia (1992) specifically discussed, based on historical sources and newly trapped material, the correctness of Fuerte

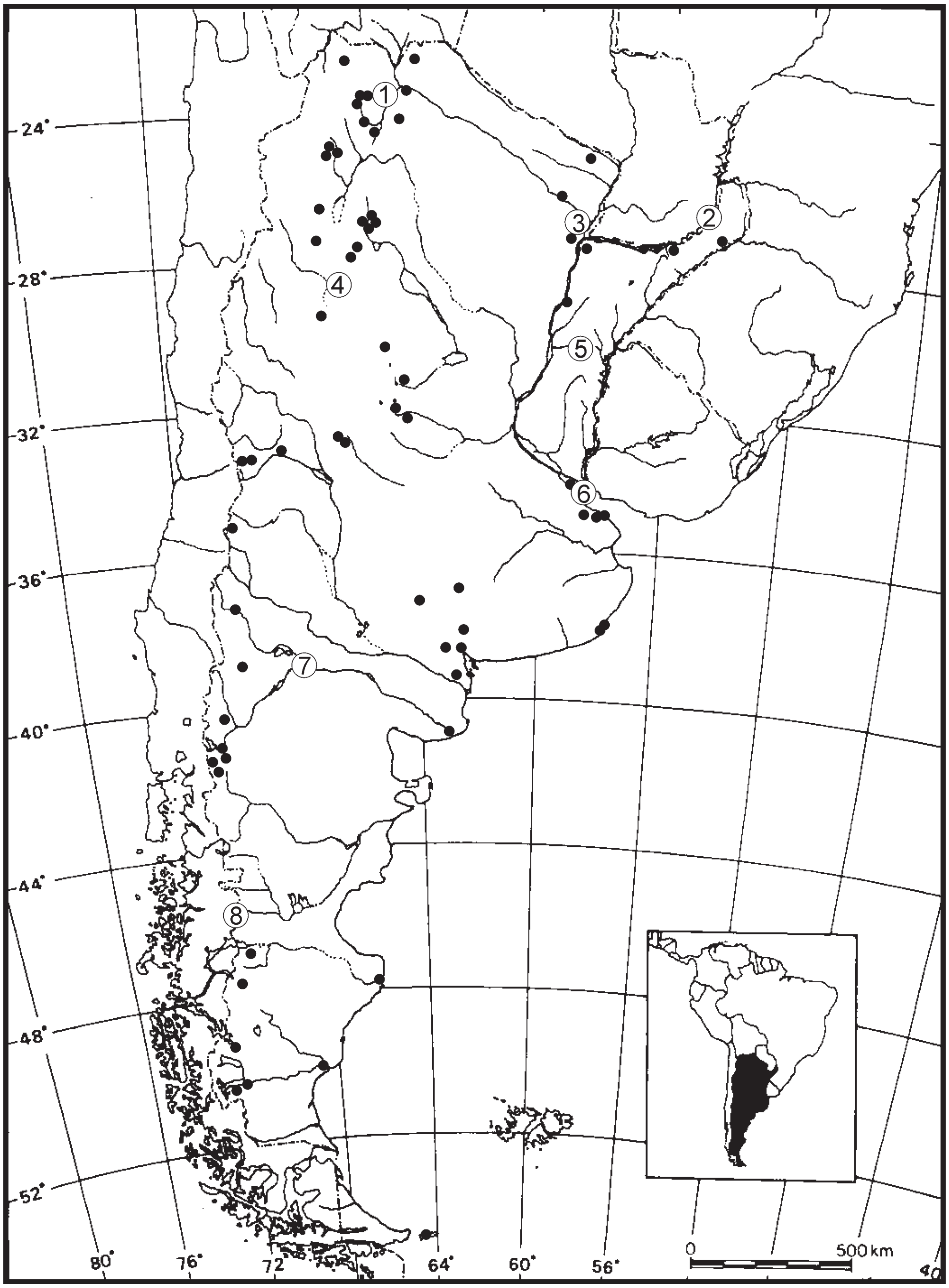

Figure 1. Argentinean sigmodontine type localities. The numbers refer to localities discussed in the text and detailed in the maps of Figs. 3, 4, and 5.

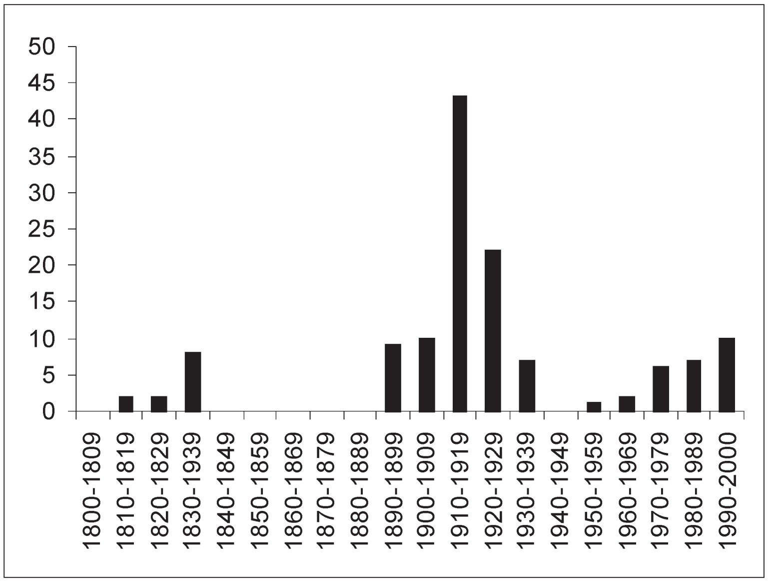

Figure 2. New taxa (binomials and trinomials) of sigmodontine rodents described per decade on the basis of Argentinean specimens.

de San Rafael (Mendoza Province) as the type locality of 3 sigmodontines. Similarly, Contreras (1992) and Contreras and Teta (2003), reinterpreting the original works of Rengger and Azara, discussed the placement of the type localities of *Calomys callosus* and *Oxymycterus rufus*, respectively.

We have 2 objectives in this report. First, we want to call attention of those working with sigmodontine rodents to the fact that the geographic origin of several type specimens is uncertain. Second, we discuss 8 of the most problematic Argentine sigmodontine type localities, to clarify their probable locations. In addition, we comment on the taxonomic uncertainties remaining with respect to several of the taxa involved.

MATERIALS AND METHODS

This paper is based on the following sources of information: a) original publications, b) public historical records, c) catalogues and field notes housed in museums, d) original labels attached to holotypes, and e) consultation with mammalogists, historians, and cartographers. As cartographic source we used historical and contemporaneous topographic maps, the latter produced mainly by the Instituto Geográfico Militar (IGM, Argentina). Most of the geographical coordinates provided in this paper (at degree and minute resolution) were obtained from the Atlas de la República Argentina (IGM, 1972, 1979). In several cases, we used GPS data obtained by us. For each locality, we also provide the names of the departments and provinces.

We discuss the type localities arranged in order of increasing latitude. In all cases, we respected the original spelling of the taxa. Finally, we followed the Article 76 of the International Code of Zoological Nomenclature (ICZN, 1999), particularly, the Recommendation 76A that states that "in ascertaining or clarifying a type locality…an author should take into account: 76A.1.1. data accompanying the original material; 76A.1.2. collector's notes, itineraries, or personal communications; 76A.1.3. the original description of the taxon; and 76A.1.4. as a last resort, and without prejudice to other clarification, localities within the known range of the taxon or from which specimens referred to the taxon had been taken."

PROBLEMATIC LOCALITIES

1. The phantom type locality called Higuerilla

History: Emilio Budin collected in this locality in 1921. Thomas (1921b, p 609) offered the original geographic reference as "Higuerilla.- 2000 m., in the Department of Valle Grande, about 10 km. east of the Zenta range and 20 km. of the town of Tilcara." Cabrera (1961, pp 451 and 466) added 2 alternative interpretations: "Higuerilla, Jujuy, 10 kilómetros al este de la Sierra de Zenta" and "Higuerilla, provincia de Jujuy, a unos 20 kilómetros al este de Tilcara y a 2.000 metros de altura." Subsequent authors repeated Thomas's reference with minor variations (e.g., Hershkovitz, 1994; Musser and Carleton, 1993; Díaz, 1999).

Problem: there is not a single place with this name on any available map of central Jujuy Province.

Present Location (Fig. 3A): Valle Grande (23° 28′ S, 64° 59′ W, 2313 m, Valle Grande, Jujuy) is the main city in the Department of Valle Grande. The region is characterized by the scarcity of roads; only provincial route 83 crosses the Calilegua National Park connecting the cities of Libertador General San Martín (23° 49′ S, 64° 47′ W, 1551 m, Ledesma, Jujuy) and Valle Grande. Searches carried out in the area recording local place names from old settlers indicate that Higuerilla was the name of an abandoned ranch (23° 33′ 35″ S, 65° 00′ 37″ W, 1804 m, Valle Grande, Jujuy) where the small village of Pampichuela is now located. It seems likely that Budin trapped in the vicinity of this ranch and recorded its name as the locality of his collections. Therefore we equate Higuerilla with the modern locality Pampichuela (23° 32′ S, 65° 02′ W, 1735 m, Valle Grande, Jujuy; IGM 1989a). Pampichuela is about 15 km (by road) south of Valle Grande, and ca. 33 km east of Tilcara (23° 34′ S, 65° 22′ W, 2461 m, Tilcara, Jujuy).

Taxonomic Implications: Higuerilla is the type locality of the sigmodontines *Phyllotis nogalaris* Thomas, 1921; *Hypsimys deceptor* Thomas, 1921; and *Oxymycterus akodontius* Thomas, 1921. Although the first species was included in several taxonomic studies of the genus *Phyllotis* (e.g., Pearson, 1958; Hershkovitz, 1962), the taxonomic status of *H. deceptor* and *O. akodontius* remains unclear. The differences between *H. deceptor* and *H. budini* Thomas, 1918 (type locality: León, 24° 03′ S, 65° 26′ W, 1754 m, Dr. Manuel Belgrano, Jujuy) were dismissed by Cabrera (1961). Now both forms are considered synonyms and placed in the genus *Akodon* (see Myers and Patton, 1989). *Oxymycterus akodontius* has been retained as a valid species but with the widespread view that it must be critically reevaluated (e.g., Cabrera, 1961; Galliari et al., 1996; Musser and

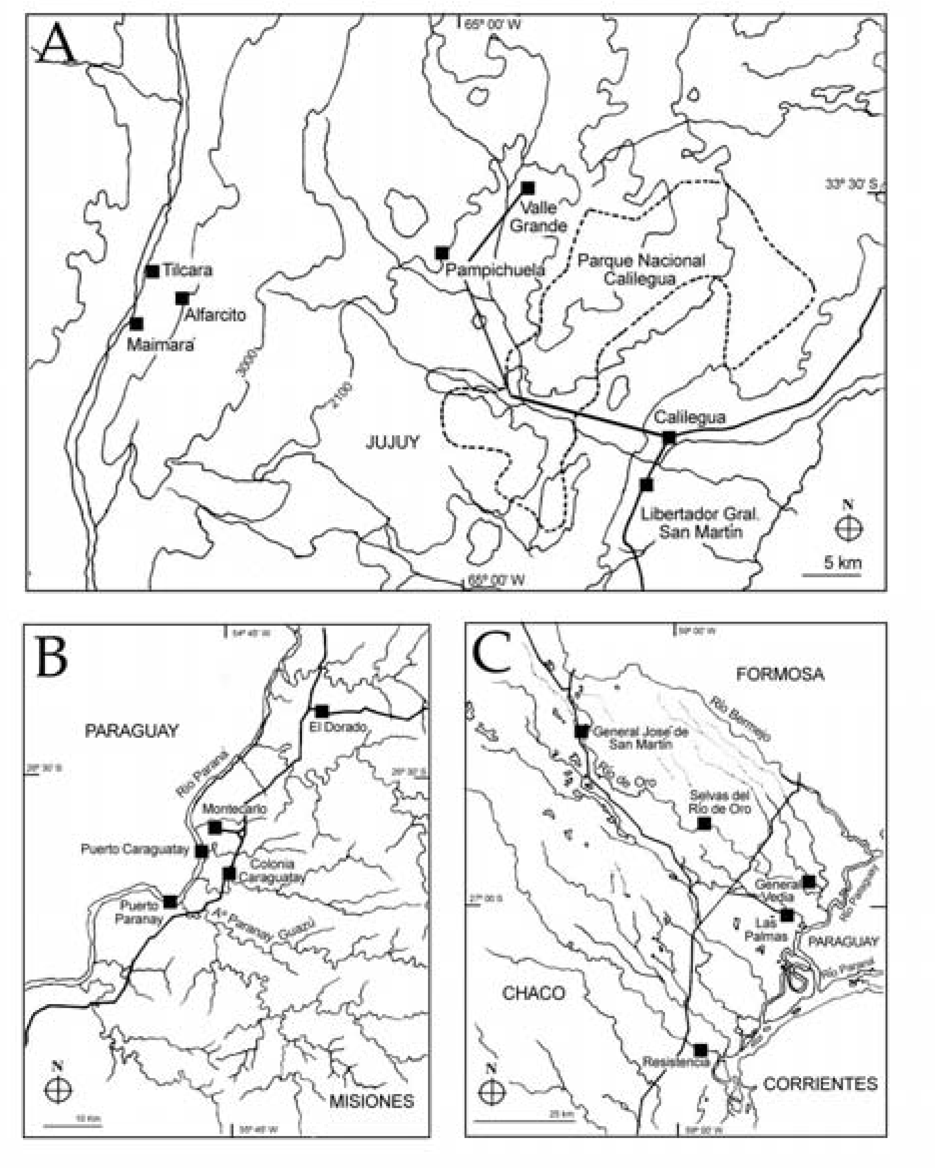

Figure 3. Detailed maps of type localities discussed in the text (numbers refer to the order of presentation in the main text; see also Fig. 1): A (Site 1 in Fig. 1). Higuerilla (Jujuy Province), B (Site 2 in Fig. 1). Caraguatay and Paranay (Misiones Province), C (Site 3 in Fig. 1). Río de Oro (Chaco Province).

Carleton, 2005). Holotypes and original series of both species were never restudied, and no new specimens from the area of the type are available.

2. Where are Caraguatay and Paranay?

History: Collin Campbell Sanborn sampled these localities during the Captain Marshall Field Brazilian Expedition (Field Museum of Natural History - Reports, 1927). The first published reference was given by Sanborn himself (1931, p 1) when describing *Oxymycterus misionalis*, as "Rio Paranay, an affluent of the Rio Parana, near Caraguatay, about 100 miles south of Rio Iguassu, Misiones Territory, Argentina." Two years later, Osgood (1933) annotated "Caraguatay, Rio Parana, 100 miles south of Rio Iguassu, Misiones, Argentina" in reference to the type locality of his *Thomasomys pictipes*. Cabrera (1961, p 467) changed the type locality of *O. misionalis*, suppressing the reference to "Rio Paranay", writing "Caraguatay, rio Paraná, Misiones, Argentina." More recently, Gonzalez (2000, p 4), misinterpreting a personal communication of Pardiñas, explained (in reference to the type locality of *T. pictipes*) that "Caraguata-i es una isla del Río Paraná frente a la localidad de Monte Carlo, Provincia de Misiones, Argentina."

Problem: Published geographic references do not provide enough information to unambiguously locate the type locality of these 2 sigmodontines.

Present Location (Fig. 3B): Information of the Field Museum of Natural History - Reports (1927, p 69) help to identify Sanborn's itinerary more precisely. The narration of the itinerary of Captain Marshall Field Brazilian Expedition indicates that "from Asuncion [Paraguay], the remaining members of the expedition went by rail to Posadas, Missiones [Misiones] Territory, Argentine Republic. Here they took a steamer on the upper Paraná for Iguazu Falls. En route, they accepted the invitation of Mr. Carlos H. Benson to camp and collect on his plantation at Caraguatay where, midway between Posadas and Iguazu Falls, Messrs. Sanborn and Ganzon stopped…The second week in Missiones was spent in camp on the Rio Paranay, a small affluent of the Paraná, where birds and amphibians were of interest but mammals and reptiles scarce." Charles Herbert Benson was one of the owners of "La Misionera S.A.I. y C.," a 4,000 ha yerba mate plantation established around 1915. By 1926 Benson had the main house of his property in Puerto Caraguatay, on the río Paraná. Sanborn (1931, p 2) also collected several specimens of his *O. misionalis* in Caraguatay, but he selected a specimen from "Rio Paranay" to serve as holotype.

At least 4 places are named "Caraguatay" or "Caraguata" in central Misiones Province, all of them are close or on the río Paraná. They are (IGM, 1994a, 1994b): Paraje Caraguatay (26° 39′ S, 54° 44′ W, 200 m, Montecarlo, Misiones), Colonia Caraguatay (26° 48′ S, 55° 20′ W, Montecarlo Misiones), Cerro Caraguatay (26° 42′ S, 55° 21′ W, Montecarlo, Misiones), and Puerto Caraguatay or Puerto Caraguatá (26° 37′ S, 54° 46′ W, 192 m, Montecarlo, Misiones). The "Rio Paranay," actually río Paranay Guazú, runs from the central Sierra de Misiones to the río Paraná, about 10 km south of Puerto Caraguatay. Near the confluence is located a small village named Puerto Paranay (26° 41′ S, 54° 48′ W, 122 m, Libertador General San Martín, Misiones). The type locality of *T. pictipes* can be restricted to Puerto Caraguatay (see above). In the case of *O. misionalis*, we restrict its type locality to the confluence of the río Paranay Guazú with the río Paraná (26° 41′ S, 54° 49′ W, 122 m, Libertador General San Martín, Misiones; IGM, 1994b).

Taxonomic Implications: González (2000) erected *Juliomys* with *Thomasomys pictipes* as type species. This author studied mainly Brazilian specimens. Recent studies have revealed an unexpected level of alpha diversity in *Juliomys* (see Oliveira and Bonvicino, 2002). In fact, the application of *pictipes* to populations in Brazil started with Pine (1980), but he pointed out several differences between the type of *pictipes* and the specimens from southern Brazil. Regrettably, nobody has recently collected at the type locality, and no new specimens are known from Misiones Province.

Oxymycterus misionalis is considered a synonym of *O. hispidus* following Cabrera (1961); however, this hypothesis never was tested studying topotypes or, at least, specimens from Misiones Province. Clearly, the collection of new specimens of both *J. pictipes* and *O. misionalis* in the type area Caraguatay-Río Paranay is necessary to clarify their taxonomic identities.

3. Río de Oro and the missing *Scapteromys chacoensis*

History: The first mention of this locality was made by Gyldenstolpe (1932a) when he described *Scapteromys chacoensis*. Gyldenstolpe (1932a, p 2) gave the type locality as "Argentine, Rio de Oro, Chaco Austral. (Caught in 'Lagunas de aqua dulce')." The holotype and only specimen known of this taxon was collected and sent to the Royal Natural History Museum of Stockholm by A. Ros in September, 1896 (Gyldenstolpe, 1932a, p 2).

Problem: There is no additional information about this type locality, the collector, or the circumstances related to the acquisition of this specimen in museum records or on the specimen label. The transcription on the latter is "Argentina, Rio de Oro, Chaco Austral. IX. 1896. A. Ros."

Present Location (Fig. 3C): The río de Oro is a tributary of the río Paraguay. With its headwaters in the vicinity of Siete Arboles (ca. 26° 18′ S, 59° 30′ W, Libertador General San Martín, Chaco), the río de Oro extends 140 km across the northeastern portion of Chaco Province. Three small towns are settled on this river (IGM, 1967), General José de San Martín (26° 33′ S, 59° 20′ W, 57 m, Libertador General San Martín, Chaco) in the upper course, Selvas del Río de Oro (26° 48′ S, 58° 57′ W, 60 m, Libertador General San Martín, Chaco) in the middle, and General Vedia (26° 56′ S, 58° 40′ W, 58 m, Bermejo, Chaco), near the mouth (27° 03′ S, 58° 33′ W, Bermejo, Chaco). At this time is not possible to restrict the type locality of *Scapteromys chacoensis* to any place along the río de Oro.

Taxonomic Implications: Scapteromys chacoensis was synonymized with *Kunsia fronto* (Winge, 1887) by Hershkovitz (1966), under the trinomial *Kunsia fronto chacoensis*. Subsequently, Avila-Pires (1972) described *K. f. planaltensis* based on a series of specimens trapped in the early 1960s by J. Moojen in Brasilia (Distrito Federal, Brazil). *Kunsia fronto* is one of the more poorly-known sigmodontines, having been recorded alive only on the río de Oro and at Brasilia. In both cases, despite intensive trapping efforts (Hershkovitz, 1990; Cirignoli et al., 2000), no new specimens were obtained.

Remarks: Despite intensive agriculture, cattle rising, and deforestation during the last 100 years, the río de Oro basin is moderately well preserved. Extensive palms and flooded grasslands remain in this area. The local extinction of *K. fronto* cannot be demonstrated until new fieldwork covering the entire river course would be made.

However, analysis of owl pellet from 12 localities from General José de San Martín to General Vedia, which included thousands of specimens of small mammals, failed to yield remains of *K. fronto* (Cirignoli et al., 2000).

4. Is Otro Cerro a fancy name?

History: The first collector to work at this locality was Emilio Budin in 1918. Thomas (1919c, p 489) discussed the real existence of Otro Cerro as follows "after making the collection at Chumbicha, Catamarca…Sr. Budin traveled westwards some 30 miles, over the Cerro de Ambato to 'another hill,' or range of hills, for which he could find no recognized name…Although Sr. Budin considered himself to be still in Catamarca…the distance and direction from Chumbicha show that he must have crossed the frontier into Rioja. Under these circumstances I have decided to use Sr. Budin's *fancy* name of 'Otro Cerro'…the locality may be stated as 45 kilometers west of Chumbicha, the specimens being taken at an altitude of about 3000 meters" (italics ours). One year later Thomas (1920, p 473) corrected himself by pointing out that Otro Cerro is located in Catamarca Province, and not in La Rioja Province (= Rioja, in his original spelling). He also wrote that "[Otro Cerro]…is in Catamarca, about 18 km. N.N.W. of Chumbicha." Almost all later authors used Thomas' (1920) second geographical reference (e.g., Hershkovitz, 1962; Williams and Mares, 1978; Mares et al., 1997; Díaz, 1999), but 3 exceptions deserve note. First, Pearson (1958, p 418), when discussing the status of *Phyllotis ricardulus*, and clearly following Thomas (1919c) in the attribution of the name to Budin, wrote "Otro Cerro is a locality name *coined* by Budin to refer to a mountain 11 miles NNW of Chumbicha" (italics ours). Second, Cabrera (1961, p 487) stated "Contra lo que supone Pearson, Otro Cerro no es un nombre inventado ('coined') por Budin para dicha localidad típica, puesto que aparece en el mapa de Catamarca de Lange y Delachaux publicado por el Museo de La Plata en 1893." Cabrera (1961, p 501) referenced this type locality as "Otro Cerro, en el extremo sur de la sierra de Ambato, al noroeste de Chumbicha, Catamarca." Third, Myers et al. (1990, p 62) mentioned Thomas' (1919c) original supposition that Budin may have confused Otro Cerro and Cerro Nunorca, speculating that Otro Cerro is "…probably in La Rioja Province…This mountain is probably within a range (for which we also have not found a name) that runs NNW from the Sierra de Valasco, originating west of La Rioja." Myers et al. (1990) tentatively changed the location of Otro Cerro back to La Rioja Province, remarking one more time on the uncertainties about the exact location of this type locality.

Problem: In spite of the fact that Otro Cerro has appeared both in old and recent official Argentine maps, uncertainties about the location of this type locality still remains (e.g., Myers et al., 1990).

Present Location (Fig. 4A): The map of Lange and Delachaux (Museo de La Plata, 1893) shows the location of Otro Cerro as a ranch in the southern end of the Sierra de Ambato, Catamarca Province. In addition, this place is figured in the topographic map IGM (1966) but, regrettably, Otro Cerro has disappeared in the most recent edition (IGM, 1989b). An *in situ* inspection of this area revealed that local settlers of the small village of Trampasacha (28° 50′ S, 66° 18′ W, 614 m, Capayán, Catamarca), the nearest habited place to Otro Cerro, know the existence of the latter as an abandoned ranch at the top of the Sierra de Ambato. The exact location of Otro Cerro is 28° 45′ S, 66° 17′ W (2023 m, Capayán, Catamarca), about 4 km SSE of Cerro Catalán (IGM, 1989b).

Taxonomic Implications: Otro Cerro is the type locality of several mammals (Thomas, 1919c, 1920), including the sigmodontines *Phyllotis ricardulus* Thomas, 1919, *Graomys edithae* Thomas, 1919, *Akodon alterus* Thomas, 1919, *Akodon orbus* Thomas, 1919, and *Reithrodon caurinus* Thomas, 1920. Of these 5 taxa, only *P. ricardulus* has been restudied, and now is considered a synonym of *P. xanthopygus* (Pearson, 1958; Hershkovitz, 1962). The status of *G. edithae* has been discussed by several authors. Cabrera (1961) treated it as a synonym of *G. griseoflavus*, without explaining his reasons. Massoia (1976) and Williams and Mares (1978) commented on the uncertainties regarding this form, but did not offer any resolution. Although this taxon is currently treated as valid species (e.g., Musser and Carleton, 1993, 2005; Mares et al., 1997) nothing is known beyond the original description. *Akodon alterus* is alternatively considered a synonym of *A. spegazzinii* (Myers et al., 1990; Musser and Carleton, 1993) or as a full species (Blaustein et al., 1992; Díaz, 1999). *Akodon orbus* was synonymyzed with *Necromys lactens* by Cabrera (1961), probably on the basis of the similarities between both taxa remarked by Thomas (1919c). However, the holotype of *A. orbus* has been never restudied or compared with other *Necromys* species. Finally, *R. caurinus* was subsumed under *R. auritus*, without any evidence favoring this hypothesis (Cabrera, 1961). Trapping efforts at Otro Cerro are essential to clarify the status of these named forms.

Remarks: In contrast with Chumbicha (28° 52′ S, 66° 14′ W, 376 m, Capayán, Catamarca; another type locality very close to Otro Cerro), where the human-disturbance can be considered as severe and the original vegetation (Montane Chaco) has been almost totally replaced, Otro Cerro remains relatively undisturbed. This fortunate situation may be due to the isolation and difficult access to this locality. The high-elevation grasslands in the southern end of the Sierra de Ambato are used by domestic cattle (goats), but probably several well-preserved places remain.

5. Why "Norte de Entre Ríos" is not a type locality

History: Azara (1802, p 94) described, under the name of "Agreste" and based on a specimen collected "...en los 30 ½ grados de latitud...," the species that Fischer (1829) later selected as the basis of his *M*[*us*]*? azarae.* Tate (1932a, 1932b, p 26) included this species in *Akodon*, recording its locality as "30 ½° (= latitude of Entre Ríos) Argentina." Later, Cabrera (1961, p 440) reported the type locality of *A. azarae* as "...los 30° 30′ de latitud sur y entre los ríos Uruguay y Paraná, o sea en *el norte de la actual provincia de Entre Ríos*" (italics ours). However, neither of these authors explained their selection of "Norte de Entre Ríos" for Azara's collections. By 1796, Azara had left Asunción, Paraguay to participate in the defense of the borders of the Spaniards colonies against the Portuguese empire in the area of the current Brazilian state of Rio Grande do Sul. There Azara participated in the establishment of the towns of San Grabriel de Batoví and Villa Esperanza (Mariluz Urquijo, 1953; Mones and Klapenbach, 1997). The reference to the 30° 30′is recurrent in the Spanish version of Azara's (1802) work, in which several sigmodontines were described. Examples are the "Orejón" (Azara, 1802, p 83), the "Blanco debaxo" (Azara, 1802, p 181), and the "cola igual al cuerpo" (Azara, 1802, p 87). Precisely, it was in the description of the later that Azara provides an additional reference of fundamental value to locate the place of his collections "...[la obtuve] en un huerto campestre de la frontera del Brasil hacia los 30 ½ grados de latitud" (Azara, 1802, p 97). This mention must correspond to San Gabriel de Batoví, because at that time there was no other locality at the same latitude along that frontier. As another piece of evidence regarding the "Murciélago orejón" (= *Histiotus velatus*, see Hershkovitz, 1987), Azara (1802, p 304) wrote "...tuve dos o tres en los 30 ½ grados de latitud..." The distribution of this species does not reach the Argentinean province of Entre Ríos (see Barquez et al. 1999), but does include the Brazilian state of Río Grande do Sul (Silva, 1985).

Problem: The selection of "Norte de Entre Ríos" as the type locality of these taxa is arbitrary and it is partially at odds with Azara's itinerary between 1796 and 1801.

Present Location: San Gabriel de Batoví, today São Gabriel (30° 19′ S, 54° 19′ W, 118 m), is in the Brazilian State of Rio Grande do Sul.

Taxonomic Implications: The relocation of the type locality of *A. azarae* to São Gabriel prompts substantial changes at the subspecific level of this complex taxon. A study of geographic variation in this species is currently underway (D'Elía, Pardiñas, and Teta, in prep). Due to geographic reasons it is probable that the "Orejón," usually included in the synonymy of *Reithrodon auritus* (Hershkovitz, 1959, 1987; Tate, 1932a) should be considered a synonym of *R. typicus* (see Pardiñas and Galliari, 2001). *Mus dubius* Fischer, 1829, based on the literal type of the "blanco debaxo," was included in *Calomys* by Cabrera (1961) and Langguth (1975), and later synonymized with *Calomys laucha* by Musser and Carleton (1993).

Remarks: Contreras and Justo (1996), in a meeting abstract, were the first authors to suggest that San Gabriel de Batoví is the true type locality of *A. azarae*. As discussed by Contreras and Teta (2003), Hershkovitz (1994) restricted the type locality of *Oxymycterus rufus* as "north of the province of Entre Ríos," based on an erroneous interpretation of Azara's work.

6. Where is Isla Ella?

History: Collections in this island were made by Robin Kemp in 1917. Thomas (1917, p 95) offered the first and unique geographical reference as "…Isla Ella, in the delta of the Rio Parana, at the top of the La Plata Estuary." Subsequent authors used Thomas' reference (e.g., Gyldenstolpe, 1932b; Cabrera, 1961; Musser and Carleton, 1993). Hershkovitz (1966, p 97) and González and Pardiñas (2002, p 3) commented explicitly about the uncertainty of the exact location of Isla Ella. Thomas (1917, p 98) presented additional information useful to locate Isla Ella when he explained the etymology of *Akodon arenicola hunteri*. This subspecies was named in honor of "Mr. James Hunter, the Managing Director of the Isla Ella Fruit and Forest Company." According to P. Pereyra (Museo Naval de la Nación, Tigre, Buenos Aires, pers. comm. 2003), the Isla Ella Fruit and Forest Company was located on the arroyo Espera, a stream selected by its good navigability. Udaondo (1942, p 121), in a historical summary of this region, wrote "Merecen especial atención...el frigorífico de Hunter, donde se preparan en envases especiales las frutas destinadas a la exportación..." In addition, Gil (1895) indicated that by that time the Hunter family tended beehives on the arroyo Esperita, and Cuomo (1967) recorded the name "Ellan" for a house (or a boat pier) in an island on the arroyo Espera. No information is available concerning when the Isla Ella Fruit and Forest Company ceased operation. Regrettably, the Public Record Office (United Kingdom; http://www.pro.gov.uk) has no record of this Company.

Problem: There is no single place recorded in any available map with the name of Isla Ella.

Present Location (Fig. 4B): The Delta del Paraná is a large region of islands, canals, and streams at the mouth of the río Paraná. Most of the numerous islands lack specific names. We believe, according to the information presented above, that Isla Ella is a small island (ca. 1 km^2) surrounded by the streams Espera and Esperita (34° 22′ S, 58° 38′ W, Primera Sección Delta del Paraná, Tigre, Buenos Aires; IGM, 1959). This island is about 8 km NNE of Tigre city (34° 25′ S, 58° 35′ W, 2 m, Tigre, Buenos Aires).

Taxonomic Implications: One genus, 3 species, and 1 subespecies were named from specimens collected in Isla Ella (Thomas, 1917, 1920). These are: *Deltamys kempi* Thomas, 1917, *Oligoryzomys delticola* Thomas, 1917, *Akodon arenicola hunteri* Thomas, 1917, and *Scapteromys aquaticus* Thomas, 1920. The generic status of *Deltamys* has been discussed by several authors (see D'Elía et al., 2003 and references therein), but no study following the original description has included specimens from this island. The status of *A. a. hunteri* remains uncertain. This subspecies was subsumed under *Akodon azarae* (see Cabrera, 1961), a widespread species of *Akodon* which has never been systematically reviewed (see comments on *A. azarae* in the "Norte de Entre Ríos" account). In addition, Thomas (1921a) pointed out striking resemblances between *A. a. hunteri* and *A. sylvanus* Thomas, 1921, the latter from Sunchal (24° 16′ S, 64° 27′ W, 1140 m, Santa Bárbara, Jujuy). Following early observations by Thomas (1921a), Cabrera (1961) synonymyzed *A. sylvanus* with *A. azarae*. In addition, Hershkovitz (1990), in a footnote, indicated the potential conspecifity of *A. sylvanus* and *A. a. hunteri*, but not with *A. azarae*. D'Elía and Pardiñas (2004) recently revised *Scapteromys*, but they did not include topotypical material. Finally, the distinctiveness of *O. delticola*, thought to be very close to *O. longicaudatus* (Osgood, 1943) has not been critically evaluated in any comprehensive review of the genus; however, recently Francés and D'Elía (in press) proposed the formal synonymy of *O. delticola* under *O. nigripes*.

7. The obvious, but neglected type locality of *Akodon neocenus*

History: A single specimen of *Akodon* trapped by E. Weiske on November 4, 1910, was made the holotype of *A. neocenus* by Thomas (1919b). Thomas (1919b, p 213) referenced its type locality as "Neuquén, Rio Limay, Upper Rio Negro, Patagonia." Subsequent authors introduced in this geographic reference minor, but important, variations. Gyldenstolpe (1932b, p 103) stated "Western Patagonia, Rio Limay, Upper Rio Negro, Neuquén Territory." Cabrera (1961, p 449) shortened it to "Río Limay, provincia de Neuquén." Finally, Myers (1989) offered a literal transcription of Thomas (1919b) early reference; he also located the place in a map (Myers, 1989: Fig. 2b), in the middle course of the río Limay. All these changes are relevant because, with the introduction of the term "territory" or "province" associated with "Neuquén," this type locality was partially diluted. However, the original reference is clear and self-explanatory

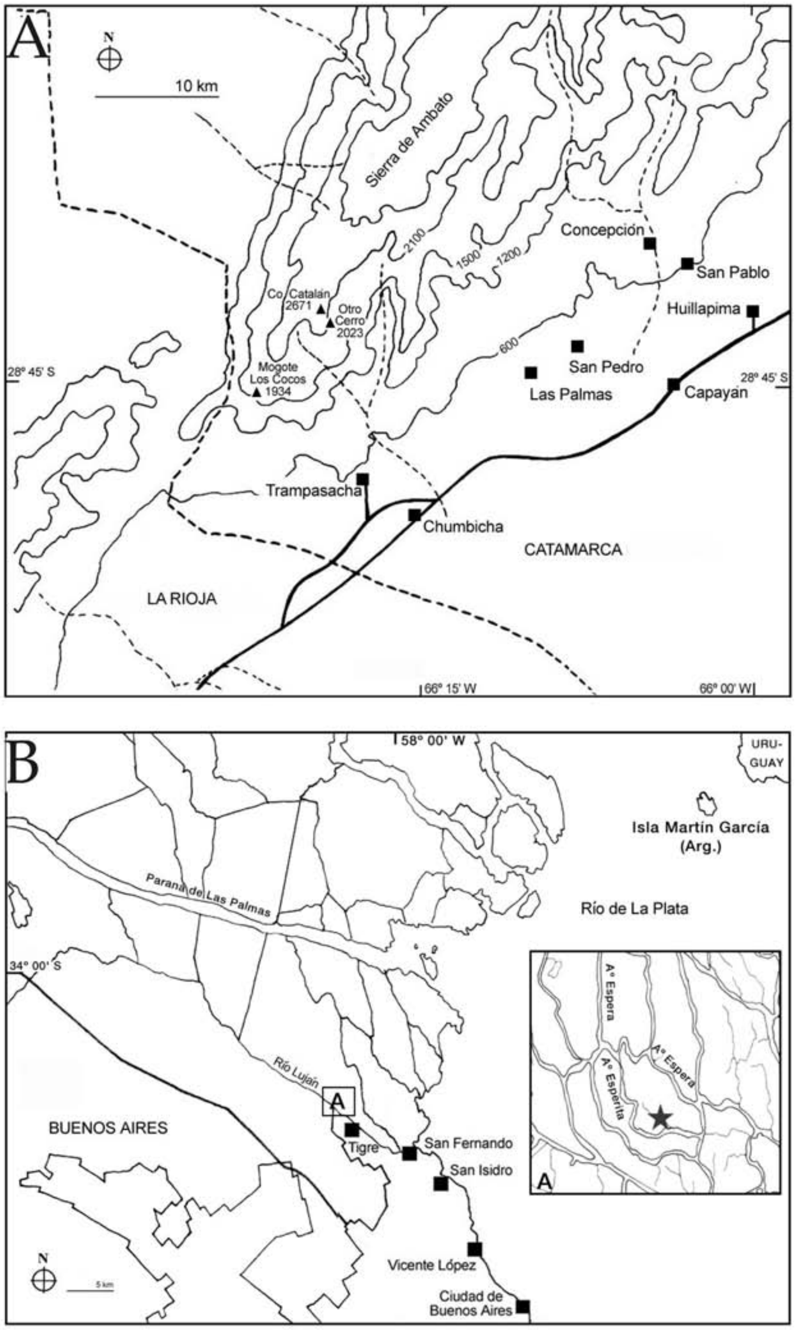

Figure 4. Detailed maps of type localities discussed in the text (numbers refer to the order of presentation in the main text; see also Fig. 1): A (Site 4 in Fig. 1). Otro Cerro (Catamarca Province), B (Site 6 in Fig. 1). Isla Ella (Buenos Aires Province); the star indicates the island tentatively identified as this type locality.

without emendations. The community of Neuquén was established a few years after the "Desert Conquest" in 1880. In 1902 the railway station of Neuquén was created, and 2 years later Neuquén was selected as main city of the territory (Alvarez, 1988). The río Limay forms the southern limit of the city; below its confluence with the río Neuquén (38° 59′ S, 68° 01′ W), it becomes the río Negro. The holotype of *A. neocenus* probably was trapped in the vicinity of Neuquén close to the río Limay. It is important to note that in 1910, the year of collection, work was begun to develop an irrigation system in the río Negro valley. In fact, the headwaters of this river are known as "Alto Valle del Río Negro," the plausible origin of "Upper Rio Negro" in the original geographic reference.

Problem: Successive alterations of the name of this type locality gradually increased the uncertainties concerning its location.

Present Location (Fig. 5A): Neuquén (38° 57′ S, 68° 04′ W, 259 m, Confluencia, Neuquén) is settled on the inner corner formed by the confluence of 2 main rivers, the northern río Neuquén, and the southern río Limay (IGM, 1994c).

Taxonomic Implications: *Akodon neocenus* was alternatively considered as a full species (e.g., Thomas, 1919b, 1927; Musser and Carleton, 1993; Galliari et al., 1996; Pardiñas et al., 2003) or as a subspecies of *A. varius* (e.g., Gyldenstolpe, 1932b; Cabrera, 1961). This fluctuating scenario is due mainly to the fragmentary nature of the holotype (an imperfect skin and skull) and to the lack of additional specimens collected in the type locality. Topotypes are fundamental to assessing not only the status of *A. neocenus*, but also that of the related species as *A. dolores*, *A. molinae*, and the recently described *A. oenos* (see Braun et al., 2000).

8. What is the Koslowsky Region or Valle del Lago Blanco?

History: The first rodents from this locality were trapped by Julio Koslowsky in 1900, and sent to Oldfield Thomas between 1900 and 1903. Thomas (1903, 1916, 1919a) referenced this locality as "Valle del Lago Blanco, Southern Chubut (Cordillera region)" (Thomas, 1903, p 241), "Valle del Lago Blanco, Cordillera region of Southern Chubut Territory, Patagonia" (Thomas, 1903, p 243), "Koslowsky Valley, 46° S., 71° W., Central Patagonia" (Thomas, 1916, p 187), or "Valle de Lago Blanco, Koslowsky region, Patagonia, 46° S." (Thomas, 1919a, p 205). In reality, there is no map that includes these place names exactly as written by Thomas. On the contrary, a small town called Lago Blanco (45° 57′ S, 71° 17′ W, 598 m, Río Senguerr, Chubut) is located in the southwestern corner of the Lago Blanco, and the ranch Estancia Lago Blanco (45° 54′ S, 71° 20′ W, Río Senguerr, Chubut) is on the northern margin of the same lake (IGM, 1950). However, the history of this type locality is more complicated; fortunately, the historical research by Aguado (2003) helps to pinpoint its exact locality (see also Aguado and Williams, 2003). Julio Koslowsky (1866-1923), the first Argentinean herpetologist, funded a colony of Russian, Polish, and Lithuanian families in 1898 on the banks of the arroyo Huemules. This colony only lasted 2 years, but Koslowsky lived there from 1898 to 1904. During these years, Koslowsky collected and sent to different museums numerous specimens of plants and vertebrates. Most of these specimens were labeled as "Valle del Lago Blanco." But this geographical reference must be understood in its historical context.

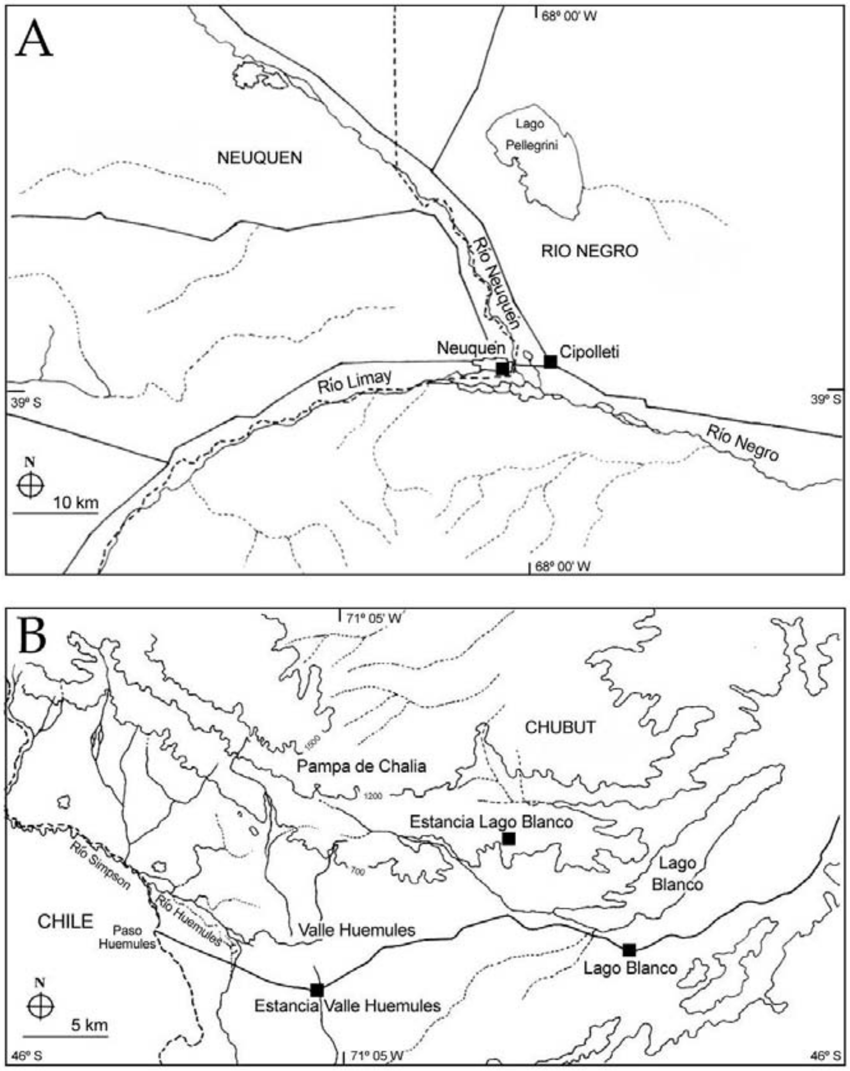

Figure 5. Detailed maps of type localities discussed in the text (numbers refer to the order of presentation in the main text; see also Fig. 1): A (Site 7 in Fig. 1). Neuquén (Neuquén Province), B (Site 8 in Fig. 1). Valle del Lago Blanco or Valle/Region Koslowsky (Chubut Province).

The place where Koslowsky's first ranch (called Estancia Los Halcones) was located is a valley (now known as Valle Huemules) that covers the area from Lago Blanco in the east to the Argentine – Chilean border in the west. So, Koslowsky used the name of "Valle del Lago Blanco" as a geographic source of his collections. This situation is revealed by Koslowsky (1904) himself when he described 2 mammals obtained in this area. The title of his 1904 article is "Dos mamíferos de Patagonia cazados en el Valle del Lago Blanco [Territorio del Chubut]." But, in the text, he wrote the exact provenance of one of these mammals as "El *Felis guigna* lo cacé el 1° de Febrero de 1902 en los bosques de la Cordillera sobre el río Aysen, cuyo lecho y orillas son la continuación oeste del valle del Lago Blanco" (Koslowsky, 1904, p 131). The río Aysen (presently in Chilean territory) was in the vicinity of the Koslowsky ranch, more than 25 km west of Lago Blanco. The names "Valle Koslowsky" or "Region Koslowsky" are historical names that were used by the commission that surveyed the Argentine- Chilean border between 1896 and 1902, and were used to reference the area occupied by Koslowsky's ranch, i.e., the present Valle Huemules (see Aguado, 2003).

Problem: There is not a single place name recorded on any available map with the name of Koslowsky Region or Valle del Lago Blanco.

Present Location (Fig. 5B): The "Koslowsky region," "Koslowsky valley," or "Valle del Lago Blanco," as used by both Koslowsky and Thomas, are historical and obsolete names applied to the Valle Huemules. This valley includes an area of subandean grasslands, oriented approximately east and west, from the Lago Blanco on the east (western margin of Lago Blanco = 45° 55′ S, 71° 19′ W; IGM, 1950) to the Chilean border in the west (the río Simpson); the northern (45° 50′ S, 71° 31′ W) and southern (46° 03′ S, 71° 31′ W) borders of this valley are surrounded by mountain ridges or basaltic plateaus. Valle Huemules covers an area of ca. 1,200 km^2. It is impossible to say where exactly in this valley Koslowsky trapped the rodents. Therefore, for taxonomic and nomenclatorial purposes, we restrict this type locality to Estancia Valle Huemules (45° 57′ S, 71° 31′ W, 593 m, Río Senguerr, Chubut). This selection appears to be adequate because this ranch is located in the middle of the Valle Huemules –an area certainly crossed by Koslowsky many times during his collecting days- and is identified on several maps (e.g., IGM, 1951). The first Koslowsky ranch (Estancia Los Halcones, ca. 45° 58′ S, 71° 36′ W, Río Senguerr, Chubut) is now part of the Estancia Valle Huemules.

Taxonomic Implications: One subgenus, 3 species, and 1 subspecies were described from specimens collected by Koslowsky in the Lago Blanco area (see Thomas, 1903, 1916, 1919a). These are: *Akodon suffusus* Thomas, 1903, *Akodon* (*Chelemys*) *vestitus* Thomas, 1903, *Oryzomys magellanicus mizurus* Thomas, 1916, and *Akodon iniscatus* Thomas, 1919. In addition, at least 1 individual of the rare sigmodontine *Notiomys edwardsii* was collected there (see Thomas, 1919a; Pardiñas and Galliari, 1998). As currently understood, *A. iniscatus*, which distributes across most of Patagonia, is a complex taxon whose geographic variation and biological boundaries have not been correctly assessed. For a revision of this species, the collection of topotypes in the Valle Huemules area is needed. *Akodon suffusus* (= *Abrothrix longipilis*), *Akodon* (*Chelemys*) *vestitus* (= *Chelemys macronyx*), and *Oryzomys magellanicus mizurus* (= *Oligoryzomys longicaudatus*) are taxa similarly widely distributed in southwestern Argentina and Chile, and lack formal taxonomic revisions (see Pardiñas et al., 2003; Palma et al., 2004; and references cited therein).

Remarks: The region of Valle Huemules was considered one of the richest in Patagonia, promoting several border conflicts between Argentina and Chile at the beginnings of the 20th century (Aguado, 2003). Photographs taken by Koslowsky between 1898 and 1910 show extensive grasslands, numerous lakes, streams, small rivers, and dense forests in the nearby mountain ridges. Intensive sheep ranging and forest extirpation started in 1908; the effects of these practices on small mammal populations have not been assessed. A fieldtrip in late 1980s, with the goal of obtaining new specimens of *A. iniscatus*, was undertaken by Orlando Scaglia (pers. comm.). He trapped, mainly in overgrazed fields, in the vicinity of the town of Lago Blanco but only captured *Abrothrix longipilis*. However, he found *A. iniscatus* remains in owl pellets gathered in this area.

SUMMARY OF FINDINGS

Type Locality: Higuerilla (Jujuy, Argentina).

Action Proposed: Equate this type locality to Pampichuela (23° 32′ S, 65° 02′ W, 1735 m, Valle Grande, Jujuy, Argentina).

Sigmodontine Taxa Affected: *Phyllotis nogalaris* Thomas, 1921; *Hypsimys deceptor* Thomas, 1921; and *Oxymycterus akodontius* Thomas, 1921.

Type Locality: Caraguatay (Misiones, Argentina).

Action Proposed: Restrict this type locality to Puerto Caraguatay (26° 37′ S, 54° 46′ W, 192 m, Montecarlo, Misiones).

Sigmodontine Taxa Affected: *Thomasomys pictipes* Osgood, 1933.

Type Locality: Río Paranay (Misiones, Argentina).

Action Proposed: Restrict this type locality to the confluence of the río Paranay Guazú with the río Paraná (26° 41′ S, 54° 49′ W, 122 m, Libertador General San Martín, Misiones).

Sigmodontine Taxa Affected: *Oxymycterus misionalis* Sanborn, 1931.

Type Locality: Río de Oro (Chaco, Argentina).

Action Proposed: None. The río de Oro is located in the northeastern portion of Chaco Province.

Sigmodontine Taxa Affected: *Scapteromys chacoensis* Gyldenstolpe, 1932.

Type Locality: Otro Cerro (Catamarca, Argentina).

Action Proposed: None. Otro Cerro is located at 28° 45′ S, 66° 17′ W (2023 m, Capayán, Catamarca).

Sigmodontine Taxa Affected: *Phyllotis ricardulus* Thomas, 1919; *Graomys edithae* Thomas, 1919; *Akodon alterus* Thomas, 1919; *Akodon orbus* Thomas, 1919; and *Reithrodon caurinus* Thomas, 1920.

Type Locality: "Norte de Entre Ríos" (Entre Ríos, Argentina).

Action Proposed: Restrict this type locality to São Gabriel (30° 19′ S, 54° 19′ W, 118 m, Rio Grande do Sul, Brazil).

Sigmodontine Taxa Affected: "Agreste" [= *Mus*? *azarae* Fischer, 1829], and "Blanco Debaxo" [= *Mus*? *dubius* Fischer, 1829].

Type locality: Isla Ella (Buenos Aires, Argentina).

Action Proposed: Identify location of Isla Ella as 34° 22′ S, 58° 38′ W (Primera Sección Delta del Paraná, Tigre, Buenos Aires).

Sigmodontine Taxa Affected: *Deltamys kempi* Thomas, 1917; *Oligoryzomys delticola* Thomas, 1917; *Akodon arenicola hunteri* Thomas, 1917; and *Scapteromys aquaticus* Thomas, 1920.

Type Locality: Neuquén, río Limay (Neuquén, Argentina).

Action Proposed: None. Neuquén is located at 38° 57′ S, 68° 04′ W (259 m, Confluencia, Neuquén).

Sigmodontine Taxa Affected: *Akodon neocenus* Thomas, 1919.

Type Locality: Valle del Lago Blanco or Valle/Region Koslowsky (Chubut, Argentina).

Action Proposed: Restrict this type locality to Estancia Valle Huemules (45° 57′ S, 71° 31′ W, Río Senguerr, Chubut).

Sigmodontine Taxa Affected: *Akodon suffusus* Thomas, 1903; *Akodon* (*Chelemys*) *vestitus* Thomas, 1903; *Oryzomys magellanicus mizurus* Thomas, 1916; and *Akodon iniscatus* Thomas, 1919.

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LITERATURE CITED

Aguado, A.
2003 El viejo oeste de la Patagonia. Lago Blanco, Valle Huemules, El Chalía -Chubut. Rawson, Chubut. Gobierno de la Provincia de Chubut. 190 pp.

Aguado, A., and J. D. Williams
2003 Julio Germán Koslowsky, científico, explorador y colono. Revista Museo 3(17):25-30.

Alvarez, G.
1988 Neuquén. Historia, Geografía, Toponimia. Gobierno de la provincia del Neuquén. 278 pp.

Avila-Pires, F. D., de.
1972 A new subspecies of *Kunsia fronto* (Winge, 1888) from Brazil (Rodentia, Cricetidae). Revista Brasileira de Biologia 32:419-422.

Azara, F. de.
1802 Apuntamientos para la Historia Natural de los Quadrúpedos del Paraguay y Río de La Plata. Tomo segundo. Imprenta de la Viuda Ibarra, Madrid. 328 pp.

Barquez, R. M., M. A. Mares, and J. K. Braun
1999 The bats of Argentina. The Museum, Texas Tech University, Special Publications 42:1-275.

Blaustein, S. A., R. C. Liascovich, L. I. Apfelbaum, L. Daleffe, R. M. Barquez, and O. A. Reig
1992 Correlates of systematic differentiation between two closely related allopatric populations of the *Akodon boliviensis* group from NW Argentina (Rodentia, Cricetidae). Zeitschrift für Säugetierkunde 57:1-13.

Braun, J. K., M. A. Mares, and R. A. Ojeda
2000 A new species of grass mouse, genus *Akodon* (Muridae: Sigmodontinae), from Mendoza Province, Argentina. Zeitschrift für Säugetierkunde 65:216-225.

Cabrera, A.
1961 Catálogo de los Mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciencias Zoológicas 4:309-732.

Cirignoli, S., C. Galliari, V. H. Merlo Alvarez, U. F. J. Pardiñas, and D. H. Podesta
2000 Pequeños mamíferos terrestres del Río de Oro (Chaco, Argentina). 15 Jornadas Argentinas de Mastozoología (La Plata, Argentina). Resúmenes:48-49.

Contreras, J. R.
1992 Acerca de la localidad típica de *Calomys callosus* (Rengger, 1830) (Mammalia: Rodentia, Cricetidae). Nótulas Faunísticas 35:1-5.

Contreras, J. R., and E. Justo
1996 Acerca de la localidad típica y la variación subespecífica de *Akodon azarae* (Fischer, 1829) (Rodentia: Cricetidae). 21 Congresso Brasileiro de Zoologia (Porto Alegre, Brazil), Res.:225.

Contreras, J. R., and P. Teta
2003 Acerca del estatus taxonómico y de la localidad típica de *Oxymycterus rufus* (Fisher, 1814) (Rodentia: Muridae: Sigmodontinae). Nótulas Faunísticas 14:1-5.

Cuomo, N. H.
1967 Guía Cuomo Delta del Paraná. Talleres Gráficos Lumi Hermanos, Buenos Aires. 97 pp.

D'Elía, G., E. M. González, and U. F. J. Pardiñas
2003 Phylogenetic analysis of sigmodontinae rodents (Muroidea), with special reference to the akodont genus *Deltamys*. Mammalian Biology 68:351-364.

D'Elía, G., and U. F. J. Pardiñas
2004 Systematics of Argentinean, Paraguayan, and Uruguayan swamp rats of the genus *Scapteromys* (Rodentia, Cricetidae, Sigmodontinae). Journal of Mammalogy 85:897-910.

Díaz, M. M.
1999 Mamíferos de la Provincia de Jujuy: Sistemática, Distribución y Ecologia. Ph.D. Dissertation, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina. 640 pp.

Field Museum of Natural History – Reports
1927 Annual report of the Director to the Board of Trustees for the Year 1926. Field Museum of Natural History 7:1-174.

Fischer, J. B.
1829 Synopsis Mammalium. Stuttgardtiae: Cottae, xlii + 752 pp.

Francés, J., and G. D'Elía
In press *Oligoryzomys delticola* es sinónimo de *O. nigripes* (Rodentia, Cricetidae, Sigmodontinae). Mastozoología Neotropical.

Galliari, C. A., U. F. J. Pardiñas, and F. J. Goin
1996 Lista comentada de los mamíferos argentinos. Mastozoología Neotropical 3:39-61.

Gil, A.
1895 Estudios Agrícolas Sobre las Islas del Paraná. Memoria Presentada por el Comisionado del Gobierno. Ministerio de Obras Públicas de la Provincia de Buenos Aires, La Plata. Taller de publicaciones del Museo. 241 pp.

González, E. M.
2000 Un nuevo género de roedor Sigmodontino de Argentina y Brasil (Mammalia: Rodentia: Sigmodontinae). Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo, 195(12):1-12.

González, E. M., and U. F. J. Pardiñas
2002 *Deltamys kempi*. Mammalian Species 711:1-4.

Gyldenstolpe, N.
1932a A new *Scapteromys* from Chaco Austral, Argentine. Arkiv för Zoologi, 24B:1-2.

1932b A manual of Neotropical sigmodont rodents. Kunglia Svenska Vetenskapsakademiens Handlingar, Stockholm, Band 11, 3. 164 pp..

Hershkovitz, P.
1959 Nomenclature and taxonomy of the Neotropical mammals described by Olfers, 1818. Journal of Mammalogy 40:337-353.

1962 Evolution of Neotropical cricetine rodents (Muridae), with special reference to the Phyllotine Group. Fieldiana: Zoology, 46:1-524.

1966 South American swamp and fossorial rats of the Scapteromyine group (Cricetinae, Muridae) with comments on the glans penis in Murid taxonomy. Zeitschrift für Säugetierkunde 2:81-149.

1987 A history of the recent mammalogy of Neotropical region from 1492 to 1850. Pp. 11-98 in Studies in Neotropical mammalogy (Patterson, B. D., and R. M. Timm, eds.). Fieldiana: Zoology, new series 39:1-506.

1990 Mice of the *Akodon boliviensis* size class (Sigmodontinae, Cricetidae), with the description of two species from Brazil. Fieldiana: Zoology, new series 57:1-35.

1994 The description of a new species of south american hocicudo, or long-nose mouse, genus *Oxymycterus* (Sigmodontinae, Muroidea), with a critical review of the generic content. Fieldiana: Zoology, new series 79:1-43.

ICZN (International Commission on Zoological Nomenclature)
1999 International Code of Zoological Nomenclature Adopted by the International Union of Biological Sciences. International Trust for Zoological Nomenclature, London, UK.

IGM (Instituto Geográfico Militar)
1950 Lago Blanco, 4572-35 [1: 100,000 topographic map]. Buenos Aires: Instituto Geográfico Militar.

1951 Valle Huemules 4572-34 [1: 100,000 topographic map]. Buenos Aires: Instituto Geográfico Militar.

1959 San Fernando, 3560-12-2, and 3557-71 [1: 50,000 topographic maps]. Buenos Aires: Instituto Geográfico Militar.

1966 Catamarca, 2966 [1: 500,000 topographic map]. Buenos Aires: Instituto Geográfico Militar.

1967 General José de San Martín, 2760-11 [1: 250,000 topographic map] . Buenos Aires: Instituto Geográfico Militar.

1972 Atlas de la República Argentina I - Parte Política. Buenos Aires: Instituto Geográfico Militar.

1979 Atlas de la República Argentina I - Parte Política. Buenos Aires: Instituto Geográfico Militar.

1989a Ciudad de Libertador General San Martín 2366-IV [1: 100,000 topographic map]. Buenos Aires: Instituto Geográfico Militar.

1989b Chumbicha, 2966-15 [1: 100,000 topographic map]. Buenos Aires: Instituto Geográfico Militar.

1994a El Dorado, 2754-8 [1: 100,000 topographic map]. Buenos Aires: Instituto Geográfico Militar.

1994b Garuhapé, 2754-14 [1: 100,000 topographic map]. Buenos Aires: Instituto Geográfico Militar.

1994c Neuquén, 3969-17 [1: 100,000 topographic map]. Buenos Aires: Instituto Geográfico Militar.

Koslowsky, J.
1904 Dos mamíferos de Patagonia cazados en el Valle del Lago Blanco (Territorio del Chubut). Revista del Museo de La Plata 11:129-132.

Langguth, A.
1975 La identidad de *Mus lasiotis* Lund y el status del género *Thalpomys* Thomas (Mammalia, Cricetidae). Papéis Avulsos de Zoologia. 29:45-54.

Mares, M. A., R. A. Ojeda, J. K. Braun, and R. M. Bárquez
1997 Systematics, distribution, and ecology of the mammals of Catamarca Province, Argentina. Pp. 89-141 in Life Among the Muses: Papers in Honor of James S. Findley (Yates, T. L., W. L. Gannon, and D. E. Wilson, eds.). Special Publication, The Museum of Southwestern Biology, The University of New Mexico, Alburquerque, New Mexico, USA.

Mariluz Urquijo, J. M.
1953 La Fundación de San Gabriel de Batoví. Revista Histórica, Montevideo, 19:1-35.

Massoia, E.
1976 La identidad del holotipo de *Graomys hypogaeus* Cabrera (Mammalia, Rodentia, Cricetidae). Revista de Investigaciones Agropecuarias, Serie 5, Patología Vegetal 13:15-20.

Massoia, E., and A. Fornes
1964 Comentarios sobre *Eligmodontia typus typus* (Rodentia-Cricetidae). Physis 24:298.

Mones, A., and M. A. Klapenbach
1997 Un ilustre aragonés en el Virreinato del Río de La Plata: Félix de Azara (1742-1821). Estudios sobre su vida, su obra y su pensamiento. Anales del Museo Nacional de Historia Natural de Montevideo. Volumen de homenaje en los 175 años de su muerte (1821-1996), serie 2, 9:i-vii + 1-231.

Museo de La Plata.
1893 Atlas geográfico de la República Argentina: mapa de la provincia de Catamarca, construido según datos recogidos y observaciones personales hechas en los años 1887-93 por Gerardo Lange y dibujado por Enrique Delachaux. Scale 1:500,000.

Musser, G. G., and M. D. Carleton

1993 Family Muridae. Pp. 501-756 in Mammal Species of the World: A Taxonomic and Geographic Reference (Wilson, D. E., and D. M. Reeder, eds.). Second ed. Smithsonian Institution Press, Washington, D.C., USA.

2005 Superfamily Muroidea. Pp. 894-1531 in Mammal Species of the World: A Taxonomic and Geographic Reference (Wilson, D. E., and D. M. Reeder, eds.). Third ed. Johns Hopkins University Press, Baltimore, Maryland, USA.

Myers, P.

1989 A preliminary revision of the *varius* group of *Akodon* (*A. dayi*, *dolores*, *molinae*, *neocenus*, *simulator*, *toba* and *varius*). Pp. 5-54 in Advances in Neotropical Mammalogy (Redford, K. H., and J. F. Eisenberg, eds.). Sandhill Crane Press, Gainesville, Florida, USA.

Myers, P., and J. L. Patton

1989 A new species of *Akodon* from the cloud forests of eastern Cochabamba Department, Bolivia (Rodentia: Sigmodontinae). Occasional Papers, Museum of Zoology, University of Michigan 720:1-28.

Myers, P., J. L. Patton, and M. F. Smith

1990 A review of the *boliviensis* group of *Akodon* (Muridae: Sigmodontinae), with emphasis on Peru and Bolivia. Miscellaneous Publications, Museum of Zoology, University of Michigan 177:iv + 1-104.

Oliveira, J. A., and C. R. Bonvicino

2002 A new species of sigmodontine rodent from the Atlantic forest of eastern Brazil. Acta Theriologica 47:307-322.

Osgood, W. H.

1933 Two new rodents from Argentina. Field Museum of Natural History, Zoology series 20:11-14.

1943 The mammals of Chile. Field Museum of Natural History, Zoology series 30:1-268.

Palma, E., E. Rivera-Milla, J. Salazar-Bravo, F. Torres-Pérez, U. F. J. Pardiñas, P. Marquet, A. Spotorno, A. Meynard, and T. L. Yates

2005 Phylogeography of *Oligoryzomys longicaudatus* (Rodentia: Sigmodontinae) in temperate South America. Journal of Mammalogy 86:191-200.

Pardiñas, U. F. J.

1996 El registro fósil de *Bibimys* Massoia, 1979 (Rodentia). Consideraciones sobre los Scapteromyini (Cricetidae, Sigmodontinae) y su distribución durante el Plioceno-Holoceno en la región pampeana. Mastozoología Neotropical 3:15-38.

Pardiñas, U. F. J., and C. A. Galliari

1998 La distribución del ratón topo *Notiomys edwardsii* (Mammalia: Muridae). Neotrópica 44:123-124.

2001 *Reithrodon auritus*. Mammalian Species 665:1-8.

Pardiñas, U. F. J., P. Teta, S. Cirignoli, and D. Podesta

2003 Micromamíferos (Didelphimorphia y Rodentia) de norpatagonia extra-andina, Argentina: taxonomía alfa y biogeografía. Mastozoología Neotropical 10:69-113.

Pearson, O. P.

1958 A taxonomic revision of the rodent genus *Phyllotis*. University of California Publications in Zoology 54:391-496.

Pearson, O. P., and H. A. Lagiglia.

1992 "Fuerte de San Rafael": una localidad tipo ilusoria. Revista del. Museo de Historia Natural de San Rafael (Mendoza) 12:35-43.

Pine, R. H.

1980 Notes on rodents of the genera *Wiedomys* and *Thomasomys* (including *Wilfredomys*). Mammalia 44:195-202.

Reig, O. A.

1964 Roedores y marsupiales del partido de General Pueyrredón y regiones adyacentes (provincia de Buenos Aires, Argentina). Publicación del Museo Municipal de Ciencias Naturales de Mar del Plata 1:203-224.

Sanborn, C. C.

1931 A new *Oxymycterus* from Misiones, Argentina. Proceedings of the Biological Society of Washington 44:1-2.

Silva, F.

1985 Guía para la Determinaçao de Morcegos: Rio Grande do Sul. Martins Livreiro-Editor. 77 pp.

Tate, G. H.

1932a The South American Cricetidae described by Felix Azara. American Museum Novitates 557: 1-5.

1932b The taxonomic history of the South and Central American akodont rodent genera: *Thalpomys*, *Deltamys*, *Thaptomys*, *Hypsimys*, *Bolomys*, *Chroeomys*, *Abrothrix*, *Scotinomys*, *Akodon* (*Chalcomys* and *Akodon*), *Microxus*, *Podoxomys*, *Lenoxus*, *Oxymycterus*, *Notiomys* and *Blarinomys*. American Museum Novitates 582:1-32.

Thomas, O.
1903 Notes on Neotropical mammals of the genera *Felis*, *Hapale*, *Oryzomys*, *Akodon*, and *Ctenomys* with descriptions of new species. Annals and Magazine of Natural History, ser. 7, 12:234-243.

1916 Notes on Argentine, Patagonian, and Cape Horn Muridae. Annals and Magazine of Natural History, ser. 8, 17:182-187.

1917 On small mammals from the Delta of the Parana. Annals and Magazine of Natural History, ser. 8, 20:95-100.

1919a On small mammals collected by Sr. E. Budin in North-western Patagonia. Annals and Magazine of Natural History, ser. 9, 3:199-212.

1919b Two new Argentine species of *Akodon*. Annals and Magazine of Natural History, ser. 9, 3:213-214.

1919c On small mammals from "Otro Cerro," north-eastern Rioja, collected by Sr. L. Budin. Annals and Magazine of Natural History, ser. 9, 3:489-500.

1920 New species of *Reithrodon*, *Abrocoma*, and *Scapteromys* from Argentina. Annals and Magazine of Natural History, ser. 9, 4:473-478.

1921a New *Rhipidomys*, *Akodon*, *Ctenomys*, and *Marmosa* from the Sierra Santa Barbara, S.E. Jujuy. Annals and Magazine of Natural History, ser. 9, 7:183-187.

1921b On a further collection of mammals from Jujuy obtained by Sr. E. Budin. Annals and Magazine of Natural History, ser. 9, 8:608-617.

1927 On further Patagonian mammals from Neuquen and the Rio Colorado collected by Señor E. Budin. Annals and Magazine of Natural History, ser. 20, 17:199-205.

Udaondo, E.
1942 Reseña histórica del partido de las Conchas. Publicaciones del Archivo Histórico de la provincia de Buenos Aires. Contribución a la historia de los Pueblos de la provincia de Buenos Aires 21:1-135.

Williams, D. F., and M. A. Mares
1978 A new genus and species of phyllotine rodent (Mammalia: Muridae) from Northwestern Argentina. Annals of Carnegie Museum 47:193-221.

THE WILD MAMMALS OF JUJUY PROVINCE, ARGENTINA: SYSTEMATICS AND DISTRIBUTION

LOS MAMÍFEROS SILVESTRES DE LA PROVINCIA DE JUJUY, ARGENTINA: SISTEMÁTICA Y DISTRIBUCIÓN

M. Mónica Díaz and Rubén M. Barquez

ABSTRACT

We present the results of extensive field surveys conducted in Jujuy Province over a 3-year period. Additionally, specimens at several collections were examined and available literature was used to supplement information. Jujuy Province supports 143 species of mammals, represented by 9 didelphimorphs, 10 edentates, 36 bats, 2 primates, 20 carnivores, 1 perissodactyl, 8 artiodactyls, 56 rodents, and 1 lagomorph. One of the species is new to science, 4 are new for Argentina, 2 are new for NW Argentina, and 14 are new for the province. Other species of mammals are here considered as probable for the province based on recent references or records we have yet to confirm; these include 1 xenarthran, 1 bat, 2 artiodactyls, and 3 rodents. Additionally, 2 artiodactyls are probable according to historical records. Four introduced species (3 Muridae and 1 Leporidae) are not included in the checklist of species, and 5 species are excluded from Jujuy Province. Using these data we conducted a biogeographic analysis to determine the degree of similarity among the phytogeographic regions of Jujuy.

Key words: Mammals, systematics, distribution, biogeography, natural history, Jujuy, Argentina.

RESUMEN

En este trabajo se presentan los resultados de muestreos extensivos de campo realizados en la provincia de Jujuy a lo largo de tres años, sumados a la revisión de ejemplares de numerosas colecciones sistemáticas, y a información procedente de la literatura. Hasta el momento la provincia de Jujuy era la menos relevada del noroeste de Argentina, y a pesar de su pequeño tamaño es una de la más diversas de la región respecto a su fauna de mamíferos. En total se confirmó la presencia de 143 especies, representados por 9 marsupiales, 10 edentados, 36 murciélagos, dos primates, 20 carnívoros, un

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Pp. 417-578 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

perisodáctilo, 8 artiodáctilos, 56 roedores y 1 lagomorfo. Una de las especies es nueva para la ciencia, 4 son nuevas para Argentina, 2 nuevas para el noroeste argentino, y 14 nuevas para la provincia. Siete especies son consideradas probables para la provincia en base a citas de la literatura o por registros que no pudieron ser verificados por nosotros; entre ellos encontramos 1 edentado, 1 murciélago, 2 artiodáctilos y 3 roedores. Dos especies de artiodáctilos son considerados probables en base a registros históricos. También se registraron cuatro especies introducidas, 3 roedores y 1 lagomorfo, que no se incluyen en la lista total de especies; y 5 especies previamente citadas para Jujuy son excluidas de la provincia. Con los datos confirmados de las especies se realizó un análisis biogeográfico para determinar el grado de similitud entre las regiones fitogeográficas de Jujuy.

Palabras clave: Mamíferos, sistemática, distribución, biogeografía, historia natural, Jujuy, Argentina.

INTRODUCTION

The mammals of northwestern Argentina are relatively well known. Many naturalists, explorers, and colonizers, have recorded their observations, particularly Emilio Budin, who collected for Oldfield Thomas from The British Museum (London, England). Thomas described a number of new species and subspecies for Argentina and new to science (e.g., Thomas, 1897, 1898, 1913, 1916a, 1916c, 1918, 1919a, 1919b, 1919c, 1920b, 1921a, 1921b, 1921c, 1926a, 1926b). Recent years have seen a number of new studies on argentine mammals (e.g., Yepes, 1929, 1930, 1944; Crespo, 1950, 1958, 1974; Olrog, 1959, 1976, 1979; Mares, 1973; Dalby and Mares, 1974; Massoia, 1976, 1980; Williams and Mares, 1978a, 1978b; Barquez, et al., 1980, 1991, 1993; Olrog and Lucero, 1981; Contreras, 1982; Barquez, 1983, 1987; Ojeda and Mares, 1989; Barquez and Lougheed, 1990; Barquez and Ojeda, 1992; Massoia et al., 1992a, 1992b; Mares et al., 1995, 1996, 1997; Díaz and Barquez, 2002), but reflecting the sheer size of the country and the diversity of habitats, further surveys are needed in many areas that remain poorly known (Pine, 1982).

Northwest Argentina has a high diversity of mammals, including 9 orders, 29 families, approximately 100 genera, and 186 species; there are 76 type localities in the area, including 16 in the province of Jujuy (Cabrera, 1958, 1961a, 1961b; Wilson and Reeder, 1993). During the last several years, new genera and species have been described in Argentina, including some from the northwest regions. These include a new species of *Cryptonanus* from the province of Jujuy (Flores et al. 2000; Díaz et al., 2002; Voss et al. 2005), and new genera and species of sigmodontines and octodontids (Díaz et al., 1999; Mares et al. 2000).

Matschie (1894) published one of the first papers concerning the mammals of NW Argentina, including the province of Jujuy. The contributions of Oldfield Thomas also were important at the beginning of the century; he added several species to the fauna of Jujuy, many of them representing species new to science, based largely on specimens collected by E. Budin. Later, some large-scale studies on the mammals of Jujuy, Salta, Tucumán, and Catamarca provinces were published (Mares et al., 1981, 1989, 1996, 1997; Ojeda and Mares, 1989; Barquez et al., 1991; Díaz et al., 1997, 2000; Díaz, 2000; Díaz and Barquez, 2002); in general, however, most of these studies were taxonomically or geographically restricted (Crespo, 1941; Olrog et al., 1976; Olrog, 1979; Cajal, 1985a, 1985b; Barquez and Ojeda, 1992; Heinonen and Bosso, 1994; Iudica, 1995; Capllonch et al., 1997; Cajal and Buenaventura, 1998 ; Perovic, 1998; Barquez et al., 1999; Jayat et al., 1999).

Until recently the province of Jujuy has not been thoroughly surveyed, in spite of being one of the most diverse provinces of Argentina with respect to mammalian species richness and taxonomic diversity. The principal objective of this investigation was focused in surveying the as many localities as possible within the province, emphasizing the less well-known areas and those that have never been studied, such as the highlands (Prepuna, Puna, High Andean). Another objective was to resolve taxonomic problems in some groups, such as rodent and marsupials, as well as to confirm the presence of species thought to occur in the province, to compare the faunal composition between phytogeographic areas of the province at species levels.

This study has permitted us to publish a field guide for the mammals of Jujuy (Díaz and Barquez, 2002), where the information was reduced and adapted to be used as an identification tool by researchers, students and rangers. Our studies in Jujuy have confirmed the presence of 143 species of mammals, plus 7 that likely occur there or that have records that could not be confirmed, and 2 species that no longer occur there. We have named 1 species new to science (Díaz et al., 2002), and added 14 species to the province, 2 to NW Argentina, and 4 to Argentina (Díaz and Barquez, 1999; Flores et al., 2000; Barquez and Díaz, 2001); we have also elevated 4 subspecies (2 marsupials and 2 rodents) to the species level (Flores et al., 2000); as a result of our studies, the information offered in this paper provides more accurate range limits for these species, and allows us to pursue several biogeographic analysis.

In spite of the extensive systematic collections and field surveys, there are still several questions to be answered, particularly concerning the identity of several taxa and their precise distributional limits.

STUDY AREA

The Province of Jujuy is located in northwestern Argentina, bordered by Bolivia to the north, Chile and Bolivia to the west, and Salta Province to the east and south (Fig. 1). It covers slightly over 53,219 km^2, representing 1.9% of the national territory. The extreme points are, the confluence of the Rivers Mojinete and Grande de San Juan (21° 46′ S, 60° 13′ W) to the north, and the headwaters of the Arroyo de Quisto, at the Cresta de Gallo mountains (24° 37′ S, 64° 39′ W) to the south, and from the a point just north of the Arroyo Ojo de Agua, at the Sierra del Maíz Gordo (24° 12′ S, 64° 09′ W), westward to the Hito in Pampa del Lari (23° 41′ S, 67° 13′ W).

In spite of its small area, Jujuy is one of richest provinces in the country in floristic terms. Its tropical location and altitudinal range (500 to 6000 m) result in a multitude of climates and habitats, with consequent variation in vegetation. As a result, the province supports subtropical forests, chacoan forests, mountain forests, xerophytic woodland, high grasslands, and High Andean steppes (Cabrera, 1977), represented by 5 phytogeographic regions (Fig. 1): High Andean, Puna, Prepuna, Yungas, and Chaco.

In the Puna of Jujuy (Fig. 2A), the climate, both daily and seasonal, is characterized by its aridity and great thermal range, with precipitation falling almost exclusively in

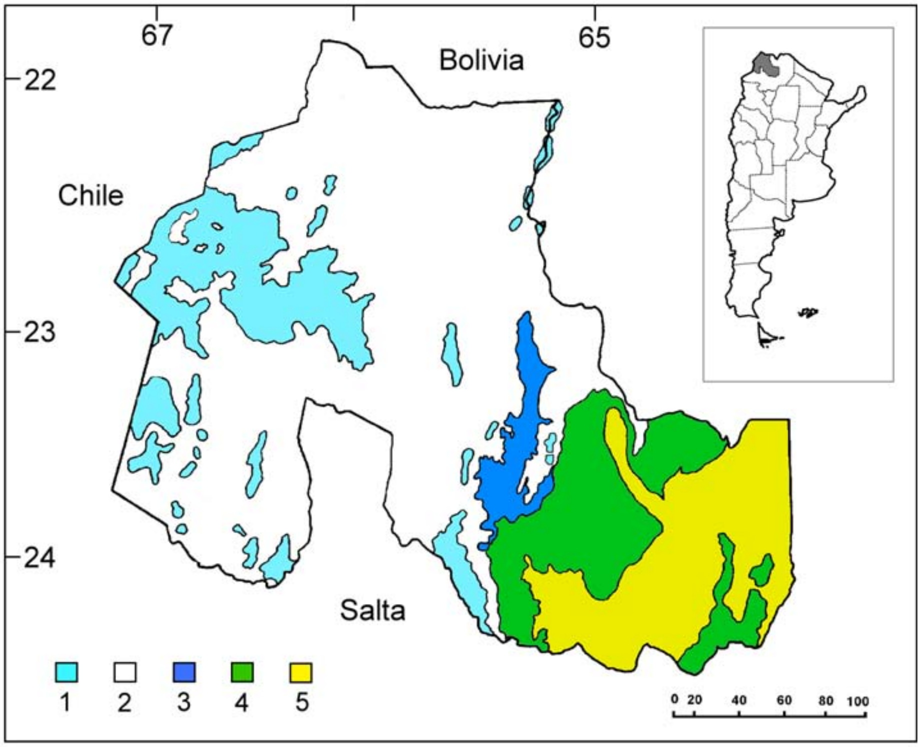

Figure 1. Map of the province of Jujuy, showing the phytogeographic provinces. The insert shows the relative position of the province within Argentina. 1) High Andean; 2) Puna; 3) Prepuna; 4)Yungas; 5) Chaco.

summer, and snow only rarely. In winter, the mean temperature is less than -1.0°C, while in the warmest month, December, it is 5.3°C (Cabrera, 1976). Rains decrease from north to south, and are practically nonexistent in the region of the large salt flats (Cabrera, 1976). Defined on the basis of vegetation, Troll (1959) defined 4 subdivisions of the Puna (humid, dry, thorny, and desert Puna). Troll's humid subdivision was considered a different province (the High Andean Province) by Cabrera (1977), because it is located at the highest part of the Andes (>4000 m elev.), and the 3 principal plant communities are associated with elevational ranges; these are the High Summit vegetation, the High Andean grassland, and the High Andean thickets (Ruthsatz and Movia, 1975).

According to Cabrera (1976) the argentine Puna (exclusive of the High Andean Province) can be climatically divided in 2 zones: to the east is the humid puna, which includes the "thorny Puna" and the "dry Puna" of Troll (1959); and to the southwest is the dry puna, corresponding to Troll's "desert Puna." However, Vervoorst (1982) recognizes Troll's authority including his 4 divisions for the Puna.

In the Prepuna (Fig. 2B) most vegetative growth occurs near ravines and dry slopes, and are dominated by columnar cacti (*Trichocereus*) and terrestrial bromeliads, ring-shaped or in cushions. In the arid zones, an ecotone with the Puna can be observed, as in the Quebrada de Humahuaca (Vervoorst, 1982). The climate is dry and warm, and

Figure 2. a) The puna at Curques, 21 km N Susques, above hwy 74. Photo taken December 1995. b) The Prepuna at Casa Colorada, approx. 2 km N Alfarcito, 3034 m. Photo taken 14 June 1997. c) The Chaco at Río Lavayén. Photo taken 4 October 1995. d) The Yungas at Río Las Capillas. Photo taken 20 August 1995. All photos by R. M. Barquez.

rain falls exclusively in summer. Climatic data are scarce, but at Humahuaca the mean temperature is 10.4°C and the annual precipitation is 175 mm; comparable metrics at Tumbaya indicate 3.6°C and 179 mm, respectively (Cabrera, 1976).

The Chaco (Fig. 2C) is located at the eastern portion of the province and contains 2 districts; the Occidental District, dominated by *Schinopsis lorentzii*, and the Serrano District, characterized by the quebracho trees (*Schinopsis haenkeana*) (Morello and Adámoli, 1968; Ragonese and Castiglione, 1970; Cabrera and Willink, 1973; Vervoorst, 1982). The region is mainly a flat plain with elevations generally no higher than 300 m, but reaching 1800 m in the Serrano District. The Occidental District has a marked continental climate, with annual precipitations between 500 and 800 mm. The Chaco has been greatly impacted by uncontrolled livestock and forest exploitation (Morello and Saravia Toledo, 1959).

The Yungas (Fig. 2D) occur along the western slopes of the mountains in the eastern portion of the province. There are different opinions with respect to the units or divisions that constitute the Yungas (Meyer, 1963; Brown, 1995; Morales et al., 1995; Prado, 1995), but we follow Cabrera (1976) and Cabrera and Willink (1973). The Yungas is limited to the northeast by the Chaco, and to the west with Prepuna or Puna (Cabrera, 1976). The principal vegetation is cloud-forest, rich in laurels (Lauraceae) and myrtles (Myrtaceae). Above the cloud-forests are deciduous woodlands of *Alnus acuminata*, forests of *Podocarpus parlatorei* (pino del cerro), and grasslands (Cabrera and Willink, 1973). The climate is warm and humid; precipitation occurs mainly in summer, and winters are characterized by occasional frost. Annual precipitation reaches 2500 mm and even more in some places. Differences in latitude, altitude, relief, and exposure result in considerable variation among localities that are relatively close to each other (Cabrera, 1976).

MATERIALS AND METHODS

The province of Jujuy was extensively sampled from January 1995 through March 1998. We personally sampled about 220 of the localities given in Appendix I and captured 806 specimens (529 collected and 277 released) belonging to 61 species in 12 families. Additionally, we have examined specimens at several collections (see below), and loans of specimens were obtained from various museums. Some private collections were also examined. These observations and records were used to supplement information available in the literature.

Collection and Preparation of Specimens. Small terrestrial mammals were captured with Sherman, Victor, and Museum Special Traps; the bats were collected with mist nets. Large mammals were recorded by direct observation, observation of tracks, signs of activity, photographic traps, and captures with leg traps.

Morphometric data were recorded for all captured specimens (Díaz et al., 1998), as well as weight, sex, reproductive condition, presence and identity of ectoparasites, and molting status. Some specimens were prepared as standard skins, skulls, and skeletons, or preserved in alcohol, and deposited at the Colección Mamíferos Lillo (CML) or Programa de Investigaciones de Biodiversidad Argentina (PIDBA), both located in the Faculty of Natural Sciences and Miguel Lillo Institute, National University of Tucumán, Tucumán, Argentina, and at the Sam Noble Oklahoma Museum of Natural History, as unaccessioned materials labeled as ARG (Catalogue of specimens from Argentina).

Specimens examined that have not been accessioned into an Institutional Collection or Museum are indicated with the initials of the collectors as follows: JPJ, Jorge Pablo Jayat; MMD, M. Mónica Díaz, and RMB, Rubén Marcos Barquez.

Specimens examined at systematic collections are indicated with the following acronyms: AMNH, American Museum of Natural History, New York, New York, United States; BMNH, British Museum (Natural History), London, England; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, United States; CEM, Colección Elio Massoia, Buenos Aires, Argentina; CML, Colección Mamíferos Lillo, Tucumán, Argentina; CR, Colección Rusconi, Tucumán, Argentina; FMNH, Field Museum of Natural History, Chicago, Illinois, United States; IADIZA, Instituto Argentino de Investigaciones de Zonas Áridas, Mendoza, Argentina; SNOMNH, Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma, United States; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; MCNS, Museo de Ciencias Naturales de Salta, Salta, Argentina; MLP, Museo de La Plata, La Plata, Argentina.

Examination of Specimens. A total of 2994 specimens were examined, comprising 180 didelphimorphs, 64 edentates, 695 bats, 4 primates, 100 carnivores, 1 perissodactyl, 37 artiodactyls, 1901 rodents, and 12 lagomorphs.

With the purpose of identifying the species, the external morphology and both external and cranial morphometrics were compared with type specimens or with original descriptions, and with published revisions (e.g., Pearson, 1958; Hershkovitz, 1962; Myers, 1989; Myers et al., 1990; Barquez et al., 1993, 1999; Braun, 1993; Steppan, 1993, 1995).

Localities and Maps. A total of 601 localities were recorded (Appendix 1), of which 42 were not located, and about 300 were located with maps of the Instituto Geográfico Militar, the department of the Dirección Provincial de Hidráulica, the Automóvil Club Argentino, and from Keegan and Keegan (1993). We have also used the following maps of the Instituto Geográfico Militar (year of publication): Chart 2363, Tartagal (1957); Chart 2366-2166, La Quiaca (1957); Chart 2563, Monte Quemado (1957); Chart 2566, Salta (1960), all at scale 1:500,000. Some localities were not found with these maps, because literature citations were not precise or there was insufficient data.

In the appendix, all localities were ordered alphabetically, with provincial departments indicated between parentheses. Geographic coordinates for localities sampled by us were obtained with Geographic Positioning System (GPS) and those for specimens not collected personally were determined with the help of the references indicated above.

The following localities were erroneously reported by E. Budin as coming from the Sierra de Zenta: La Laguna, Sierra de Zenta, 4500 m; Sierra de Zenta, 4000 m; Sierra de Zenta, 4500 m, E de Maimará; and Sierra de Zenta; all with voucher specimens deposited at the BMNH, MACN, CML, and CR. Budin's original notes are deposited at the CML, however, and these, along with information in Budin (1931), allowed us to

Figure 3. Campo Laguna (a Type Locality; mentioned either as La Laguna, Cerro Lagunita, Cerro de Lagunita, Cerro de la Lagunita, or Lagunita). This site is located in Sierras de Tilcara, and O. Thomas referred it as to Sierras de Zenta. Photograph taken 16 June 1997 by D. A. Flores.

Figure 4. Photo of Emilio Budin in his campsite at Campo Laguna on February 1931. Vicuñas hunted by him can be seen on the ground.

confirm the exact location of these localities, which in fact must be located in Sierra de Tilcara. The place is known by the local residents as Lagunita, or Campo Laguna (Figs. 3, 4), as mentioned in some of Thomas' publications (e.g., Thomas, 1913). The locality is in the Sierras de Tilcara, in the mountains E of Tilcara, approximately 70 km S to the locality indicated by Thomas, and in a different mountain chain. Consequently, the type locality must be changed to the location given here.

BIOGEOGRAPHICAL ANALYSIS

To evaluate biogeographic patterns among phytogeographic areas we compared the species, genera, and families shared between these areas using similarity indices. Faunal similarity between phytogeographical areas was estimated with simple presence/absence data for species, genera, and families, to analyze the degree of interrelation among regions at different taxonomic levels. We applied both Jaccard's Coefficient (J) (Jaccard, 1908; Sneath, 1957) and the Simple Matching Coefficient (S_{SM}) (Sokal and Michener, 1958). Jaccard's Coefficient was calculated with the formula:

$$J = a/(a+u)$$

where a is the number of shared species and u is the number unshared species between the phytogeographic areas. This metric does not incorporate absences shared by 2 areas. The Simple Matching Coefficient was calculated as:

$$S_{SM} = m/(m+u) = m/n$$

where m corresponds to the sum of the shared presences (e.g., a) and the number of shared absences (species known for the area but not sharing the phytogeographic regions under comparison), and u is the sum of the unshared species. Thus, this metric does consider shared absences in assessing overall similarity. Both indices range from

0 (minimum similarity) to 1 (maximum similarity).

Phytogeographic regions were grouped using the unweighted pair-group arithmetic averaging cluster algorithm (UPGMA) based on similarity values, and expressed in a dendrogram. Cophenetic correlation coefficients between the resultant phenogram and the original similarity matrix estimate the degree to which the relationships suggested by clustering are representative of the actual relation among elements in the original similarity matrix (Sokal and Rohlf, 1962). Generally the values oscillated between 0.6 and 0.9, the values greater than 0.8 indicate a good representation of the matrix of similarity for the dendrogram (Sneath and Sokal, 1973).

A consensus between S_{SM} and J was performed to indicate the relationships common to both analyses. Phenetic analyses were performed using NTSYS-pc (Rohlf, 1993).

SPECIES ACCOUNTS

In this section we report on all species known to occur in Jujuy Province, based either on published literature (with confirmed identity) or our observations. Accounts include scientific name, author, literature citation, and broader distribution in Argentina. Taxonomic arrangement follows Wilson and Reeder (1993) and McKenna and Bell (1997) with some exceptions indicated under comments for each species. The distribution in Jujuy is based on the Specimens Examined and Additional Records; the latter includes records from the literature, interviews with local residents, and personal observations. Unless noted otherwise all specimen localities are from Jujuy Province. Under the "Comments" section we summarize available information about natural history and taxonomy, incorporating unpublished data obtained during this study, especially pertaining to reproduction, molting, habitat preferences, and feeding habits, among others.

RESULTS

Order Didelphimorphia
Family Didelphidae
Subfamily Didelphinae

Genus *Didelphis*

Didelphis albiventris Lund, 1840
White-eared Opossum

Didelphis albiventris Lund, 1840. Konigelige Danske Videnskabernes Selskabs Afhandlinger, Kjöbenhavn, p. 20.

Distribution in Argentina.--Subtropical and Pampean regions, extending southward to Río Negro province, at 40° S latitude; in Jujuy it is found up to 2600 m (Cabrera, 1958; Barlow, 1965; Olrog, 1979; Olrog and Lucero, 1981; Crespo, 1982; Cerqueira, 1984, 1985).

Specimens Examined (17).--Caimancito, FCCNA, 1 (MACN 30.348); "Jujuy," 4 (MACN 31.14, 36.102, 36.103, 36.104); Maimará, 2230 m, 2 (MACN 27.97, 27.98); Palpalá, 1 km al E, entre rutas 66 and 1, 2 (MMD 404, 405); Parque Nacional Calilegua, Aguas Negras, 1 (CML 4067); Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20, 1 (MMD 340); San Salvador de Jujuy, 1 (CML 1639); Yuchán, 1 (MACN 34.586); Yuto, 4 (AMNH 179892, 179893, 179894, 185206).

Additional Records.--Cercanías de El Simbolar (census); Cerro Calilegua (Olrog, 1979); El Arenal (Yepes, 1944); Puente sobre el Río San Francisco, cruce entre Ruta 1 y el Río San Francisco (M.M. Díaz, personal observation); Río Blanco (Yepes, 1944).

Comments.--Records of this species in Jujuy correspond to the Yungas, Chaco, and Prepuna. Several specimens were collected alongside roads. Although *Didelphis albiventris* is more common in rural regions, 1 specimen was captured in a pristine dense forest at Las Capillas. Heinonen and Bosso (1994) reported this species from Mesada de las Colmenas, Abra de Cañas and from Duraznillar, 2 localities that are included in Cerro Calilegua as mentioned by Olrog (1979). We have recorded a female with developed mammae in February and young specimens in March and July.

Genus *Cryptonanus*

Recently described by Voss et al. (2005), this genus was included in northwestern Argentina, in the provinces of Jujuy and Salta, by Flores et al. (2000, as *Gracilinanus*). It is apparently uncommon or difficult to capture, and records are scarce. Flores et al. (2000) cited 1 species for Jujuy, *Cryptonanus chacoensis* (as *Gracilinanus agilis chacoensis*) and Díaz et al. (2002) described *Cryptonanus ignitus* (as *Gracilinanus ignitus*).

Cryptonanus chacoensis (Tate, 1931)
Agile Gracile Mouse Opossum

Marmosa agilis chacoensis Tate, 1931. American Museum Novitates 493:10.

Distribution in Argentina.--This species is found in Corrientes, Chaco, Formosa, Misiones, Entre Ríos, Buenos Aires, Jujuy, and Salta provinces (Massoia and Fornes, 1972; Contreras, 1982, 1984; Flores et al., 2000; Voss et al., 2005).

Specimens Examined (3).--Ingenio La Esperanza, 1 (CEM 4691); Santa Bárbara, 2 (AMNH 167851, 185270).

Comments.--This species was previously considered as a subspecies of *Gracilinanus agilis*, which is now restricted to Brazil, Peru, and probably Paraguay. The records from Jujuy correspond to the Yungas and Chaco.

Cryptonanus ignitus (Díaz et al. 2002)
Red-bellied Gracile Mouse Opossum

Gracilinanus ignitus Díaz, Flores, and Barquez, Journal of Mammalogy, 83, 2002:824.

Distribution in Argentina.--Known only from the type locality in Yuto, Jujuy Province.

Specimens Examined (1).--Yuto, 1 (AMNH 167852, holotype).

Comments.--Nothing is known about the natural history of this species. It was described based on a single specimen deposited at AMNH, collected by F. Contino in 1962, when the province of Jujuy was less disturbed by agricultural development. The holotype is the only specimen known for this species.

Genus *Lutreolina*

Lutreolina crassicaudata (Desmarest, 1804)
Thick-tailed Opossum

Didelphis crassicaudata Desmarest, 1804. Nouveau dictionnaire d`histoire naturelle, appliqueé aux arts, à l`agriculture, à l`économie rurale et domestique, à la médicine, etc. par une société de naturalistes et d`agriculteurs, noveau édition, Ch. Deterville, Paris, 24:19.

Distribution in Argentina.--It is found Jujuy, Salta, Formosa, Chaco, Tucumán, Misiones, Corrientes, Entre Ríos, Córdoba, Santa Fe, Buenos Aires, La Pampa, and Mendoza provinces (Flores, 2003).

Specimens Examined (4).--Abra de Cañas, El Monolito, 1 (CML 1759); El Duraznal, Santa Bárbara, 1800 m, 2 (CML 1596, 1597); "Jujuy," 1 (MACN no number).

Additional Records.--Abra de Cañas, 1700 m (Olrog, 1976); Aguas Negras, 600 m (Heinonen and Bosso, 1994); Arroyo Sauzalito (R. M. Barquez, personal observation); Cerro Calilegua (Olrog, 1979); Cerro Santa Bárbara, 1800 m (Olrog, 1976); Parque Nacional Calilegua (Heinonen Fortabat and Chébez, 1997).

Comments.--Cabrera (1958) considered 2 subspecies to be present in Argentina, *L. c. crassicaudata* and *L. c. paranalis*; the former occurs in Misiones and Formosa provinces, and the latter in Corrientes, Santa Fe, Buenos Aires, west to La Rioja and San Juan provinces. He did not mentioned specimens from northwestern Argentina, in spite of having records being reported since the beginning of the 19th century. According to Massoia (1973) the specimens cited from northwestern Argentina may be not assigned with certainty to any of the known argentine subspecies, but he indicated that they were more similar to *L. c. crassicaudata*. This taxon is in need of a detailed revision to determine if the different geographical populations should be recognized as subspecies or species; the populations from northwestern Argentina are smaller and darker than those from southern and eastern Argentina (D. A. Flores, personal communication 1995).

Heinonen and Bosso (1994) attributed the localities Abra de Cañas and Mesada de las Colmenas to Olrog (1979); however, although Abra de Cañas was noted by Olrog in 1976, Mesada de las Colmenas is not indicated by him in any of his publications. The record by Olrog (1976) for Cerro Santa Bárbara probably corresponds to specimens at the CML from El Duraznal. Records of *L. crassicaudata* are scarce in Jujuy Province and all are from the Yungas. A specimen has been observed attacking individuals of *Didelphis albiventris* in the water while swimming (D. A. Flores, personal communication).

Genus *Micoureus*

Micoureus constantiae (Thomas, 1904)
Pale-bellied Woolly Mouse Opossum

Marmosa constantiae Thomas, 1904. Proceedings of the Zoological Society of London, 2:243.

Distribution in Argentina.--Northwestern Argentina, in Jujuy, Salta, and Tucumán provinces (Cabrera, 1958; Olrog and Lucero, 1981; Mares et al., 1989; Redford and Eisenberg, 1992; Flores and Díaz, 2002).

Specimens Examined (8).--Aguas Negras, 5 (2 CML 2921, 5688; 3 MACN 19425, 19426, 19427); Caimancito, 1 (MACN 30297); Calilegua, 1 (CEM 4886); Río San Francisco, altura de Yuto, 500 m, 1 (BMNH 20.1.7.134 holotype of *Marmosa budini*).

Additional Records.--Aguas Negras, Camping, Parque Nacional Calilegua (M. M. Díaz, personal observation); Mesada de las Colmenas, 1150 m (Heinonen and Bosso, 1994).

Comments.--Aguas Negras is the correct locality for the specimen at the CML, cited by Heinonen and Bosso (1994) for Caimancito. All records of Jujuy are from a National Park (Parque Nacional Calilegua) in the Yungas. In specimens collected at Aguas Negras, Camping, Parque Nacional Calilegua, we have observed an aggressive behavior, and a great ability to climb the trees. At the same locality a female captured in June had mammae pigmented strongly ochraceous. The subspecies from Jujuy is *M. c. budini* (Thomas, 1919), whose type locality is in the province.

Genus *Thylamys*

Four species of *Thylamys* are known from Jujuy: *T. cinderella*, *T. sponsorius*, *T. pallidior*, and *Thylamys* sp. According to Palma (1994, 1995) and Palma and Yates (1998) the specimens cited as *T. elegans* from Argentina are *T. venustus* whereas *T. elegans* is restricted to Chile. According to Flores et al. (2000), not all the specimens from northwestern Argentina correspond to *T. venustus*. When specimens from northwestern Argentina were compared, we found characters that allow the recognition of the subspecies described by Thomas for this region, *Marmosa elegans sponsoria*, from Jujuy and *M. e. cinderella*, from Tucumán. Cabrera (1958) considered these 2 subspecies as synonyms, and Gardner (1993) included them within *T. elegans*. Tate (1933), in spite of showing sympatry between *T. cinderella* and *T. sponsorius*, considered the 2 taxa as subspecies of *T. venustus*. However, in his list of specimens examined, some individuals were listed for both taxa. For example, he cited León, and Carmencito (=Caimancito) for *T. venusta cinderella* and also for *T. v. sponsorius*, but in both cases referenced the same specimen (Flores et al., 2000).

Two groups, differing in cranial characters, body size, and a tendency to inhabit different habitats, can be recognized. Based on this information, *T. sponsorius* and *T.*

cinderella are considered to be valid species (Flores et al., 2000). It is possible that these 2 taxa can live in sympatry in some places because some collecting localities are in close proximity.

Actual records of *T. pusillus* for Jujuy Province were not found. Currently the records in the literature (Olrog and Lucero, 1981; Honacki et al., 1982; Redford and Eisenberg, 1992) correspond to *T. pallidior*, which is the typical form of the Puna and is considered by some authors as a subspecies of *T. pusillus* (Cabrera, 1958; Olrog, 1979). *Thylamys pusillus* inhabits the Chaco, which is a small and extremely disturbed area in Jujuy Province.

Thylamys cinderella (Thomas, 1902)
Cinderella fat-tailed Opossum

Marmosa elegans cinderella Thomas, 1902. Annals and Magazine of Natural History, ser. 7, 10:159.

Distribution in Argentina.--Found only in the NW part of the country, previously known from the provinces of Jujuy and Tucumán (Tate, 1933) but recently reported for Salta Province by Flores et al. (2000).

Specimens Examined (48).--4 km W jct Hwys 34 & 3, along Hwy 3, 1 (CM 42779); Caimancito, 400 m, 1 (BMNH 21.1.2.17); Caimancito, 600 m, 1 (FMNH 41266); Caimancito, 700 m, 1 (MACN 30.299); Cruce camino a Puesto Viejo y Ruta 34, 4 km al E, sobre camino a Puesto Viejo, 5 (4 MMD 102, 106, 107, 108; 1 released); Jujuy, 1258 m, 5 (BMNH 20.1.7.135, 20.1.7.136, 20.1.7.137, 20.1.7.138, 20.1.7.139); Laguna La Brea, 1 (MMD 49); Laguna La Brea, 25 km antes de Palma Sola (Ruta 1), 1 (SNOMNH 19580); León, 1500 m, 5 (BMNH 18.1.1.47, 18.1.1.48, 18.1.1.49, 18.1.1.50, 18.1.1.51); On highway 9 at border with Salta, at campground on the way to El Carmen, 4600 ft., 4 (ARG 2496, 2516, 2598, 2623); Oyeros, 3 km al N, camino entre rutas 61 and 43, 1 (MMD 210); Santa Rita, 2 km al NO, sobre ruta provincial N° 1, 2 (MMD 216, 217); Santa Rita, 4 km al NO, sobre ruta provincial N° 1, 1 (MMD 215); Sobre ruta 9 en el límite con Salta, sobre camino a El Carmen, 12 (6 CML 3175, 3176, 3177, 3178, 3179, 3180; 6 IADIZA 4642, 4646, 4648, 4649, 4652, 4657); Villa Carolina, Río Lavallén, 500 m, 3 (BMNH 20.1.7.140, 20.1.7.141, 20.1.7.142); Yuto, 4 (1 CML 486; 3 AMNH 167853, 185271, 186948).

Comments.--Records are known mainly from the Chacoan vegetation. Some localities are in Yungas or transitional forests, but always near the Chaco or arid areas, where they may be found in sympatry with *T. sponsorius* (Flores et al., 2000). On a specimen label at the BMNH (18.1.1.49), E. Budin wrote that rodents in his traps were eaten by this marsupial. According to information on the original label, the holotype was captured by hand (BMNH 0.7.9.20).

A lactating female with open vagina was captured in February. Juveniles were collected in February and May, and subadults in May, July, August, September, and October.

Thylamys pallidior (Thomas, 1902)
Pallid Fat-tailed Opossum

Marmosa elegans pallidior Thomas, 1902. Annals and Magazine of Natural History, ser. 7, 10:161.

Distribution in Argentina.--Lower elevations in the Monte and in the northern part of the Patagonian Region from the provinces of Jujuy south to Chubut near the coast (Palma, 1995; Flores et al., 2000).

Specimens Examined (35).--9 km NW Bárcena, 2 (ARG 4603, 4627); 11 km east of Humahuaca, 2 km east of Pucará on road to Cianzo, 1 (ARG 2690); Abra Pampa, 4 (3 CML 1028, 1030, 1031; 1 MACN 15602); Abrapampa, 3500 m, 1 (BMNH 19.8.1); Alfarcito, 2600 m, 1 (BMNH 21.11.1.105); Casabindo, 4000 m, 6 (BMNH 19.8.2.35, 19.8.2.36, 19.8.2.40, 19.8.2.41, 19.8.2.42, 19.8.2.44); Cerro Casabindo, 4500 m, 2 (BMNH 19.8.2.39, 19.8.2.43); Cuesta del Hurón, 29 km al O de Cineguillas sobre ruta provincial N° 64, 3835 m, 3 (MMD 441, 463, 466); Curques, 24 km al N de Susques, sobre ruta provincial N° 74, 4100 m, 1 (MMD 286); La Quiaca, 17 km al O and 3 km al S, sobre ruta provincial N° 5, 3711 m, 1 (MMD 418); Laguna de Pozuelos, 2 (MACN 19399, 19413); Maimará, 2230 m, 3 (2 BMNH 12.12.12.53, 12.12.12.54; 1 MACN 31.108); Maimará, 2500 m, 2 (MACN 31.40, 31.41); Mina Pan de Azúcar, 13 km al S, sobre Río Cincel, 1 (MMD 535); Mina Pirquitas, 31 km al SE, Sierra de Quichagua, sobre ruta 74b, 4200 m, 2 (MMD 528, 529); Miyuyoc, 3750 m, 1 (MMD 399); Salar Cauchari, 31 km al N de Cauchari, sobre ruta 70, 3840 m, 1 (MMD 313); Sierra de Zenta, 4500 m, 1 (MACN 31.107; see comments under *Localities and maps*).

Additional Records.--Casabindo (Tate, 1933); Casabindo, 4000-4500 m (Thomas, 1919b, as *Marmosa elegans pallidior*); Humahuaca (Thomas, 1919a, as *Marmosa elegans pallidior*).

Comments.--All records of this species correspond to the High Andean, Puna, and Prepuna regions. At 9 km NW Bárcena, this species was collected with *T. sponsorius*, a species known only from the Yungas and Chaco provinces. Bárcena is in an ecotone between Prepuna and Yungas. Offspring were recorded in February and April, juveniles in February and March, and subadults in April and May. A lactating female was captured in December, with 9 abdominal mammae, 8 forming a circle around a central one, and as is typical for this genus the hair around the mammae was pigmented. Specimens with incrassate tails were recorded in February, March, and December. Molting specimens were observed in February and March. The specimen from Mina Pan de Azúcar is represented by a toothrow found in feces.

Thylamys sp.

Specimens Examined (1).--Cerro Calilegua, El Duraznillo, 3000 m, 1 (CML 1718).

Comments.--The specimen cited by Heinonen and Bosso (1994) as *Thylamys elegans* is deposited at the CML and the same as that cited by Olrog (1979) as *M. pusilla pallidior.* This specimen was examined at CML and does not correspond with any of the known species from northwestern Argentina (Flores et al., 2000), so it is here treated as

Thylamys sp.

The record is from a region of alder (*Alnus*) forests with some specimens of queñoa trees (*Polylepis*), according to Olrog (1979) and Heinonen and Bosso (1994). Additional specimens from the area are needed to confirm the identity of this species.

Thylamys sponsorius (Thomas, 1921)
Fat-tailed Mouse Opossum

Marmosa elegans sponsoria Thomas, 1921. Annals and Magazine of Natural History, ser. 9, 7:186.

Distribution in Argentina.--In Argentina this species was only known for the province of Jujuy, but recently was reported from Salta and Tucumán provinces (Flores et al., 2000).

Specimens Examined (63).--2.5 km W El Bananal, 1 (PIDBA 892); 9 km NW Bárcena, 2 (ARG 4609, 4620); Abra de Cañas, 2 (MACN 19434, 19435); Abra de Cañas, El Monolito, 1700 m, 6 (CML 1781, 1782, 1785, 1786, 1787, 1788); Aguas Negras, 1 (MACN 19429); Aguas Negras, 600 m, 1 (MACN 19428); Arroyo La Horqueta, 3 km al SE de las Lagunas de Yala, 2100 m, 1 (MMD 182); Arroyo La Horqueta, 6 km el SE de las Lagunas de Yala, 2100 m, 1 (MMD 191); Arroyo Yuto, 13 km al SO de Yuto, 2 (MMD 68, 69); Calilegua, 2 (1 CEM 4885; 1 FMNH 22353); Cerro Hermoso, 3 (MACN 19431, 19432, 19433); El Simbolar, 25 km al SO de Palma Sola, 3 (2 CM 42780, 42783; 1 SNOMNH 19579); Higuerilla, 2000 m, 6 (BMNH 21.11.1.100, 21.11.1.101, 21.11.1.102, 21.11.1.103, 21.11.1.104, 21.11.1.99); Mesada de las Colmenas, 5 (MACN 19436, 19437, 19438, 20280, 20281); Mountains W of Yala, 1 (FMNH 22354); On highway 29 (east off of hwy 9), 10 km west of Tiraxi, 1 (ARG 2659); Palma Sola, 1 (AMNH 183307); Parque Nacional Calilegua, Aguas Negras, camping, 5 (CML 5695, 5696, 5697); Parque Nacional Calilegua, Arroyo Sauzalito, 2 (CML 5698); Río Blanco, 9 km SW San Antonio, 1495 m, 2 (PIDBA 622, 623); Río Tesorero, 4 km al N de Tiraxi, sobre ruta provincial N° 29, 2 (MMD 192, 200); Río Tiraxi, 1.5 km al E de Tiraxi, sobre ruta provincial N° 29, 1 (PIDBA 671); Santa Bárbara, 1 (AMNH 185323); Sunchal, Sierra Santa Bárbara, 1200 m, 9 (BMNH 21.1.1.82, 21.1.1.83, 21.1.1.84, 21.1.1.85 *Marmosa elegans sponsoria* holotype; 21.1.1.86, 21.1.1.87, 21.1.1.88, 21.1.1.89, 21.1.1.90); Sunchal, Sierra Santa Bárbara, 1400 m, 1 (BMNH 21.1.1.81); Tumbaya, 1 (IADIZA 4641).

Comments.--All localities for this species in Jujuy Province correspond to the Yungas, except for a few that are in the Prepuna and Chaco. This distribution indicates a preference for humid and dense vegetation, contrasting with *T. cinderella*, which prefers dry and disturbed areas in the Chaco, as well as transitional and Yungas forest. The type specimen was captured in Yungas inside of a hole in a cedar tree (*Cedrela* sp.); other specimens were collected in trees or fallen logs at the localities Arroyo Yuto, Sunchal, and Higuerilla.

Specimens at CML cited by Olrog (1979) as *Marmosa elegans cinderella* from Cerro Calilegua are here reidentified as *Thylamys sponsorius*; the precise locality is Abra de Cañas, El Monolito. The locality "Near Vala" (cited by Tate, 1933) for *Marmosa venustus sponsoria,* is indicated in the original specimen label as "Mountains W of Yala" and the correct name of the locality indicated by this author as Carmencito is Caimancito. Tate

(1933) included *M. v. cinderella* and *M. v. sponsoria* in Caimancito, 400 m; however, this was based on the error of assigning the same specimen (BMNH 21.1.2.17) to 2 different subspecies at 1 locality.

A pregnant female and a lactating female were collected in December. Subadults were captured in May, July, and August. Specimens with incrassated tails have been recorded in June and July.

Magnorder Xenarthra
Order Pilosa Flower
Suborder Phyllophaga (=Tardigrada)
Family Bradypodidae

Genus *Bradypus*

Bradypus variegatus Schinz, 1825
Brown-throated Three-toed Sloth

Bradypus variegatus Schinz, 1825. Naturgeschichte und Adildungen der Säugethiere. Das Thierreich eingetheilt nach dem Bau der Thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie von dem Herrn Ritter von Cuvier. Säugethiere und Vögel. J. G. Cottaíschen Buchhandlung, Stuttgart und Tübingen, 4:510.

Distribution in Argentina.--Probable in Jujuy and Misiones provinces (Vizcaíno et al., in press.).

Specimens Examined (1).--“Jujuy,” 1 (FMNH 21672).

Comments.--Although Chébez (1994) stated that there are no well-documented records to confirm the presence of this species in Argentina, we examined a specimen from Jujuy at FMNH. Additionally, Redford and Eisenberg (1992) mentioned this species from Misiones, Formosa, and Chaco provinces, and reported 2 individuals from Jujuy, at the Zoo in Buenos Aires. The record at the FMNH corresponds to a tanned skin of a specimen captured during the “Argentine Commission Panama Pacific Exposition” in 1916. During our field trips, this species was not observed by us and was not reported by rural residents.

Order Cingulata
Family Dasypodidae
Subfamily Dasypodinae

Genus *Chaetophractus*

Chaetophractus nationi (Thomas, 1894)
Andean Hairy Armadillo

Dasypus nationi Thomas, 1894. Annals and Magazine of Natural History, ser. 6, 13:70.

Distribution in Argentina.—This species is known only from Jujuy Province and its presence in Salta is probable (Díaz, 2000; Díaz et al., 2000).

Specimens Examined (9).--Abra Pampa, 1 (MACN 35.308); La Quiaca, 1 (MACN 14.10); Salinas Grandes, al O de Tilcara, 2400 m, 5 (CML 1095, 1096, 1097, 1098, 1099); Santa Catalina, 2 (MACN 41.155, 41.160).

Additional Records.--Abra Pampa, 3500 m (Thomas, 1919b, as *Dasypus nationi*); Río Ajedrez; Río Coyaguaima; Río Orosmayo; Río Salitre (Crespo, 1944, as *C. v. vellerosus*).

Comments.--According to Wetzel (1985) this species might be a highland subspecies of *C. vellerosus*, although material is lacking to confirm this conclusion (Chébez, 1994). This species is found only in the Andean grasslands and shrubs (Redford and Eisenberg, 1992; Anderson, 1997). The specimens cited by Crespo (1944) as *C. v. vellerosus*, based on distribution, were reidentified by us and are here considered to be *C. nationi*, because of the size and shape of the cephalic shield.

Chaetophractus vellerosus (Gray, 1865)
Screaming Hairy Armadillo

Dasypus vellerosus Gray, 1825. Proceedings of the Zoological Society of London, 376.

Distribution in Argentina.--In Argentina this species is distributed from Jujuy south to Mendoza, San Luis, La Pampa, and Buenos Aires (Vizcaíno et al., in press).

Specimens Examined (28).--Chanchillos, 2 (MACN 42.99, 42.98); "Jujuy," 20 (MACN 30.400, 31.177, 31.178, 31.179, 32.43, 32.44, 32.78, 34.576, 34.577, 34.578, 34.591, 34.652, 34.655, 34.641, 34.642, 34.643, 34.644, 34.646, 34.648, 36.105); Perico, 2 (MACN 30.255, 30.256); San Antonio, 2 (MACN 27.133, 27.134); Vinalito, Yuto, 1 (CML 398); Yuto, 1 (AMNH 179897).

Additional Records.--E of El Palmar, Sierra de Santa Bárbara (J. K. Braun, personal communication).

Comments.--The specimens from Chanchillos were cited by Yepes (1944) as *C. v. pannosus*, but according to Cabrera (1958) the northern limits for the distribution of this subspecies is Tucumán Province.

Genus *Dasypus*

Dasypus hybridus (Desmarest, 1804)
Southern Long-nosed Armadillo

Loricatus hybridus Desmarest, 1804. Nouveau dictionnaire d`histoire naturelle, appliqueé aux arts, à l`agriculture, à l`économie rurale et domestique, à la médicine, etc. par une société de naturalistes et d`agriculteurs, noveau édition, Ch. Deterville, Paris, 24:28.

Distribution in Argentina.--This species is distributed in the provinces of Corrientes, Chaco, Formosa, and Jujuy, southward to Mendoza and Río Negro; it likely occurs in Misiones as well (Cabrera, 1958; Wetzel and Mondolfi, 1979).

Specimens Examined (2).--"Jujuy," 2 (MACN 35.148, 34.669).

Comments.--Only 2 specimens of this species were examined for the province of Jujuy, both without specific locality, collected by Dr. S. Mazza in 1930.

Dasypus novemcinctus Linnaeus, 1758
Nine-banded Armadillo

Dasypus novemcinctus Linnaeus, 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:51.

Distribution in Argentina.--Previously, this species was known from Misiones, Formosa, Chaco, eastern Salta, and Santiago del Estero provinces (Cabrera, 1958; Wetzel, 1985). It is here included in the fauna of Jujuy Province (Díaz and Barquez, 1999).

Specimens Examined (1).--"Jujuy," 1 (MACN 34.590).

Comments.--The specimen examined, representing the first record of the species for the province (Díaz and Barquez, 1999), was collected by A. Fiora in 1934.

Dasypus yepesi Vizcaíno, 1995
Yepes´ Armadillo

Dasypus yepesi Vizcaíno, 1995. Mastozoología Neotropical, 2(1):5-13

Distribution in Argentina.--Salta and Jujuy provinces (Vizcaíno, 1995).

Specimens Examined (1).--Abra de Cañas, El Monolito, 1700 m, 1 (CML 1809).

Additional Records.--Abra de Cañas, 1700 m (Olrog, 1976, as *D. mazzai*), Cerro Calilegua (Olrog, 1979, as *D. mazzai*); El Alto, Río Caulario, 1200 m; El Caulario, Río Caulario, 940 m; Finca La Mauricia, 5-10 km al E de Caimancito, 500 m; Finca La Realidad, Río San Francisco, 5 km al E de Caimancito, 440 m (Vizcaíno, 1995).

Comments.--Vizcaíno (1995) agreed with Hamlett (1939) and Wetzel and Mondolfi (1979) that the holotype of *D. mazzai* corresponds to *D. novemcinctus*, while the paratype corresponds to *D. yepesi*. Consequently, all of the specimens of *D. mazzai* in systematic collections require re-examination. Olrog (1976, 1979) reported *D. mazzai* in 2 localities of Jujuy, which probably correspond to a single specimen deposited at the CML (1809), and here re-identified as *D. yepesi*. Moreover, the armadillo from Palpalá that was cited as *D. mazzai* by Yepes (1933b) could correspond to any of the species actually cited for the province. All records correspond to the Yungas.

Genus *Euphractus*

Euphractus sexcinctus (Linnaeus, 1758)

Dasypus sexcinctus Linnaeus, 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:51.

Distribution in Argentina.--Northern Argentina in the provinces of Catamarca, Corrientes, Chaco, Entre Ríos, Formosa, Jujuy, Misiones, Salta, Santiago del Estero, and Tucumán (Vizcaíno et al., in press.).

Specimens Examined (8).--Cuyaya, 1 (MACN 42.104); El Pongo, 1 (MACN 34.714); "Jujuy," 2 (MACN 34.592, 49.38); Laguna La Brea, 2 (collected by hunters); Sierra El Centinela, 1 (CR 455); Yuto, 1 (AMNH 185324).

Additional Records.--Agua Salada (local residents, personal communication); Chalicán (Yepes, 1944); E of El Palmar, Sierra de Santa Bárbara (J. K. Braun, personal communication); Perico (Yepes, 1944); Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20 (local residents, personal communication); San Francisco, 1550 m (Olrog, 1979); San Lorenzo (Matschie, 1894; Trouessart, 1897-1905); Zapla (Yepes, 1944).

Comments.--Heinonen and Bosso (1994) have included this species in Abra de Cañas under the argument that this was a locality indicated by Olrog (1979) for this species; however, Olrog only reported *E. sexcinctus* for the locality San Francisco. This species is found in dry savannas; according to local residents, it is a good predator and may eat small vertebrates.

Genus *Tolypeutes*

Tolypeutes matacus (Desmarest, 1804)
Southern Three-banded Armadillo

Loricatus matacus Desmarest, 1804. Nouveau dictionnaire d`histoire naturelle, appliqueé aux arts, à l`agriculture, à l`économie rurale et domestique, à la médicine, etc. par une société de naturalistes et d`agriculteurs, noveau édition, Ch. Deterville, Paris, 24:28.

Distribution in Argentina.--Northern and central Argentina, extending southward to Río Negro Province (Cabrera, 1958).

Specimens Examined (10).--"Jujuy," 7 (MACN 34.595, 34.637, 34.638, 34.639, 34.64, 31.201, 31.221); Perico, 1 (MACN 31.91); San Pedro, 1 (MACN 41.399); Yuto, 1 (CML 490).

Additional Records.--Agua Salada (local residents, personal communication); Aguas Negras, 600 m (Heinonen and Bosso, 1994); Chanchillos (Yepes, 1944).

Comments.--The specimen examined from Yuto is a neonate individual preserved in ethanol 70%.

Suborder Vermilingua
Family Myrmecophagidae

Genus *Myrmecophaga*

Myrmecophaga tridactyla Linnaeus, 1758
Giant Anteater

Myrmecophaga tridactyla Linnaeus, 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:35.

Distribution in Argentina.--Northern Argentina, in Misiones, Formosa, Salta, and Jujuy provinces, and probably in Chaco and Santiago del Estero (Wetzel, 1982).

Specimens Examined (1).--Yuto, 1 (MCNS no number).

Additional Records.--Laguna La Brea (local residents, personal communication); Departamento Santa Bárbara (Massoia et al., 1992a); Parque Nacional Calilegua (P. Perovic, personal communication); San Lorenzo (Matschie, 1894; as *Myrmecophaga jubata*).

Comments.--Massoia et al. (1992a) mentioned a specimen from Jujuy, kept in captivity at a breeding station of regional fauna in San Salvador de Jujuy. At Laguna La Brea, local residents have observed this species on the dry side of the lake, where the chacoan vegetation is dominant.

Genus *Tamandua*

Tamandua tetradactyla (Linnaeus, 1758)
Southern Tamandua

Myrmecophaga tetradactyla Linnaeus, 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:35.

Distribution in Argentina.--Northern Argentina, in Misiones, Santa Fe, Chaco, Formosa, Salta, Jujuy, and Tucumán provinces (Vizcaíno et al., in press, Wetzel, 1975, 1982, 1985). Díaz and Ojeda (2000) mention the presence of this species in Corrientes. Additionally, information published in local newspapers indicates its presence in the provinces of Catamarca and Santiago del Estero.

Specimens Examined (3).--"Jujuy," 2 (MACN 33.255, 42.11); Reyes, 1 (MACN 33.255).

Additional Records.--Laguna La Brea (local residents, personal communication); Palos a pique (Matschie, 1894; as *Tamandua tridactyla*); Parque Nacional Calilegua (P. Perovic, personal communication); Río Grande de Jujuy (Matschie, 1894; as *Tamandua tridactyla*).

Comments.--Yepes (1944) gave much importance to the locality "Reyes" for this species, because it is a western area that is quite far from the Chaco; however, we have registered additional localities from transitional and Yungas forest.

Order Chiroptera
Family Noctilionidae

Genus *Noctilio*

Noctilio leporinus (Linnaeus, 1758)
Greater Bulldog Bat

Vespertilio leporinus Linnaeus, 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:32.

Distribution in Argentina.--Salta, Jujuy, Santiago del Estero, Formosa, Chaco, Santa Fe, Misiones, and Corrientes provinces (Barquez et al., 1993, 1999).

Specimens Examined (2).--Río Las Capillas, 15 km al N de Las Capillas, por ruta 20, 1 (ARG 4246); Yuto, 1 (AMNH 182734).

Additional Records.--Santa Clara (Yepes, 1944).

Comments.--Although common in Argentina (Barquez et al. 1993), this species is rare in Jujuy Province, with only 2 known records from the eastern part of the province. The last published record for this species in Jujuy was that reported by Davis (1973), based on a specimen deposited at the AMNH, captured in 1959 in Yuto. During our research we recently captured 1 specimen at Río Las Capillas (Barquez and Díaz, 2001), a locality from the western part of Yungas of Jujuy; this specimen was a male with abdominal testes collected in the month of July.

Family Phyllostomidae
Subfamily Phyllostominae

Genus *Chrotopterus*

Chrotopterus auritus (Peters, 1856)
Woolly False Vampire Bat

Vampyrus auritus Peters, 1856. Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin, p. 415.

Distribution in Argentina.--Salta, Jujuy, Tucumán, Formosa, Chaco, Corrientes, and Misiones provinces (Barquez et al., 1999).

Specimens Examined (9).--Abra de Cañas, El Monolito, 1700 m, 1 (CML 1803); Aguas Negras, 600 m, 1 (MACN 19440); Aguas Negras, Camping, 1 (CML 5694); La Brea, 1

(MACN 17016); Laguna La Brea, 3 (1 MACN 17015; 2 MMD 31, 32); Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20, 1 (PIDBA 1011); Ruta 83, camino a Valle Grande, 9 km al N de San Francisco, 1200 m, 1 (MMD 322).

Additional Records.--Cerro Calilegua (Olrog, 1979); Palma Sola (Barquez et al., 1999).

Comments.--Two specimens were captured at Laguna La Brea in May (a male with abdominal testes and a female with a closed vagina) in a net close to water and dense vegetation. One specimen was captured just above the ground. Males with abdominal testes were captured in June and August.

Genus *Tonatia*

Tonatia bidens (Spix, 1823)
Greater Round-eared Bat

Vampyrus bidens Spix, 1823. Simiarum et Vespertilionum Brasiliensium species novae ou histoire naturelle des species nouvelles de singes et de chauve-souris observées et recueillies pendant le voyage dans l'intérieur du Bresil execute par ordre de S. M. le Roi de Baviere dans les annees 1817, 1818, 1819, 1820. Francisci Seraphici Hübschmanni, p. 65.

Distribution in Argentina.--Jujuy and Misiones provinces (Barquez et al., 1993, 1999).

Specimens Examined (8).--Finca Quema Azupera, Palma Sola, 135 km de San Salvador de Jujuy, 1 (MACN 20339); Laguna La Brea, 6 (MACN 17110, 17111, 17112, 17113, 17114, 17115); Laguna La Brea, 25 km antes de Palma Sola, Ruta 1, 1 (SNOMNH 18788).

Additional Records.--Palma Sola, 550 m (Fornes et al., 1967, as *T. sylvicola*); Palma Sola, Mina de Azufre (Barquez et al., 1999).

Comments.--This species feeds on fruits, insects, and small vertebrates. The stomach of a specimen from Laguna La Brea (SNOMNH 18788) was filled with down feathers, indicating the consumption of a young bird (Barquez et al., 1999); this specimen was a male with scrotal testes captured in mid-June.

Subfamily Glossophaginae

Genus *Anoura*

Anoura caudifer (É. Geoffroy Saint-Hilaire, 1818)
Hairy-legged Long-tongued Bat

Glossophaga caudifer É. Geoffroy Saint-Hilaire, 1818. Mémoires du Muséum d'histoire Naturelle, Paris, 4:418.

Distribution in Argentina.--Salta and Jujuy provinces (Barquez et al., 1993, 1999).

Specimens Examined (3).--Arroyo Sauzalito, 1 (CML 2922); Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20, 1 (PIDBA 1008); San Francisco, aproximadamente dos km, pasando el pueblo, camino a Valle Grande, 1 (CML 5578).

Comments.--Previously, this species was known only from Arroyo Sauzalito. Here we include 2 new localities for the distribution of this species. The specimen from Arroyo Sauzalito was a male with abdominal testes captured in June, and represents the first record of this species for Jujuy; this specimen was erroneously cited by Heinonen and Bosso (1994) as collected in Caimancito. In October we captured a pregnant female, with a large fetus (16.3 x 10.3 mm) at Río Las Capillas; at the same site a lactating female was released.

Genus *Glossophaga*

Glossophaga soricina (Pallas, 1766)
Pallas' Long-tongued Bat

Vespertilio soricinus Pallas, 1766. Miscellanea zoologica, quibus nov imprimis atque obscur animalium species describuntur et observationibus i conibusque illustratur. Hagae Comitum, apud Petrum van Cleef, p. 48.

Distribution in Argentina.--Salta, Jujuy, Chaco, and Misiones provinces (Barquez et al., 1993). Historical records are known from Buenos Aires Province (Barquez et al., 1999).

Specimens Examined (2).--Planta Caimancito, Parque Nacional Calilegua, 2 (CML 5588, 5589).

Comments.--The specimens examined are 1 male and 1 female, captured in July.

Subfamily Stenodermatinae

Genus *Artibeus*

Artibeus planirostris (Spix, 1823)
Flat-faced Fruit-eating Bat

Phyllostoma planirostre Spix, 1823. Simiarum et Vespertilionum Brasiliensium species novae ou histoire naturelle des species nouvelles de singes et de chauve-souris observées et recueillies pendant le voyage dans l'intérieur du Bresil execute par ordre de S. M. le Roi de Baviere dans les annees 1817, 1818, 1819, 1820. Francisci Seraphici Hübschmanni, p. 66.

Distribution in Argentina.--Salta, Jujuy, Tucumán, and Formosa provinces (Barquez et al., 1993, 1999).

Specimens Examined (71).--Abra de Cañas, 1700 m, 1 (MACN 19441); Abra de Santa Laura, límite entre Salta y Jujuy, sobre ruta nacional N° 9, 1397 m, 9 (PIDBA 567, 568, 570, 573, 575, 579, 580); Aguas Negras, 2 (1 CML 1703; 1 MACN 19442); Aguas Negras, Camping, 1 (CML 6111); Arroyo Yuto, 13 km al SO de Yuto, 3 (released); Caimancito, 2 (MACN not number); Cruce camino a Puesto Viejo y Ruta 34, 4 km al E, sobre camino a Puesto Viejo, 1 (MMD 105); Fraile Pintado, 12 km al SO, sobre Río Ledesma, 2 (released); Laguna La Brea, 2 (1 MMD 37; 1 released); Laguna La Brea, 25 km al O de Palma Sola, 9 (CML 3131, 3132, 3133, 3134, 3135, 3136, 3137, 3138, 3139); Laguna La Brea, 25 km antes de Palma Sola, sobre Ruta 1, 3 (1 AMNH 256981; 2 SNOMNH 18942, 18943); On highway 9 at border with Salta, at campground on the way to El Carmen, 4600 ft., 3 (1 IADIZA 4542; 2 SNOMNH 23510, 23511); Río Blanco, 9 km SW San Antonio, 1495 m, 9 (2 ARG 4308, 4309; 7 PIDBA 598, 599, 600, 602, 603, 606, 608); Río de Zora, en cruce con ruta 34, 1 (CML 3140); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20, 11 (7 ARG 4215, 4216, 4223, 4230, 4243, 4248, 4249; 2 MMD 342, 352, 2 released); Río Lavayén, app 1 km al N de Santa Rita, 2 (MMD 220, 221); Ruta 83, camino a Valle Grande, 9 km al N de San Francisco, 1200 m, 1 (MMD 323); Vinalito, 2 km al SE, al borde del 2° canal, 5 (released); Yuto, 4 (3 AMNH 179981, 180303, 185267; 1 CML 1595).

Additional Records.--Abra de Cañas (=El Monolito) (Barquez et al., 1999); Aguas Negras, 600 m (Heinonen and Bosso, 1994); Calilegua (Barquez et al., 1999); Camino de Cornisa, 10 km al O de Dique La Ciénaga (Barquez et al., 1999); Cerro Calilegua (Olrog, 1979); Finca El Remate, 24 km al SE de San Salvador de Jujuy, 740 m; Finca La Carolina, Los Perales, 1310 m (Villa-R. and Villa-C., 1971).

Comments.--The localities of the specimens examined are from the Yungas, Transitional forests, and Chaco phytogeographic provinces. Males with abdominal testes were reported from May through August, males with scrotal testes in February and May, females with closed vaginas in May, females with open vaginas in February, May, July, and August, and females with developed mammae in May.

Artibeus sp.

Specimens Examined (3).--Abra de Santa Laura, límite entre Salta y Jujuy, sobre ruta nacional N° 9, 1397 m, 2 (PIDBA 572, 587); Río Blanco, 9 km SW San Antonio, 1495 m, 1 (PIDBA 609).

Comments.--Specimens were captured in Yungas forests in the same nets as *A. planirostris*. The external differences between these species are mostly in coloration, but further comparisons are needed to determine if they belong to a known species but not yet reported to Argentina, or if they represent a species new to science.

A female with closed vagina and 2 females with open vaginas, 1 with well-developed mammae, were captured in May.

Genus *Sturnira*

Sturnira erythromos (Tschudi, 1844)
Hairy Yellow-shouldered Bat

Ph (*yllostoma*) *erythromos* Tschudi, 1844. Therologie. Untersuchungen ünder die Fauna

Peruana. Scheitlin und Zollikofer, St. Gallen, Switzerland, p. 64.

Distribution in Argentina.--Salta, Jujuy, Tucumán, and Catamarca provinces (Barquez et al., 1993).

Specimens Examined (48).--Abra de Cañas, 4 (2 CML 2086, 2087; 2 MACN 19447, 19448); Abra de Cañas, 1710 m, 3 (MACN 19444, 19445, 19446); Abra de Cañas, approx 30 km NW of Calilegua on Valle Grande Rd, 1 (CM 42828); Abra de Santa Laura, límite entre Salta y Jujuy, sobre ruta nacional N° 9, 1397 m, 3 (PIDBA 569, 574, 578); Aguas Blancas, 14 km al E de Santa Clara, 9 (SNOMNH 18690, 18691, 18692, 18693, 18694, 18695, 18696, 18697, 18698); Aguas Negras, Camping, 2 (CML 2926, 2928); Alto Calilegua, El Duraznillo, 3000 m, 3 (CML 1715, 1716, 1717); Arroyo Sauzalito, 5 (CML 2924, 2925, 2927, 5703, 5704); Arroyo Yuto, 13 km al SO de Yuto, 1 (MMD 92); Calilegua, El Monolito, 1 (CML 1891); Cerro El Morado, 11 km al NO de San Antonio, sobre Río El Morado, 4 (3 MMD 119, 125, 126; 1 released); El Simbolar, 25 km al SO de Palma Sola, 1000 m, 1 (CM 42830); Laguna La Brea, 25 km antes de Palma Sola, 1 (SNOMNH 18689); Laguna La Brea, 25 km antes de Palma Sola, sobre ruta 1, 1 (SNOMNH 18688); On Hwy 9 at border with Salta Province, at campground on the way to El Carmen, 4600 ft., 1 (SNOMNH 23518); Río Blanco, 9 km SW San Antonio, 1495 m, 3 (1 ARG 4315; 2 PIDBA 604, 605); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20, 4 (ARG 4218, 4221, 4227, 4251); Yuto, 1 (CML 2717).

Additional Records.--Abra de Cañas, 1700 m (Heinonen and Bosso, 1994).

Comments.--This species is more common than previously reported in NW Argentina. We found males with scrotal testes in May and June, females with closed vaginas in May, June, and July, and females with open vaginas in February, May, and July.

Sturnira lilium (É. Geoffroy Saint-Hilaire, 1810)
Common Yellow-shouldered Bat

Phyllostoma lilium É. Geoffroy Saint-Hilaire, 1810. Annales du Muséum d'histoire Naturelle, Paris, 15:181.

Distribution in Argentina.--Salta, Jujuy, Tucumán, Catamarca, Formosa, Chaco, Santa Fe, Entre Ríos, Misiones, and Corrientes provinces (Barquez et al., 1993, 1999).

Specimens Examined (369).--Abra de Cañas, approx. 30 km NW of Calilegua on Valle Grande Rd, 1 (CM 42826); Aguas Blancas, 14 km al E de Santa Clara, 4 (SNOMNH 18718, 18920, 18921, 18922); Aguas Negras, 12 (CML 1704, 1705, 1706, 1707, 1708, 1709, 1710, 1711, 1712, 1713, 1714, 2090); Aguas Negras, 500 m, 2 (CML 2088, 2089); Aguas Negras, 600 m, 1 (MACN 20279); Aguas Negras, 650 m, 1 (MACN 19443); Aguas Negras, Camping, 1 (CML 5686); Arroyo Sauzalito, 4 (2 CML 2929, 2930; 2 RMB 1411, 1412); Arroyo Yuto, 13 km al SO de Yuto, 131 (7 MMD 73, 75, 76, 78, 81, 82, 83; 124 released); Cruce camino a Puesto Viejo y Ruta 34, 4 km al E, sobre camino a Puesto Viejo, 3 (1 MMD 103, 2 released); El Simbolar, 25 km al SO de Palma Sola, 1000 m, 2 (CM 42831, 42832); Fraile Pintado, 12 km al SO, sobre Río Ledesma, 67 (3 MMD 93, 97, 98; 64 released); Laguna La Brea, 41 (4 MMD 33, 34, 35, 47; 2 CML 5686, 5690;

35 released); Laguna La Brea, 25 km al O de Palma Sola, 13 (CML 3087, 3088, 3089, 3090, 3091, 3092, 3093, 3094, 3095, 3096, 3097, 3098, 3099); Laguna La Brea, 25 km antes de Palma Sola, 5 (SNOMNH 18709, 18710, 18711, 18918, 18919); Laguna La Brea, 25 km antes de Palma Sola, sobre ruta 1, 7 (SNOMNH 18712, 18713, 18714, 18715, 18716, 18717, 18917); Río de Zora, cruce con ruta 34, 4 (CML 5705, 5706, 5707, 5708); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20, 6 (4 ARG 4217, 4224, 4228, 4229; 2 MMD 406, 407); Vinalito, 2 km al SE, al borde del 2° canal, 61 (4 MMD 56, 58, 59, 60; 57 released); Yuto, 3 (AMNH 185320, 185321, 186949).

Additional Records.--Arroyo La Urbana, 45 km E y 5.4 km N de San Salvador de Jujuy, 620 m (Villa-R. and Villa-C., 1971); Caimancito, 550 m (Heinonen and Bosso, 1994); Camino de Cornisa, 10 km W Dique La Ciénaga (Barquez et al., 1999); Cerro Calilegua (Olrog, 1979); El Duraznillo, 3000 m, Cerro Calilegua (Barquez et al., 1999); Finca El Remate, 24 km al SE de San Salvador de Jujuy, 740 m (Villa-R. and Villa-C., 1971); Mesada de las Colmenas, 1150 m (Heinonen and Bosso, 1994); Palma Sola (Villa-R. and Villa-C., 1971); Paraje Palo Blanco, Parque Nacional Calilegua (Iudica, 1995).

Comments.--This species is very abundant. The coloration is highly variable even between individuals of the same population. Males with abdominal testes and females with closed vaginas were captured in May, June, and July, males with scrotal testes in May, June, and July, and lactating females and females with open vaginas in May.

Sturnira oporaphilum (Tschudi, 1844)
Big Yellow-shouldered Bat

Ph (*yllostoma*) *oporaphilum* Tschudi, 1844. Therologie. Untersuchungen ünder die Fauna Peruana. Scheitlin und Zollikofer, St. Gallen, Switzerland, p. 64.

Distribution in Argentina.--Salta, Jujuy, and Tucumán provinces (Barquez et al., 1993).

Specimens Examined (5).--Arroyo Sauzalito, 2 (CML 2931, 2932); Calilegua, El Monolito, 1 (CML 1892); Laguna La Brea, 25 km antes de Palma Sola, 1 (SNOMNH 18685); Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20, 1 (PIDBA 1023).

Comments.--Barquez et al. (1999) identified the specimens from Argentina as *S. oporaphilum*, indicating that they were identical to those from Bolivia housed at the AMNH, even though the identity of the different species in northern Bolivia is not yet completely clear. Anderson (1997) established the southern limits for this species in Bolivia, about 200 km N of the border with Argentina. A male with abdominal testes was captured in June. A specimen cited by Barquez et al. (1999) from Fraile Pintado, 12 km W, sobre Río Ledesma (MMD 93), was reidentified as *Sturnira lilium*.

Subfamily Desmodontinae

Genus *Desmodus*

Desmodus rotundus (É. Geoffroy Saint-Hilaire, 1810)
Vampire Bat

Phyllostoma rotundum É. Geoffroy Saint-Hilaire, 1810. Annales du Muséum d'Histoire Naturelle, Paris, 15:181.

Distribution in Argentina.--Salta, Jujuy, Tucumán, Catamarca, La Rioja, San Juan, San Luis, Córdoba, Santiago del Estero, Formosa, Chaco, Entre Ríos, Corrientes, Mendoza, and Misiones provinces (Barquez et al., 1993; Barquez, in press).

Specimens Examined (14).--Abra de Cañas, 1730 m, 1 (CML 2063); Abra de Santa Laura, límite entre Salta y Jujuy, sobre ruta nacional N° 9, 1397 m, 3 (PIDBA 571, 576, 577); Aguas Negras, Camping, 2 (CML 5685, 5702); Dique Las Maderas, 1 (MACN 17190); Laguna La Brea, 25 km al O de Palma Sola, 2 (CML 3148, 3149); Laguna La Brea, 25 km antes de Palma Sola (Ruta 1), 1 (AMNH 256983); Palma Sola, 1 (AMNH 183304); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20, 2 (1 ARG 4231; 1 MMD 353); Ruta 83, camino a Valle Grande, 9 km al N de San Francisco, 1200 m, 1 (released).

Additional Records.--Aguas Negras, 600 m (Heinonen and Bosso, 1994); Angosto El Duraznal, 15 km al S de Palma Sola, 1225 m; Arroyo La Urbana, 45 km E y 5.4 km N de San Salvador de Jujuy, 620 m; Cercanías de San Pedro (Villa-R. and Villa-C., 1971); Cerro Calilegua (Olrog, 1979); Cueva del Tigre, 74 km al N de Pampa Blanca, 700 m; Dique Las Maderas, 42 km de San Salvador de Jujuy, 920 m; Finca Catamontaña, 33 km al SSE de San Salvador de Jujuy, 925 m; Finca El Olvido, 15 km al E de Palma Sola (Villa-R. and Villa-C., 1971); Finca El Pongo, Estación Perico (Barquez et al., 1999); On highway 9 at border with Salta, at campground on the way to El Carmen (Mares et al., 1995); Puesto Viejo, 16 km al N de General Güemes, Río Las Pavas (Villa-R. and Villa-C., 1971).

Comments.--Unlike *Diaemus youngi* this species is very common in NW Argentina. In this study, males with abdominal testes were collected in June and August, males with scrotal testes in May and July, and females with closed and open vaginas in May.

Genus *Diaemus*

Diaemus youngi (Jentink, 1893)
White-winged Vampire Bat

Desmodus youngi Jentink, 1893. Notes of the Leiden Museum, 15:282.

Distribution in Argentina.--Jujuy and Misiones provinces (Barquez, 1984; Barquez et al., 1993).

Specimens Examined (1).--Agua Salada, app 15 km al SE de Agua Caliente, del lado oriental del Río San Francisco, 1 (CML 1343).

Comments.--The record of Jujuy is the only known locality in NW Argentina. The specimen was a female with open vagina captured in August, in a mist net about 4 m above the ground. About 60 cm below the bat, a small owl (*Otus choliba*) was also trapped in the net and, upon examination, was found to have spots of blood probably produced by bites from the vampire (Barquez et al., 1999).

Family Vespertilionidae
Subfamily Vespertilioninae

Genus *Dasypterus*

Dasypterus ega (Gervais, 1856)
Southern Yellow Bat

Nycticeius ega Gervais, 1855 (1856). Deuxième Mémoire. Documents zoologiques pour servir à la monographie des Chéiroptères Sud-Américains. Pp. 25-88, i*n*: P. Gervais, ed., Mammiféres. *In* Animaux nouveaux ou rares recueillis pendant l'expédition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro a Lima, et Lima au Para; exécutée par ordre du gouvernement français pendant les annés 1843 à 1847, sous la direction du comte Francis de Castelnau (F.Castelnau, ed.). P. Bertrand, Paris, 1 (2):77.

Distribution in Argentina.--Salta, Jujuy, Tucumán, Catamarca, Córdoba, Buenos Aires, Santa Fe, Formosa, Corrientes, Entre Rios, La Pampa, Santiago del Estero, and Misiones provinces (Barquez et al., 1993, 1999; Barquez, in press).

Specimens Examined (2).--Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20, 1 (MMD, 351); Yuto, 1 (AMNH 183305).

Additional Records.--Arroyo La Urbana, 45 km E y 5.4 km N de San Salvador de Jujuy, 620 m (Villa-R. and Villa-C., 1971).

Comments.--Morales and Bickham (1995) suggested that the frosted and red bats (*Lasiurus borealis*, *L. blossevillii*, and *L. cinereus*) constitute a group separate from the yellow bats (*L. ega*). The latter has been placed in a different genus by several authors (Miller, 1907; Cabrera, 1958; Husson, 1962, 1978; Barquez et al., 1999). This is also suggested by studies of dental (Tate, 1942) and bacular morphology (Hill and Harrison, 1987). We follow Barquez et al (1999) for the use of *Dasypterus*. A female with an open vagina was captured in August.

Genus *Eptesicus*

Eptesicus diminutus Osgood, 1915
Diminutive Serotine

Eptesicus diminutus Osgood, 1915. Field Museum of Natural History, Zoological Series,

10:197.

Distribution in Argentina.--Salta, Jujuy, Tucumán, Misiones, Corrientes, Santa Fe, Santiago del Estero, and Buenos Aires provinces and 1 isolated record from La Pampa Province (Barquez et al., 1999).

Specimens Examined (2).--Laguna La Brea, 25 km al O de Palma Sola, 2 (CML 3084, 3086).

Comments.--Barquez and Lougheed (1990) included this species in the province of Jujuy. Later, Barquez et al. (1999) erroneously included Palma Sola, as a locality indicated by Villa-R. and Villa-C. (1971) for the species, since these authors never mentioned this locality for this species. The specimens examined were 2 females captured in July.

Eptesicus furinalis (d´Orbigny, 1847)
Argentine Brown Bat

Vespertilio furinalis d´Orgbigny, 1847. Mammifères. En Voyage dans l'Amérique Méridionale (le Brésil, la Republique orientale de Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivia, la République du Péru), exécuté pendant les années 1826, 1827, 1828, 1830, 1831, 1832, et 1833. Tome Quatrième. 2e Partie. (A. d'Orbigny, ed.). Pitois Levrault, et cie, Paris, 4:13.

Distribution in Argentina.--Found in almost all the provinces of northern and central Argentina as far south as 37° S, but not reported for the provinces of San Juan and San Luis (Barquez et al., 1993, 1999).

Specimens Examined (23).--Aguas Negras, 600 m, 1 (MACN 19449); Laguna La Brea, 25 km al O de Palma Sola, 1 (CML 3085); Oyeros, 3 km al N, camino entre rutas 61 y 43, 2 (MMD 206, 207); Río de Zora, en cruce con ruta 34, 1 (CML 5224); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20, 2 (1 ARG 4222, 1 MMD 411); Río Lavayén, app 1 km al N de Santa Rita, 1 (MMD 237); Río Ledesma, app 14 km al S de Pueblo Ledesma, sobre ruta 34, 1 (CML 5223); Ruta 83, camino a Valle Grande, 9 km al N de San Francisco, 1200 m, 1 (MMD 324); Santa Bárbara, Santa Bárbara, 1 (AMNH 185209); Yuto, 12 (2 MACN 13163, 13162; 10 AMNH 181530, 181531, 182735, 182568, 183306, 184655, 185215, 185217, 185318, 185319).

Additional Records.--Caimancito, 550 m (Heinonen and Bosso, 1994); Laguna La Brea (Barquez and Lougheed, 1990); Ledesma (Barquez et al., 1999); Palma Sola, 550 m (Villa-R. and Villa-C., 1971); Yuto, Río San Francisco (Thomas, 1920a, as *E. hilairei*).

Comments.--According to Barquez et al. (1999), the specimens from Jujuy correspond to *E. furinalis*. Males with abdominal testes were captured in October, males with scrotal testes in July and August, females with closed vaginas in June and October, and 2 females, each with 2 well-developed fetuses, in November.

Genus *Histiotus*

Histiotus laephotis Thomas, 1916
Northern Big-eared Brown Bat

Histiotus laephotis Thomas, 1916. Annals and Magazine of Natural History, ser. 8, 17:275.

Distribution in Argentina.--Jujuy, Salta, Tucumán, Catamarca, and Santiago del Estero provinces (Barquez et al., 1999; Barquez and Díaz, 2001).

Specimens Examined (6).--Arroyo Sauzalito, 1 (CML 2923); Cucho, San Salvador de Jujuy, 1 (CML 1682); Cueva del Tigre, El Milagro, 1 (MACN 16811); Río Lavayén, app 1 km al N de Santa Rita, 1 (MMD 212); Yuto, 2 (AMNH 181527, 181528).

Additional Records.--Dique La Ciénaga, casa del club náutico, 30 km al SSO de San Salvador de Jujuy, 1000 m (Villa-R. and Villa-C., 1971, as *H. montanus montanus*); El Palmar del Río San Francisco (Del Ponte, 1944); Finca El Palmar (Romaña and Abalos, 1950); Finca La Toma, 25 km al SO de San Salvador de Jujuy (Villa-R. and Villa-C., 1971, as *H. montanus montanus*); Jujuy, ciudad (Romaña and Abalos, 1950); San Lorenzo (Thomas, 1898, as *H. velatus*); San Salvador de Jujuy (Del Ponte, 1944).

Comments.--This species was treated as a subspecies of *H. montanus* by Anderson (1997), and of *H. macrotus* by Barquez et al. (1999). Barquez and Díaz (2001) subsequently elevated this to a valid species; they provide characters, which allow clear differentiation of both forms.

Thomas (1898) identified a specimen from San Lorenzo (Jujuy) together with others from Salta, and from Caiza (Bolivia) as *H. velatus;* subsequently (Thomas, 1916b), he described *H. laephotis* based on 4 of the specimens from Caiza, without mentioning the identity of those from San Lorenzo. Thus, we consider that the specimen from San Lorenzo also corresponds to *H. laephotis* because of its original inclusion in the same series. At Río Lavayén a male with abdominal testes was captured in October, in a net placed parallel to the river.

Histiotus macrotus (Poeppig, 1835)
Big-eared Brown Bat

Nycticeius macrotus Poepping, 1835. Reise in Chile, Peru und auf dem Amazonenstrome während der Jahre 1827-1832. Friedrich Fleischer, Leipzig, 1:451.

Distribution in Argentina.--Catamarca, Córdoba, Jujuy, Salta, Tucumán, Neuquén, Río Negro, San Juan, and San Luis provinces (Barquez et al., 1999, Barquez and Lougheed, 1990).

Specimens Examined (4).--Tres Cruces, 8 km S, al lado de ruta 9, 3 (CML 5408, 5409, 6066); Yavi, 6.8 km al SE de Suripujies, sobre ruta provincial N° 5, 3991 m, 1 (ARG 4734).

Comments.--Barquez and Lougheed (1990) extended the distribution of this species to Jujuy, Salta, and Tucumán provinces. The phytogeographic regions occupied by *H. laephotis* and *H. macrotus* in Jujuy are clearly segregated. *H. laephotis* inhabits the lowlands in the Yungas and the Chaco, while *H. macrotus* is found only at higher altitudes, mainly in Prepuna and Puna. The skins of specimens examined from both species are very similar, but there are clear differences in the skulls, with the rostrum being wider and the external breadth across M3 >7 mm in *H. macrotus*, in contrast to a narrower rostum and M3 <7 mm in *H. laephotis*.

It is possible that populations of *H. macrotus* from northern Argentina, inhabiting high altitudes, represent a different subspecies than specimens from southern Argentina. The record from Yavi is the second known locality for Jujuy, and represents the northernmost record for the species; the specimen was a male with abdominal testes collected in November.

Histiotus velatus (I. Geoffroy Saint-Hilaire, 1824)
Tropical Big-eared Brown Bat

Plecotus velatus I. Geoffroy Saint-Hilaire, 1824. Annales des Sciences Naturelles, Zoologie, Paris, ser. 1, 3:446.

Distribution in Argentina.--Previously this species was known only from NE Argentina in Misiones and Corrientes provinces (Barquez et al., 1999); it was recently included in Jujuy by Barquez and Díaz (2001).

Specimens Examined (1).--Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20, 1 (MMD 414).

Comments.--The specimen examined is the first record of the species for the Province of Jujuy and extends the distribution of *H. velatus* to NW Argentina. The specimen mentioned by Thomas (1898) as *H. velatus* is here considered to be *H. laephotis*.

The specimen examined was a female collected in June, in a net placed across a river in pristine Yungas forest.

Genus *Lasiurus*

Lasiurus blossevillii (Lesson and Garnot, 1826)
Western Red Bat

Vespertilio blossevillii Lesson and Garnot, 1826. Bulletin des Sciences Naturelles et de Géologie, 8:95.

Distribution in Argentina.--Salta, Jujuy, Tucumán, Catamarca, Santiago del Estero, San Juan, Córdoba, La Pampa, Buenos Aires, Entre Ríos, Corrientes, Chaco, Formosa, Santa Fe, and Misiones provinces (Barquez et al., 1993).

Specimens Examined (18).--Aguas Negras, 600 m, 1 (MACN 19451); Caimancito, El Arroyo, 600 m, Parque Nacional Calilegua, 1 (MACN 19450); Laguna La Brea, 25 km al O de Palma Sola, 2 (CML 5255, 5256); Río Blanco, 9 km SW San Antonio, 1495 m, 2 (1 ARG 4291, 1 PIDBA 601); Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20, 1 (MMD 413); Río Tiraxi, 1.5 km al E de Tiraxi, sobre ruta provincial N° 29, 3 (PIDBA 648, 657, 677); Yuto, 8 (7 AMNH 167854, 181525, 181526, 184651, 184652, 184653, 185266; 1 CML 483).

Additional Records.--Cerro Calilegua (Olrog, 1979); El Monolito (Barquez et al., 1999).

Comments.--We follow Baker et al. (1988) and Morales and Bickham (1995) in treating this species as *L. blossevillii*.

At Río Tiraxi a dark gray specimen was captured. Some authors have considered specimens with gray coloration to be *L. salinae* (Mares et al., 1995, 1997; Tiranti Paz and Torres Martínez, 1998), but Barquez et al. (1999) considered *L. salinae* to be a synonym of *L. blossevillii*. The type specimen of *L. borealis salinae* is a young individual with cartilaginous phalanges, and examination of this and other specimens of this species confirm that young individuals usually are darker than adults. However, there also are adults with dark coloration indicating the possibility that this species may have several color phases, depending on age and or habitat. More specimens are needed to resolve this issue. Males with abdominal testes were captured in May and July, and females with open vaginas in August .

Lasiurus cinereus (Beauvois, 1769)
Hoary Bat

Vespertilio cinereus Beauvois, 1769. A scientific and descriptive catalogue of Peale's museum. S. H. Smith, Philadelphia, p. 18.

Distribution in Argentina.--Salta, Jujuy, Tucumán, Catamarca, La Rioja, Mendoza, San Luis, Santiago del Estero, Córdoba, La Pampa, Río Negro, Buenos Aires, Santa Fe, Entre Ríos, Corrientes, and Misiones provinces (Barquez et al., 1993; Díaz and Barquez, 1999).

Specimens Examined (2).--Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20, 1 (PIDBA 1006); Río Lavayén, app 1 km al N de Santa Rita, 1 (MMD 238).

Additional Records.--León (R. M. Barquez, personal observation).

Comments.--The observation from León represents the first record of this species for Jujuy Province; although collected by S. Lougheed and examined by RMB, the specimen probably is lost. A male with abdominal testes was captured in October at Río Lavayén in a net placed across the river.

Genus *Myotis*

Myotis albescens (É. Geoffroy Saint-Hilaire, 1806)
Silver-tipped Myotis

Vespertilio albescens É. Geoffroy Saint-Hilaire, 1810. Annales du Muséum d'histoire Naturelle, Paris, 8:204-205.

Distribution in Argentina.--Salta, Tucumán, Santiago del Estero, Formosa, Chaco, Buenos Aires, Entre Ríos, Corrientes, and Misiones provinces (Barquez et al., 1993). Recently included in Jujuy by Díaz and Barquez (1999).

Specimens Examined (9).--Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20, 3 (1 ARG 4238; 2 MMD 354, 415); Río Lavayén, app 1 km al N de Santa Rita, 6 (4 MMD 227, 232, 234, 242; 2 released).

Comments.--Specimens captured at Río Lavayén are the first records of the species for Jujuy Province. We captured a male with abdominal testes in August and a male with scrotal testes in July; a male with scrotal testes, a female with an open vagina, and a pregnant female were captured in October.

Myotis keaysi Allen, 1914
Hairy-legged Myotis

Myotis ruber keaysi Allen, 1914. Bulletin of the American Museum of Natural History, 33:383.

Distribution in Argentina.--*Myotis keaysi* was known in Argentina only for the provinces of Salta and Tucumán (Barquez et al., 1999), but recently was included in Jujuy by Barquez and Díaz (2001).

Specimens Examined (1).--Río Tiraxi, 1.5 km al E de Tiraxi, sobre ruta provincial N° 29, 1 (PIDBA 647).

Comments.--The nearest localities for this species are in Salta (Capital) and Bolivia, about 50 km N of the border with Argentina. The specimen examined was a female with open vagina captured in August, in a dense forest of the Yungas.

Myotis levis (I. Geoffroy Saint-Hilaire, 1824)
Yellowish Myotis

Vespertilio levis I. Geoffroy Saint-Hilaire, 1824. Annales des Sciences Naturelles, Zoologie, Paris, ser. 1, 3:444-445.

Distribution in Argentina.--All of central and northern Argentina; the subspecies *M. l. dinellii* is found in Salta, Jujuy, Tucumán, Catamarca, La Rioja, San Juan, Mendoza, Neuquén, La Pampa, south of Buenos Aires, San Luis, and Córdoba provinces (Barquez et al., 1993, 1999).

Specimens Examined (2).--Río Blanco, 9 km SW San Antonio, 1495 m, 1 (ARG 4290); Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20, 1 (PIDBA 1024).

Comments.--This species was reported for Jujuy by Barquez et al. (1993) based on a specimen from El Simbolar; this specimen was reidentified as *M. riparius*, however, so that *M. levis* was not recorded from the province (Díaz and Barquez, 1999). However, based on its distribution, the presence of this species was highly probable; we finally captured a specimen at Río Blanco, which represents the first confident record for the province (Barquez and Díaz, 2001). The specimen was captured in July and was a male with abdominal testes. A female with open vagina was collected in October at Río Las Capillas.

Myotis nigricans (Schinz, 1821)
Black Myotis

Vespertilio nigricans Schinz, 1821. Naturgeschichte und Abbildungen der Säugethiere. Das Thierreich eingetheilt nach dem Bau der Thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie von dem Herrn Ritter von Cuvier. Säugethiere und Vögel. J. G. Cotta'schen Buchhandlung, Stuttgart und Tübingen, 1:179.

Distribution in Argentina.--Salta, Jujuy, Tucumán, Catamarca, Santiago del Estero, Formosa, Chaco, Corrientes, and Misiones provinces (Barquez et al., 1999).

Specimens Examined (4).--Caimancito, 600 m, 1 (MACN 19452); Laguna La Brea, 1 (MMD 36); Laguna La Brea, 25 km al O de Palma Sola, 1 (CML 3082); Río Lavayén, app 1 km al N de Santa Rita, 1 (MMD 233).

Additional Records.--Arroyo La Urbana, 45 km E y 5.4 km N de San Salvador de Jujuy, 620 m (La Val, 1973); Caimancito, 550 m (Heinonen and Bosso, 1994); Cerro Calilegua (Olrog, 1979); Santa Bárbara, Valle Grande (Barquez, 1987); Yuto (Olrog, 1959), Yuto, Río San Francisco (Thomas, 1920a).

Comments.--Identification of this species in Argentina is quite difficult and confusing; several specimens belonging to other species have frequently been cited as *M. nigricans*, but later reidentified by different authors. This is largely a consequence of the lack of studies in the southern part of South America, where most aspects of the biology and variations of this species are not well known. Our review of numerous specimens lead us to define a series of characters that can help to identify *M. nigricans*. Among other characters, one of the most useful was the lack of sagittal crest in *nigricans*; the majority of similar specimens having a sagittal crests were *M. riparius*. With this criterion the majority of the specimens deposited in systematic collections cataloged as *M. nigricans* have been reallocated to *M. riparius*.

Males with abdominal testes were registered in October and females with closed vaginas in May and July.

Myotis riparius Handley, 1960
Riparian Myotis

Myotis simus riparius Handley, 1960. Proceedings of the United States National Museum, 112:466-468.

Distribution in Argentina.--Misiones, Corrientes, Chaco, Formosa, Tucumán, and Santiago del Estero provinces (Barquez et al., 1993, 1999). Díaz and Barquez (1999) included this species in Jujuy Province, and Barquez and Díaz (2001) in Salta Province.

Specimens Examined (5).--El Simbolar, 25 km al SO de Palma Sola, 1000 m, 1 (CML 2359); Laguna La Brea, 1 (MMD 38); Laguna La Brea, 25 km antes de Palma Sola, sobre Ruta 1, 2 (SNOMNH 18890,18891); Yuto, 1 (AMNH 185210).

Comments.--The specimen from El Simbolar is the first record of this species for the Province (Díaz and Barquez, 1999). We reidentified the specimen cited by LaVal (1973) and Barquez et al. (1999) as *M. nigricans*, AMNH 185210, as *M. riparius* based on the presence of a sagittal crest; the locality, as indicated in the original tag, is Yuto, and not Santa Bárbara W of San Pedro ca 1000 m as reported by LaVal (1973).

Males with abdominal testes were collected in May, males with scrotal testes in April, and females with closed vaginas in June.

Family Molossidae

Genus *Cynomops*

Cynomops planirostris (Peters, 1865)
Southern Dog-faced Bat

Molossus planirostris Peters, 1865. Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin, p. 575.

Distribution in Argentina.--Salta and Jujuy provinces (Barquez et al., 1993, 1999).

Specimens Examined (4).--Arroyo Yuto, 13 km al SO de Yuto, 1 (MMD 72); Caimancito, 2 (MACN 16620, 16621); Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20, 1 (MMD 410).

Comments.--The previous and the only known locality of this species in the province was Caimancito, with specimens collected in 1970. The specimen from Yuto is the second known for Jujuy; this was a female with open vagina captured in a net placed across the river in May. The specimen from Río Las Capillas, a female captured in June, extends the distribution westward of the province (Díaz and Barquez, 1999).

Genus *Eumops*

Eumops glaucinus (Wagner, 1843)
Wagner's Bonneted Bat

Dysopes glaucinus Wagner, 1843. Wiegmann's Archiv für Naturgeschichte, Jahrgang, 9(1):368.

Distribution in Argentina.--Salta, Jujuy, La Rioja, Misiones, and Tucumán provinces (Barquez et al., 1993, 1999).

Specimens Examined (5).--Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20, 3 (PIDBA 1004, 1005, 1009); Río Lavayén, app 1 km al N de Santa Rita, 1 (MMD 231); Yuto, 1 (CML 492).

Comments.--The previous record of *Eumops glaucinus* for the province of Jujuy was 1 specimen collected at Yuto, in 1955 by F. Contino. The specimen from Río Lavayén represents the second record of the species for Jujuy, extending the known distribution to the south of the province (Díaz and Barquez, 1999). This was a female with open vagina captured in a net placed across a river in October. The locality Río Las Capillas represents the third locality for Jujuy province, the specimens were 2 pregnant females with large fetuses (CRL = 9.9 and 10.0 mm), and 1 male with scrotal testes.

Eumops patagonicus Thomas, 1924
Patagonia's Bonneted Bat

Eumops patagonicus Thomas, 1924. Annals and Magazine of Natural History, ser. 9, 13:234.

Distribution in Argentina.--Salta, Jujuy, Tucumán, Santiago del Estero, Formosa, Chaco, Santa Fe, Corrientes, and Misiones provinces; isolated records are known from Chubut and Buenos Aires province (Barquez et al., 1993, 1999; Díaz and Barquez, 1999).

Specimens Examined (7).--"Jujuy," 6 (MACN 39760, 39761, 39762, 39763, 39764, 39765); Río Lavayén, app 1 km al N de Santa Rita, 1 (MMD 230).

Comments.--The specimens at the MACN are not well preserved, but we were able to determine that they are *E. patagonicus*, a species recently captured by us in Jujuy (Díaz and Barquez, 1999). The specimens at the MACN were collected in December 1939 by S. Mazza. The only specimen of this species collected after Mazza's specimens, is from Río Lavayén, a male with abdominal testes captured in October.

Eumops perotis (Schinz, 1821)
Western Bonneted Bat

Molossus perotis Schinz, 1821. Naturgeschichte und Adildungen der Säugethiere. Das Thierreich eingetheilt nach dem Bau der Thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie von dem Herrn Ritter von Cuvier. Säugethiere und Vögel. J. G. Cotta'schen Buchhandlung, Stuttgart und Tübingen, 1:870.

Distribution in Argentina.--Salta, Jujuy, Tucumán, La Rioja, Santiago del Estero, Córdoba, Formosa, Chaco, Corrientes, and Misiones provinces (Barquez et al., 1993, 1999; S. Heinonen, personal comunication).

Specimens Examined (1).--Yuto, 1 (AMNH 185208).

Additional Records.--Dique La Ciénaga, casa del club náutico, 30 km al SSO de San Salvador de Jujuy (Villa-R. and Villa-C., 1971); Libertador General San Martín; San Salvador de Jujuy (Eger, 1977).

Comments.--The specimen from Yuto was a male with scrotal testes captured in May 1960. All localities are in the Yungas Phytogeographic Province.

Genus *Molossops*

Molossops temminckii (Burmeister, 1854)
Dwarf Dog-faced Bat

Dysopes temminckii Burmeister, 1854. Systematische Üebersicht der Thiere Brasiliens, welche während einer Reise durch die Provinzen von Rio de Janeiro und Minas Geraës...gesamnelt oder beobachtat wurden von Dr. Hermann Burmeister. Pt. 1. Georg Reimer, Berlin, p. 72.

Distribution in Argentina.--In the provinces of Salta, Jujuy, Tucumán, Santiago del Estero, Córdoba, Chaco, Formosa, northern Santa Fe, Buenos Aires, Corrientes, and southern Misiones; there is also a specimen from "Chubut" at the BMNH (Barquez et al., 1993, 1999).

Specimens Examined (28).--Laguna La Brea, 25 km al O de Palma Sola, 1 (CML 3083); Ledesma, 1 (AMNH 185213); Oyeros, 3 km al N, camino entre rutas 61 and 43, 2 (MMD 208, 209); Río Lavayén, app 1 km al N de Santa Rita, 7 (MMD 213, 214, 228, 229, 243, 244, 245); Río Lavayén, sobre ruta 6 al N de Santa Clara, 1 (CML 5331); Yuto, 16 (AMNH 180310, 181532, 181533, 181534, 181535, 181536, 181537, 181538, 181539, 181540, 181541, 181542, 182736, 182569, 185212, 186950).

Additional Records.--Laguna La Brea (Barquez and Lougheed, 1990); Palma Sola, 550 m (Villa-R. and Villa-C., 1971); San Lorenzo (Thomas, 1898); Yuto, Río San Francisco (Thomas, 1920a).

Comments.--Males with abdominal and scrotal testes, and females with open and closed vaginas were captured in October; females with open vaginas were captured in July.

Genus *Molossus*

Molossus molossus Pallas, 1766
Velvety Free-tailed Bat

V(*espertilio*) *molossus* Pallas, 1766. Miscellanea zoologica, quibus nov imprimis atque obscur animalium species describuntur et observationibus i conibusque illustratur. Hagae Comitum, apud Petrum van Cleef, p. 49-50.

Distribution in Argentina.--Salta, Jujuy, Tucumán, La Rioja, Santiago del Estero, Córdoba, Formosa, Chaco, Corrientes, Misiones, Entre Ríos, Santa Fe, and Buenos Aires provinces (Barquez et al., 1993).

Specimens Examined (5).--Arroyo Sauzalito, 1 (CML 5701); Calilegua, 2 (FMNH 23633, 23634); Yuto, 2 (AMNH 185211, 185322).

Additional Records.--San Salvador de Jujuy, 20 km al O (Villa-R. and Villa-C., 1971).

Comments.--Some of the specimens considered by López González and Presley (2001) to be *Molossus currentium*, in particular those from the northestern part of the country, were considered to be *M. molossus* by Barquez et al. (1999). The status of the species inhabiting Argentina is now unclear because the 2 smaller species of the genus have not been studied along their distributional ranges within the country. The specimens from the northeast, now considered as *M. currentium*, were not compared with those from the northwest.

Molossus rufus É Geoffroy Saint-Hilaire, 1805
Black Mastiff Bat

Molossus rufus É Geoffroy Saint-Hilaire, 1805. Annales Muséum National D'Histoire Naturelle, 6:155. Nouveau bulletin des sciences par la Société Philomatique, Paris, 3(96):279.

Distribution in Argentina.--Salta, Jujuy, Córdoba, Formosa, Chaco, Corrientes, Santa Fe, and Misiones provinces (Barquez et al., 1993, 1999).

Specimens Examined (1).--Río de Zora, en cruce con ruta 34, 1 (CML 5330).

Additional Records.--Dique La Ciénaga, 13 km al SSO de San Salvador de Jujuy (Villa-R. and Villa-C., 1971).

Comments.--This is an uncommon species in NW Argentina. The specimen examined was a female with open vagina captured in October. The 2 known localities in Jujuy belong to the Yungas forests. This species has frequently been treated as *M. rufus* (Dolan, 1989; Anderson, 1993), although other authors have applied *M. ater* (Goodwin 1960, Husson 1962, Koopman 1993); we agree with Simmons and Voss (1998), who follow Dolan (1989) for the use of *rufus* as the correct name for this species.

Genus *Nyctinomops*

Nyctinomops laticaudatus (É. Geoffroy Saint-Hilaire, 1805)
Broad-eared Free-tail Bat

Molossus laticaudatus É. Geoffroy Saint-Hilaire, 1805. Annales du Muséum d'histoire Naturelle, Paris, 6:156.

Distribution in Argentina.--This species was previously known from the provinces of Salta, Formosa, and Misiones (Barquez et al., 1999). It has been recently included in Jujuy and Tucumán provinces (Díaz and Barquez, 1999; Barquez and Díaz, 2001).

Specimens Examined (3).--Río Lavayén, app 1 km al N de Santa Rita, 3 (MMD 235, 236, 239).

Comments.--The specimens examined represent the first record of this species for the province of Jujuy (Díaz and Barquez, 1999). They include a male with abdominal testes and 2 females with open vaginas captured in October.

Nyctinomops macrotis (Gray, 1839)
Big Free-tailed Bat

Nyctinomus macrotis Gray, 1839. Annals and Magazine of Natural History, ser. 11, 4:5.

Distribution in Argentina.--Salta, Jujuy, Tucumán, Catamarca, and La Rioja provinces (Barquez et al., 1993, 1999).

Specimens Examined (1).--Yuto, 1 (MACN 13217).

Comments.--The specimen examined is the only known record for the province of Jujuy; it was captured by F. Contino in April 1957. According to the information written in the catalog at the MACN, there also is a specimen from "Jujuy," but we were not able to find this specimen.

Genus *Promops*

Promops nasutus (Spix, 1823)
Brown Mastiff Bat

Molossus nasutus Spix, 1823. Simiarum et Vespertilionum Brasiliensium species novae ou histoire naturelle des species nouvelles de singes et de chauve-souris observées et recueillies pendant le voyage dans l'intérieur du Bresil execute par ordre de S. M. le Roi de Baviere dans les annees 1817, 1818, 1819, 1820. Francisci Seraphici Hübschmanni, p. 58

Distribution in Argentina.--Salta, Jujuy, Tucumán, Catamarca, Santiago del Estero, Córdoba, Chaco, Formosa, and Misiones provinces (Barquez et al., 1993, 1999).

Specimens Examined (5).--Arroyo Sauzalito, 1 (CML 2940); Yuto, 4 (AMNH 184647, 184648, 184649, 184650).

Comments.--Specimens from Yuto were captured by F. Contino in 1959. This seems to be a rare species in the province, and only 1 specimen was captured during this study, after almost 40 years since the date of the specimens collected by Contino. Barquez et al. (1999) indicated that no characters have been found that can be used to differentiate populations from NW Argentina from those of NE Argentina.

Genus *Tadarida*

Tadarida brasiliensis (I. Geoffroy Saint-Hilaire, 1824)
Brazilian Free-tailed Bat

Nyctinomus brasiliensis I. Geoffroy Saint-Hilaire, 1824. Annales des Sciences Naturelles, Zoologie, Paris, ser. 1, 3:343.

Distribution in Argentina.--This species occupies all of the continental area of the country to about 43° S and Islas Malvinas; there are no records from Chaco or Corrientes provinces (Barquez et al., 1993, 1999).

Specimens Examined (21).--El Talar, 2 (PIDBA 936, 937); "Jujuy," 5 (MACN 26.2, 31.318, 32.22, 32.79, 39.778); Perico, 1 (MACN 40.82); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20, 3 (MMD 350; PIDBA 999, 1000); Río Lavayén, app 1 km al N de Santa Rita, 5 (4 MMD 224, 225, 226, 246; 1 released); Río Tiraxi, 1.5 km al E de Tiraxi, sobre ruta provincial N° 29, 1 (PIDBA 676); Yuto, 4 (3 AMNH 179978, 184654, 186951, 186952; 1 CML 489).

Additional Records.--Dique La Ciénaga, 13 km al SSO de San Salvador de Jujuy (Villa-R. and Villa-C., 1971); El Carmen (Yepes, 1944); Los Perales, San Salvador de Jujuy (Barquez et al., 1999).

Comments.--In August we captured a male with abdominal testes and a female with an open vagina; females with closed vaginas were captured in August and October.

Order Primates
Family Cebidae
Subfamily Aotinae

Genus *Aotus*

Aotus azarae (Humboldt, 1811)
Azara's Night Monkey

Simia azarae Humboldt, 1811 (1812). Tableau synotique des singes de l'Amerique. *En:* A. Humboldt and A. Bonpland, Voyage aux regions equinoxiales du noveau continent fait en 1799-1804. Pt. II. Recueil d'observations de zoologie et d'anatomie camparée, volumen 1:353-363 pp. Paris: Schoell, p. 359.

Distribution in Argentina.--Previously known from NE Argentina, in Formosa and Chaco provinces (Cabrera, 1958; Arditi et al., 1989) but recently included in the province of Jujuy by Díaz and Barquez (1999).

Specimens Examined (1).--Ledesma, 1 (CML 237).

Comments.--The record for Jujuy Province greatly extends the distribution of this species in Argentina. S. Pierotti, a reliable collector, collected the only known specimen for the province in 1944. There are no recent records documented with specimens in collections, and even though we have not observed this species during our field studies, a local resident recently commented to us about the presence of nocturnal monkeys in the province.

Subfamily Cebinae

Genus *Cebus*

Cebus apella (Linnaeus, 1758)
Brown Capuchin

Simia apella Linnaeus, 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:28.

Distribution in Argentina.--Jujuy, Salta, Formosa, Chaco, and Misiones provinces (Cabrera, 1958).

Specimens Examined (3).--"Jujuy," 2 (MACN 34.587, 34.588); Zapla, 1 (MACN 34.700).

Additional Records.--Aguas Blancas, 14 km al E de Santa Clara, 900 m (rural residents, personal communication); Aguas Negras, 600 m; Caimancito, 550 m (Heinonen and Bosso, 1994); Cerro Calilegua (Olrog, 1979); El Simbolar, a 2 km (rural residents, personal communication); Garrapatal, 150 km N de Jujuy (Matschie, 1894, as *Cebus azarae*); Ledesma (CML, not found); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20 (M. M. Díaz, personal observation; rural residents, personal communication); Sierra Santa Bárbara, app 6 km al E de El Palmar (R. M. Barquez, personal observation).

Comments.--The inclusion of this species at Río Las Capillas was based on information given by the local people in the area, and also because of the observation of signs that are typical of the activity of this species, including bromeliads with marks of the teeth in the leaves. A specimen from Ledesma, collected by L. Dinelli in 1906, is registered in the catalogs of the CML, but the specimen probably has been lost and was not found in the collection.

Order Carnivora
Family Canidae

Two genera and 4 species have been registered in Jujuy: *Cerdocyon thous*, *Pseudalopex culpaeus*, *P. griseus*, and *P. gymnocercus*. *Pseudalopex* was considered a subgenus of *Canis* (Kraglievich, 1930; Langguth, 1975; Van Gelder, 1978) or *Dusicyon* (Cabrera, 1958; Clutton-Brock et al., 1976), but Berta (1988) treated *Pseudalopex* as a full genus and considered *D. australis* to be the only living species of *Dusicyon*. Zunino et al. (1995) considered *Lycalopex* as a valid genus for South American species due to priority over *Pseudalopex*. Nevertheless, a phylogenetic study of the caninae (Tedford et al. 1995) argued for the distinction of *Pseudalopex* and *Lycalopex*. Recent work (Wayne et al., 1997) suggested that these groups are not high distinct genetically, and should be merged. Novaro (1997) and Bininda-Emonds et al. (1999) included the argentine taxa within *Pseudalopex*, which we follow in this paper. We consider *P. griseus* and *P. gymnocercus* as different species (Wozencraft, 1993), since specimens with diagnostic characters for each species were observed around the same localities, thus they cannot be considered as clinal variations.

Genus *Cerdocyon*

Cerdocyon thous (Linnaeus, 1766)
Crab-eating fox

Canis thous Linnaeus, 1766. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Volumen 1. Regnum Animale. 12th edition. Laurentii Salvii, Stockholm, 1:60.

Distribution in Argentina.--This species is found in northern Argentina, from east of the Andes to Misiones Province; it has been documented in southern Tucumán, northern Santiago del Estero, and northern Santa Fe provinces (Barquez et al., 1991).

Specimens Examined (11).--"Jujuy," 2 (MACN 32.75, 36.938); Oyeros, 3 km al N, camino entre rutas 61 y 43, 2 (1 CML 5966, 1 released); Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20, 2 (MMD 408, 409); Río Lavayén, app 1 km al N de Santa Rita, 2 (1 CML 5967, 1 released); San Rafael, Sierra Santa Bárbara, 1000 m, 1 (BMNH 21.1.1.3); Río Blanco, 9 km SW San Antonio, 1495 m, 2 (1 ARG 4292; 1 released).

Additional Records.--Aguas Negras, Camping, Parque Nacional Calilegua (R. M. Barquez, personal observation); Aguas Negras, 600 m (Heinonen and Bosso, 1994); Aival (=Aibal) (Matschie, 1894, as *Canis cancrivorus*); Arroyo Yuto, 13 km al SO de Yuto (park ranger G. Sosa, personal communication); Caimancito, 550 m (Heinonen and Bosso, 1994); Cerro Calilegua (Olrog, 1979); Juntas (Matschie, 1894, as *Canis cancrivorus*); Mesada de las Colmenas, 1150 m (Heinonen and Bosso, 1994); Río Colorado, Parque Nacional Calilegua (G. Gil, personal communication); Río Lavayén, 4 km al E, sobre ruta provincial N° 1 (M. M. Díaz, P. Jayat, and R. M. Barquez, personal observation); San Rafael, 1000 m; Sierra de Santa Bárbara, E de Jujuy (Thomas, 1921b); Sierra Santa Bárbara, app 6 km al E de El Palmar (R. M. Barquez, personal observation); Sunchal, 1000 m (Thomas, 1921b, type locality of *C. t. jucundus*; Kraglievich, 1930); Zapla (Yepes, 1944, as *C. t. jucundus*).

Comments.--Although Yepes (1944) recognized the subspecies *C. t. jucundus* described by Thomas (1921b), Cabrera (1958) established that is not possible to differentiate a race from Jujuy.

We observed 1 pair of *C. thous* at Río Las Capillas in June, and another at Río Blanco in July. The male from Río Blanco was a very old specimen with scrotal testes, while the female was young. At Oyeros a young male was captured in October.

Genus *Pseudalopex*

Pseudalopex culpaeus (Molina, 1782)
Andean Red Fox

Canis culpaeus Molina, 1782. Saggio sulla storia naturale del Chili. S. Tommaso d'Aquino, Bologna, p.293.

Distribution in Argentina.--From the Andes in Jujuy Province south to Córdoba and through La Pampa to the Atlantic coast of Río Negro, then south to Tierra del Fuego (Cabrera, 1958; Olrog and Lucero, 1981; Mares et al., 1989; Barquez et al., 1991).

Specimens Examined (7).--Abra Pampa, 3500 m, 1 (MACN 39.493); Alfarcito, 2600 m, 1 (BMNH 21.11.1.1); Cochinoca, 3500 m, 1 (MACN not number); "Jujuy," 1 (MACN 38.39); Norte de Lizoite, 2 (MACN 41.55, 41.56); Sierra de Zenta, 4500 m, 1 (BMNH 21.11.1.2; see comments under *Localities and maps*).

Additional Records.--Abra Blanca (Zunino et al., 1995); Alto Calilegua, 3000 m (Olrog, 1979; as *Dusicyon culpaeus andinus*); Cerro Calilegua, 2300-2600 m (Olrog, 1979; as *Dusicyon culpaeus andinus*); Cordillera de Jujuy (Yepes, 1929); Cuesta del Hurón, 29 km al O de Cienegüillas sobre Ruta provincial N° 64 (observation of tracks); Laguna de Pozuelos (Perovic, 1998); Purmamarca, 10 km al O, sobre ruta 52 (N. P. Giannini and S. Adams, personal communication); Reserva Olaroz-Cauchari, 3903 m (P. J. Martinez, personal communication); Santa Catalina (Zunino et al., 1995); Tocomar, 3 km al NO, sobre ruta nacional N° 51 (R. M. Barquez, M. M. Díaz, and P. Martinez; personal observation); Vilama (P. G. Perovic, R. S. Walter, and A. J. Novaro, in litt. – available at http://www.felidae.org/LIBRARY/perovic_et_al_1999.html).

Comments.--All records are from Prepuna or Puna, except that of Olrog (1979) for Cerro Calilegua, which is a grassland limited by the *Alnus* forests at an altitude of 2600 m. The specimen from Tocomar was observed during the day, at the side of the road. There is a large series of specimens at the BMNH, collected by E. Budin, erroneously treated as being from Sierra de Zenta.

Pseudalopex griseus (Gray, 1837)
Argentine Gray Fox

Vulpes griseus Gray, 1837. Magazine of Natural History (Charlesworth's), 1:578.

Distribution in Argentina.--The distribution of this species is similar to that of the Andean red fox (*L. culpaeus*). According to Barquez et al. (1991) and Olrog and Lucero (1981), the distribution of this species does not include Jujuy and eastern Salta. However, there are several records (see additional records) suggesting the presence of this species in Jujuy (Díaz and Barquez, 1999).

Specimens Examined.--None.

Additional Records.--Puente sobre el Arroyo Sapagua, ruta nacional N° 9, entre Humahuaca and desvío a Iruya (G. Gil, personal communication); Purmamarca, 10 km al O, sobre ruta 52 (S. P. Adams, in litt.; N. P. Giannini, personal communication); Laguna de Pozuelos (Perovic, 1998); Santa Laura, camino de cornisa (P. Perovic, personal communication).

Comments.--The observations from Purmamarca, a locality in the Prepuna, correspond to a female with 2 young, recorded in February 1991. Abra de Santa Laura is situated in the Yungas, and Laguna Pozuelos and Arroyo Sapagua are in the Puna.

Pseudalopex gymnocercus (Fischer, 1814)
Pampa Fox

Procyon gymnocercus Fischer, 1814. Zoognosia tabulis synopticis illustrata, in usum praelectionum Academie imperialis medico-chirugicae mosquensis edita…. N. S. Vsevolozsky, Mosquae, 3:178.

Distribution in Argentina.--From northern Argentina to northern Río Negro and Neuquén provinces (Cabrera, 1958; Massoia, 1982).

Specimens Examined (3).--Chalicán, 1 (MACN 35.241); "Jujuy," 1 (MACN 32.252); Puente sobre el Arroyo Sapagua y ruta nacional N° 9, 3500 m, 1 (MMD 394).

Additional Records.--Aguas Negras, 600 m (Heinonen and Bosso, 1994); Cercanías de la ciudad de San Pedro, sobre ruta nacional N° 34 (Massoia, 1982); Cruce de las rutas nacional 34 and provincial 43, camino a Monterrico, km 1160; Dique Las Maderas; Ruta nacional N° 34, cerca de Pampa Blanca (J. P. Jayat, personal communication); Santa Rita, 4 km al NO, sobre ruta provincial N° 1 (P.J. Martinez, J.P. Jayat, R.M. Barquez, D.A. Flores, and M.M. Díaz, personal observation, photos); Sierra de Aguilar, 3800 m (Massoia, 1981); Sierra Santa Bárbara, app 6 km al E del Palmar (R.M. Barquez, personal observation); Tanques, 7 km al SE sobre Ruta provincial N° 74 (R.M. Barquez, M.M. Díaz, D.A. Flores, and J.P. Jayat, personal observation).

Comments.--Massoia (1981) identified the specimen from Sierra de Aguilar, as *Dusicyon inca*; however, this taxon was included either in *P. culpaeus* or in *P. gymnocercus* (Langguth, 1975). According to Massoia (1982) this species inhabits the Chaco-Yungas ecotonal area in Jujuy and Salta provinces, but we have found that in Jujuy; it can be found in all habitats from the Puna to the Chaco and Yungas.

The specimen from "Puente sobre el Arroyo Sapagua" was found dead at the side of the road and only 1 mandible was collected. The specimen from Tanques, a locality in the Puna region, was observed hunting a mountain vizcacha (*Lagidium vizcacia*) on the rocky hills.

Family Felidae
Subfamily Felinae

Genus *Herpailurus*

Herpailurus yagouarondi (É. Geoffroy Saint-Hilaire, 1803)
Jaguarundi

É. Geoffroy Saint-Hilaire, 1803. Annales du Muséum d'histoire Naturelle, Paris, 1803:124.

Distribution in Argentina.--Mountainous areas from Jujuy to Neuquén and Río Negro (approximately 39° S), east to Buenos Aires Province (Cabrera, 1958; de Oliveira, 1998a).

Specimens Examined (4).--"Jujuy," 1 (MACN 38.43); Villa Carolina, Río Lavallén, 500 m, 1 (BMNH 20.1.7.4); Yuto, 2 (1 CR 407; 1 AMNH 183120).

Additional Records.--Abra de Cañas, 1700 m; Aguas Negras, 600 m; Mesada de las Colmenas, 1150 m (Heinonen and Bosso, 1994); Villa Carolina, 500 m (Thomas, 1920a, as *Felis yaguarondi*).

Comments.--The specimen from Villa Carolina (Thomas, 1920a), was captured in July by E. Budin, who indicated that it was a female with 3 pairs of well marked mammae.

Genus *Leopardus*

Leopardus pardalis (Linnaeus, 1758)
Ocelot

Felis pardalis Linnaeus, 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis…. Tenth edition. Laurentii Salvii, Stockholm,1:42.

Distribution in Argentina.--Northern Argentina, from Misiones and Corrientes provinces, west to Salta and Tucumán (Cabrera, 1958; Murray and Gardner, 1997; Jayat et al., 1999). For Jujuy it was only cited for Departamento Ledesma by Chébez (1994).

Specimens Examined.--None.

Additional Records.--Arroyo Negrito, Parque Nacional Calilegua (G. Gil, personal communication); Arroyo Yuto, 13 km al SO de Yuto (Park guard G. Sosa, personal communication); E of El Palmar, Sierra de Santa Bárbara (J. K. Braun, personal communication); Juntas; Palos a pique (Matschie, 1894, as *Felis mitis*); Río Tesorero, 4 km al N de Tiraxi, sobre ruta provincial N° 29 (J. P. Jayat and P. J. Martinez, personal communication); Vecindades del Parque Nacional Calilegua (Heinonen and Bosso, 1994).

Comments.--Inhabits forests in highlands or plains with forests that are nor very extensive (Nowak and Paradiso, 1991). According to Olrog (1976), this species is extremely rare in Jujuy and Salta, because of unrestricted hunting. There are no specimens from Jujuy deposited at any of the collections studied. The specimen from El Palmar was observed in the mountains of Sierra de Santa Bárbara.

Leopardus tigrinus (Schreber, 1775)
Little Spotted Cat

Felis tigrina Schreber, J. C. D. von, 1775. Die Säugethiere in Abbildungen nach der Natur, mit Beschreibungen von D. Johan Christian Daniel von Schreber. Walther'sche Kunst- und Buchhandlung, Erlangen, Vol. 2 (15):pl. 106 [1775]; Wolfgang Walther, Erlangen, text, Vol. 3(23): 396 [1777].

Distribution in Argentina.--Northern Argentina, in Misiones, Jujuy, and Salta Provinces (Díaz and Lucherini, in press). The observation from Jujuy extends the distribution of this species to western Argentina.

Specimens Examined.--None.

Additional Records.--Ocloyas (J. P. Jayat, personal communication).

Comments.--The record from Ocloyas is the first of this species for the province of Jujuy.

Leopardus wiedii (Schinz, 1821)
Margay

Felis wiedii Schinz, 1821. Naturgeschichte und Adildungen der Säugethiere. Das Thierreich eingetheilt nach dem Bau der Thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie von dem Herrn Ritter von Cuvier. Säugethiere und Vögel. J. G. Cotta'schen Buchhandlung, Stuttgart und Tübingen, 1:235.

Distribution in Argentina.--Eastern Jujuy, northern Salta, Misiones and probably northeastern Corrientes (Olrog and Lucero, 1981; Massoia et al., 1992b; Chébez, 1994) and Tucumán provinces (de Oliveira, 1998b).

Specimens Examined (2).--Calilegua, 1 (MCNS 32); Cucho, 1 (CML 5738).

Additional Records.--Cerro Calilegua, 1500 m (Olrog, 1979); El Simbolar, 25 km al SO de Palma Sola, 1000 m (R. M. Barquez, personal observation); San Francisco, 1400 m, Valle Grande (Olrog, 1976); Yuto (local residents, personal communication; Ojeda and Mares, 1989).

Comments.--Inhabits humid forests. According to Olrog (1976), this species is abundant in Cerro Calilegua, in southeastern Jujuy Province. Olrog (1979) reported 8 skins confiscated in Valle Grande.

Genus *Lynchailurus*

Lynchailurus pajeros (Desmarest, 1816)
Pampas Cat

Felis pajeros Desmarest, 1816. Tableau Méthodique des mammiferes, *in* Nouveau dictionnaire d`histoire naturelle, appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à la médicine, etc. Par une société de naturalistes et d'agriculteurs. Nouveau édition, presqú entièrement refondue et considérablement augmentée. Ch. Deterville, Paris,6:114.

Distribution in Argentina.--Eastern slopes of the Andes in northwestern Argentina, and lowlands of northwestern, central, and southern Argentina (García-Perea, 1994).

Specimens Examined (1).--Abra de Fundición, 20 km al O de Rinconada and app 50 km al O de Pozuelos, 1 (MCNS no number).

Additional Records.--Alto Calilegua (Olrog, 1979; as *Felis colocolo crespoi*); Cerro Hermoso (cercanías), 2800 m (Heinonen and Bosso, 1994; as *Lynchailurus colocolo*); "Jujuy" (Matschie, 1894); Laguna de Pozuelos (Perovic, 1998; as *Oncifelis colocolo*); Sierra de Santa Victoria, 3000 a 5000 m (García-Perea, 1994); Valle Morado (Olrog, 1979, as *Felis colocolo crespoi*).

Comments.--Johnson et al. (1999) considered only 1 species for the genus *Lynchailurus* (*L. colocolo*). They recognize variations, based on mtDNA from small samples of each group, that support several commonly recognized subspecific divisions for this species, but not those subdivisions at species level suggested by García-Perea (1994). We follow García-Perea (1994, 2002) with respect to the composition of the genus (*L. colocolo*, *L. pajeros*, and *L. braccatus*). According to Cabrera (1958), 2 subspecies occur in the province of Jujuy, *L. p. budini* and *L. p. crespoi*, and he indicated that the 2 species could be differentiated by the length of the fur, coloration and length of the mane, coloration of spots on the sides, and on the venter and limbs. None of these characters concerning the coloration is coincident with the type specimen. *L. p. budini* inhabits open areas in high grasslands, and preferentially hunts on the ground; although this subspecies is known from more records than *L. p. crespoi*, it remains scarce and constantly hunted (Chébez, 1994). *L. p. crespoi* is typical of the transitional forest between Chaco and Yungas, and is considered to be rare (Chébez, 1994). According to García-Perea (1994), *L. p. crespoi* and *L. p. budini* might be synonyms because of the similarities of their external characters and habitat. Based on genetic variation Johnson et al. (1999) note several geographical divisions (including *budini* and *crespoi*), but acknowledged that their sample size was small. Consequently, because the differences are unclear we do not make any subspecific distinctions. Matschie (1894) cited this species for the Puna of Jujuy Province.

Genus *Oncifelis*

Oncifelis geoffroyi (d'Orbigni and Gervais, 1844)
Geoffroy's Cat

Felis geoffroyi d'Orbigni and Gervais, 1844. Nouveau bulletin des sciences par la Société Philomatique, Paris, 1844:40.

Distribution in Argentina.--All of Argentina, except Tierra del Fuego (Ximénez, 1975); the subspecies of Jujuy (*O. g. salinarum*) inhabits the mountainous areas of Jujuy and Salta, south to Mendoza and San Luis provinces (Cabrera, 1958).

Specimens Examined (6).--Chalicán, 1 (MACN 35.240); "Jujuy," 2 (MACN 33.500, 34.702); Mountains W of Yala, 1 (FMNH 24360); Palpalá, 1 (MCNS not catalogued); Sunchal, Sierra Santa Bárbara, 1200 m, 1 (BMNH 21.1.1.1).

Additional Records.--Agua Salada (local residents, personal communication); Aguas Calientes, Finca Los Melados (J. P. Jayat, personal communication); Alrededores de la ciudad (Yepes, 1944); E of El Palmar, Sierra de Santa Bárbara (J. K. Braun, personal communication); El Simbolar, 25 km al SO de Palma Sola, 1000 m (R. M. Barquez, personal observation); Laguna de Pozuelos (Perovic, 1998); Yuto (local residents, personal communication).

Comments.--This subspecies was described by Thomas (1903) as different from *O. geoffroyi*; according to Cabrera (1958) and Yepes (1944), however, it should be considered a western representative of *O. geoffroyi*. The known records are from Yungas, Chaco, and Puna. The specimen from Yala was a young female. Matschie (1894) cited *Felis geoffroyi* d'Orbigni and Gervais, and *Felis guigna* Molina, for Jujuy Province; both taxa are considered synonyms of *O. g. geoffroyi.*

Genus *Oreailurus*

Oreailurus jacobita (Cornalia, 1865)
Andean Cat

Felis jacobita Cornalia, 1865. Memorie Societa di Scienze Naturali e Museo Civico di Storia Naturale de Milano, 1:3.

Distribution in Argentina.--Northwestern Argentina, in arid and semiarid zones, from Jujuy to San Juan provinces (Cabrera, 1958; Yensen and Seymour, 2000).

Specimens Examined.--None.

Additional Records.--Laguna de Pozuelos (Perovic, 1998, as *Oncifelis jacobita*); Laguna de Vilama (P. Perovic, personal communication); Paso de Jama, inmediaciones (Chébez, 1994).

Comments.--This species is endemic to the High Andean phytogeographic province

(Scrocchi and Halloy, 1986), and it can be confused with the sympatric pampas cat (*Lynchailurus pajeros*); for this reason García-Perea (2002) analyzed the differences and offered descriptions and a key to separate the 2 species. It is known from only a few specimens and, although its distribution is wide, it is not a common species (Chébez, 1994).

The type locality "South of the Bolivian department of Potosí, near the border with Argentina, between Potosí and Humahuaca" should be in error, because the department of Potosí abuts the departments of Santa Catalina and Yavi (Jujuy, Argentina), and is far away from Humahuaca.

Genus *Puma*

Puma concolor (Linnaeus, 1771)
Mountain Lion

Felis concolor Linnaeus, 1771. Mantissa plantarum altera generum editionis VI & specierum editionis II. Laurentii Salvii, Stockholm, 2:522.

Distribution in Argentina.--All the country from the north to the Estrecho de Magallanes (Cabrera, 1958).

Specimens Examined (6).--El Bananal, Urundel, 1 (MACN no number); "Jujuy," 2 (MACN 34.594, 38.44); Las Escaleras, 1 (MCNS no number); Quera, Pozuelos, 1 (MCNS 118); Sierra Santa Bárbara, 1200 m, 1 (CR 453).

Additional Records.--9 km NW Bárcena, (local residents, personal communication); Agua Salada (local residents, personal communication); Aguas Negras, 600 m (Heinonen and Bosso, 1994); Al E de Yuto, cruzando el Río San Francisco (local residents, personal communication); Alto Laguna (Anonymous, 1996); Campo Laguna (local residents, personal communication); Cerro El Morado (local residents, personal communication); Cerro Hermoso (cercanías), 2800 m (Heinonen and Bosso, 1994); E of El Palmar, Sierra de Santa Bárbara (J. K. Braun, personal communication); "Jujuy" (Matschie, 1894); Laguna de Pozuelos (Perovic, 1998); La Quiaca, 17 km al O and 3 km al S, sobre ruta provincial N° 5, 3711 m (local residents, personal communication); Lipán, 10 km al O de Purmamarca (local residents, personal communication); Mesada de las Colmenas, 1150 m (Heinonen and Bosso, 1994); Mina Pirquitas, 31 km al SE, Sierra de Quichagua, sobre ruta 74b, 4200 m (local residents, personal communication); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20 (local residents, personal communication); San Juancito (J. P. Jayat, personal communication); Sierra de Zenta, entre Iturbe and Chaupe Rodeo, sobre ruta provincial N° 13 (local residents, personal communication); Sobre ruta 40, 29 km al N del empalme con ruta 52 (J. P. Jayat and P. J. Martinez, personal communication).

Comments.--In Bárcena, local residents informed us that pumas are becoming a serious problem due to the frequent attacks to livestock; the specimen from Alto Laguna was killed because it was attacking sheep. Matschie (1894) reported this species from the Puna of Jujuy.

Subfamily Pantherinae

Genus *Panthera*

Panthera onca (Linnaeus, 1758)
Jaguar

Felis onca Linnaeus, 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis…. Tenth edition. Laurentii Salvii, Stockholm, 11:42.

Distribution in Argentina.--Northern half of Misiones, northern and eastern Salta, eastern Jujuy, northeastern Santiago del Estero, and northwestern Chaco and Formosa provinces (Chébez, 1994)

Specimens Examined (3).--"Jujuy," 1 (MACN 31.203); Las Animas, Fraile Pintado, 1 (MCNS no number); Urundel, 1 (MCNS 1).

Additional Records.--Agua Salada (local residents, personal communication); Caimancito (local residents, personal communication); Cerro Calilegua (Olrog, 1979); Franja E del departamento de Santa Bárbara (Arra, 1974); "Jujuy," (Matschie, 1894); Las Escaleras (Chébez, 1994); Maíz Gordo; Normenta (Perovic and Herrán, 1998); Parque Nacional Calilegua (Heinonen Fortabat and Chébez, 1997); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20 (local residents, personal communication).

Comments.--The majority of localities from Jujuy are from Parque Nacional Calilegua and from the eastern part of the province, in forests and Chaco. A specimen was killed by hunters in Paraje Escaleras (Chébez, 1994). According to local residents, at Las Capillas this species attacks horses, cows, and sheeps; they also informed that a young was captured and given to the city zoo of Jujuy.

Family Mephitidae

Mephitidae is here recognized as a family different from Mustelidae following Dragoo and Honeycutt (1997). Based on mitochondrial DNA, these authors proposed that Mustelidae is a paraphyletic group.

Genus *Conepatus*

Conepatus chinga (Molina, 1782)
Molina's Hog-nosed Skunk

Viverra chinga Molina, 1782. Saggio sulla storia naturale del Chili. S. Tommaso d'Aquino, Bologna, p. 288.

Distribution in Argentina.--Northern Argentina south to Neuquén and Río Negro provinces (Cabrera, 1958).

Specimens Examined (18).--Abra Pampa, Criadero,1 (MACN 52.89); Alfarcito, 2600 m, 1 (BMNH 21.11.1.3); Casa Colorada, app 2 km al N de Alfarcito, 3034 m, 1 (MMD 375); Cerro El Morado, 11 km al NO de San Antonio, sobre Río El Morado, 1 (CML 5972); Cochinoca, 3500 m, 4 (MACN 39.495, 39.496, 39.497, 39.498); Cuesta de Lipán, 15 km al O de Purmamarca, sobre ruta provincial N° 52, 3156 m, 1 (MMD 304); Humahuaca, 1 (MACN 26.182); "Jujuy," 2 (1 MACN not number; 1 FMNH 21675); La Laguna, 4500 m, Sierra de Zenta, E de Maimará, 1 (MACN 27.101; see comments under *Localities and maps*); Maimará, 2230 m, 2 (BMNH 12.12.12.1 *Conepatus ajax* holotype, 12.12.12.2); Mina Pan de Azúcar, 8 km al N and 5 km al O camino a Herrana, 3820 m, 1 (MMD 500); Sierra de Zenta, 1 (CML 602; see comments under *Localities and maps*); Tres Cruces, 1 (CML 187).

Additional Records.--Aguas Blancas, 14 km al E de Santa Clara, 900 m (R.M. Barquez, personal observation); Alto Calilegua, 3000 m (Olrog, 1979, as *C. chinga budini*); Arroyo Yuto, 13 km al SO de Yuto (M. M. Díaz, personal observation of footprints); Cerro Calilegua, 1500 m (Olrog, 1979, as *C. chinga budini*); El Perchel (G. Gil, personal communication); Laguna de Pozuelos (Perovic, 1998); Palma Sola, 18 km al S (R. M. Barquez, personal observation).

Comments.--According to Cabrera (1958) and Chébez (1994), the species from NW Argentina is *C. rex*, although most authors cited *C. chinga* for the region (Mares et al., 1989, 1995, 1997; Barquez et al., 1991). Osgood (1943) reported that *C. rex* occurs at high and semiarid regions in northern Argentina. Olrog (1979) considered that the subspecies from NW Argentina is *C. c. budini* Thomas, 1919. However, all original descriptions of the species were based on pelage banding patterns, which our examination indicates are highly variable. To determine if 1 or 2 species of *Conepatus* inhabit Jujuy Province, 1 from high altitudes and another from lowlands, additional specimens require examination. In Uruguay, Van Gelder (1968) reported that an analysis of color pattern indicates considerable individual variation but no sex or age differences. Most of the records in Jujuy are from the Puna and Prepuna, although it has been reported also in the Yungas. All records obtained in this study correspond to animals killed by hunters.

Family Mustelidae
Subfamily Lutrinae

Genus *Lontra*

Lontra longicaudis (Olfers, 1818)
Neotropical River Otter

L[*utra*] *longicaudis* Olfers, 1818. Bemerkingen zu Illiger's Ueberblick der Säugethiere nach ihrer Vertheilung uber die Welttheile, rücksichtlich der Südamerikanischen Arten (species). Abhandlung 10 of Wilhelm Ludwig Eschwege's Journal von Brasilien..., vol. 15, heft 2:192-237, *in* Neue Bibliothek des wichtigsten Reisenbeschreibungen zur Erweiterung der Erdund Volkerkunde...F. T. Bertuch (ed.), Weimar, p. 233.

Distribution in Argentina.--From northern Argentina south to Buenos Aires Province

(Redford and Eisenberg, 1992). In Jujuy, it was recorded only at the departments of Valle Grande and Ledesma (Redford and Eisenberg, 1992; Chébez, 1994).

Specimens Examined (1).--Caimancito, pozos petroleros 38 and 39, 1 (MCNS 108).

Additional Records.--Aguas Negras, 1400 m (Olrog, 1979, as *Lutra platensis*); Arroyito Negro, Parque Nacional Calilegua (P. Blendinger, personal communication); Arroyo Negrito, Parque Nacional Calilegua (G. Gil, personal communication, observation of tracks); Valle Grande Department (Chébez, 1994); Río Grande de Jujuy bei Aival (Matschie, 1894, as *Lontra paranensis*); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20 (local residents, personal communication).

Comments.--According to Van Zyll de Jong (1987), the New World otters belong to the genus *Lontra*, although other authors (Corbet, 1978; Hall, 1981; Corbet and Hill, 1986; Jones et al., 1986), do not consider *Lontra* to be a valid genus

According to Olrog (1979), tracks and feces of this species at Aguas Negras, a stream originated in Cerro Amarillo at 3000 m of altitude, indicate that this species may occur at higher elevations than supposed. Information given by local residents indicate that some years ago this species was observed frequently at Río Las Capillas.

Genus *Pteronura*

Pteronura brasiliensis (Gmelin, 1788)
Giant Otter

Mustela lutris brasiliensis Gmelin, 1788. Pp. 93. *In*: Caroli a Linnaeus... Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis synonymis, locis. Editio decima tertia, aucta, reformata. Lipseae: Georg. Emanual Beer, Volumen 1. pt. 1, Mammalia. pp. 10 (unnumbered) + 1-232.

Distribution in Argentina.--Northeastern Argentina, in Misiones, and historical records for Corrientes, Jujuy, Santa Fe, and Formosa provinces (Díaz and Lucherini, in press).

Specimens Examined (1).--Alrededores de la ciudad, 1 (MACN 31.333).

Additional Records.--Río San Francisco (Chébez, 1994).

Comments.--Chébez (1994) mentioned the historical presence of this species in Jujuy, in the 18th century in Río San Francisco and Río Bermejo or Teuco in the extreme eastern Jujuy along the border with Salta Province. The record from "alrededores de la ciudad" corresponds to a young individual collected by Salvador Mazza and Arístedes Fiora; somewhere around San Salvador de Jujuy.

Subfamily Mustelinae

Genus *Eira*

Eira barbara (Linnaeus, 1758)
Tayra

Mustela barbara Linnaeus, 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis.... Tenth edition. Laurentii Salvii, Stockholm, 1:46.

Distribution in Argentina.--Northern Argentina, from Jujuy to Catamarca, east to Misiones and south to northern Santa Fe Province (Cabrera, 1958).

Specimens Examined (5).--Arroyo del Medio, Parque Nacional Calilegua, 1 (MCNS not number); Arroyo Zanjón Seco, 20 a 30 km al N de Libertador General San Martín, 1 (MCNS not number); "Jujuy," 1 (MACN 32,11); Santa Bárbara, Santa Bárbara, 1 (MCNS not number); Yuto, 1 (AMNH 185325).

Additional Records.--Agua Caliente (Matschie, 1894, as *Galictis barbara*); Agua Salada (local residents, personal communication); Aguas Blancas, 14 km al E de Santa Clara, 900 m (R. M. Barquez, personal observation); Aguas Negras, 600 m (M. M. Díaz, personal observation); Arroyo Colorado, cerca de Santa Clara (P. Perovic, personal communication); Cerro Calilegua, 1400 m (Olrog, 1979); E of El Palmar, Sierra de Santa Bárbara (J. K. Braun, personal communication); Laguna La Brea, 25 km antes de Palma Sola (R. M. Barquez, personal observation); Libertador General San Martín límite del Parque Nacional Calilegua (P. Perovic, personal communication); Mesada de las Colmenas, 1150 m (Heinonen and Bosso, 1994).

Comments.--Inhabits forests up to 2000 m (Mares et al., 1989); records in Jujuy Province correspond to forest and transitional forest. We observed a pair of *Eira* at mid-day at Laguna La Brea, 1 on a branch of a tree and the other at the ground on the side of a path; both animals, a male and a female, made alarm calls. At Parque Nacional Calilegua, we observed a specimen on a tree attempting to reach a magpie's (*Cyanocorax chrysops*) nest.

Genus *Galictis*

Galictis cuja (Molina, 1782)
Lesser Grison

Mustela cuja Molina, 1782. Saggio sulla storia naturale del Chili. S. Tommaso d'Aquino, Bologna, p. 291.

Distribution in Argentina.--From northern Argentina south to Chubut Province (Redford and Eisenberg, 1992; Yensen and Tarifa, 2003).

Specimens Examined (12).--Chalicán, 1 (MACN 35.242); Cruce de las rutas 34 y la que se dirige a Vinalito, 1 (MCNS no number); "Jujuy," 4 (MACN 31.171, 33.101, 33.102, 35.348); Sobre ruta 34, Colonia Libertad, 1 (MCNS no number); Tilcara, 1 (MCNS no number); Yavi Chico, 2 (MACN 36.631, 41.190); Yavi Chico, El Habal, 1 (MACN 36.488); Yuto, 1 (MACN 18201).

Additional Records.--Agua Salada (local residents, personal communication); Aguas Calientes, Finca Santa Victoria (local residents, personal communication); Aguas Negras, 600 m (Heinonen and Bosso, 1994); Bordo La Isla, Finca La Nación (C. F. Jayat, personal communication); Caimancito (P. Perovic, personal communication); Cerro Calilegua, 1700 m (Olrog, 1979); Laguna de Pozuelos (Perovic, 1998); Las Lajitas (P. Perovic, personal communication); Río Grande de Jujuy (Matschie, 1894); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20 (local residents, personal communication); Ruta nacional N° 34, entre Ciudad Perico and San Pedro de Jujuy, app 10 km al E de Ciudad Perico (J. P. Jayat, personal communication).

Comments.--In Jujuy this species was observed in all habitats from the forests to the Puna. In Yuto a young was reported in June.

Family Procyonidae
Subfamily Procyoninae

Genus *Nasua*

Nasua nasua (Linnaeus, 1766)
South American Coati

Viverra nasua Linnaeus, 1766. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Volumen 1. Regnum Animale. 12th edition. Laurentii Salvii, Stockholm, 1:64.

Distribution in Argentina.--Two populations are thought to inhabit Argentina, 1 in the northwest, in Salta, Jujuy, and Tucumán provinces, and another in the eastern and central part of the country from the provinces of Chaco, Formosa, Corrientes, and northern Santa Fe, to Mendoza (Olrog and Lucero, 1981; Barquez et al., 1991). However, the records from Salta, Formosa, and Chaco provinces (Heinonen Fortabat and Chébez, 1997; Jayat et al., 1999), suggest that these populations are not completely isolated (Jayat et al., 1999).

Specimens Examined (7).--El Bananal, Urundel, 1 (MACN not number); "Jujuy," 3 (MACN 26.122, 31.222, 35.329); Ramal de Perico a Embarcación, 1 (MACN not number); San Francisco, Macizo de Calilegua, 1 (MACN 41.235); Yuto, 1 (AMNH 183294).

Additional Records.--Agua Salada (local residents, personal communication); Aguas Negras, 600 m (Heinonen and Bosso, 1994); Arroyo Sauzalito (A. G. Autino, personal communication); Caimancito, 550 m (Heinonen and Bosso, 1994); Cerro Calilegua, 1300 m (Olrog, 1979, as *N. nasua cinerascens*); Mesada de las Colmenas, 1150 m (Heinonen and Bosso, 1994); Palos a pique; Río Grande de Jujuy (Matschie, 1894).

Comments.--Although Cabrera (1958) reported 3 subspecies in Argentina – *N. n aricana*, *N. n. cinerascens*, and *N. n. solitaria* – the variation in coloration and cranial and dental structure led him to note that his taxonomic decision was provisional. Cabrera considered that the subspecies from northern Argentina was *N. n. aricana* Vieira, 1945. In contrast, Olrog and Lucero (1981) considered *N. n. cinerascens* Lönnberg, 1921 to be the taxon represented in Jujuy Province, although they did not justify this decision; Cabrera (1958) considered this subspecies to be restricted to Eastern Argentina. Gompper and Decker (1998) considered Argentine animals to represent *N. n. spadicea,* including *aricana* and *cinerascens* as synonyms. Juveniles were collected in August and October.

Genus *Procyon*

Procyon cancrivorus (G. Cuvier, 1798)
Crab-eating Raccoon

Ursus cancrivorus G. Cuvier, 1798. Tableau élémentaire de l'histoire naturelle des Animaux. Baudouin, Paris, p. 113.

Distribution in Argentina.--Northern Argentina, south to Santa Fe Province (Redford and Eisenberg, 1992).

Specimens Examined (13).--"Jujuy," 8 (MACN 31.170, 31.171, 31.200, 32.254, 33.101, 33.102, 35.218, 37.84); Río Blanco, 2 (MACN 32.275, 32.276); Yavi Chico, 3 (MACN 41.109, 41.153, 41.154).

Additional Records.--Aguas Negras, 600 m (Heinonen and Bosso, 1994); Aguas Negras, Camping, Parque Nacional Calilegua (M. M. Díaz, personal observation); Alrededores de la Capital (Yepes, 1944); Arroyo Negrito, Parque Nacional Calilegua (G. Gil, personal communication); Arroyo Sauzalito (P. Martinez, personal communication); Arroyo Yuto, 13 km al SO de Yuto (Park guard G. Sosa, personal communication); Caimancito, 550 m (Heinonen and Bosso, 1994); Cerro Calilegua, 2000 m (Olrog, 1979); "Jujuy" (Matschie, 1894); Laguna La Brea, ruta 1, km 134 (P. Martinez, personal communication); Mesada de las Colmenas, 1150 m (Heinonen and Bosso, 1994); Oyeros, 3 km al N, camino entre rutas 61 and 43 (J. P. Jayat and P. J. Martinez, personal communication); Río Blanco, 9 km SW San Antonio, 1495 m (local residents, personal communication); Río Colorado, Parque Nacional Calilegua (G. Gil, personal communication); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20 (M. M. Díaz, personal observation); Río Tesorero, 4 km al N de Tiraxi, sobre ruta provincial N° 29 (J. P. Jayat and P. J. Martinez, personal communication); Río Tiraxi, app 5 km al S, de Tiraxi, sobre ruta provincial N° 29 (P. J. Martinez, personal communication); Sierra Santa Bárbara, app 6 km al E de El Palmar (R. M. Barquez, personal observation).

Comments.--Although this species is easy to observe in northeastern Argentina, in the northwest the majority of records correspond to tracks observed along rivers and streams. In Jujuy, most records for this species are from Yungas forest; additionally, some records are from the Chaco and there is a record from Yavi Chico, in the Puna region. The last locality was cited by Yepes (1942), who mentioned that although the locality is in the Puna, it is located near a habitat that is typical for this species. Heinonen and Bosso (1994) included *P. cancrivorus* in Abra de Cañas, following Olrog (1979), although the latter author only mentioned Cerro Calilegua as the locality.

Order Perissodactyla
Family Tapiridae

Genus *Tapirus*

Tapirus terrestris (Linnaeus, 1758)
South American Tapir

Hippocamelus terrestris Linnaeus, 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:74.

Distribution in Argentina.--Central and northern Misiones, northern and eastern Salta, southeastern Jujuy, extreme northeastern Santiago del Estero, and western Chaco and Formosa provinces (Chébez, 1994).

Specimens Examined (1).--Arroyo Pedregoso, 1250 m, 1 (MACN 36.139).

Additional Records.--Aguas Blancas, 14 km al E de Santa Clara, 900 m (local residents, personal communication); Aguas Negras, 600 m (Heinonen and Bosso, 1994); Arroyo Sauzalito (R. M. Barquez, personal observation); Arroyo Yuto, 13 km al SO de Yuto (M. M. Díaz and D. A. Flores, personal observation of tracks, photos); Caimancito, 550 m (Heinonen and Bosso, 1994); Cercanías de El Simbolar (R. M. Barquez, personal observation); Cerro Calilegua (Olrog, 1979); "Jujuy" (Matschie, 1894 as *Tapirus americanus*); Laguna La Brea (local residents, personal communication); Mesada de las Colmenas, 1150 m (Heinonen and Bosso, 1994); Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20 (local residents, personal communication).

Comments.--According to Olrog (1979), tapirs can be found at Cerro Calilegua at 2000 m, although they might descend to lower elevations during the winter. At Arroyo Yuto, tracks were observed and 1 individual was heard during the night. The record from Cercanías de El Simbolar corresponds to a specimen hunted in the area.

Order Artiodactyla
Family Tayassuidae

Genus *Pecari*

Pecari tajacu (Linnaeus, 1758)
Collared Peccary

Sus tajacu Linnaeus, 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis.... Tenth edition. Laurentii Salvii, Stockholm, 1:50.

Distribution in Argentina.--Northern Argentina, extending southward to northern San Luis, southeastern San Juan, and northern Mendoza, and through the east to Corrientes and Misiones provinces (Cabrera, 1961a; Ortiz Jaureguizar and López Armengol, 1984).

Specimens Examined (1).--None.

Additional Records.--Agua Salada (local residents, personal communication); Cafatales (=Cafetales) (Matschie, 1894; as *Dicotyles torquatus*); Cerro Calilegua (Olrog, 1979, as *Dicotyles tajacu tajacu*); "Jujuy" (Wetzel, 1977); Laguna La Brea; Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20; Sierra Santa Bárbara, app 6 km al E de El Palmar (local residents, personal communication).

Comments.--This species has been observed in the Chaco as well as in the Yungas. This species is persecuted for food, leather, and sport hunting (Sowls, 1984; Mares et al., 1989).

Genus *Tayassu*

Tayassu pecari (Link, 1795)
White-lipped Peccary

Tayassu pecari Link, 1795. Beiträge zur Naturgeschichte, 2:104.

Distribution in Argentina.--Misiones, Corrientes, Formosa, Chaco, northern Santa Fe and Santiago del Estero, eastern Jujuy and Salta, and Tucumán Province (Díaz and Barquez, 2002).

Specimens Examined.--None.

Additional Records.--Agua Salada (local residents, personal communication); Aguas Blancas, 14 km al E de Santa Clara, 900 m; Cafatales (=Cafetales) (Matschie, 1894; as *Dicotyles labiatus*); Cerro Calilegua (Olrog, 1979); Laguna La Brea (local residents, personal communication); Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20 (local residents, personal communication).

Comments.-- This species is found in both wet and arid areas (Sowls, 1984); in Jujuy, records are known from the Yungas and Chaco, based on information from local residents. Pecaris are sensitive to changes in habitat, and have difficulty adapting to areas of secondary growth or disturbance; thus, they require very large zones of undisturbed habitat (Sowls, 1984).

Family Camelidae

Genus *Lama*

Lama glama (Linnaeus, 1758)
Llama

Camelus glama Linnaeus, 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis.... Tenth edition. Laurentii Salvii, Stockholm, 1:65.

Distribution in Argentina.--Northwestern Argentina, domesticated specimens (Cabrera, 1961a), from 2300 to 4000 m.

Specimens Examined (3).--Abra Pampa, 1 (MACN 39.502); Rinconada, 6 km al N, camino a Timón Cruz, 4286 m, 1 (MMD 489); Río Orosmayo, Peñas Blancas, 1 (MACN 39.501).

Additional Records.--Abra Pampa, 13 km al NO sobre ruta provincial N° 7; Abra Pampa, 20 km al O sobre ruta provincial N° 71; Abra Pampa, 21 km al NO sobre ruta provincial N° 7; Abra Pampa, 29 km al NO sobre ruta provincial N° 7; Abra Pampa, 32 km al NO sobre ruta provincial N° 7; Abra Pampa, 4 km al O sobre ruta provincial N° 71; Abra Pampa, 9 km al O sobre ruta provincial N° 71; Alto de Yoscaba, 4320 m; Alto de Yoscaba, 3 km al S, camino a Rinconada; Alto de Yoscaba, 12 km al S, camino a Rinconada; Camino a Santa Catalina, 8 km al N del cruce de las rutas provinciales 64 y 65, sobre ruta provincial N° 65; Cienegüillas, 25 km al O, sobre ruta provincial N° 64; Cienegüillas, 4 km al E sobre ruta provincial N° 5; Cienegüillas, 6 km al E sobre ruta provincial N° 5; Cochinoca, 11 km al NO sobre ruta provincial N° 71; Cochinoca, 16 km al NO sobre ruta provincial N° 71; Cochinoca, 2 km al NO sobre ruta provincial N° 71; Cochinoca, 8 km al NO sobre ruta provincial N° 71; Coranzulí; Coranzulí, 10 km al SO sobre ruta provincial N° 74; Coranzulí, 18 km al SO sobre ruta provincial N° 74; Coranzulí, 7 km al SO sobre ruta provincial N° 74; Cruce camino a Rinconada y Oros, 4 km al S, sobre camino a Rinconada; Cruce Coranzulí-Rachayte, 2 km al S, sobre ruta provincial N° 74; Cruce de las rutas provinciales 64 y 65, 5 km al S sobre ruta provincial N° 65; Cruce de las rutas provinciales 70 y 71, 5 km al O sobre ruta provincial N° 70; Cruce de las rutas provinciales 70 y 71, 7 km al O sobre ruta provincial N° 70; Cuesta del Hurón, 4 km al O sobre ruta provincial N° 64; Curques, 3 km al N sobre ruta provincial N° 74 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation); Mina El Porvenir (R. M. Barquez, M. M. Díaz, and P. Martinez, personal observation); Mina El Porvenir, 29 km al NE, camino a Susques (R. M. Barquez, M. M. Díaz, and P. Martinez, personal observation); Mina Pan de Azúcar, 10 km al N, 1 km al N del Río Colquimayo; Mina Pan de Azúcar, 2 km al S sobre ruta provincial N° 71; Mina Pan de Azúcar, 6 km al NO camino a Rinconada; Mina Pan de Azúcar, 8 km al N y 1 km al O; Mina Pirquitas, 10 km al SE sobre ruta provincial N° 74b; Mina Pirquitas, 15 km al SE sobre ruta provincial N° 74b; Mina Pirquitas, 19 km al SE sobre ruta provincial N° 74b; Mina Pirquitas, 22 km al SE sobre ruta provincial N° 74b; Mina Pirquitas, 28 km al SE sobre ruta provincial N° 74b; Mina Pirquitas, 31 km al SE, Sierra de Quichagua, sobre ruta provincial N° 74b, 4200 m; Mina Pirquitas, 4 km al E, sobre ruta provincial N° 70 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation); Miniaio, 2 km al E sobre ruta provincial N° 71 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation); Rinconada, 20 km al SE sobre ruta provincial N° 7; Río Cincel, 2 km al N de Miniaio, sobre ruta provincial N° 71 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation); Salar Cauchari, 31 km al N de Cauchari, sobre ruta provincial N° 70 (R. M. Barquez, M. M. Díaz, and P. Martinez, personal observation); Santa Catalina, 8 km al S por ruta provincial N° 65, 3845 m; Santo Domingo; Susques, 1 km al N sobre ruta provincial N° 74; Susques, 10 km al N sobre ruta provincial N° 74; Tanques; Tanques, 1 km al N sobre ruta provincial N° 74; Tanques, 1 km al S sobre ruta provincial N° 74; Tanques, 2 km al N sobre ruta provincial N° 74 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation); Timón Cruz, 1 km al S camino a Rinconada; Tocomar (R. M. Barquez, M. M. Díaz, and P. Martinez, personal observation); Tres Pozos, 10 km al E, km 15 sobre ruta provincial N° 16 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation); Tres Pozos, 10 km al O del empalme de las rutas 40 y 52 (R. M. Barquez, M. M. Díaz, D. A. Flores, P. Jayat, and P. Martinez, personal observation); Tres Pozos, 5 km al O, sobre ruta provincial N° 16 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation); Tres Pozos, 6 km al E sobre ruta provincial N° 16; Yoscaba, 5 km al NE (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation).

Comments.--All specimens observed in the province were in large domesticated groups. Wild animals were probably extirpated during the Hispanic times (Cabrera, 1961a).

According to Franklin (1982) the llama and the alpaca were domesticated between 4000 and 5000 years ago. Populations of llamas have declined corresponding to a decline in its use as a beast of burden; still today, it is used in the Puna as a source of food and for the value of its wool (Cajal, 1985b).

Lama guanicoe (Müller, 1776)
Guanaco

Camelus guanicoe Müller, 1776. Mit einer ausführlichen Erklärung ausgefertiget. Des ritters Carl von Linné ...Vollständigen Natursystems Supplements-und Register-band über aller sechs Theile oder Classen des Thierreichs. G. N. Raspe, Nurnberg, p.50.

Distribution in Argentina.--In northwestern Argentina to Catamarca and La Rioja provinces (Sierra de Velasco), southward to La Pampa Province, at Sierra de Curamalal and Sierra de la Ventana, in Buenos Aires Province; all Patagonia, including Tierra del Fuego and Navarino Island, but excluding the Andean forests (Cabrera, 1961a).

Specimens Examined (3).--Campo Laguna, 1 (MMD 392); "Jujuy," 2 (MACN 34.585; 39.585).

Additional Records.--Cerro Negro (local residents, personal communication); Ovejería (local residents, personal communication).

Comments.--In northwestern Argentina with few exceptions, like Campo Laguna, the distribution of *L. guanicoe* and *V. vicugna* do not overlap (Pujalte and Reca, 1985).

According to Franklin (1982) the subspecies *L. g. voglii* Krumbiegel, 1944 is distributed north to the 32° latitude, but Cabrera (1961a) considered it a synonym of *L. g. guanicoe*.

Genus *Vicugna*

Vicugna vicugna (Molina, 1782)
Vicugna

Camellus (*sic*) *vicugna* Molina, 1782. Saggio sulla storia naturale del Chili. S. Tommaso d'Aquino, Bologna, p. 313.

Distribution in Argentina.--According to Cabrera (1961a) this species is distributed in northwestern Argentina, S to La Rioja near the border with San Juan Province. Currently, it is found only in northern and western Jujuy and Catamarca, western Salta, La Rioja, and northern San Juan Province (Chébez, 1994).

Specimens Examined (17).--Abra Pampa, 3 (CR 357, 358, 403); Alto de Yoscaba, 10 km al S, camino a Rinconada, 1 (MMD 488); Campo Laguna, 1 (MMD 393); Cerro Guadalupe, 4300 m, 1 (MACN 39.494); Curques, 24 km al N de Susques, sobre ruta provincial N° 74, 4100 m, 1 (MMD 530); "Jujuy," 3 (MACN 38.36, 38.37, 38.38); Tres Cruces, 5 (MACN 45.13, 45.14, 45.15, 45.16, 45.17); Tres Cruces, Mina Aguilar, 1 (MACN 44.15); Sierra de Zenta, 1 (PIDBA 764).

Additional Records.--11-16 km E of Humahuaca, 2 km E of Pucará, on road to Cianzo (R. M. Barquez, personal observation); Abra Pampa, 13 km al O sobre ruta provincial N° 71 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation, 4 specimens); Al E de la Laguna Vilama (G. Gil, personal communication, 18 specimens); Al N de la Laguna Vilama (G. Gil, personal communication, 16 specimens); Al NE de la Laguna Vilama (G. Gil, personal communication, 58 specimens); Alto de Yoscaba, 4320 m (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation); Alto de Yoscaba, 7 km al S, camino a Rinconada (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation); Camino a Santa Catalina, 500 m al N del cruce de las rutas provinciales 64 y 65, sobre ruta provincial N° 65 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation, 7 specimens); Camino a Santa Catalina, 8 km al N del cruce de las rutas provinciales 64 y 65, sobre ruta provincial N° 65 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation); Campo Morro (G. Gil, personal communication, 8 specimens); Cerro Negro (local residents, personal communication); Cienegüillas, 4 km al E sobre ruta provincial N° 5 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 40 specimens, 32 adults, and 8 offspring); Cruce de las rutas provinciales 70 y 71, 5 km al O sobre ruta provincial N° 70 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 10 specimens, 8 adults, and 2 offspring); Cruce de las rutas provinciales 70 y 71, 7 km al O sobre ruta provincial N° 70 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 3 specimens); Empalme rutas 40 y 52 (R. M. Barquez, M. M. Díaz, D. A. Flores, P. Jayat, and P. Martinez, personal observation; 2 specimens, photos); Entre el empalme con ruta 40 y Quera (G. Gil, personal communication, 12 specimens); Entre el SE de la Laguna Vilama y Laguna Palar (G. Gil, personal communication, 1 specimen); Entre la casa del Guardaparque y Lagunillas (G. Gil, personal communication, 10 specimens); Entre Laguna Chica y Culi Culi (G. Gil, personal communication, 34 specimens); Entre Mina Campanario y Ojo Catal (G. Gil, personal communication, 29 specimens); Entre Pozo Colorado y el cruce con ruta 52 (G. Gil, personal communication, 1 specimen); Entre Santo Domingo y la casa del Guardaparque (G. Gil, personal communication, 6 specimens); Laguna de Leandro, 4455 m (R. M. Barquez, personal observation, 17 specimens in groups of 4-6-7, 2 juveniles, photos); Laguna de Pozuelos, acceso sur (G. Gil, personal communication, 20 specimens); Laguna Isla Chica, 3,5 km antes (G. Gil, personal communication, 9 specimens); Mina El Porvenir, 23 km al N, cerca del camino al Paso de Jama (R. M. Barquez, M. M. Díaz, and P. Martinez, personal observation; 13 specimens, photos); Mina Pan de Azúcar, 11 km al N, 2 km al N del Río Colquimayo (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 3 specimens); Mina Pan de Azúcar, 2 km al NE sobre ruta provincial N° 71 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation); Mina Pan de Azúcar, 8 km al N y 1 km al O (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 5 specimens); Mina Pan de Azúcar, 8 km al N y 3 km al O (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 24 specimens); Mina Pan de Azúcar, 9 km al N (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 9 specimens, 8 adults, and 1 offspring); Miniaio, 2 km al E sobre ruta provincial N° 71 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 1 specimen); Miniaio, 5 km al E sobre ruta provincial N° 71 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 6 specimens); Orosmayo, 11 km al NE sobre ruta provincial N° 70 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 1 specimen); Orosmayo, 9 km al NE sobre ruta provincial N° 70 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 4 specimens); Ovejería (local residents, personal communication); Reserva Provincial Olaroz-Cauchari, 35 km al O de Susques, sobre ruta provincial N° 70 (R. M. Barquez, M. M. Díaz, and P. Martinez, personal observation); Rinconada, 20 km al SE sobre ruta provincial N° 7 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 3 specimens); Rinconada, 22 km al SE sobre ruta provincial N° 7 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 5 specimens); Rinconada, 23 km al SE sobre ruta provincial N° 7 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 5 specimens, 4 adults, and 1 offspring); Rinconada, 25 km al SE sobre ruta provincial N° 7 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 12 specimens, 11 adults, and 1 offspring); Rinconada, 28 km al SE sobre ruta provincial N° 7 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 10 specimens); Rinconada, 30 km al SE sobre ruta provincial N° 7 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 4 specimens); Rinconada, 3 km al E sobre ruta provincial N° 7 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 6 specimens); Rinconada, 32 km al SE sobre ruta provincial N° 7 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 2 specimens); Salar Cauchari, 13 km al N de Cauchari, sobre ruta provincial N° 70 (R. M. Barquez, M. M. Díaz, and P. Martinez, personal observation); Salinas Grandes, 15 km al E de Tres Pozos sobre ruta provincial N° 16 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 5 specimens); Salinas Grandes, 2 km al E de Tres Pozos sobre ruta provincial N° 52 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation); Salinas

Grandes, sobre ruta 52 (R. M. Barquez, M. M. Díaz, D. A. Flores, P. Jayat, and P. Martinez, personal observation; 6 specimens, photos); Santa Catalina, 8 km al S por ruta provincial N° 65 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 3 specimens); Santo Domingo (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 1 specimen); Sobre ruta nacional 52, 10 km al O de Ronqui Angosto (G. Gil, personal communication, 9 specimens); Susques, 21 km al O, sobre ruta provincial N° 16 (R. M. Barquez, M. M. Díaz, and P. Martinez, personal observation); Susques, 26 km al O, sobre ruta provincial N° 16 (R. M. Barquez, M. M. Díaz, and P. Martinez, personal observation; 1 specimen, photo); Susques, 27 km al O, sobre ruta provincial N° 16 (R. M. Barquez, M. M. Díaz, and P. Martinez, personal observation; 4 specimens); Susques, 28 km al O, sobre ruta provincial N° 16 (R. M. Barquez, M. M. Díaz, and P. Martinez, personal observation; 4 specimens); Susques, 30 km al O, sobre ruta provincial N° 16 (R. M. Barquez, M. M. Díaz, and P. Martinez, personal observation; 5 specimens); Tafna, 7 km al O sobre ruta provincial N° 5 (R. M. Barquez, M. M. Díaz, D.A. Flores, and P. Jayat, personal observation; 8 specimens, 7 adults, and 1 cría; 37 specimens, 36 adults, and 1 offspring); Tanques, 1 km al S sobre ruta provincial N° 74 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 2 groups of 12 specimens, 20 adults, and 4 offspring); Tanques, 6 km al N sobre ruta provincial N° 74 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation; 1 specimen); Tanques, 8 km al N, sobre ruta provincial N° 74 (R. M. Barquez, M. M. Díaz, D. A. Flores, and P. Jayat, personal observation, 1 specimen); Tres Pozos, 10 km al O del empalme de las rutas 40, and 52 (R. M. Barquez, M. M. Díaz, D. A. Flores, P. Jayat, and P. Martinez, personal observation; 5 adults, and 1 offspring); Vega entre Laguna Caití y Laguna Isla Grande (G. Gil, personal communication, 5 specimens).

Comments.--The vicuña have suffered largely as a consequences of human predation due to the great value of their wool, but in the early 1970s Argentina applied regulations to protect this species (Cajal, 1985b). In Jujuy, during the course of the present study many specimens, in small groups, were observed along routes in the Puna.

Family Cervidae
Subfamily Odocoileinae

Genus *Hippocamelus*

Hippocamelus antisensis (d'Orbigny, 1834)
Peruvian Guemal

Cervus antisensis d'Orbigny, 1834. Annales Museum d'Histoire Naturelle, Paris, 3:91.

Distribution in Argentina.--Northwestern Argentina, from Jujuy Province to the Sierras de Catamarca and Serranías de Famatina (in La Rioja Province), where its southern limit is located; it is found between 2500 and 5000 m (Cabrera, 1961a; Olrog and Lucero, 1981). Within Jujuy, it has been reported in the departments of Tilcara, Valle Grande, Capital, and Ledesma (Chébez, 1994).

Specimens Examined (4).--"Jujuy," 1 (MACN 26.5); Mountains W of Yala, 2 (FMNH, 29380, 29381); Ruinas de Tilcara, 1 (AMNH 207049).

Additional Records.--9 km NW Bárcena (local residents, personal communication); Alto Calilegua (Chébez, 1994); Cerro Hermoso (cercanías), 2800 m (Heinonen and Bosso, 1994); "Jujuy" (Matschie, 1894); Lagunas de Yala (local residents, personal communication); Miyuyoc, 3750 m (local residents, personal communication); Parque Nacional Calilegua; Parque Provincial de Yala; San Francisco, Valle Grande (Chébez 1994).

Comments.--According to Massoia et al. (1992b), citing unpublished information from S. Heinonen, this species is found at Cerro Hermoso and Cerro Amarillo, but the last locality was not cited by Heinonen and Bosso (1994).

This species is found in the rocky slopes of the Prepuna and in the Yungas, above the alder forests (Chébez, 1994); most of the records for Jujuy correspond to the Yungas. Matschie (1894), cited this species for the Puna of Jujuy, and we are including a locality (Miyuyoc) for these phytogeographic region. In Jujuy, it is used in local rituals, where 1 or 2 individuals are hunted on Good Friday, and offered in sacrifice (Chébez, 1994).

Genus *Mazama*

Mazama americana (Erxleben, 1777)
Red Brocket Deer

Morchus americanus Erxleben, 1777. Systema regni animalis per classes, ordines, genera, species, varietates, cum synonymia et historia animalium. Classis. I. Mammalia. Weygandianis, Lipsiae, 1:324.

Distribution in Argentina.--Northern Argentina, in Corrientes, Chaco, Formosa, Jujuy, Misiones, Salta, and Tucumán Provinces (Merino, in press).

Specimens Examined (1).--Yuto, 1 (AMNH 185207).

Additional Records.--Abra de Cañas, 1700 m (Heinonen and Bosso, 1994); Camino a Yuto, cerca del Río San Francisco (R. M. Barquez, personal observation); Cercanías de El Simbolar (local residents, personal communication); "Jujuy" (Matschie, 1894); Mesada de las Colmenas, 1150 m (Heinonen and Bosso, 1994); Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20 (local residents, personal communication); Santa Rita, app 5 km al NO, sobre ruta provincial N° 1 (D. A. Flores, personal communication).

Comments.--Brocket deer live on the slopes of the humid forest, although they also may be found in zones of dense vegetation and agriculture (Mares et al., 1989); in Jujuy, they have been observed as frequently in Yungas as in Chaco. The specimen examined from Yuto corresponds to an offspring collected in May.

Mazama gouazoupira (G. Fischer, 1814)
Gray Brocket Deer

Cervus gouazoupira G. Fischer, 1814. Zoognosia tabulis synopticis illustrata, in usum praelectionum Academie imperialis medico-chirugicae mosquensis edita…. N. S. Vsevolozsky, Mosquae, 3:465, 1814.

Distribution in Argentina.--Northern Argentina southward to San Luis and Santa Fe, and through the east to Entre Ríos and Correientes Provinces (Merino, in press).

Specimens Examined (9).--"Jujuy," 8 (MACN 26.111, 32.137, 32.141, 32.264, 34.582, 34.589, 35.34, 36.32); Rumi Cruz, 1 (MACN 32.87).

Additional Records.--Aguas Negras, 600 m; Caimancito, 550 m (Heinonen and Bosso, 1994); Camino al Río San Francisco, 12 km al O de ruta provincial N° 1, entre el Sauzalito and El Palmar (M. M. Díaz, personal observation); Catamontaña; El Cuarteadero, km 1177 sobre ruta nacional N° 34 (J. P. Jayat, personal communication); E of El Palmar, Sierra de Santa Bárbara (R. M. Barquez, personal observation); El Simbolar, 25 km al SO de Palma Sola, 1000 m (R. M. Barquez, personal communication); "Jujuy" (Matschie, 1894); Río Tiraxi, app 5 km al S de Tiraxi, sobre ruta provincial N° 29 (P. J. Martinez, personal communication); Yuto (local residents, personal communication).

Comments.--This species is not confined to the forest, and it was reported in the dry zone of the Chaco (Redford and Eisenberg, 1992). Is mainly nocturnal or crepuscular, although Husson (1978) mentioned that in Surinam it is diurnal; in Jujuy, diurnal activity was observed. The observations from Camino al Río San Francisco in December correspond to a female with a young. One juvenile collected in April and other collected in March are deposited at the MACN, but there is no information about the specific locality, except that they are from "Jujuy." The locality Rumi Cruz is located in the Puna. This record needs confirmation, since this species is not known to inhabit in that region.

Order Rodentia
Suborder Sciuromorpha
Family Sciuridae
Subfamily Sciurinae

Genus *Sciurus*

Sciurus ignitus (Gray, 1867)
Bolivian Squirrel

Macroxus ignitus Gray, 1867. Annals and Magazine of Natural History, ser. 3, 20:429.

Distribution in Argentina.--Mountains forests of the extreme NW Argentina (Yepes, 1935b, 1944; Cabrera, 1961a) in Salta and Jujuy provinces.

Specimens Examined (27).--Calilegua, 3 (1 CML 1914, 2 MACN 26.79, 26.78); Camino de

San Francisco a El Duraznillo, 1 (CML 1753); Chijra, 3 (MACN 34.717, 35.300, 35.301); El Jordán, camino a Calilegua, 1700 m, 1 (CML 1684); Higuerilla, 2000 m, 7 (BMNH 21.11.1.4, 21.11.1.5, 21.11.1.6, 21.11.1.7, 21.11.1.8 *Sciurus argentinius* holotype, 21.11.1.9, 21.11.1.10, 21.11.1.106); "Jujuy," 1 (MACN 34.598); San Francisco, 5 (CML 1124, 1125, 1126, 1127, 1128); San Francisco, 1500 m, 1 (CML 1752); San Francisco, 60 km de Ledesma, camino a Valle Grande, 1800 m, 4 (CML 60, 120, 137, 151); Valle Grande, 1 (CML 63).

Additional Records.--Abra de Cañas, 1700 m (Heinonen and Bosso, 1994); Abra de Cañas, El Monolito (R. M. Barquez, personal observation); Aguas Blancas, 14 km al E de Santa Clara, 900 m (local residents, personal communication); Arroyo Yuto, 13 km al SO de Yuto (D. A. Flores, personal communication); Capillas, 25 km N von Jujuy (Matschie, 1894); Duraznillar, 2500 m; Mesada de las Colmenas, 1150 m (Heinonen and Bosso, 1994); Río Blanco (Yepes, 1944); Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20 (local residents, personal communication); Tilquiza (Yepes, 1944).

Comments.--All records from Jujuy correspond to the Yungas, up to 2000 m. According to Olrog (1979), and Ojeda and Mares (1989), this species has been observed up to 2600 m in alder forests. Generally considered a diurnal species (Mares et al., 1989), 1 specimen was observed during the night at Arroyo Yuto (D. A. Flores, personal communication). According to information written by C. Olrog on the original labels of some specimens from San Francisco, they were captured on a walnut tree, where they had their nests. Juveniles were captured in October and November; in these specimens the M2 was erupting and the M3 was not erupted; in some specimens both molars were not erupted.

Suborder Myomorpha
Family Cricetidae
Subfamily Sigmodontinae
"Abrothricines"

Only 2 "abrothricines" occur in Jujuy Province. Both electrophoretic analysis of allozymes (Patton et al., 1989) and study of mitochondrial DNA (Smith and Patton, 1991) supported the allocation of "*Akodon andinus*" and "*A. jelskii*" to *Chroeomys*. Subsequently, Smith and Patton (1993, 1999) found *Abrothrix* to be paraphyletic with respect to *Chroeomys jelskii*. For this reason and for the low degree of morphological variation among the species of *Chroeomys*, and those traditionally considered *Abrothrix*, D'Elía (2003) recommended placing all forms within *Abrothrix*. Pending resolution of this ongoing debate, we accept allocation of *andinus* to *Abrothrix* but we leave *jelskii* in *Chroeomys*.

Genus *Abrothrix*

Abrothrix andinus (Philippi, 1858)
Andean Altiplano Mouse

Mus andinus Philippi, 1858. Archiv für Naturgeschichte, 23(1):77.

Distribution in Argentina.--Arid and semiarid mountains of the north, in Jujuy and Salta provinces extending E to Aconquija, between Catamarca and Tucumán region, to NE Mendoza (Cabrera, 1961a; Mares et al., 1981, 1997; Díaz, 1999, Díaz et al., 2000).

Specimens Examined (6).--Cerro de Lagunita al Este de Maimará, 4500 m, 1 (BMNH 12.12.12.12 *Akodon jucundus* holotype); La Laguna 4500 m, Sierra de Zenta, E de Maimará, 1 (MACN 27.111 as *Akodon jucundus*; see comments under *Localities and maps*); Sierra de Zenta, 4500 m, 2 (BMNH 21.11.1.38, 21.11.1.39 as *A. jucundus*; See comments under *Localities and maps*); Rinconada, 6 km al N, camino a Timón Cruz, 4286 m, 1 (MMD 483); Tres Cruces, 3700 m, 1 (FMNH 35244).

Comments.--Osgood (1943) and Cabrera (1961a) considered this species to be a synonym of *Akodon jucundus*. Thomas (1913, 1921c), Yepes (1935b), and Gyldenstolpe (1932) treated *A. jucundus* as a distinct species, whereas Honacki et al. (1982) and Wilson and Reeder (1993) did not mentioned *Akodon jucundus*. At Rinconada males with abdominal testes and molting, were recorded in March; the specimen from Tres Cruces was a young collected in April.

Genus *Chroeomys*

Chroeomys jelskii (Thomas, 1894)
Jelski's Altiplano Mouse

Akodon jelskii Thomas, 1894. Annals and Magazine of Natural History, ser. 8, 18:340.

Distribution in Argentina.--Although reported from Salta and Jujuy provinces (Yepes, 1935b; Cabrera, 1961a; Gardner and Patton, 1976; Reig, 1978) this species has been is confirmed only for the latter province (Díaz et al., 2000; Díaz and Barquez, 2002).

Specimens Examined (19).--Cerro de la Lagunita al Este de Maimará, 4500 m, 3 (BMNH 12.12.12.17, 12.12.12.19, *Akodon bacchante sodalis* holotype, 12.12.12.20); Cerro de Lagunita, 4500 m, 1 (BMNH 12.12.12.18); La Laguna 4500 m, Sierra de Zenta, E de Maimará, 2 (MACN 27.75, 27.76; see comments under *Localities and maps*); Sierra de Zenta, 2 (CML 94, 609; see comments under *Localities and maps*); Sierra de Zenta, 4500 m, 8 (3 MACN 31.116, 31.117, 31.118; 5 BMNH 21.11.1.55, 21.11.1.56, 21.11.1.57, 21.11.1.58, 21.11.1.59; see comments under *Localities and maps*); Sierra de Zenta, 4500 m, E de Maimará, 3 (MACN 27.73, 27.74, 27.77; see comments under *Localities and maps*).

Comments.--The type locality for *C. j. sodalis*, "Cerro de Lagunita, al Este de Maimará, 4500 m, Jujuy, Argentina," was erroneously reported by Thomas (1913). For the exact location of Sierras de Zenta, see comments under *Localities and maps*. This species is difficult to capture and records are scarce in Argentina. It is known from Peru and Bolivia (Anderson, 1997; Eisenberg and Redford, 1999) but from only a single locality in Jujuy Province. It is not strictly nocturnal, and feeds in the first hours in the morning (Thomas, 1913). According to Thomas (1913), E. Budin said that he caught this specimen using meat as bait and that this species frequently feed on seeds.

Specimens from Sierra de Tilcara (Sierra de Zenta on the specimen tags) were subadults captured in February and May.

Tribe Akodontini

The tribe Akodontini comprises 13 extant genera (D'Elía, 2003) widely distributed in the temperate and tropical areas, and subtropical lowlands. According to D'Elía (2003) this tribe is well supported and composed of 5 main clades (the *Akodon*, the *Bibimys*, the *Blarinomys*, the *Oxymycterus*, and the *Scapteromys* Divisions).

Genus *Akodon*

Northwestern Argentina, and particularly Jujuy Province, has a number of species of this genus. The "*varius*" group (Myers, 1989) includes *A. toba* and *A. simulator*. The latter was represented by 2 subspecies, *A. S. simulator* and *A. S. tartareus*; we found both of these in sympatry, however, and their characters lead us to treat them as different species, as originally described. We also report on 4 species from the "*boliviensis*" group (Myers et al., 1990), including *A. spegazzinii* (historically included in *A. alterus*, but here considered as a valid species), *A. puer*, and *A. caenosus* (considered as a subspecies of *puer*). *A. puer* is considered a subspecies of *lutescens* following Anderson (1997). *Akodon tucumanensis* was treated as a subspecies of *spegazzinii* by Myers et al. (1990); however the range given for *A. spegazzinii* (their Fig. 11) was entirely S of Jujuy Province, although their gazetteer included 1 specimen of *A. S. tucumanensis* from Santa Bárbara. We have reidentified this specimen as *A. budini* (this manuscript), however, and so do not consider *A. S. tucumanensis* to occur in Jujuy. Finally, the "*fumeus*" group (Myers and Patton, 1989) is represented in Jujuy by *A. fumeus*, only recently added to the fauna of Argentina (Díaz and Barquez, 1999). *A. albiventer*, *A. budini*, and *A. sylvanus* cannot be confused with other species. Thomas (1920a) indicated the presence of an *Akodon*, comparable to *A. dolores*, from Villa Carolina, which according to Myers (1989) might correspond to *A. simulator* or *A. toba*.

Akodon albiventer Thomas, 1897
White-bellied Grass Mouse

Akodon albiventer Thomas, 1897. Annals and Magazine of Natural History, ser. 6, 20:217.

Distribution in Argentina.--Mountains of the extreme NW Argentina, in Jujuy and Salta provinces (Cabrera, 1961a).

Specimens Examined (191).--11 km al E de Humahuaca, 2 km al E de Pucará sobre camino a Cianzo, 6 (CML 3287, 3288, 3289, 3290, 3291, 3292); 11 km al E de Humahuaca, 2 km al E de Pucará sobre camino a Cianzo, 11,500 ft, 3 (SNOMNH 23619, 23620, 23621); "Jujuy," 5 (MACN 17440, 36.432, 36.453, 36.455, 36.458); Abra Pampa, 20 (CML 1253, 1260, 1267, 1268, 1270, 1271, 1275, 2491, 2492, 2493, 2494, 2495, 2496, 2497, 2498, 2499, 2500, 2501, 2502, 2503); Abra Pampa, 3500 m, 21 (1 FMNH 29161; 1 MLP 11-II-36-7; 19 BMNH 19.8.1.35, 19.8.1.36, 19.8.1.37, 19.8.1.38, 19.8.1.39, 19.8.1.40, 19.8.1.41, 19.8.1.42, 19.8.1.43, 19.8.1.44, 19.8.1.45, 19.8.1.46, 19.8.1.47, 19.8.1.48, 19.8.1.49, 19.8.1.50, 19.8.1.51, 19.8.1.52, 19.8.1.53); Alfarcito, 2600 m, 2 (BMNH 21.11.1.49, 21.11.1.50); Campo Laguna, 2 (MMD 387, 388); Casa Colorada, app 2 km al N de Alfarcito, 3034 m, 11 (9 MMD 366, 368, 369, 370, 371, 372, 377, 378, 383; 2 released); Casabindo, 4000 m, 5

(BMNH 19.8.2.21, 19.8.2.22, 19.8.2.23, 19.8.2.24, 19.8.2.25); Cerro de la Lagunita al Este de Maimará, 4500 m, 2 (BMNH 12.12.12.14, 12.12.12.15); Cerro de la Lagunita, 4500 m, 1 (BMNH 12.12.12.16); Cuesta del Hurón, 29 km al O de Cieneguillas, sobre ruta provincial N° 64, 3835 m, 9 (MMD 442, 445, 446, 447, 453, 454, 460, 464, 467); Curques, 24 km al N de Susques, sobre ruta provincial N° 74, 4100 m, 2 (MMD 282, 287); El Toro, 55 km O de Susques, 3 (IADIZA 3336, 3346, 1 not numbered); La Ciénaga, 3 (CML 1252, 1261, 1262); La Ciénaga, Abra Pampa, 3 (CML 1269, 1272, 1284); La Ciénaga, Tres Cruces, 1 (CML 1263); La Laguna 4500 m, Sierra de Zenta, E de Maimará, 4 (MACN 27.102, 27.103, 27.104, 27.106; see comments under *Localities and maps*); La Quiaca, 17 km al O y 3 km al S, sobre ruta provincial N° 5, 3711 m, 7 (MMD 422, 423, 427, 430, 431, 432, 437); Laguna de Pozuelos, 24 (5 IADIZA 3332, , 3334, 3335, 3337, 3338; 19 MACN 19390, 19394, 19396, 19397, 19398, 19403, 19404, 19405, 19406, 19407, 20288, 20290, 20291, 20292, 20293, 20294, 20296, 20297, 20298); Laguna, Durazno, 4500 m, 1 (BMNH 12.12.12.13); Lagunillas, 1 (MACN 19300); Mina Pan de Azúcar, 8 km al N y 5 km al O, camino a Herrana, 3820 m, 5 (MMD 493, 496, 498, 501, 502); Mina Pirquitas, 31 km al SE, Sierra de Quichagua, sobre ruta provincial N° 74 b, 4200 m, 4 (MMD 515, 520, 521, 526); Miyuyoc, 3750 m, 2 (MMD 389, 391); Pirquita, 10 km antes de la mina, 1 (IADIZA 3339); Pirquita, 20 km NO de Coranzulí, 2 (IADIZA 3327, 3330); Reserva Provincial Olaroz-Cauchari, 30 km al O de Susques, sobre ruta provincial N° 70, 1 (MMD 314); Rinconada, 6 km al N, camino a Timón Cruz, 4286 m, 7 (MMD 474, 476, 477, 479, 480, 481, 482); Sierra de Zenta, 3 (BMNH 21.11.1.51, 21.11.1.52, 21.11.1.54; see comments under *Localities and maps*); Sierra de Zenta, 4500 m, 5 (1 BMNH 21.11.1.53; 1 FMNH 41286, 3 MACN 31.109, 31.113, 47.35; see comments under *Localities and maps*); Sierra de Zenta, ruta provincial N° 13, entre Chaupe Rodeo e Iruya, 12 km al N de Chaupe Rodeo, 3 (MMD 362, 363, 365); Sobre ruta 40, 29 km al N del empalme con ruta 52, 4 (MMD 270, 271, 275, 276); Tres Cruces, 4000 m, 1 (CML 108); Yavi, 2 (CML 4597, 4598); Yavi, 3640 m, 1 (CML 2667); Yavi, 6.8 km al SE de Suripujies, sobre ruta provincial N° 5, 1 (ARG 4732); Yavi Chico, 13 (MACN 36.441, 36.442, 36.448, 36.449, 36.451, 36.454, 36.456, 36.459, 36.461, 36.462, 36.466, 36.45, 36.46).

Additional Records.--Cerrito Leones, near the mine of Pan de Azúcar, Man and Biophere Reserve of Laguna de Pozuelos (Ortiz et al., 2000); Humahuaca, 16 km al E, sobre camino a Cianzio (SNOMNH, J. K. Braun, personal communication); Laguna de Pozuelos, 3700 m (G. Gil, personal communication); Lagunita (Liascovich, 1991).

Comments.--In our experience, *A. albiventer* appear to be less common and more diurnal where populations of *Eligmodontia* are high. This is a typical species of high altitudes, and all records correspond to the Andean, Puna, and Prepuna regions; in some places, they are found together with *Octodontomys gliroides*. For all the specimens examined at the BMNH, FMNH, and MACN, when Sierra de Zenta is indicated, the correct locality is Sierra de Tilcara (see comments under *Localities and maps*).

The specimen from Laguna, Durazno, 4500 m, was cited by Thomas (1913) as Laguna, Durazno, Maimará, 4500 m. At the locality Rinconada, 6 km al N, we observed a specimen feeding on grass. Young have been collected in January, March, April, May, and June, and a juvenile in March. Males with abdominal testes were captured in February, March, May, June, and November, males with scrotal testes in February, March, and December; females with closed vaginas were collected in February, March, and June, and females with open vaginas in February, March, and December. We have captured females that were both lactating and pregnant in February (1 female with 3 fetuses and another with 6), in March (1 females with 3 fetuses), and December (1 female with 3 fetuses and another with 4). Molting specimens were collected in February, March, June, and December.

Akodon alterus Thomas, 1919
Bunchgrass Grass Mouse

Akodon alterus Thomas, 1919. Annals and Magazine of Natural History, ser. 9, 3:496.

Distribution in Argentina.--Northwestern Argentina in Jujuy, Salta, Tucumán, and Catamarca provinces (Yepes, 1935b).

Specimens Examined (1).--Miyuyoc, 3750 m, 1 (MMD 395).

Comments.--Cabrera (1961a) considered this to be a synonym of *A. boliviensis tucumanensis*; Myers et al. (1990) noted that the pelage color *A. alterus* is intermediate between *A. tucumanensis* and *A. spegazzinii*, and the skull is very similar to that of *A. spegazzinii*. Musser and Carleton (1993) treated *A. alterus* and *A. tucumanensis* as synonyms of *A. spegazzinii*. Other authors have treated *A. alterus* as a valid species (Barquez et al., 1991; Blaustein et al., 1992; Mares et al., 1997). Blaustein et al. (1992) noted that although allozymic and cytogenetic data suggested a close relationship between *A. tucumanensis* and *A. alterus*, they are morphological different and exploit different habitats.

This species is typical of grasslands, and has been reported from the Yungas as well as in the Prepuna and Puna. The specimen from Miyuyoc is the first documented record of the species for the province of Jujuy; the area corresponds to the Puna. This individual was a male captured in June near a stone corral.

Akodon budini (Thomas, 1918)
Budin's Grass Mouse

Hypsimys budini Thomas, 1918. Annals and Magazine of Natural History, ser. 9, 1:190.

Distribution in Argentina.--Mountains forests of NW of Argentina, in Jujuy, Tucumán, and Salta provinces (Yepes, 1935b; Cabrera, 1961a; Myers et al., 1990; Redford and Eisenberg, 1992). However its presence in Salta and Tucumán was not confirmed. According to Olrog (1979), in Jujuy this is a common species above 2500 m, although it is found in many localities below 2500 m.

Specimens Examined (84).--Abra de Cañas, 18 (MACN 19483, 19484, 19492, 19493, 19494, 19495, 19496, 19498, 19499, 19500, 19501, 19502, 19503, 19506, 19510, 19591, 20283, 20285); Arroyo La Horqueta, 3 km SE Laguna Yala, 2100 m, 1 (MMD 180); Caimancito, 600 m, 1 (MACN 20282); Cerro El Morado, 11 km al NO de San Antonio, sobre Río El Morado, 6 (MMD 115, 122, 123, 124, 141, 144); Cerro Hermoso, 3 (MACN 19475, 19480, 20284); El Simbolar, 25 km al SO de Palma Sola, 5 (CML 2025, 2030, 2102, 2106, 2109); Higuerilla, 2000 m, 12 (11 BMNH 21.11.1.61, 21.11.1.62, 21.11.1.63, 21.11.1.64, 21.11.1.65, 21.11.1.66 *Akodon deceptor* holotype, 21.11.1.67, 21.11.1.68, 21.11.1.69, 21.11.1.70, 21.11.1.71; 1

FMNH 46121); León, 1500 m, 6 (BMNH 18.1.1.41, 18.1.1.42, 18.1.1.43, 18.1.1.44 *Akodon budini* holotype, 18.1.1.45, 18.1.1.46); Mesada de las Colmenas, 9 (MACN 19507, 19508, 19509, 19512, 19513, 19514, 19515, 19516, 20286); Mountains W of Yala, 3 (FMNH 23351, 23357, 23360); On highway 29 (E off of hwy 9), 10 km W of Tiraxi, 5800 ft., 2 (1 ARG 2635; 1 SNOMNH 23616); Palma Sola, 1 (AMNH 183308); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20, 14 (5 ARG 4220, 4233, 4235, 4240, 4247, 9 MMD 341, 343, 349, 355, 358, 359, 412, 416, 417); Río Tiraxi, app 5 km al S de Tiraxi, sobre ruta provincial N° 29, 2 (MMD 154, 196); Santa Bárbara, Santa Bárbara, 1 (AMNH 179977).

Additional Records.--Duraznillar, 2500 m (Heinonen and Bosso, 1994); León; San Pablo (Liascovich, 1991).

Comments.--This species was described by Thomas (1918) from Jujuy, and included in the genus *Hypsimys*. Later, Thomas (1921c) described *H. deceptor*, considered by both Honacki et al. (1982) and Musser and Carleton (1993) to be a synonym of *A. budini*. Thomas (1921c) mentioned size as the only difference between these taxa, but the holotype of *budini* examined at the BMNH is a young individual. Although Yepes (1935b) considered both forms to be distinct species, Cabrera (1961a) noted that it would be unusual for 2 forms so closely related to coexist in the same region. Our examination of the holotypes supports the conjecture that they differ only slightly in size and coloration, and we consider the 2 taxa to be synonymous.

According to notes written on the specimen tag of the holotype, *A. budini* lives in very humid forests at the base of trees; a specimen from León was captured among roots of a pine tree.

All localities for this species correspond to the Yungas. We have registered young individuals in February, June, and July, subadults in June, males with abdominal testes in June, July, August, and September, males with scrotal testes in February and July, females with closed vaginas and females with open vaginas in June and August. Also, specimens molting were collected in June. A specimen at the AMNH (179977) cited by Myers et al. (1990) as *A. spegazzinii tucumanensis* it was reidentified by us and is here treated as *A. budini*.

Akodon caenosus Thomas, 1918
Unicolored Grass Mouse

Akodon puer caenosus Thomas, 1918. Annals and Magazine of Natural History, ser. , 9, 1:189-190.

Distribution in Argentina.--Mountains forest of NW Argentina, in Jujuy, Tucumán, Catamarca (Cabrera, 1961a; Barquez et al., 1980; Myers et al., 1990), and Salta (Díaz et al., 2000).

Specimens Examined (46).--Along Yala Laguna Rd, ? km W jct it and Hwy 9, 5 (CM 43050, 43053, 43054, 43056, 43406); Arroyo La Horqueta, 3 km SE Laguna Yala, 2100 m, 2 (MMD 179, 183); Arroyo La Horqueta, 6 km SE Laguna Yala, 2100 m, 1 (MMD 185); Cerro El Morado, 11 km al NO de San Antonio, sobre Río El Morado, 9 (1 JPJ 2; 7 MMD 20, 21, 23, 121, 129, 138, 143; 1 released); El Sunchal, Sierra de Santa Bárbara, 1400 m, 1 (FMNH 29126); Higuerilla, 2000 m, 8 (BMNH 21.11.1.40, 21.11.1.42, 21.11.1.43, 21.11.1.44, 21.11.1.45, 21.11.1.46, 21.11.1.47, 21.11.1.48); Jujuy, 1258 m, 9 (BMNH 20.1.7.104, 20.1.7.105, 20.1.7.106, 20.1.7.107, 20.1.7.108, 20.1.7.109, 20.1.7.110, 20.1.7.111, 20.1.7.112); León, 1500 m, 2 (BMNH 18.1.1.38 *Akodon caenosus* holotype, 18.1.1.39, 18.1.1.40); Mountains W of Yala, 1 (FMNH 23384); Sunchal, Sierra de Santa Bárbara, 1200 m, 2 (1 BMNH 21.1.1.91; 1 MACN 20269); Sunchal, Sierra de Santa Bárbara, 1300 m, 1 (BMNH 21.1.1.96); Sunchal, Sierra de Santa Bárbara, 1500 m, 3 (BMNH 21.1.1.100, 21.1.1.95, 66. 1840); Sunchal, Sierra de Santa Bárbara, 1600 m, 1 (BMNH 21.1.1.98).

Additional Records.--Ruta a Las Lagunas de Yala, al O de la unión con ruta 9 (Barquez et al., 1980); León (Liascovich, 1991).

Comments.--Myers et al. (1990) treated *A. caenosus* as a subspecies of *A. puer*, while other authors (Cabrera, 1961a; Gyldenstolpe, 1932; Barquez et al., 1980, 1991; Honacki et al., 1982; Mares et al., 1997) considered it a valid species.

Females with closed vaginas were captured in July, males with abdominal testes in June, and males with scrotal testes in December and January. Specimens from Cerro El Morado were molting in June.

Akodon fumeus Thomas, 1902
Smoky Grass Mouse

Akodon fumeus Thomas, 1902. Annals and Magazine of Natural History, ser. 7, 9:137-138.

Distribution in Argentina.--In Bolivia this species is found near Cuyambuyo (departamento de Tarija), along the border with Argentina (Anderson, 1997); we reported this species for Argentina, including records from Jujuy Province (Díaz and Barquez, 1999).

Specimens Examined (39).--A 2.5 km del Río Santa Rita, sobre camino al Fuerte, 1 (CML 2039); Abra de Cañas, approx 30 km NW of Calilegua on Valle Grande Rd, 1700 m, 4 (CM 43134, 43139, 43146, 43150); Abra de Cañas, El Monolito, 1700 m, 18 (CML 1775, 1776, 1789, 1790, 1791, 1792, 1793, 1794, 1796, 1797, 1798, 1799, 1800, 1801, 1802, 1806, 1807, 1808); Cerro Calilegua, El Duraznillo, 2600 m, 15 (CML 1734, 1735, 1738, 1739, 1740, 1741, 1743, 1744, 1745, 1746, 1747, 1748, 1749, 1750, 1751); On Valle Grande Rd, 2 km de Abra de Cañas, 1 (CM 95446).

Comments.--This species has only recently been recorded for Argentina (Díaz and Barquez, 1999), and previously was known only from Bolivia and Peru (Myers and Patton, 1989). Localities of all specimens examined correspond to the Yungas. The specimens from Abra de Cañas, approx. 30 km NW of Calilegua on Valle Grande Rd, were cited by Myers and Patton (1989) as *Akodon budini*.

Akodon lutescens Allen, 1901
Altiplano Grass Mouse

Akodon lutescens Allen, 1901. Bulletin of the American Museum of Natural History,

14:46.

Distribution in Argentina.--This species has been reported only for Bolivia (Myers et al., 1990; Anderson, 1997); herein this species is added to the fauna of Argentina, with records from Jujuy Province.

Specimens Examined (24).--9 km NW Bárcena, 1 (ARG 4619); Abra de Santa Laura, límite entre Salta y Jujuy, sobre ruta nacional N° 9, 1397 m, 1 (PIDBA 591); Cerro Calilegua, El Duraznillo, 2600 m, 1 (CML 1734); Río Blanco, 9 km SW San Antonio, 1495 m, 21 (3 PIDBA 617, 618, 621; 18 ARG 4267, 4268, 4269, 4270, 4277, 4278, 4279, 4281, 4282, 4285, 4287, 4298, 4300, 4301, 4304, 4305, 4306, 4313).

Comments.--The subspecies from Jujuy is *A. l. puer*. Myers et al. (1990) considered *lutescens* to be a subspecies of *puer*; however, the name *lutescens* has priority as it was described by Allen in 1901 and *puer* was not described until 1902 (Thomas, 1902); thus, Anderson (1997) recognized the latter as a subspecies of *lutescens*.

Records in Jujuy correspond to the Yungas (Alder forests, grasslands, and Myrtaceae and laurel cloud forests) below the known altitude for this species. Females with closed vaginas were captured in May, July, and September; males with abdominal testes and young were collected in July.

Akodon simulator Thomas, 1916
Gray-bellied Grass Mouse

Akodon simulator Thomas, 1916. Annals and Magazine of Natural History, ser. 8, 18:335.

Distribution in Argentina.--Eastern Jujuy, central Salta, and Tucumán provinces, at elevations from 500 to 2400 m (Myers, 1989, for *A. S. simulator*).

Specimens Examined (59).--Abra de Santa Laura, límite entre Salta y Jujuy, sobre ruta nacional N° 9, 1397 m, 6 (PIDBA 582, 583, 584, 586, 588, 596); Arroyo El Cano, 7 km al N del Río Saladillo, 1 (MMD 29); Caimancito, 400 m, 1 (BMNH not numbered); Cerro El Morado, 11 km al NO de San Antonio, sobre Río El Morado, 22 (17 MMD 24, 25, 26, 110, 112, 117, 118, 120, 128, 130, 131, 132, 133, 134, 136, 137, 140; 5 released); Fraile Pintado, 12 km al SO, sobre Río Ledesma, 1 (MMD 100); "Jujuy," 1 (MACN 19456); Mesada de las Colmenas, 3 (MACN 19458, 19459, 19461); Río Blanco, 9 km SW San Antonio, 1495 m, 8 (5 ARG 4257, 4283, 4286, 4288, 4294; 3 PIDBA 607, 615, 616); Sunchal, 1500 m, 1 (MLP 11-XII-35-10); Sunchal, 1600 m, 1 (MLP 11-XII-35-11); Sunchal, Sierra de Santa Bárbara, 5 (BMNH 21.1.1.19, 21.1.1.20, 21.1.1.24, 21.1.1.25, 21.1.1.26); Sunchal, Sierra de Santa Bárbara, 1200 m, 3 (BMNH 21.1.1.21, 21.11.1.19, 21.11.1.23); Villa Carolina, 2 (BMNH 20.1.7.27, 20.1.7.29); Villa Carolina, Río Lavallén, 500 m, 4 (BMNH 20.1.7.81, 20.1.7.95, 20.1.7.96, 20.1.7.98).

Additional Records.--Cerro Calilegua (Olrog, 1979, as *A. varius simulator*); Villa Carolina, 500 m (Thomas, 1920a).

Comments.--This species was described by Thomas (1916c) and later was considered a subspecies of *A. varius* (Thomas, 1926a; Gyldenstolpe, 1932; Cabrera, 1961a). Myers (1989) considered *Akodon simulator* to be a valid species and included *glaucinus* and *tartareus* as subspecies. Among the specimens examined, there is considerable variation in coloration of individuals from the same locality or nearby localities. In specimens from Villa Carolina, the venters are reddish or grayish. We recorded females with closed vaginas in January, May, June (2 lactating), and July, and females with open vaginas and lactating in May; males with abdominal testes were recorded in May, June, and July, and males with scrotal testes in January and May. Young specimens were captured in January, February, and June. The specimens from Villa Carolina were trapped in a cornfield and at the base of a tree, and the majority from Cerro El Morado were collected in traps placed at the side of a road.

Akodon spegazzinii Thomas, 1897
Spegazzini's Grass Mouse

Akodon spegazzinii Thomas, 1897. Annals and Magazine of Natural History, ser. 6, 20:216.

Distribution in Argentina.--Northwestern Argentina, in Salta, Jujuy Tucumán, and Catamarca provinces (Yepes, 1935b; Cabrera, 1961a; Musser and Carleton, 1993; Mares et al., 1997).

Specimens Examined (28).--JUJUY: Arroyo La Horqueta, 6 km SE Laguna Yala, 2100 m, 1 (MMD 189); Camino a Las Capillas, 2 km de la intersección de las rutas 56 y 20, por ruta provincial N° 20, 1 (JPJ 1); On highway 29 (E off of hwy 9), 10 km W of Tiraxi, 5800 ft., 6 (ARG 2638, 2642, 2644, 2645, 2650, 2666); On highway 9 at border with Salta, at campground on the way to El Carmen, 4600 ft., 2 (ARG 2565, 2624); Río Tiraxi, app 5 km al S de Tiraxi, sobre ruta provincial N° 29, 9 (MMD 145, 149, 151, 152, 155, 157, 161, 162, 167); Río Tiraxi, 1,5 km al E de Tiraxi, sobre ruta provincial N° 29, 7 (PIDBA 646, 649, 651, 655, 659, 660, 672). SALTA: Cachi, 2500 m, 1 (BMNH 6.5.8.17); Lower Cachi, 1 (BMNH 97.5.5.14 holotype).

Comments.--This species is readily recognized by its reddish and uniform coloration, which distinguishes it from *A. tucumanensis*, which is pale reddish brown dorsally mixed with gray and with a buffy gray venter (Allen, 1901). Cabrera (1961a) considered *tucumanensis* to be a subspecies of *A. boliviensis* whereas Myers et al. (1990) included it as a subspecies of *A. spegazzinii*. A detailed study including specimens of different age groups and seasons, and including specimens from Río Tiraxi, is necessary to verify whether more than 1 species of *Akodon* of the *boliviensis* group is present. This locality is close to the type locality of *A. caenosus* and the habitat is similar to that of *A. lutescens puer*.

All localities for this species in Jujuy Province are in the Yungas Phytogeographic Province, up to 1000 m. The environment in Tiraxi is a mix of grasses and pines (*Podocarpus parlatorei*); at the campground on highway 9 at the border with Salta, the dominant vegetation is forest with walnut, palo blanco, and laurel trees.

Females with closed vaginas were registered in July and August, whereas females with open vaginas, 1 with 6 fetuses and another with 7, were captured in February; males with abdominal testes in February, July, and August, and males with scrotal testes in February. Young were captured in July, and August. Specimens molting were registered in July and February.

Akodon sylvanus Thomas, 1921
Forest Grass Mouse

Akodon sylvanus Thomas, 1921. Annals and Magazine of Natural History, ser. 9, 7:184.

Distribution in Argentina.--Northwestern Argentina, in the mountains of Jujuy (Yepes, 1935b; Cabrera, 1961a; Myers, 1989), and probably in Salta Province.

Specimens Examined (54).--El Simbolar, 25 km al SO de Palma Sola, 36 (4 CM 43394, 43395, 43396, 43397; 32 CML 1984, 1985, 1986, 1987, 1988, 1990, 1991, 1994, 1995, 1996, 1997, 2019, 2026, 2027, 2028, 2029, 2032, 2033, 2034, 2035, 2036, 2097, 2099, 2100, 2101, 2103, 2104, 2105, 2108, 2110, 2111, 2112); El Sunchal, Sierra de Santa Bárbara, 1200 m, 1 (FMNH 29125); Sierra Santa Bárbara, 1200 m, 1 (MACN 20.257); Sunchal, Santa Bárbara, 1200 m, 9 (BMNH 21.1.1.27 *Akodon sylvanus* holotype, 21.1.1.30, 21.1.1.32, 21.1.1.35, 21.1.1.36, 21.1.1.37, 21.1.1.38, 21.1.1.39, 66. 1830); Sunchal, Santa Bárbara, 1400 m, 2 (BMNH 21.1.1.28, 21.1.1.29); Sunchal, Santa Bárbara, 1500 m, 3 (BMNH 21.1.1.33, 66.1831, 66.1832); Sunchal, Santa Bárbara, 1600 m, 2 (BMNH 21.1.1.31, 66.1833).

Comments.--Localities of all specimens examined are in the Yungas, in the type locality and surrounding areas. On the label of one specimen, the collector, E. Budin, wrote that this species lives between roots of trees or at the bases of walnut trees; some were captured in dense forests, and other in the humid forest of a ravine. He also indicated that this species feeds on nuts . Young were collected in June and July.

Akodon tartareus Thomas, 1919
Tartagal's Grass Mouse

Akodon tartareus Thomas, 1919. Annals and Magazine of Natural History, ser. 9, 4:155.

Distribution in Argentina.--In NW Argentina, from Jujuy to Tucumán Province (Myers, 1989 as *A. S. tartareus*; Yepes, 1935b).

Specimens Examined (79).--4 km W jct Hwys 34 and 3, along Hwy 3, Valle Grande Rd, 1 (CM 43404); 6 km W jct Hwys 34 and 3, along Hwy 3, Valle Grande Rd, 1 (CM 44025); A 2.5 km del Río Santa Rita, sobre camino al Fuerte, 2 (CML 2038, 2040); Aguas Negras, 3 (MACN 19453, 19454, 19460); Arroyo Yuto, 13 km al SO de Yuto, 1 (MMD 63); Bomba YPF márgenes del Arroyo Sauzalito, 4 (CML 2934, 2935, 5699, 5700); Caimancito, 2 (1 FMNH 29134, 1 MACN 19455); Caimancito FCCNA, 700 m, 4 (MACN 30.306, 30.314, 30.315, 30.316); Caimancito, 600 m, 1 (MACN 19457); El Palmar, 1.6 km al E, Sierra de Santa Bárbara, 2 (ARG 3429, 3452); El Palmar, 2.9 km al E, Sierra de Santa Bárbara, 1 (ARG 3412); El Palmar, 5.9 km al E, Sierra de Santa Bárbara, 4 (ARG 3436, 3440, 3441, 3442); El Palmar, 8.4 km al E, Sierra de Santa Bárbara, 1 (ARG 3467); El Simbolar, 25 km al SO de Palma Sola, 8 (CML 1992, 1993, 2020, 2022, 2023, 2024, 2037, 2044); Jujuy, 1000 m, 1 (CML 95); Jujuy, 1250 m, 14 (BMNH 20.1.7.78, 20.1.7.80, 20.1.7.82, 20.1.7.83, 20.1.7.84, 20.1.7.86, 20.1.7.88, 20.1.7.89, 20.1.7.90, 20.1.7.91, 20.1.7.92, 20.1.7.93, 20.1.7.94, 20.1.7.101); Jujuy, 1258 m, 5 (BMNH 66. 1784, 66. 1785, 66. 1786, 66. 1787, 66. 1788); Laguna La Brea, 6 (2 MMD 42, 53; 4 RMB 1567, 1573, 1574, 1575); On highway 9 at border with Salta, at campground on the way to El Carmen, 4600 ft., 5 (ARG 2510, 2520, 2545, 2570, 2608); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20, 1 (ARG 4225); Ruta 83, camino a Valle Grande, 9 km al N de San Francisco, 1200 m, 6 (MMD 326, 328, 331, 332, 335, 336); Santa Bárbara, Santa Bárbara, 1 (AMNH 185221); Villa Carolina, 2 (BMNH 20.1.7.27, 20.1.7.29); Villa Carolina, Río Lavallén, 500 m, 2 (BMNH 20.1.7.87, 20.1.7.100); Yuto, 1 (AMNH 182572).

Comments.--This species was described by Thomas (1919c) and considered to be valid by Gyldenstolpe (1932); however most subsequent authors have treated this species either as a subspecies or as a synonym of *simulator* or *varius* (Cabrera, 1961a; Mares et al., 1981; Myers, 1989; Anderson, 1997). In Jujuy, it was found in sympatry with *A. simulator*, which we consider an additional argument to support the validity of the 2 forms as different species. They also are morphologically different, and are not difficult to differentiate in the field in Jujuy Province. The coloration is copper gray, more clear toward the flanks, so that the change of coloration from the dorsum to the venter is gradual. In *simulator* the coloration is dark gray with the head and shoulders more grayish than the rest of the dorsum. The periocular rings are drab while in *simulator* they are lighter. The flanks are lighter in *simulator*, a grizzly or purplish gray, while in *A. tartareus* they are ochraceous. The chin has some white hairs, but the typical “white spot” is not in fact evident, in contrast to *simulator* in which the spot is quite evident and well expanded. The skull is robust; and the nasal bones are longer than in *A. simulator*. The crests are prominent, especially the lambdoids. The Eustacian tubes are longer and wider than in *simulator*. The incisive capsule is located near the posterior border of the coronoid process, while in *simulator* this is merely back of the coronoid process. The upper incisors are orthodont and the molars do not reveal a marked hypsodonty, while in *simulator* these are clearly hypsodont.

The specimen from Santa Bárbara cited by Myers (1989) as *A. simulator simulator*, is here reidentified as *A. tartareus*. The skin of the specimen from Villa Carolina, Río Lavallén, 500 m (BMNH 20.1.7.100) was mistakenly identified (according to the specimen tag) as *Bolomys lactens*, whereas the skull corresponds to a species of *Calomys*.

Except for Villa Carolina, a locality in the Chacoan region, the rest of the localities belong to the Yungas, and the majority within transitional areas. Females with closed vaginas were captured in February, May, June, July, and August, lactating females in April, and a lactating female and other with 7 fetuses in February; males with abdominal testes were recorded in May, July, and August, and males with scrotal testes in February and June. Young have been captured in December, May, June, and July. We recorded specimens molting in February, May, and July.

Akodon toba Thomas, 1921
Chaco Grass Mouse

Akodon toba Thomas, 1921. Annals and Magazine of Natural History, ser. 9, 7:178.

Distribution in Argentina.--Jujuy, Salta, Chaco, and Formosa provinces (Massoia, 1971;

Myers, 1989).

Specimens Examined (26).--Abra de Santa Laura, límite entre Salta y Jujuy, sobre ruta nacional N° 9, 1397 m, 2 (PIDBA 585, 589); Aguas Negras, 1 (CML 2936); Arroyo Yuto, 13 km al SO de Yuto, 5 (MMD 61, 64, 66, 87, 90); Bomba YPF márgenes del Arroyo Sauzalito, 1 (CML 2933); Caimancito, 600 m, 1 (FMNH 41283); El Palmar, 2.9 km al E, Sierra de Santa Bárbara, 2 (ARG 3413, 3415); Laguna La Brea, 8 (5 MMD 39, 40, 44, 45, 54; 3 RMB 1566, 1568, 1570); Río Blanco, 9 km SW San Antonio, 1495 m, 2 (ARG 4254, 4256); Río Tiraxi, 1,5 km al E de Tiraxi, sobre ruta provincial N° 29, 1 (PIDBA 670); Sunchal, Sierra de Santa Bárbara, 1 (BMNH 21.1.1.22); Villa Carolina, Río Lavallén, 500 m, 2 (BMNH 20.1.7.97, 20.1.7.99).

Comments.--Some authors considered *A. toba* as a subspecies of *A. varius* (Cabrera, 1961a; Massoia, 1971, Wetzel and Lovett, 1974), but Myers (1989) treated it as a valid species, on the basis of cranial and pelage differences.

According to Myers (1989) *A. toba* is restricted to the Chaco, but the locality Caimancito in Jujuy, cited by him, is in the Yungas. The majority of the localities for the specimens examined correspond to the Yungas. Specimens from Arroyo Yuto and El Palmar were captured near a stream.

Females with closed vaginas were captured in May, July, and August, and females with open vaginas in June and July; males with abdominal testes were captured in May and July. Young were registered in May, July, and August, and molting specimens in May and July.

Genus *Necromys*

Massoia and Pardiñas (1993) revalidated the genus *Necromys* described by Ameghino (1889), and included *Bolomys* as a synonym. This criterion was followed by many authors (Liascovich and Reig, personal communication 1990; Smith and Patton, 1999; Galliari and Pardiñas 2000; D'Elía, 2003).

Necromys lactens (Thomas, 1918)
Rufous-bellied Bolo Mouse

Akodon lactens Thomas, 1918. Annals and Magazine of Natural History, ser. 9, 1:188.

Distribution in Argentina.--Northwestern Argentina, in the eastern mountain range of Jujuy and Salta provinces, and Sierra Peninsulares of Tucumán and Catamarca provinces (Thomas, 1918; Yepes, 1935b; Cabrera, 1961a; Honacki et al., 1982; Lucero, 1983).

Specimens Examined (10).--9 km NW Bárcena, 2 (ARG 4617, 4618); Alto Calilegua, El Duraznillo, 3000 m, 1 (CML 1719); Calilegua, 1 (FMNH 23433); Cerro Calilegua, El Duraznillo, 2600 m, 2 (CML 1737, 1736); Cerro Hermoso, 1 (MACN 19517); Chilcayoc, 2 (MMD 168, 171); León, 1500 m, 1 (BMNH 18.1.1.37 *Bolomys lactens* holotype).

Additional Records.--Cerro Hermoso (cercanías), 2800 m (Heinonen and Bosso, 1994; as *Necromys lactens*).

Comments.--The records of this species correspond to the Yungas and to an ecotone between Yungas and Prepuna. The specimens from Cerro Hermoso and Chilcayoc were captured near water. Females with closed vaginas and males with abdominal testes were recorded in July and September, and a female with developed mammae was captured in July.

Genus *Oxymycterus*

Oxymycterus akodontius Thomas, 1921
Argentine Hocicudo

Oxymycterus akodontius Thomas, 1921. Annals and Magazine of Natural History, ser. 9, 8:615.

Distribution in Argentina.--Cited for NW Argentina, in Catamarca and Jujuy provinces (Cabrera, 1961a; Mares et al., 1997; Díaz and Barquez, 2002). The specimen cited by Mares et al. (1997) from Catamarca corresponds to a specimen of *Abrothrix illuteus* (Pardiñas et al., in press).

Specimens Examined (2).--Higuerilla, 2000 m, 2 (BMNH 21.11.1.72, holotype; 21.11.1.73).

Comments.--Several authors (Cabrera, 1961a; Honacki et al., 1982; Reig, 1987; Vitullo et al., 1986; Hershkovitz, 1994), considered this species as likely to be conspecific with *O. paramensis*; however, 2 young male specimens examined at the BMNH are not similar to young specimens of *paramensis* captured in the province. The young of *paramensis* have a coloration that is similar to the adults, uniformly reddish, while the young of *akodontius* are dorsally more blackish, and buffy on the venter. The specimens examined were captured in May and June. *O. akodontius* lives in the ground in burrows, and in abandoned burrows of *Ctenomys*, as well as in wet places, among mounds, in the densest parts of the forest (Thomas, 1921c).

Oxymycterus paramensis Thomas, 1902
Paramo Hocicudo

Oxymycterus paramensis Thomas, 1902. Annals and Magazine of Natural History, ser. 7, 9:139.

Distribution in Argentina.--Salta, Jujuy, and Tucumán provinces (Cabrera, 1961a; Mares et al., 1989; Barquez et al., 1991).

Specimens Examined (41).--Abra de Cañas, El Monolito, 1 (CML 1761); Arroyo La Horqueta, 6 km al SE de Lagunas de Yala, 2100 m, 3 (MMD 186, 187, 190); Caimancito, 600 m, 1 (FMNH 41280); Calilegua, Mesada de las Colmenas, 1150 m, 1 (MACN 20657); Cerro El Morado, 11 km al NO de San Antonio, sobre Río El Morado, 12 (5 MMD 22, 111, 113, 114, 116; 7 liberados); Cerro Hermoso, 1 (MACN 19519); Chilcayoc, 1 (MMD 170); León, 1500 m, 4 (BMNH 18.1.1.33, 18.1.1.34, 18.1.1.35, 18.1.1.36); Mesada de las Colmenas, 1150 m, 2 (MACN 19518, 19520); Mountains W of Yala, 2 (FMNH 22234, 23325); On highway 29 (E off of hwy 9), 10 km W of Tiraxi, 5800 ft., 2 (ARG 2634, 2656); On Valle Grande Rd, about 20 km NW Calilegua, 1 (CM 95445); Río Blanco, 9 km SW San Antonio, 1495 m, 3 (ARG 4289; 4293, 4314); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20, 2 (ARG 4219, 4234); Río Tesorero, 4 km al N de Tiraxi, sobre ruta provincial N° 29, 1 (MMD 194); Río Tiraxi, app 5 km al S de Tiraxi, sobre ruta provincial N° 29, 3 (MMD 148, 153, 159); Río Tiraxi, 1,5 km al E de Tiraxi, sobre ruta provincial N° 29, 1 (PIDBA 664).

Additional Records.--Aguas Negras, 600 m, Caimancito, 550 m (Heinonen and Bosso, 1994); "Jujuy" (Yepes, 1935b; Steppan, 1995); León (Liascovich, 1991).

Comments.--In Jujuy and Salta this species is abundant. Localities of all specimens examined correspond to the Yungas, with the exception of Chilcayoc, which is an ecotone between Yungas and Prepuna. The specimen captured at this locality is more grayish than other specimens.

Females with closed vaginas were captured in February, June, and July; males with abdominal testes were captured in January, June, July, and August, and a male with small scrotal testes was collected in February. We have recorded young in February and subadults in August. Molting specimens were collected in February, June, July, and September.

Tribe Oryzomyini

Genus *Holochilus*

Holochilus chacarius Thomas, 1906
Chacoan Marsh rat

Holochilus chacarius Thomas, 1906. Annals and Magazine of Natural History, ser. 7, 18:446.

Distribution in Argentina.--In the provinces of Buenos Aires, Córdoba, Corrientes, Chaco, Entre Ríos, Formosa, Jujuy, Salta, Santa Fe, Santiago del Estero. and Tucumán (Massoia, 1976, 1980; Vidal et al., 1976; Rivas et al., 1977). According to Honacki et al. (1982), and Musser and Carleton (1993), this species is only found in northeastern Argentina, but they include *balnearum* as synonym of *chacarius*, whose type locality is in Tucumán Province, in NW Argentina.

Specimens Examined (28).--6 km W jct Hwys 34 and 3, along Hwy 3, Valle Grande Rd, 1 (CM 43789); Calilegua, 2 (FMNH 23308, 23311); Ingenio Ledesma, 1 (MACN 48.51); Río San Francisco, 1 (MACN 27.58); Villa Carolina, Río Lavallén, 500 m, 17 (BMNH 20.1.7.10, 20.1.7.11, 20.1.7.12, 20.1.7.13, 20.1.7.14, 20.1.7.15, 20.1.7.16, 20.1.7.18, 20.1.7.19, 20.1.7.20, 20.1.7.21, 20.1.7.8, 20.1.7.9, 2 not numbered; 1 FMNH 29158; 1 MLP 11-XII-35-3); Yuto, 6 (AMNH 184656, 183311, 183310, 183309, 182574, 182931).

Additional Records.--Rio San Francisco Valley (Hershkovitz, 1955, as *H. b. balnearum*); Villa Carolina, 500 m (Thomas, 1920a, as *H. balnearum*).

Comments.--According to information written by E. Budin on specimen labels at the BMNH, this species lives along the banks of rivers among trunks and logs that have accumulated from river action. Juveniles were recorded in April and November; and 1 juvenile and 1 offspring were registered in June. One specimen of *Holochilus* from Pampa Blanca, deposited at the MACN (35.249), is coincident with the range of measurements established for *H. brasiliensis*, especially in the size of the hind foot. However, as the skull of the specimen was not found, some characteristics could not be observed; additionally, the distribution of this species, as mentioned by some authors (Massoia, 1976; Musser and Carleton, 1993; Voss and Carleton, 1993) is far from Jujuy Province.

Genus *Oligoryzomys*

In NW Argentina 4 species of *Oligoryzomys* have been recorded -- *O. chacoensis*, *O. flavescens*, *O. longicaudatus* (Mares et al., 1989, 1997; Barquez et al., 1991; Redford and Eisenberg, 1992; Heinonen and Bosso, 1994), and *O. destructor* (Capllonch et al., 1997). Many specimens cited in the literature as *O. longicaudatus* could represent a different species, from a complex of species formed by *O.longicaudatus*, *O.destructor*, and *O.nigripes*; although Carleton and Musser (1989) indicated that *O. nigripes* and *O. destructor* are not present in northern Argentina and Chile, we captured the later species in Jujuy, Salta, and Tucumán provinces. In addition, *O. microtis* has been reported from adjacent areas of Bolivia (Anderson, 1997) and likely occurs in Jujuy as well. Specimens identified by us as *O. destructor* and *O. flavescens* were compared with type descriptions and with specimens identified by G. Musser at the AMNH and SNOMNH.

Oligoryzomys chacoensis (Myers and Carleton, 1981)
Chacoan Pygmy Rice Rat

Oryzomys chacoensis Myers and Carleton, 1981. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 161:19.

Distribution in Argentina.--Jujuy, Salta, Formosa, and Chaco provinces (Contreras and Berry, 1983; Olds and Anderson, 1987; Musser and Carleton, 1993).

Specimens Examined (57).--4 km W jct Hwys 34 and 3, along Hwy 3, Valle Grande Rd, 1 (CM 43853); 6 km W jct Hwys 34 and 3, along Hwy 3, Valle Grande Rd, 2 (CM 43849, 43850); Agua Salada, 2 (SNOMNH 18648, 18649); Aguas Negras, Camping, 1 (CML 2939); Arroyo Yuto, 13 km al SO de Yuto, 6 (5 MMD 62, 71, 79, 84, 86; 1 liberado); Calilegua, 1 (FMNH 23428); Chilcayoc, 1 (MMD 169); El Palmar, 1.6 km al E, Sierra de Santa Bárbara, 7 (ARG 3424, 3425, 3431, 3433, 3453, 3454, 3465); El Palmar, 2.9 km al E, Sierra de Santa Bárbara, 1 (ARG 3411); El Simbolar, 25 km al SO de Palma Sola, 2 (1 CML 2121; 1 CM 43847); Fraile Pintado, 12 km al SO, sobre Río Ledesma, 1 (MMD 101); Laguna La Brea, 6 (4 MMD 41, 46, 48, 50; 2 RMB 1576, 1581); Laguna La Brea, 25 km antes de Palma Sola, sobre ruta 1, 1 (SNOMNH 18650); Oyeros, 3 km al N, camino entre rutas 61 y 43, 1 (MMD 201); Río Blanco, 9 km SW San Antonio, 1495 m, 3 (ARG 4261, 4266, 4307); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20, 1 (ARG 4242); Río Tiraxi, app 5 km al S de Tiraxi, sobre ruta provincial N° 29, 2 (MMD

164; 166); Río Tiraxi, 1,5 km al E Tiraxi, sobre ruta provincial N° 29, 2 (PIDBA 654, 668); Santa Bárbara, Santa Bárbara, 4 (AMNH 185224, 185225, 185228, 186954); Vinalito, 2 km al SE, al borde del 2° canal, 1 (MMD 57); Yuto, 11 (AMNH 167855, 179976, 179980, 182570, 182571, 182738, 182739, 183312, 185226, 185227, 185269).

Additional Records.--Aguas Negras, 600 m; Mesada de las Colmenas, 1150 m (Heinonen and Bosso, 1994).

Comments.--In spite of being a typical species of the Chaco, in Jujuy several localities of the specimens examined correspond to the Yungas, in transitional forests and grasslands. Also, chacoan localities (Oyeros and Agua Salada), and an ecotone between Yungas and Prepuna (Chilcayoc), were recorded for this species. Females with closed vaginas were captured in May, June, August, and October, 1 female with open vagina was recorded in June, and lactating females in April and July; males with abdominal testes were captured in May, June, July, and August, and 1 male with scrotal testes was registered in May. Molting specimens were observed in May and July.

Oligoryzomys destructor (Tschudi, 1844)
Destructive Pygmy Rice Rat

Hesperomys destructor Tschudi, 1844. Therologie. Untersuchungen über die Fauna Peruana. Scheitlin und Zollikofer, St. Gallen, Switzerland, 1:182.

Distribution in Argentina.--Tucumán, Salta, and Jujuy provinces (Capllonch et al., 1997; Díaz et al., 2000; Díaz and Barquez, 2002).

Specimens Examined (135).--4 km W jct Hwys 34 and 3, along Hwy 3, Valle Grande Rd, 1 (CM 43852); Abra de Cañas, aprox 30 km NW of Calilegua on Valle Grande Rd, 1700 m, 1 (CM 43843); Abra de Santa Laura, límite entre Salta y Jujuy, sobre ruta nacional N° 9, 1397 m, 4 (PIDBA 592, 593, 594, 595); Arroyo La Horqueta, 3 km al SE de Laguna de Yala, 2100 m, 1 (MMD 178); Arroyo La Horqueta, 6 km al SE de Lagunas de Yala, 2100 m, 2 (MMD 184, 188); Arroyo Yuto, 13 km al SO de Yuto, 1 (MMD 91); El Simbolar, 25 km al SO de Palma Sola, 11 (9 CML 2042, 2045, 2115, 2116, 2117, 2118, 2119, 2120, 2122; 2 SNOMNH 19796, 19797); El Simbolar, 25 km SW Palma Sola, 2 (CM 43844, 43848); Higuerilla, 2000 m, 8 (BMNH 21.11.1.11, 21.11.1.12, 21.11.1.13, 21.11.1.14, 21.11.1.15, 21.11.1.16, 21.11.1.17, 66.1902); Jujuy, 900 m, 1 (FMNH 35252); Laguna La Brea, 1 (MMD 55); León, 1 (BMNH 18.1.1.19); León, 1200 m, 2 (BMNH 18.1.1.14, 18.1.1.15); León, 1500 m, 8 (BMNH 18.1.1.10, 18.1.1.11, 18.1.1.12, 18.1.1.13, 18.1.1.16, 18.1.1.17, 18.1.1.18, 18.1.1.9); Maimará, 2230 m, 1 (FMNH 129274); Mountains W of Yala, 2 (FMNH 23421, 23427); Río Blanco, 9 km SW San Antonio, 1495 m, 31 (24 ARG 4255, 4258, 4259, 4260, 4262, 4263, 4264, 4265, 4271, 4272, 4273, 4274, 4275, 4276, 4284, 4295, 4296, 4297, 4299, 4302, 4303, 4310, 4311, 4312; 7 PIDBA 610, 611, 612, 613, 614, 619, 620); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20, 11 (4 ARG 4236, 4244, 4245, 4250; 7 MMD 344, 345, 346, 347, 348, 356, 357); Río Tesorero, 4 km al N de Tiraxi, sobre ruta provincial N° 29, 3 (MMD 195, 197, 198); Río Tiraxi, app 5 km al S de Tiraxi, sobre ruta provincial N° 29, 9 (MMD 146, 147, 150, 156, 160, 163, 165, 193, 199); Río Tiraxi, 1,5 km al E de Tiraxi, sobre ruta provincial N° 29, sobre Río Tiraxi, 5 (PIDBA 650, 658, 661, 674, 675); Ruta 83, camino a Valle Grande, 9 km al N de San Francisco, 1200 m, 8 (MMD 321, 325, 327, 329, 333, 334, 337, 338); San Rafael, Sierra Santa Bárbara, 1000 m, 2 (BMNH 21.1.1.16, 66.1901); Sierra Santa Bárbara, El Sunchal, 1200 m, 1 (BMNH 66.1900); Sunchal, Sierra Santa Bárbara, 1200 m, 5 (BMNH 21.1.1.10, 21.1.1.11, 21.1.1.12, 21.1.1.8, 21.1.1.9); Sunchal, Sierra Santa Bárbara, 1400 m, 2 (BMNH 21.1.1.13, 21.1.1.14); Sunchal, Sierra Santa Bárbara, 1600 m, 1 (BMNH 21.1.1.7); Villa Carolina, Río Lavallén, 500 m, 10 (BMNH 20.1.7.58, 20.1.7.59, 20.1.7.60, 20.1.7.61, 20.1.7.62, 20.1.7.63, 20.1.7.64, 20.1.7.65, 66.1898, 66.1899).

Comments.--Espinosa and Reig (1991) suggested that the karyotypes of the specimens from Horco Molle, Tucumán, and from León, Jujuy, were not like those of *O. longicaudatus*, and they found sufficient differences to believe that these specimens may represent a different species such as *O. stolzmanni*, considered by Musser and Carleton (1993) a junior synonym of *O. destructor*. According to Carleton and Musser (1989) the specimens reported by Gardner and Patton (1976) and Olds and Anderson (1987) as *O. longicaudatus* are *O. destructor*.

The specimens from Abra de Cañas (CM 43843) and from El Simbolar (CM 43844), were considered by Carleton and Musser (1989) to be *O. chacoensis*. The specimens at the BMNH from Villa Carolina, Río Lavallén, 500 m (20.1.7.61 and 20.1.7.63) were identified by Thomas (1920a) as belonging to the *flavescens* group. All the localities from Jujuy correspond to the Yungas, including transitional areas, montane forest, and grasslands, except Villa Carolina, which is a chacoan locality. At Higuerilla, according to annotations of Mr. Budin, 1 specimen was collected in the walnuts and in Villa Carolina some specimens were collected at the bank of the river; also this species make their nests in climbing plants or build spherical nests made of straw.

Females with closed vaginas were captured in May, July, August, and September, and 1 female with open vagina in July; males with abdominal testes were captured in May, July, August, and September, and males with scrotal testes in September. In addition, young have been recorded in May, June, and July. A specimen from El Simbolar had insects and plants in the stomach.

Oligoryzomys flavescens (Waterhouse, 1837)
Yellow Pygmy Rice Rat

Mus flavescens Waterhouse, 1837. Proceedings of the Zoological Society of London, p. 19.

Distribution in Argentina.--North and central Argentina (Olrog and Lucero, 1981). Records exist for Misiones, Chaco, Salta, Jujuy, Tucumán, Mendoza, Córdoba, San Luis, and Buenos Aires provinces (Thomas, 1920a; Contreras and Rosi, 1980; Myers and Carleton, 1981; Massoia et al., 1987)

Specimens Examined (10).--Cerro Calilegua, El Duraznillo, 2 (CML 1728, 1729); Cerro Calilegua, El Duraznillo, 2600 m, 3 (CML 1731, 1732, 1733); El Palmar, 1.6 km al E, Sierra de Santa Bárbara, 1 (ARG 3464); El Palmar, 8.4 km al E, Sierra de Santa Bárbara, 1 (ARG 3472); San Francisco, 1 (CML 1591); San Francisco, Calilegua, 1 (CML 389); Sunchal, Sierra Santa Bárbara, 1200 m, 1 (BMNH 21.1.1.15).

Additional Records.--Maimará (Espinosa and Reig, 1991, as *Oligoryzomys cf. flavescens*);

Villa Carolina, 500 m (Thomas, 1920a, as a species of the *flavescens* group).

Comments.--All localities in specimens examined correspond to the Yungas, while Espinosa and Reig (1991) and Thomas (1920a) reported the species from Prepuna and Chaco habitats, respectively. In July, we collected 1 female with closed vagina, and 1 male with abdominal testes.

Oligoryzomys sp.

Specimens Examined (7).--Cerro El Morado, 11 km al NO de San Antonio, sobre Río El Morado, 4 (MMD 127, 135, 139, 142); On highway 29 (E off of hwy 9), 10 km W of Tiraxi, 5800 ft., 1 (ARG 2671); On highway 9 at border with Salta, at campground on the way to El Carmen, 2 (ARG 2583, 2592).

Comments.--The specimens examined likely belong to an undescribed species. Most belong to what Diaz (1999) refered to as *O. longicaudatus*. All the localities belong to the Yungas, montane forests, and grasslands. We have found males with abdominal testes in February and June, and males with scrotal testes in February and June.

Genus *Oryzomys*

Oryzomys legatus (Thomas, 1925)
Big-headed Rice Rat

Oryzomy legatus Thomas, 1925. Annals and Magazine of Natural History, ser. 9, 15:577.

Distribution in Argentina.--Northwest of Salta and Jujuy provinces (Mares et al., 1989; Ojeda and Mares, 1989; Musser et al., 1998 as *Oryzomys russatus*).

Specimens Examined (24).--Aguas Negras, Camping, Parque Nacional Calilegua, 2 (CML 5692, 5693); Arroyo El Sauzalito, 2 (CML 2938; 5691); Arroyo Yuto, 13 km al SO de Yuto, 2 (MMD 77, 89); El Palmar, 2.9 km al E, Sierra de Santa Bárbara, 4 (ARG 3414, 3446, 3449, 3450); El Palmar, 8.4 km al E, Sierra de Santa Bárbara, 1 (ARG 3471); El Simbolar, 25 km al SO de Palma Sola, 3 (2 CM 43819, 43820; 1 SNOMNH 19798); El Simbolar, 25 km al SO de Palma Sola, 1000 m, 2 (CML 2013, 2014); Laguna La Brea, 1 (RMB 1577); Laguna La Brea, 25 km antes de Palma Sola, 1 (RMB 900); Laguna La Brea, 25 km antes de Palma Sola, sobre ruta 1, 1 (SNOMNH 19799); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20, 5 (ARG 4226, 4237, 4239, 4241, 4253).

Comments.--We follow Patton et al. (2000) in considering *legatus* as a valid species, including the specimens from NW Argentina. The elevation range reported for this species extends from near sea level to 2100 m, so the presence of a specimen in the Puna (Yavi Chico) as indicated in the Catalog of the MACN (not examined) is extremely rare. The other localities in general correspond to transitional forests of the Yungas. Females with closed vagina were observed in May, June, and July, 1 female with open vagina was captured in July; males with abdominal testes were collected in May, June, and July. Juveniles were recorded in June, and molting specimens in May and July.

Tribe Phyllotini

Genus *Andinomys*

Andinomys edax Thomas, 1902
Andean Mouse

Andinomys edax Thomas, 1902. Proceedings of the Zoological Society of London, 1:116.

Distribution in Argentina.--Northwestern Argentina, in Jujuy and Salta provinces, between 2000 and 5000 m (Yepes, 1935a; Cabrera, 1961a; Hershkovitz, 1962).

Specimens Examined (52).--11 km al E de Humahuaca, 2 km al E de Pucará sobre camino a Cianzo, 2 (ARG 2689, 2709); Abra Pampa, 1 (CML 1220); Alfarcito, 2600 m, 2 (BMNH 21.11.1.18, 21.11.1.19); Cerro Casabindo, 4500 m, 6 (BMNH 19.8.2, 19.8.2.1, 19.8.2.2, 19.8.2.3, 19.8.2.4, 19.8.2.8); Cerro Casabindo, 4800 m, 2 (BMNH 19.8.2.5, 19.8.2.9); Cerro de la Lagunita, 1 (BMNH 12.12.12.36); Cerro Lagunita, Maimará, 4500 m, 1 (BMNH not number); Cuesta del Hurón, 29 km al O de Cienegüillas, sobre ruta provincial N° 64, 3835 m, 3 (MMD 455, 462, 470); "Jujuy," 1 (MACN 4.103); La Laguna 4500 m, Sierra de Zenta, E de Maimará, 1 (MACN 27.125, 27.85; see comments under *Localities and maps*); Maimará, 2200 m, 2 (CML 372, 373); Maimará, 2230 m, 9 (7 BMNH 12.12.12.28, 12.12.12.29, 12.12.12.30, 12.12.12.31, 12.12.12.32, 12.12.12.34, 12.12.12.35; 2 MACN 27.83, 27.84); Maimará, 2328 m, 1 (BMNH 17.12.31.3); Maimará, 2500 m, 5 (2 CML 109, 111; 3 MACN 31.25, 31.26; 31.27); Maimará, 3000 m, 1 (CML 279); Mina Pan de Azúcar, 13 km al S, sobre Río Cincel, 1 (MMD 531); Mountains W of Yala, 1 (FMNH 23435); Rinconada, 6 km al N, camino a Timón Cruz, 4286 m, 2 (MMD 473, 486); Sierra de Zenta, 4500 m, 6 (1 BMNH 21.11.1.20; 5 MACN 17822, 31.114, 31.122, 31.123, 32.58; see comments under *Localities and maps*); Tilcara, 2400 m, 3 (MACN 17562, 17563, 17564); Tres Cruces, 4000 m, 1 (CML 380).

Additional Records.--Cerro Casabindo, 4000-4800 m (Thomas, 1919b); Cerro de Lagunita, E de Maimará, 4500 m (Thomas, 1913); La Laguna, Sierra de Zenta, 4500 m (Yepes, 1935a; see comments under *Localities and maps*); Sierra de Zenta (Yepes, 1935a; see comments under *Localities and maps*).

Comments.--All specimens examined are from the Prepuna and Puna regions. For the specimen from the "Mountains W of Yala" the locality is not clearly indicated, but probably also belong to the upper part of the mountains, and not to the Yungas where Yala is located.

Females with closed vaginas were found in February and March, a lactating female and 1 with 3 fetuses were collected in February, and females with open vaginas were collected in March (1 with 2 fetuses). Young specimens were collected in February, June, and July. Molting specimens were observed in February and March. Specimens from Cuesta del Hurón were captured during the night, in an area between the road and a stream. The record from Mina Pan de Azúcar corresponds to an upper tooth row extracted from feces of an undetermined carnivore.

Andinomys lineicaudatus Yepes, 1935
Forest Mouse

Andinomys edax lineicaudatus Yepes, 1935. Anales del Museo Argentino de Ciencias Naturales, 38:342.

Distribution in Argentina.--Northwestern Argentina, in the Sierras Peninsulares of Tucumán, Catamarca (Yepes, 1935a; Cabrera, 1961a; Hershkovitz, 1962), and Jujuy provinces (Díaz and Barquez, 1999).

Specimens Examined (8).--Abra de Cañas, 2 (MACN 19542, 19543); Abra de Cañas, approx 30 km NW of Calilegua on Valle Grande Rd, 1700 m, 2 (CM 43492, 43493); Abra de Cañas, El Monolito, 1700 m, 2 (CML 1760, 1805); Cerro Hermoso, 1 (MACN 19544); Maimará, 2500 m, 1 (MACN 31.24).

Comments.--We consider *A. lineicaudatus* to be a valid species and distinct from *A. edax* following Díaz (1999), because they were found in sympatry and the characters to separate both species are clear. Unlike *A. edax*, the tail of this species has a dark middle line ventrally, and the feet are >30 mm. In contrast to *A. edax* the majority of the records for this species, with the exception of Maimará (Prepuna), are in the Yungas Phytogeographic Province; some specimens were captured below 2000 m, the lower altitudinal range established by Hershkovitz (1962); in Tucumán Province this species has been captured at an altitude of 500 m. The inclusion of this species in Cerro Calilegua, as cited by Olrog (1979), is probably based in the specimens from Abra de Cañas deposited at the CML. A male with scrotal testes was captured in November.

Genus *Auliscomys*

Auliscomys sublimis (Thomas, 1900)
Andean Big-eared Mouse

Phyllotis sublimis Thomas, 1900. Annals and Magazine of Natural History, ser. 7, 6:467.

Distribution in Argentina.--In NW Argentina, in the Altiplano, between 4500 and 4700 m, in Salta and Jujuy provinces (Pearson, 1958; Cabrera, 1961a; Hershkovitz, 1962).

Specimens Examined (5).--La Laguna 4500 m, Sierra de Zenta, E. de Maimará, 1 (MACN 27.72; see comments under *Localities and maps*); Lagunita, Tilcara, 1 (BMNH 19.7.10.3 *Euneomys leucurus* holotype); Sierra de Zenta, 4500 m, 3 (BMNH 21.11.1.30, 21.11.1.31, 21.11.1.32; see comments under *Localities and maps*).
Additional Records.--Cerrito Leones, near the mine of Pan de Azúcar, Man and Biophere Reserve of Laguna de Pozuelos (Ortiz et al., 2000); La Lagunita (Thomas, 1921c, as *Euneomys* (*Auliscomys*) *leucurus*; Yepes, 1935b); La Lagunita, 4500 m (Pearson, 1958); Maimará (Thomas, 1921c, as *Euneomys* (*Auliscomys*) *leucurus*; Yepes, 1935b).

Comments.--According to the labels on specimens at the BMNH, written by E. Budin, this species lives in open places, below rocks, and along the banks of streams. A young individual was recorded in May at Sierra de Tilcara.

Genus *Calomys*

This genus has been reviewed by several authors (Hershkovitz,1962; Olds, 1988; Vitullo et al., 1990; Braun, 1993; Steppan, 1993, 1995). Recently, Salazar-Bravo et al. (2001) demonstrated, based on the cytochrome *b* gene sequence, that this genus is monophyletic and composed of 2 main clades; 1 comprised of species found in highlands, and other distributed in lowland habitats.

Calomys boliviae (Thomas, 1901)
Bolivian Vesper Mouse

Eligmodontia callosa boliviae Thomas, 1901. Annals and Magazine of Natural History, ser. 7, 8:253.

Distribution in Argentina.--This species was cited by Musser and Carleton (1993) for western Bolivia. Anderson (1997) indicates their distribution to near the limits with Argentina. This species is cited for Tucumán and Santiago del Estero provinces (Salazar-Bravo et al., 2001 as *C. fecundus*; Dragoo et al., 2002), and its distribution is here included in Jujuy Province.

Specimens Examined (59).--4 km W jct Hwys 34 and 3, along Hwy 3, Valle Grande Rd, 2 (CM 43513, 43514); 6 km W jct Hwys 34 and 3, along Hwy 3, Valle Grande Rd, 2 (CM 43524, 43525); Arroyo El Cano, 7 km al N de Río Saladillo, 1 (MMD 28); Arroyo Yuto, 13 km al SO de Yuto, 3 (MMD 67, 70, 88); El Palmar, 2.9 km al E, Sierra de Santa Bárbara, 1 (ARG 3447); El Palmar, 1.6 km al E, Sierra de Santa Barbara, 9 (ARG 3417, 3418, 3419, 3430, 3432, 3451, 3461, 3462, 3463); El Palmar, 5.9 km al E, Sierra de Santa Bárbara, 4 (ARG 3477, 3483, 3484, 3485); El Palmar, 8.4 km al E, Sierra de Santa Bárbara, 2 (ARG 3470, 3473); Fraile Pintado, 12 km al SO, sobre Río Ledesma, 3 (MMD 95, 96, 99); Jujuy, 1258 m, 5 (BMNH 20.1.7.22, 20.1.7.23, 20.1.7.24, 20.1.7.25, 20.1.7.26); On highway 9 at border with Salta, at campground on the way to El Carmen, 2 (ARG 2556, 2569); Palma Sola, 3 (AMNH 183313, 183314, 185234); Santa Bárbara, Santa Bárbara, 7 (AMNH 185230, 185231, 185232, 185233, 185235, 185236, 185238); Villa Carolina, Río Lavallén, 500 m, 14 (BMNH 20.1.7.27, 20.1.7.28, 20.1.7.29, 20.1.7.30, 20.1.7.31, 20.1.7.32, 20.1.7.33, 20.1.7.34, 20.1.7.35, 20.1.7.36, 20.1.7.37, 20.1.7.38, 20.1.7.39, 20.1.7.40); Villa Carolina, Río Lavayén, 500 m, 1 (MLP 11-XII-35-24).

Additional Records.--La Mendieta (Olds, 1988 as *C. venustus*).

Comments.--This species was originally described as a subspecies of *Eligmodontia callosus* by Thomas (1901) and considered as such by Cabrera (1961a) and Thomas (1916a); Musser and Carleton (1993) considered it to be a valid species including *fecundus* as a synonym, while Anderson (1997) and Olds (1988) considered *boliviae* and *fecundus* to be synonyms of *venustus*. Salazar-Bravo et al. (2001) considered *venustus* to be a valid species and distinct from *callosus* and *fecundus*. They included *fecundus* in Argentina, previously reported only for Bolivia, and considered that *callosus* is present in Paraguay and Bolivia and *venustus* in Argentina. Olds (1988) and Thomas (1920a) identified the specimens from Jujuy, 1258 m, and from Villa Carolina as *C. venustus*;

while Herskovitz (1962) considered them as *C. c. callosus*; Olds (1988) determined the specimens from Palma Sola as *C. venustus*.

Collecting localities all are from the Yungas and Chaco phytogeographic provinces. According to information on the specimen tags, written by Mr. Budin, the animals from Jujuy, 1258 m, were captured in cornfields and in grasses, and some from Villa Carolina were collected along the bank of the river. The specimen from Arroyo El Cano was captured near a cultivated area. Olds (1988) erroneously placed the locality La Mendieta in the province of Catamarca, but Mares et al. (1997) clarified that it is in Jujuy Province. Females present 7 pairs of mammae located in the chest and abdomen. Females with closed vaginas and inflated mammae were captured in February, females with closed vaginas in May and July, and a female with 10 fetuses in February. Males with abdominal testes were registered in May and July, and males with scrotal testes in February and May. Young were collected in April, May, June, July, and August. Molting specimens were observed in February, May, and July.

Calomys lepidus (Thomas, 1884)
Andean Vesper Mouse

Hesperomys (*Calomys*) *bimaculatus lepidus* Thomas, 1884. Proceedings of the Zoological Society of London, p. 454.

Distribution in Argentina.--Northwestern Argentina, in high altitudes grasslands between 3000 and 5000 m (Yepes, 1935b; Cabrera, 1961a; Hershkovitz, 1962; Olds, 1988; Salazar-Bravo et al., 2001); its presence has been confirmed in Jujuy and Salta Provinces (Ortiz et al., 2000; Díaz and Barquez, 2002).

Specimens Examined (23).--Abrapampa, 3500 m, 6 (BMNH 19.8.1.17, 19.8.1.18, 19.8.1.19, 19.8.1.20, 19.8.1.21 *Hesperomys carillus argurus* holotype, 19.8.1.22); El Toro, 50 km al O de Susques, 1 (IADIZA 3387); Laguna de Pozuelos, 14 (3 IADIZA 3384, 3385, 3388; 11 MACN 19414, 20299, 20300, 20301, 20302, 20303, 20304, 20305, 20306, 20307, 20308); Mina Pan de Azúcar, 8 km al N y 5 km al O, camino a Herrana, 3820 m, 1 (MMD 507); Sierra de Zenta, ruta provincial N° 13, entre Chaupe Rodeo e Iruya, 12 km al N de Chaupe Rodeo, 1 (MMD 364).

Additional Records.--Cerrito Leones, near the mine of Pan de Azúcar, Man and Biophere Reserve of Laguna de Pozuelos (Cirignoli et al., 2001).

Comments.--According to the labels of the specimens at the BMNH, written by Mr. Budin, specimens from Abrapampa were captured at the bank of a lagoon in humid grasses. All the localities are in the Puna. In March, a female with closed vagina and males with scrotal testes were captured, and males with abdominal testes were captured in November. Young were captured in February and December.

Calomys musculinus (Thomas, 1913)
Drylands Vesper Mouse

Eligmodontia laucha musculina Thomas, 1913. Annals and Magazine of Natural History, ser. 8, 11:138.

Distribution in Argentina.--Most of Argentina from Jujuy, S to northern Patagonia (Yepes, 1935b; Cabrera, 1961a; Hershkovitz, 1962).

Specimens Examined (43).--9 km NW Bárcena, 2 (ARG 4601, 4622); Along Yala Laguna Rd, ? km W jct it and Hwy 9, 1 (CM 43609); Casa Colorada, app 2 km al N de Alfarcito, 3034 m, 2 (MMD 367, 376); Chilcayoc, 1 (MMD 175); Cuesta de Lipán, 15 km al O de Purmamarca, sobre ruta 52, 1 (MMD 303); Jujuy, 1258 m, 15 (BMNH 20.1.7.43, 20.1.7.44, 20.1.7.45, 20.1.7.46 *Hesperomys musculinus cortensis* holotype, 20.1.7.47, 20.1.7.48, 20.1.7.49, 20.1.7.50, 20.1.7.51, 20.1.7.52, 20.1.7.53, 20.1.7.54, 20.1.7.55, 20.1.7.56, 20.1.7.57); La Quiaca, 1 (MACN 36.873); Maimará, 1 (BMNH 12.12.12.10); Maimará, 2230 m, 8 (6 BMNH 12.12.12.7, 12.12.12.8, 12.12.12.9 *Hesperomys laucha musculina* holotype, 12.12.12.11, 34.11.4.57, not number; 1 CML 375; 1 MACN 27.109); Maimará, 2300 m, 1 (MACN 27.108); Río Tiraxi, 1,5 km al E de Tiraxi, sobre ruta provincial N° 29, 2 (PIDBA 656, 673); Santa Catalina, 4500 m, 2 (BMNH 26.6.12.43, 26.6.12.44); Sierra de Zenta, 4500 m, 1 (MACN 31.109; see comments under *Localities and maps*); Sunchal, Sierra Santa Bárbara, 1200 m, 1 (BMNH 21.1.1.41); Tilcara, 8000 ft., 1 (AMNH 41878); Yavi Chico, El Habal, 3 (MACN 36.440, 36.452, 36.465).

Additional Records.--León, 1.6 km al O, 1770 m; Sunchal, Santa Bárbara, 1200-1500 m (Olds, 1988).

Comments.--There likely are 2 subspecies in Jujuy, 1 from higher elevations at the Prepuna, Puna, and High Andean (*C. m. musculinus*), and another from the lower parts in the Yungas (*C. m. cortensis*). Cabrera (1961a), and Musser and Carleton (1993) considered these to be synonyms.

In the Prepuna several captures were made trapping in stone fences or mud walls built beside rivers. At Maimará, according to the annotations of Mr. Budin, a specimen was captured in the gorge of the Río Humahuaca; at Yavi, according to annotations of J. Yepes, specimens were captured along the banks of a river among agricultural stubble. In general, this genus is associated with cultivated fields in the Yungas or in the Chaco, but also with the secondary growth vegetation or altered zones. The holotype of *C. m. cortensis* was captured in a cornfield.

A pregnant female was recorded in March, females with closed vaginas in June and August, and a young female with closed vagina and molting in July; a young male with scrotal testes and molting was captured in December, and males with abdominal testes in August and September. Juveniles were registered in February, March, April, May, June, and November.

Calomys venustus (Thomas, 1894)
Charming Vesper Mouse

Oryzomys? *venustus* Thomas, 1894. Annals and Magazine of Natural History, ser. 6, 14:359.

Distribution in Argentina.--From Jujuy and Salta to Córdoba Province (Yepes, 1935b; Cabrera, 1961a; Hershkovitz, 1962; Myers, 1982; Lucero, 1983; Dragoo et al., 2002).

Specimens Examined (49).--Abra de Santa Laura, límite entre Salta y Jujuy, sobre ruta nacional N° 9, 1397 m, 1 (PIDBA 590); Along Hwy 9 at border with Salta Prov., 4600 ft., 2 (CML 3600, 3601); Arroyo Yuto, 13 km al SO de Yuto, 4 (MMD 65, 74, 80, 85); Bomba YPF en márgenes del Arroyo Sauzalito, 1 (CML 2937); Caimancito, 400 m, 2 (BMNH 21.1.2.1, 21.1.2.2); Calilegua, 3 (FMNH 22235, 23372, 23377, 23431); Cruce camino a Puesto Viejo y Ruta 34, 4 km al E, sobre camino a Puesto Viejo, 1 (MMD 104); El Simbolar, 25 km al SO de Palma Sola, 1 (CML 2114); El Simbolar, 25 km SW Palma Sola, 1 (CM 43508); Laguna La Brea, 4 (3 MMD 51, 52, 109; 1 RMB 1572); Río Blanco, 9 km SW San Antonio, 1495 m, 1 (ARG 4280); Sobre ruta 9 en el límite con Salta, sobre camino a El Carmen, 2 (IADIZA 5543, 5544); Sunchal, Sierra Santa Bárbara, 1200 m, 10 (BMNH 21.1.1.42, 21.1.1.43, 21.1.1.44, 21.1.1.45, 21.1.1.46, 21.1.1.48, 21.1.1.49, 21.1.1.51, 21.1.1.52, 21.1.1.53); Sunchal, Sierra Santa Bárbara, 1300 m, 1 (BMNH 21.1.1.47); Sunchal, Sierra Santa Bárbara, 1500 m, 1 (BMNH 21.1.1.50); Yuto, 14 (AMNH 167856, 179974, 179975, 179979, 181544, 182573, 182737, 182740, 182926, 182927, 182928, 182929, 182930, 185229).

Additional Records.--Aguas Negras, 600 m (Heinonen and Bosso, 1994); Calilegua, 470 m (Osgood, 1943); Mesada de las Colmenas, 1150 m (Heinonen and Bosso, 1994); San Lorenzo (Thomas, 1898, as *Oryzomys callosus*); Vecindades del Parque Nacional Calilegua (Heinonen and Bosso, 1994).

Comments.--Musser and Carleton (1993) considered *C. venustus* as a synonym of *C. callosus*; this approach was followed by Díaz and Barquez (2002). Anderson (1997) and Olds (1988) treated *callosus* and *venustus* as distinct species; Olds (1988) distinguished these 2 species on the basis of body size, and considered *boliviae* to be a synomyn of *venustus*. Recent molecular studies have confirmed the distinctiveness of these species (Salazar-Bravo et al., 2001; Dragoo et al., 2002), and indicated that *callosus* is not present in Argentina. Consequently, we treat the specimens from Jujuy under the name *C. venustus*. Some specimens cited in additional records were not examined by us, so there is a possibility that they may correspond to *C. boliviae*. The majority of the localities are in the Yungas, with the exception of Puesto Viejo, a chacoan locality. According to Mr. Budin's notes in the label of a specimen from Sunchal at the BMNH, this was captured in a slope with grasses; he also indicated that a specimen from Caimancito was captured among tree trunks. We found females with closed and open vaginas in May., and a lactating female and a female with 7 offspring in February. Males with abdominal testes were registered in May, and July, and males with scrotal testes were collected in February. Young were collected in March, April, May, June, and August; and molting specimens in February and May.

Genus *Eligmodontia*

Pearson (1957) considered *Eligmodontia* to be monotypic, comprised of *E. puerulus puerulus* and *E. p. hirtipes*. Cabrera (1961a) and Mann Fischer (1978) recognized 2 species of *Eligmodontia*: *E. typus* and *E. puerulus*, but Hershkovitz (1962) treated *typus* and *puerulus* as subspecies of *E. typus*. Later, Musser and Carleton (1993), considered *Eligmodontia* to comprise 4 species (*E. moreni, E. morgani, E. puerulus,* and *E. typus*) and included *E. moreni* and *E. puerulus* in NW Argentina. Some authors have considered *E. hirtipes* either as a synonym (Cabrera, 1961a; Musser and Carleton, 1993) or as a subspecies of *puerulus* (Mann Fischer, 1945; Pearson, 1951), but their morphology

(Osgood, 1943; Mann Fischer, 1978) and karyotypes (Ortells et al., 1989; Kelt et al., 1991) support their identity as different species. In Jujuy, both taxa were found in sympatry and we treat them as separate species.

Eligmodontia hirtipes (Thomas, 1902)
Silky-feet Gerbil Mouse

Phyllotis hirtipes Thomas, 1902. Annals and Magazine of Natural History, ser. 7, 9:225.

Distribution in Argentina.--Jujuy and Salta provinces (Díaz and Barquez, 1999; Díaz et al., 2000).

Specimens Examined (34).--Abrapampa, 3500 m, 12 (BMNH 19.8.1.23, 19.8.1.24, 19.8.1.25, 19.8.1.26, 19.8.1.27, 19.8.1.28, 19.8.1.29 *Eligmodontia hirtipes jucunda* holotype, 19.8.1.30, 19.8.1.31, 19.8.1.32, 19.8.1.33, 19.8.1.34); Reserva Olaroz-Cauchari, 3903 m, 2 (MMD 317, 318); Reserva Provincial Olaroz-Cauchari, 35 km al O de Susques, sobre ruta provincial N° 70, 2 (MMD 316, 320); Sobre ruta 40, 29 km al N del empalme con ruta 52, 18 (MMD 247, 248, 249, 251, 252, 253, 254, 255, 260, 262, 263, 264, 265, 268, 269, 272, 274, 277).

Comments.--All specimens collected by us were captured at night, in sandy soils with widely scattered bushes, in the Puna. Females with closed vaginas and males with abdominal testes were captured in May, and females with closed vaginas and males with scrotal testes in December. Juveniles were recorded in January.

Eligmodontia puerulus (Phillipi, 1896)
Andean Gerbil Mouse

Hesperomys puerulus Phillipi, 1896. Anales del Museo Nacional de Chile, Zoología, entr. 13a:20.

Distribution in Argentina.--Jujuy and Salta provinces (Díaz and Barquez, 1999; Díaz et al., 2000).

Specimens Examined (13).--Curques, 24 km al N de Susques, sobre ruta 74, 1 (MMD 285); Reserva Olaroz-Cauchari, 3903 m, 2 (MMD 315, 319); Salar Cauchari, 31 km al N de Cauchari, sobre ruta provincial N° 70, 3840 m, 1 (MMD 312); Sobre ruta 40, 29 km al N del empalme con ruta 52, 9 (MMD 250, 256, 257, 258, 259, 261, 266, 267, 273).

Additional Records.--Cerrito Leones, near the mine of Pan de Azúcar, Man and Biophere Reserve of Laguna de Pozuelos (Ortiz et al., 2000); Laguna de Vilama, 4500 m (G. Gil, personal communication).

Comments.--This species was collected in dunes and rocks. Females with open vaginas in December; 1 female was lactating and another aborted 4 fetuses. Males with scrotal testes were collected in December. A juvenile female was captured in May.

Genus *Graomys*

Graomys domorum (Thomas, 1902)
Pale Leaf-eared Mouse

Eligmodontia domorum Thomas, 1902. Annals and Magazine of Natural History, ser. 7, 9:132.

Distribution in Argentina.--Salta, Jujuy and Tucumán provinces, in the western portion of the Chaco (Yepes, 1935b; Cabrera, 1961a; Capllonch et al., 1997).

Specimens Examined (4).--Laguna La Brea, 2 (1 CML 5985; 1 MMD 43); Maimará, 2500 m, 1 (MACN 31.37), Ruta 83, Camino a Valle Grande, 9 km al N de San Francisco, 1200 m, 1 (MMD 339).

Comments.-- The holotype comes from an area of low transitional forest as well as the specimens examined from Laguna La Brea. The locality Maimará corresponds to the Prepuna, and although this area is not typical for this species, there also are records from the Puna of Tupiza in Bolivia, for *G. lockwoodi* (Thomas, 1926b). We captured males with abdominal testes in May (1 specimen was molting) and August.

Graomys griseoflavus (Waterhouse, 1837)
Gray Leaf-eared Mouse

Graomys griseoflavus chacoensis (Allen, 1901)

Phyllotis chacoensis Allen, 1901. Bulletin of the American Museum of Natural History, 14:405-412.

Distribution in Argentina.--Cabrera (1961a) considered it likely that this species occurred in the province of Formosa. However, on the base of specimens examined it is clear that the distribution of this species is wider than thought and includes the provinces of Jujuy, Tucumán, Formosa, Catamarca, Salta, and San Juan.

Specimens Examined (2).--La Quiaca, 1 (MACN 36.802); Oyeros, 3 km al N, camino entre rutas 61 y 43, 1 (MMD 202).

Comments.--We expect that further study will support specific recognition for this species. The specimens of *chacoensis* have a pure white venter, while in the type specimens of *G. g. cachinus*, the ventral hairs are gray at the base. Both taxa are present in Jujuy and other provinces of NW Argentina, in areas very close to each other, but analysis of full series' of specimens from throughout their distribution is needed to resolve their taxonomy. The locality Oyeros is in the Chaco region and La Quiaca is in the Puna. At the first locality a female with open vagina was captured in October.

Graomys griseoflavus cachinus (Allen, 1901)

Phyllotis cachinus Allen, 1901. Bulletin of the American Museum of Natural History,

14:409.

Distribution in Argentina.--Jujuy and Salta provinces (Yepes, 1935b; Cabrera, 1961a).

Specimens Examined (15).--Palma Sola, 2 (AMNH 185223, 185272); Santa Bárbara, Santa Bárbara, 1 (AMNH 185222); Villa Carolina, Río Lavallén, 500 m, 12 (BMNH 20.1.7.66, 20.1.7.67, 20.1.7.68, 20.1.7.69, 20.1.7.70, 20.1.7.71, 20.1.7.72, 20.1.7.73, 20.1.7.74, 20.1.7.75, 20.1.7.76, 20.1.7.77).

Comments.--Hershkovitz (1962) identified the specimens from Villa Carolina (cited by Thomas, 1920a, as *Graomys lockwoodi*) as *Phyllotis griseoflavus griseoflavus*. We consider these specimens to be *G. g. cachinus* on the basis of pelage coloration and the size of the bullae. The collecting localities are in the Chaco and in the Yungas regions. At Villa Carolina, the specimens were captured among fallen trunks and hollow trees. A juvenile was captured at Palma Sola in July. Matschie (1894) cited *Phyllotis griseoflavus* for the locality Aival.

Genus *Neotomys*

Neotomys ebriosus Thomas, 1894
Andean Swamp Mouse

Neotomys ebriosus Thomas, 1894. Annals and Magazine of Natural History, ser. 6, 14:348.

Distribution in Argentina.--Northwestern Argentina to Sierra de Aconquija; confirmed in Jujuy, Salta, Catamarca, and San Juan provinces (Barquez, 1983; Pardiñas and Ortiz, 2001).

Specimens Examined (17).--Cerro de Tilcara, 1 (CML 614); La Lagunita, Maimará, 2 (BMNH 19.7.10.1, 19.7.10.2); Sierra de Zenta, 6 (MACN 27.78; 27.79, 27.80, 27.81, 27.82, 31.112; see comments under *Localities and maps*); Sierra de Zenta, 4500 m, 8 (BMNH 21.11.1.33, 21.11.1.34 *Neotomys vulturnus* holotype, 21.11.1.35, 21.11.1.36, 21.11.1.37; 2 CML 115, 307; 1 FMNH 41282; see comments under *Localities and maps*).

Additional Records.--La Lagunita, Maimará, 4300 m (Thomas, 1921c, como *N. vulturnus*); Yavi (Pardiñas and Ortiz, 2001).

Comments.--According to Thomas (1921c) this is a rare species and lives in isolation from other rodents; it is found near streams or among isolated rocks. Barquez (1983) mentioned that this species lives in dense grasslands in "vegas." The holotype of *N. vulturnus* was collected at the border of a stream beneath a stone, similar to other specimens that were captured along streams or in marshes. Juveniles were captured in May and July. All records correspond to the High Andean area.

Genus *Phyllotis*

Phyllotis caprinus Pearson 1958
Capricorn Leaf-eared Mouse

*Phyllotis caprinus*_Pearson 1958. University of California Publications in Zoology, 56:435.

Distribution in Argentina.--Jujuy and Salta provinces (Pearson, 1958; Díaz et al., 2000).

Specimens Examined (34).--9 km NW Bárcena, 6 (ARG 4598, 4602, 4606, 4608, 4613, 4623); Chilcayoc, 4 (1 ARG 4615; 3 MMD 172, 173, 177); Maimará, 2200 m, 1 (MACN 27.120); Maimará, 2230 m, 11 (6 BMNH 12.12.12.21, 12.12.12.22, 12.12.12.23, 12.12.12.24, 12.12.12.25, 12.12.12.26; 1 FMNH 85847; 4 MACN 27.112, 27.113, 27.114, 27.115); Maimará, 2328 m, 1 (BMNH 17.12.31.1); Maimará, 2500 m, 8 (2 CML 98, 282; 6 MACN 31.31, 31.32, 31.33, 31.34, 31.35, 31.36); Sierra de Zenta, 4500 m, 1 (FMNH 41287; see comments under *Localities and maps*); Tilcara, 2350 m, 1 (BMNH 17.12.31.2); Tilcara, 8000 ft., 1 (AMNH 41879).

Additional Records.--Humahuaca, 2355 m (Pearson, 1958); La Laguna; Maimará (Steppan, 1995); Tilcara, 2330 m (Pearson, 1958; Hershkovitz, 1962 as *P. darwini caprinus*).

Comments.--The localities cited by Pearson (1958) for *caprinus* are the same as those cited by Thomas (1913) for *P. wolffshoni*, who later corrected the identification of this species to *P. ricardulus* (Thomas, 1919b), because the toothrows of these specimens were shorter than in *wolffshoni*. The specimens from Maimará were treated by Yepes (1933a) as *P. wolffshoni*, and by Pearson (1958) as *caprinus*. The specimens from Alfarcito cited by Pearson (1958) as *caprinus* are here considered *P. wolffshoni*. The majority of the collecting localities are from the Prepuna or High Andean region, but Chilcayoc and Bárcena occur in an ecotone between Yungas and Prepuna. Females with closed vaginas and males with abdominal testes were collected in July and September; and males with scrotal testes in September. In July, we recorded a molting juvenile.

Phyllotis osilae J. A. Allen, 1901
Bunchgrass Leaf-eared Mouse

Phyllotis osilae osilae J. A. Allen, 1901

Phyllotis osilae J. A. Allen, 1901. Bulletin of the American Museum of Natural History, 14:44.

Distribution in Argentina.--Northern of Argentina, in patches of grasslands from 2700 to 4100 m, below 1800 m in some places (Pearson, 1958).

Specimens Examined (36).--9 km NW Bárcena, 8 (ARG 4596, 4597, 4600, 4605, 4611, 4612, 4614, 4624); Arroyo La Horqueta, 3 km al SE de las Laguna de Yala, 2100 m, 1 (MMD 181); Casa Colorada, app 2 km al N de Alfarcito, 3034 m, 6 (MMD 374, 380, 381, 382, 384, 385); Chilcayoc, 2 (1 ARG 4616; 1 MMD 174); León, 1500 m, 13 (BMNH 18.1.1.20, 18.1.1.21, 18.1.1.22, 18.1.1.23, 18.1.1.24, 18.1.1.25, 18.1.1.26, 18.1.1.27, 18.1.1.28, 18.1.1.29, 18.1.1.30, 18.1.1.31, 18.1.1.32); Miyuyoc, 3750 m, 2 (MMD 398, 400); Mountains W of Yala, 1 (FMNH 22341); Mountains W of Yala, 10000 ft., 2 (FMNH 22342, 22343); Río Tiraxi, app 5 km al S de Tiraxi, sobre ruta provincial N° 29, 1 (MMD 158).

Additional Records.--León (Thomas, 1918, as *Phyllotis darwini tucumanus*); León, 1 mile west, 5800 ft. (Pearson, 1958; Hershkovitz, 1962).

Comments.--According to Pearson (1958), this subspecies lives in grasslands on the W slope of the Andes. In Jujuy, most localities are W of Quebrada de Humahuaca in Yungas or Prepuna, with the exception of Casa Colorada, which is W of the Sierra de Tilcara, and Miyuyoc, near Sierra de Zenta, and is in the Puna.

We recorded females with closed vaginas in July and September; and males with abdominal testes in June, July, and September. A young specimen was recorded in June and molting specimens in June and July.

Phyllotis osilae nogalaris Thomas, 1921

Phyllotis nogalaris Thomas, 1921. Annals and Magazine of Natural History, ser. 9, 8:611.

Distribution in Argentina.--Mountains of Salta and Jujuy provinces (Cabrera, 1961a).

Specimens Examined (9).--Abra Pampa, 2 (CML 1276, 1283); Cerro Calilegua, El Duraznillo, 2600 m, 2 (CML 1724, 1725); Higuerilla, 1 (BMNH 21.11.1.23); Higuerilla, 2000 m, 1 (BMNH 21.11.1.22 *Phyllotis nogalaris* holotype); La Ciénaga, 3700 m, 1 (CML 1259); La Ciénaga, Abra Pampa, 1 (CML 1280); Rinconada, 6 km al N, camino a Timón Cruz, 4286 m, 1 (MMD 487).

Comments.--Until now, the type locality, situated in the Yungas, was the only known locality for this subspecies. Here we are adding a new locality close to the type locality but in the Puna region.

According to notes of E. Budin, the collector of the original specimens, this subspecies lives among walnut trees, a reason for which he call them “rata de los nogales.” Pearson (1958) noted that this species is isolated and distributed E of the slopes of the Andes; but we extend its distribution to the W of Jujuy Province. Cabrera (1961a) indicated the presence of this subspecies in Salta and Jujuy provinces, whereas Hershkovitz (1962) recognized it only from the type locality. We documented overlap in the distribution of both subspecies, but because of the scarcity of specimens and localities, we provisionally retain their taxonomic distinctiveness. A male with scrotal testes was collected in March.

Phyllotis wolffshoni Thomas, 1902
Wolffsohn’s Leaf-eared Mouse

Phyllotis wolffsohni Thomas, 1902. Annals and Magazine of Natural History, ser. 7, 9:131

Distribution in Argentina.--According to Pearson (1958) and Hershkovitz (1962), this species is not present in Argentina. Anderson (1997) cited a locality near the Argentine border, in Tarija Department, Bolivia. Reidentification of specimens from Alfarcito at the BMNH documents that this species ranges to Argentina.

Specimens Examined (8).--Alfarcito, 2600 m, 4 (BMNH 21.11.1.24, 21.11.1.26, 21.11.1.27, 21.11.1.28); La Quiaca, 17 km al O y 3 km al S sobre ruta provincial N° 5, 3711 m, 4 (MMD 433, 434, 436, 438).

Comments.--This species it is being transferred to *Tapecomy*s (see Steppan et al., this volume). The specimens from Alfarcito were cited by Thomas (1921c) as *P. ricardulus* and by Pearson (1958) as *P. caprinus*. Alfarcito is a locality in the Prepuna and La Quiaca is in the Puna, near the border with Bolivia. In February we recorded a female with closed vagina, a male with abdominal testes, 2 males with scrotal testes, and a single juvenile.

Phyllotis xanthopygus (Waterhouse, 1837)
Yellow-rumped Leaf-eared Mouse

Mus xanthopygus Waterhouse, 1837. Proceedings of the Zoological Society of London, p. 28.

Distribution in Argentina.--Widely distributed in the country, in the mountain chains of NW Jujuy Province, S to Santa Cruz (Steppan, 1998; Kramer et al., 1999).

Specimens Examined (138).--10 km west of Purmamarca on highway 52, 3 (1 ARG 2684; 2 CML 3941, 3942); 11 km east of Humahuaca, 2 km east of Pucará on road to Cianzo, 11500 ft., 2 (ARG 2692, 2694); A 12 km cruce con ruta 40, sobre ruta 52, 3700 m, 1 (IADIZA 3533); Abra Pampa, 2 (CML 1277, 1278); Abra Pampa, 3480 m, 1 (CML 1285); Abrapampa, 3500 m, 11 (BMNH 19.8.1.1, 19.8.1.10, 19.8.1.12, 19.8.1.15, 19.8.1.16, 19.8.1.2, 19.8.1.4, 19.8.1.5, 19.8.1.7, 66.1678, 66.1679); Casa Colorada, app 2 km al N de Alfarcito, 3034 m, 1 (MMD 373); Casabindo, 4000 m, 5 (BMNH 19.8.2.10, 19.8.2.11, 19.8.2.12, 19.8.2.13, 19.8.2.16); Cerro Casabindo, 4500 m, 3 (BMNH 19.8.2.15, 19.8.2.19, 19.8.2.20); Cerro de Lagunita al Este de Maimará, 4500 m, 1 (BMNH 12.12.12.27); Cerro Hermoso, 17 (MACN 19521, 19523, 19524, 19525, 19526, 19527, 19528, 19529, 19530, 19531, 19532, 19534, 19535, 19536, 19537, 19539, 19540); Cuesta de Lipán, 15 km al O de Purmamarca, sobre ruta 52, 3156 m, 11 (MMD 292, 293, 294, 295, 296, 305, 306, 307, 308, 309, 310); Cuesta del Hurón, 29 km al O de Cienegüillas sobre ruta provincial N° 64, 3835 m, 6 (MMD 448, 449, 452, 456, 458, 459), Curques, 24 km al N de Susques, sobre ruta provincial N° 74, 7 (MMD 280, 281, 284, 288, 289, 290, 291); Humahuaca, 16 km al E, camino a Cianzio, 2 (CML 3939, 3940); La Ciénaga, Cochinoca, 1 (CML 1264); La Ciénaga, Abra Pampa, 2 (CML 1274, 1281); La Laguna 4500 m, Sierra de Zenta, E de Maimará, 4 (MACN 27.117, 27.118, 27.119, 27.121; see comments under *Localities and maps*); La Quiaca, 17 km al O y 3 km al S, sobre ruta provincial N° 5, 3711 m, 4 (MMD 420, 421, 425, 439); Laguna de Pozuelos, 11 (MACN 19391, 19392, 19393, 19395, 19400, 19401, 20309, 20310, 20311, 20312, 20313); Maimará, 1 (CML 328); Maimará, 2500 m, 2 (CML 317, 338); Mina Pan de Azúcar, 8 km al N y 5 km al O camino a Herrana, 3820 m, 5 (MMD 492, 494, 495, 505, 508); Mina Pirquitas, 31 km al SE, Sierra de Quichagua, sobre ruta provincial N° 74b, 4200 m, 5 (MMD 513, 517, 518, 522, 523); Miyuyoc, 3750 m, 3 (MMD 396, 401, 402); Pirquita, 10 km antes de la mina, 3 (IADIZA 3358, 3360, 3361); Pirquita, 20 km NO de Coranzulí, 1 (IADIZA 3351); Rinconada, 6 km al N, camino a Timón Cruz, 4286 m, 2 (MMD 484, 485); Río Yacoraite, 7 km al N de Huacalera y 3 km al O de ruta 9, 2740 m, 1 (MMD 386); Sierra de Zenta, 5 (2 CML 285, 320; 3 MACN 47.23, 47.22, 47.23; see comments under *Localities and maps*); Sierra de Zenta, 4500 m, 10 (1 BMNH 21.11.1.29; 1 CML 378; 8 MACN 32.50, 32.51, 32.52, 32.53, 32.54, 32.55, 32.56, 32.57; see comments under *Localities and maps*); Tres Cruces, 4000 m, 2 (FMNH 41288, 41289); Yavi Chico, 1 (MACN 36.446); Yavi, 3600 m, 2 (CML 2870, 2871).

Additional Records.--Alfarcito, 2600 m (Pearson, 1958 as *P. darwini rupestris*); Casabindo (Osgood, 1943, as *P. darwini rupestris*); Casabindo, 4000-4500 m (Thomas, 1919b, as *P. ricardulus*); Cerro Casabindo, 4000-4800 m (Pearson, 1958, as *P. darwini rupestris*); Cerro de Lagunita, 4500 m (Thomas, 1913, as *P. arenarius*; Pearson, 1958, as *P. darwini rupestris*); Cerro Hermoso (cercanías), 2800 m; Duraznillar, 2500 m (Heinonen and Bosso, 1994, as *P. darwini*); Tilcara, 0.8 km E, 2600 m (Pearson, 1958; Hershkovitz, 1962); Tilcara, 2600 m (Pearson, 1958, as *P. darwini rupestris*; Hershkovitz, 1962, as *P. darwini rupestris*).

Comments.--Two subspecies may occur in Jujuy Province, *P. x. ricardulus* and *P. x. rupestris* (Cabrera, 1961a; Steppan, 1998). Under *P. d. rupestris*, Hershkovitz (1962) included specimens cited by Thomas (1921c) and Yepes (1935b) as *P. ricardulus*, and he did not recognize *P. d. ricardulus* as a valid subspecies. Pearson (1958) considered *ricardulus* to be a valid subspecies but not present in the province of Jujuy. La Laguna 4500 m, Sierra de Zenta was cited by Yepes (1933a) for *P. d. rupestris*, but later (Yepes, 1935b) he cited the same locality for *P. d. ricardulus*. The localities of the specimens examined and additional records belong to the Prepuna, Puna, High Andean, and grasslands in the Yungas. In general, this species is captured in rocky areas with sparse vegetation of grasses, shrubs, and cacti.

Females with closed vaginas were recorded in February, March, June, and December, females with open vaginas in February, March, and December, pregnant females in February (1 with 3 fetuses, 1 with 6 fetuses, and 1 with 7 fetuses) and December (1 with 3 fetuses), and lactating females in March and December. We collected males with abdominal testes in March and June, and males with scrotal testes in February, March, October, and December. Juveniles have been reported in February, April, November, and October. Molting specimens were recorded in February, March, June, and December.

Genus *Reithrodon*

Reithrodon auritus (Fischer, 1814)
Bunny Rat

Mus auritus Fischer, 1814. Zoognosia, 3:71.

Distribution in Argentina.--Northern Argentina, in Jujuy, Tucumán, Catamarca, and Córdoba south to Tierra del Fuego (Barquez et al., 1991; Mares et al., 1997; Pardiñas and Galliari, 2001).

Specimens Examined.--None.

Additional Records.--Cochinoca (Pardiñas and Galliari, 2001).

Comments.--Dalby and Mares (1974) cited this species for Jujuy, based on a specimen from the MACN (31.37), which was reidentified as *Graomys domorum*. Consequently the species was excluded from Jujuy (Díaz and Barquez, 1999), and our inclusion of this species in the province is based on a specimen deposited at the BMNH (21.4.21.3), whose identity was verified by E. González (personal communication).

Tribe Thomasomyini

Genus *Rhipidomys*

Rhipidomys austrinus Thomas, 1921
Southern Climbing Mouse

Rhipidomys austrinus Thomas, 1921. Annals and Magazine of Natural History, ser. 9, 7:183.

Distribution in Argentina.--Mountain forests of NW Argentina, in Jujuy and Salta provinces (Cabrera, 1961a).

Specimens Examined (4).--Abra de Cañas, El Monolito, 1700 m, 1 (CML 1804); El Palmar, 2.9 km E, Sierra de Santa Bárbara, 1 (ARG 3443); Sunchal, Sierra Santa Bárbara, 1200 m, 1 (BMNH 21.1.1.17 *Rhipidomys austrinus* holotype); Sunchal, Sierra Santa Bárbara, 1600 m, 1 (BMNH 21.1.1.18 paratype).

Additional Records.--Cerro Calilegua (Olrog, 1979; as *R. leucodactylus austrinus*).

Comments.--According to annotations of E. Budin, the specimens from Sunchal live in large walnut trees. The specimen from El Palmar was captured in a transitional area near a river, in July; the specimen is a molting juvenile male with scrotal testes. Records of this species are scarce and all correspond to the Yungas region.

Olrog (1979) cited a record from Cerro Calilegua that was based in the specimen examined from Abra de Cañas deposited in the CML.

Suborder Histricognatha
Family Erethizontidae
Subfamily Erethizontinae

Genus *Coendou*

Coendou bicolor (Tschudi, 1844)
Bicolor-spined Porcupine

Sphingurus bicolor Tschudi, 1844. Theriologie. Untersuchungen ünder die Fauna Peruana. Scheitlin und Zollikofer, St. Gallen, Switzerland, p.186.

Distribution in Argentina.--Jujuy Province (Lucero, 1987; Heinonen and Bosso, 1994).

Specimens Examined (1).--Yuto, 1 (CML 591).

Additional Records.--Abra de Cañas, 1700 m; Aguas Negras, 600 m (Heinonen and Bosso, 1994).

Comments.--Records of this species are scarce in Argentina (Chébez, 1994). The records from Jujuy are located in the Yungas region. The specimen examined was a female captured in October 1979.

Family Chinchillidae
Subfamily Chinchillinae

Genus *Chinchilla*

Chinchilla brevicaudata Waterhouse, 1848
Short-tailed Chinchilla

Chinchilla brevicaudata Waterhouse, 1848. The natural history of the mammalia. Hippolyte Bailliere, Publisher, London, 2:241.

Distribution in Argentina.--High Andean region in the western portions of Jujuy, Salta, and Catamarca provinces (Cabrera, 1961a).

Specimens Examined (15).--Abra Pampa, 5 (1 CM 44100, 4 MACN 13.037, 28.164, 16371, 16372); Abra Pampa, Criadero, 3 (MACN 52.9, 52.91, 52.92); Abra Pampa estación INTA (Instituto Nacional de Tecnología Agropecuaria), 3 (MACN 16.261,16.267, 16.268); Criadero Nacional, 3 (MACN 39.389, 39.390, 39.391); "Jujuy," 1 (MACN 36118).

Additional Records.--Susques (Cajal and Bonaventura, 1998).

Comments.--The composition of this genus is controversial. Cabrera (1961a) recognized 2 species (*C. brevicaudata* and *C. lanigera*), an opinion that was followed by most later authors, although Pine et al. (1979) treated *C. brevicaudata* as a subspecies of *C. lanigera* (Chébez, 1994). Anderson (1997) considered the 2 species as *Chinchilla chinchilla* Lichtenstein, 1830, suggesting that it likely is extinct in Bolivia. According to Chébez (1994), the 2 species are present in NW Argentina. Yepes (1929) cited *C. lanigera* from western Catamarca, Salta, and Jujuy provinces, whereas Woods (1993) cited only *C. brevicaudata* for Argentina. Cajal and Bonaventura (1998) mentioned that, according to the local residents, there likely is a relictual population of *C. brevicaudata* in the high rocky areas of Salta and Catamarca provinces, and at high altitudes of Susques in the province of Jujuy.

The species cited by Crespo (1941) as *C. intermedia*, was later considered by Cabrera (1961a) as *C. brevicaudata boliviana*, who mentioned that its distribution in the Altiplano of Jujuy is restricted to the highest and most remote areas of the district, due to the persecution suffered by this species.

Specimens examined are all from the "Criadero Nacional de Abra Pampa," from where they were released because of limited resources to feed them. An unidentified epizootic in 1982 produced more losses (Chébez, 1994). This species lives in the Puna and the High Andean region. After 5 years of field trips through the province of Jujuy (1994-1998), we have not recorded any wild specimen but, according to Chébez (1994), a Provincial Reserve was established for the species.

Genus *Lagidium*

Lagidium viscacia (Molina, 1782)
Southern Vizcacha

Lepus viscacia Molina, 1782. Saggio sulla storia naturale del Chili. S. Tommaso d'Aquino, Bologna, p.307.

Lagidium viscacia vulcani Thomas, 1919

Lagidium vulcani Thomas, 1919. Annals and Magazine of Natural History, ser. 9, 4:133.

Distribution in Argentina.--Northern Jujuy and NW portion of Salta Province (Yepes, 1929; Cabrera, 1961a).

Specimens Examined (24).--Casabindo, 2 (BMNH 19.8.2.30, 19.8.2.34); Casabindo, 4000 m, 1 (BMNH 19.8.2.31); Cerro Casabindo, 4800 m, 2 (BMNH 19.8.2.32 *Lagidium vulcani* holotype, 19.8.2.33); Cerro Guadalupe, 4100 m, 1 (MACN 39.499); Cuesta del Hurón, 29 km al O de Cienegüillas, sobre ruta provincial N° 64, 3835 m, 1 (MMD 443); Curques, 24 km al N de Susques, sobre ruta provincial N° 74, 2 (MMD 278, 279); Mina Pan de Azúcar, 13 km al S, sobre Río Cincel, 1 (MMD 532); Mina Pirquitas, 31 km al SE, Sierra de Quichagua, sobre ruta provincial N° 74 b, 4200 m, 3 (MMD 516, 519, 534); Norte de Lizoite, 5 (MACN 41.26, 41.27, 41.37, 41.54, 41.97); Rinconada, 13 km al N camino a Timón Cruz, 1 (MMD 490); Río Coyaguaima, 4000 m, 1 (MACN 39.500); Sierra de Cochinoca, 1 (MACN 14708); Yavi Chico, 3 (MACN 36.432, 41.115, 41.130).

Additional Records.--Algunos kilómetros al WNW de Cerro Casabindo (Crespo, 1941); Laguna de Pozuelos (Massoia, 1993); Miyuyoc, 3750 m (local residents, personal communication).

Comments.--This subspecies was frequently observed during the our surveys to the Puna in Jujuy; they were seen in groups of several individuals living in rocky areas. They are diurnal and use holes and crevices in the rocks as shelters. In March, a pregnant female, a female with closed vagina, and a male with abdominal testes were recorded. Two specimens, 1 from Mina Pan de Azúcar, 13 km al S, and another from Mina Pirquitas, 31 km al SE (MMD 534), consist of postcranial bones extracted from feces.

Lagidium viscacia tucumanum (Thomas, 1907)

Viscacia tucumana Thomas, 1907. Annals and Magazine of Natural History, ser. 7, 19:444.

Distribution in Argentina.--Mountains of Salta and Jujuy provinces, reaching the center of the latter province (Cabrera, 1961a).

Specimens Examined (17).--Alfarcito, 2600 m, 2 (BMNH 21.11.1, 21.11.1.90); Cerro de Lagunita al Este de Maimará, 4500 m, 1 (BMNH 12.12.12.48); La Laguna 4500 m, Sierra de Zenta, E de Maimará, 2 (MACN 27.99, 27.100; see comments under *Localities and maps*); Maimará, 1 (CR 15); Maimará, 2230 m, 2 (BMNH 12.12.12.46, 12.12.12.47); Mountains W of Yala, 12000 ft., 2 (FMNH 24095, 24096); Sierra de Zenta, 5 (2 CML 441, 442; 1 CR 16; 2 MACN 32.66, 32.67; see comments under *Localities and maps*); Tilcara, 2 (MACN 8.18, 8.19).

Additional Records.--Cerro Hermoso (cercanías), 2800 m (Heinonen and Bosso, 1994); Cerro Negro (local residents, personal communication); Laguna Colorada (Yepes, 1944, juvenile cited as *L. vulcani*).

Comments.--The records for this subspecies in Jujuy are in the High Andean region and in the Prepuna, clearly separated from *L. v. vulcani*, which occurs in the northern portion of the province. The locality "Mountains W of Yala" is not accurate, and even though cited for other species typical of Yungas forests, the indication of this locality for this species should be in reference to a place at higher altitude. The specimen cited by Yepes (1944) was not examined. A juvenile specimen was captured in April.

Subfamily Lagostominae

Family Caviidae

Subfamily Caviinae

Genus *Cavia*

Cavia tschudii Fitinger, 1857
Montane Guinea Pig

Cavia tschudii Fitzinger, 1857. Sitzungsberchte Akademie der Wissenschaften in Wien., p.154.

Distribution in Argentina.--Northwestern Argentina, in the mountains E of the High Andes, from Tarija in Bolivia, to Tucumán Province in Argentina (Cabrera, 1961a). Yepes (1935b) suggested that this species should be found in Jujuy (Cabrera, 1953), a prediction later confirmed by Olrog (1979).

Specimens Examined (2).--Cerro Calilegua, El Duraznillo, 1 (CML 1754); Mountains W of Yala, 1 (FMNH 23306).

Additional Records.--Cerro Calilegua (Olrog, 1979), Inca Cueva 5 site; La Cueva site (Ortiz, 2003).

Comments.--The specimen examined at the CML, is a very young specimen, probably the same specimen cited by Olrog (1979).

Genus *Galea*

Galea musteloides Meyen, 1832
Common Yellow-toothed Cavy

Galea musteloides Meyen, 1832. Nouva Acta Acad. Caesareae Leop.-Carol. Natur. Curiosorum, 16:567.

Distribution in Argentina.--Northwestern Argentina, S to northern Chubut, and eastward in all provinces except in Misiones, Corrientes, and Entre Ríos provinces (Cabrera, 1953, 1961a).

Specimens Examined (100).--11 km east of Humahuaca, 2 km east of Pucará on road to Cianzio, 11.500 ft., 1 (ARG 2722); Abra Pampa, 14 (9 CML 1113, 1114, 1115, 1116, 1117, 1118, 1119, 1120, 1121; 4 CR 30, 31, 32, 40; 1 MACN 27.57); Abra Pampa, 3500 m, 3 (BMNH 19.8.1.73, 19.8.1.74, 19.8.1.75); Abra Pampa, 3800 m, 4 (CML 1104, 1106, 1107, 1108); Alfarcito, 2600 m, 5 (4 BMNH 21.11.1.91, 21.11.1.92, 21.11.1.93, 21.11.1.94; 1 FMNH 46105); Cuesta del Hurón, 29 km al O de Cienegüillas, sobre ruta provincial N° 64, 3835 m, 1 (MMD 471); La Ciénaga, Abra Pampa, 2 (CML 1105, 1112); La Laguna 4500 m, Sierra de Zenta, E de Maimará, 3 (MACN 27.89, 27.90, 27.91; see comments under *Localities and maps*); La Quiaca, 1 (MACN not number); Maimará, 2230 m, 5 (4 BMNH 12.12.12.49, 12.12.12.50, 12.12.12.52 como *Kerodon boliviensis*, 12.12.12.53 *Galea comes* holotype; 1 MACN 27.88); Maimará, 2500 m, 3 (MACN 31.28, 31.29, 31.30); Mina Pan de Azúcar, 13 km al S, sobre Río Cincel, 1 (MMD 533); Mina Pan de Azúcar, 8 km al N y 5 km al O, camino a Herrana, 3820 m, 1 (MMD 503); Miyuyoc, 3750 m, 2 (MMD 390, 397); Perico, 4000 ft., 5 (AMNH 41580, 41581, 41582, 41583, 41584); Rinconada, 6 km al N, camino a Timón Cruz, 4286 m, 1 (MMD 475); Santa Bárbara, Santa Bárbara, 1 (AMNH 185268); Santa Catalina, 7 km al S, sobre ruta provincial N° 65, 3845 m, 1 (MMD 472); Sierra de Zenta, 4500 m, 5 (3 BMNH 21.11.1.95; 21.11.1.96, 21.11.1.97; 2 MACN 32.64, 32.65; see comments under *Localities and maps*); Sunchal, Sierra Santa Bárbara, 1200 m, 5 (BMNH 21.1.1.71, 21.1.1.72, 21.1.1.73, 21.1.1.74, 21.1.1.75); Tilcara, 8000 ft., 9 (AMNH 41571, 41572, 41573, 41574, 41575, 41576, 41577, 41578, 41579); Tres Cruces, 3700 m, 1 (CML 73); Villa Carolina, Río Lavallén, 500 m, 10 (BMNH 20.1.7.121, 20.1.7.122, 20.1.7.123, 20.1.7.124, 20.1.7.125, 20.1.7.126, 20.1.7.127, 20.1.7.128, 20.1.7.129, 20.1.7.130); Yavi Chico, 16 (MACN 36.419, 36.420, 36.422, 36.423, 36.424, 36.425, 36.426, 41.110, 41.111, 41.112, 41.113, 41.118, 41.119, 41.120, 41.121, 41.122).

Additional Records.--Laguna de Pozuelos (Massoia, 1993); Perico (Yepes, 1944); San Pedro (Matschie, 1894, as *Cavia leucoblephara*); Villa Carolina, 1258 m (Thomas, 1920a, as *Galea comes*).

Comments.--*Galea comes*, described by Thomas (1919b), is considered a synonym of *G. musteloides*; the holotype of the former (BMNH 12.12.12.53) was collected in Maimará, but erroneously indicated as Abrapampa. There is also an error in the citation by Thomas (1920a) of the locality Villa Carolina, 1258; the original specimen tags specify Villa Carolina, Río Lavallén, 500 m. In Jujuy, this species has been found in all phytogeographic regions from the Chaco through the Yungas to 4500 m in the High Andean region. We captured a female with closed vagina in March, a male with scrotal testes in March, and males with abdominal testes in March and June. Juveniles were collected in February and March; the latter was molting. The majority of the specimens were captured with a shotgun, but some were collected with live traps (Sherman trap). One specimen was captured in a trap set near a stone fence, at the same place that a specimen of *Octodontomys gliroides* was collected. The record from Mina Pan de Azúcar, 13 km al S, is represented by an upper toothrow and upper incisors which were extracted from an unidentified canid feces.

Genus *Microcavia*

Microcavia australis (I. Geoffroy Saint-Hilaire and d'Orbigny, 1833)
Southern Mountain Cavy

C[*avia*] *australis* I. Geoffroy Saint-Hilaire and d'Orbigny, 1833. Magazin de Zoologie, p. 3.

Distribution in Argentina.--From Jujuy in NW Argentina, to Santa Cruz Province in the south (Tognelli et al., 2001).

Specimens Examined.--None.

Additional Records.--Yavi Chico (Cabrera, 1953).

Comments.--The only known record for Jujuy is in the Puna region.

Subfamily Dolichotinae

Genus *Dolichotis*

Dolichotis salinicola Burmeister, 1876
Chacoan Mara

Dolichotis salinicola Burmeister, 1876. Proceedings of the Zoology Society of London, p. 634.

Distribution in Argentina.--From the salt flats areas of San Luis and Córdoba provinces, N through the eastern part of La Rioja and Catamarca; W of Santiago del Estero, Tucumán, and Salta, to the S end of Bolivia (Cabrera, 1953, 1961a); recently included in Jujuy Province (Díaz and Barquez, 1999).

Specimens Examined.--None.

Additional Records.--E of El Palmar, Sierra de Santa Bárbara (J. K. Braun, personal communication); "Jujuy" (MACN catalogue, not found); Palma Sola (local residents, personal communication).

Comments.--According to the curator (O. Vaccaro and M. Piantanida, personal communication), the identity of the specimen registered at the MACN is correct, but the skin was disposed of because of its poor condition, and the skull was donated to another institution. This specimen represented the only documented record for the species in Jujuy Province. This species lives in the Chaco whose deterioration may have affected the wild populations; a few years ago this species was abundant in the area of Palma Sola.

Family Hydrochoeridae

Genus *Hydrochoerus*

Hydrochoerus hydrochaeris (Linnaeus, 1766)
Capybara

Sus hydrochaeris Linnaeus, 1766. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Volumen 1. Regnum Animale. 12th edition. Laurentii Salvii, Stockholm, 1:103.

Distribution in Argentina.--From NW Argentina, in Jujuy, Salta, and Formosa province, SE through Santiago del Estero, Chaco, and Santa Fe to Buenos Aires Province; and in the NE in Misiones, Corrientes, and Entre Ríos provinces (Mones and Ojasti, 1986; Alvarez, 2002).

Specimens Examined.--None.

Additional Records.--Agua Salada (local residents, personal communication); Aguas Negras, 600 m (Heinonen and Bosso, 1994); Laguna La Brea (local residents, personal communication); Río de Las Pavas (local residents, personal communication).

Comments.--Some authors restricted its distribution in Argentina to the NE portion of the country (Honacki et al., 1982; Woods, 1993), but its presence is confirmed in Salta and Jujuy provinces, in the NW (Mares et al., 1989; Aceñolaza, 1991; Redford and Eisenberg, 1992; Alvarez, 2002). In Jujuy, the records are from the transitional forests of the Yungas and from the Chaco.

Family Agoutidae
Subfamily Dasyproctinae

Genus *Dasyprocta*

Dasyprocta punctata Gray, 1842
Central American Agouti

Dasyprocta punctata Gray, 1842. Annals and Magazine of Natural History, ser. 1, 10:264.

Distribution in Argentina.--Jujuy and Salta provinces (Cabrera, 1961a).

Specimens Examined (5).--"Jujuy," 2 (MACN 9.29, 32.102); Yuto, 3 (1 MCNS, not numbered; 1 CR 8; 1 AMNH 179895).

Additional Records.--Agua Salada (local residents, personal communication); Aguas Negras, 600 m (Heinonen and Bosso, 1994); Aguas Negras, Camping, Parque Nacional Calilegua (M. M. Díaz, personal observation); Arroyo El Cano, 7 km al N del Río Saladillo (local residents, personal communication); Arroyo Sauzalito (R. M. Barquez, personal observation); Caimancito, 550 m (Heinonen and Bosso, 1994); Camino a Vinalito, entre Las Siete Aguas y Vinalito (M. M. Díaz, P. Diosque, and D. A. Flores, personal observation); Cercanías de El Simbolar (local residents, personal communication); Cerro Calilegua (Olrog, 1979); El Simbolar, 25 km al SO de Palma Sola (R. M. Barquez, personal observation); Mesada de las Colmenas, 1150 m (Heinonen and Bosso, 1994); Palma Sola, 18 km al S (local residents, personal communication); Río Jordán (Olrog, 1979); Sierra Santa Bárbara, app 6 km al E de El Palmar (R. M. Barquez, personal observation); Villa Carolina, 500 m (Thomas, 1920a, as *D. variegata boliviae*)

Comments.--This is a common species in Jujuy, but only are few specimens have been deposited in systematic collections. The records correspond to the Yungas and Chaco phytogeographic provinces. At Aguas Negras, 1 specimen was observed during the day, at about 1000 hrs near our campsite. In Yuto, a juvenile with M4 not completely erupted was captured in June.

Family Ctenomyidae

Genus *Ctenomys*

Ctenomys frater Thomas, 1902
Forest's Tuco-tuco

Ctenomys frater Thomas, 1902. Annals and Magazine of Natural History, ser. 7, 9:185.

Ctenomys frater barbarus Thomas, 1921

Ctenomys budini barbarus Thomas, 1921. Annals and Magazine of Natural History, ser. 9, 7:185

Distribution in Argentina.--Northwestern Argentina, in the mountains of S Jujuy and adjacent portion of Salta (Cabrera, 1961a).

Specimens Examined (20).--San Rafael, Sierra Santa Bárbara, 1000 m, 7 (BMNH 21.1.1.65, 21.1.1.66, 21.1.1.67, 21.1.1.68, 21.1.1.69, 21.1.1.70, 66. 1952); Sunchal, Sierra de Santa Bárbara, 1200 m, 8 (7 BMNH 21.1.1.54 *Ctenomys budini barbarus* holotype, 21.1.1.57, 21.1.1.59, 21.1.1.61, 21.1.1.62, 21.1.1.63, 21.1.1.64; 1 FMNH 29051); Sunchal, Sierra de Santa Bárbara, 1300 m, 1 (BMNH not numbered); Sunchal, Sierra de Santa Bárbara, 1800 m, 4 (BMNH 21.1.1.55, 21.1.1.56, 21.1.1.58, 21.1.1.60).

Comments.--Thomas (1921a) described *C. barbarus* as a subspecies of *budini*, and considered *budini* and *sylvanus* as valid species (Thomas, 1913, 1919c). Later, Cabrera

(1961a) and Woods (1993) treated *barbarus, budini*, and *sylvanus* as subspecies or synonyms of *C. frater*. This subspecies is known only from the localities of the specimens examined, all located E of the Río San Francisco in Santa Bárbara department, in Yungas forest. Notes on some specimen tags by the collector, E. Budin, indicate that they were captured in red soils and vegetal soils, under large forests; 1 specimen was collected in the sands of a dry river-bed.

Ctenomys frater budini Thomas, 1913

Ctenomys budini Thomas, 1913. Annals and Magazine of Natural History, ser. 8, 1:141.

Distribution in Argentina.--Andean area of Jujuy, and central and western Salta Provinces (Cabrera, 1961a).

Specimens Examined (15).--Cerro de la Lagunita al Este de Maimará, 4500 m, 4 (BMNH 12.12.12.37 *Ctenomys budini* holotype; 12.12.12.38, 12.12.12.39, 12.12.12.40); La Laguna 4500 m, Sierra de Zenta, E de Maimará, 2 (MACN 27.86, 27.87; see comments under *Localities and maps*); Sierra de Zenta, 5 (1 CML 610; 4 MACN 26.110, 31.128, 31.129, 32.61; see comments under *Localities and maps*); Sierra de Zenta, 4500 m, 4 (3 BMNH 21.11.1.81, 21.11.1.82, 21.11.1.83; 1 CML 84; see comments under *Localities and maps*).

Comments.--According to Thomas (1913), *budini* is closely related to *C. frater* but is larger. It is a typical species of high altitudes and open areas; they are shy according to Mr. Budin (Thomas, 1919c). Specimens examined all are from the type locality and surrounding areas and correspond to the High Andean region.

Ctenomys frater sylvanus Thomas, 1919

Ctenomys sylvanus Thomas, 1919. Annals and Magazine of Natural History, ser. 9, 4:155.

Distribution in Argentina.--Eastern Jujuy and Salta, at the base of the mountains (Yepes, 1930; Cabrera, 1961a).

Specimens Examined (43).--Abra de Cañas, 1 (MACN 19541); Abra de Cañas, approx 30 km NW of Calilegua on Valle Grande Rd, 1700 m, 1 (CM 86607); Caimancito, 400 m, 18 (16 BMNH 21.1.2.10, 21.1.2.11, 21.1.2.12, 21.1.2.13, 21.1.2.14, 21.1.2.15, 21.1.2.16, 21.1.2.3, 21.1.2.4, 21.1.2.5, 21.1.2.6, 21.1.2.7, 21.1.2.8, 21.1.2.9, 66.1949, 66.1950; 2 FMNH 29048, 29049); Caimancito, 700 m, 8 (1 CML 255; 7 MACN 30.269, 30.270, 30.271, 30.272, 30.273, 30.275, 30.276); Higuerilla, 2000 m, 6 (BMNH 21.11.1.84, 21.11.1.85, 21.11.1.86, 21.11.1.87, 21.11.1.88, 21.11.1.89); "Jujuy," 1 (CML 260); Mountains W of Yala, 12000 ft., 1 (FMNH 23241); Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20, 2 (ARG 4232, 4252); Río San Francisco, altura de Yuto, 500 m, 2 (BMNH 20.1.7.113, 20.1.7.114 *Ctenomys sylvanus utibilis* holotype); Yuto, 2 (1 AMNH 179896; 1 MACN 13161); Yuto, 700 m, 1 (MACN 27.59).

Additional Records.--Abra de Cañas, 1700 m (Heinonen and Bosso, 1994); Caimancito, near Yuto (Thomas, 1921a, as *C. budini utibilis*)

Comments.--The specimens collected by Mr. Budin were captured in dense forest; a specimen from Río San Francisco was captured among fallen trunks in sandy soils.

In July, 1 female with an open vagina and another with a closed vagina were captured. A juvenile was collected in November. All localities are in the Yungas. The specimens from Caimancito, identified at MACN as *budini*, correspond to the description and type of habitat indicated by Thomas for *C. f. sylvanus*. Thomas (1921c) identified the specimens from Higuerilla as *C. budini*, but he mentioned that they are darker and closer to *C. sylvanus*, or to *C. utibilis*; moreover, *budini* is a species typical from the High Andean region.

Ctenomys juris Thomas, 1920
Jujuy Tuco-tuco

Ctenomys juris Thomas, 1920. Annals and Magazine of Natural History, ser. 9, 5:194.

Distribution in Argentina.--East of the mountains of Jujuy and Salta provinces (Yepes, 1930; Cabrera, 1961a).

Specimens Examined (5).--El Chaguaral, entre San Pedro y Villa Carolina, 500 m, 1 (BMNH 20.1.7.116 *Ctenomys juris* holotype); El Chaguaral, 500 m, 4 (BMNH 20.1.7.115, 20.1.7.117, 20.1.7.118, 20.1.7.119).

Comments.--Cabrera (1961a) considered this species as a subspecies of *C. mendocinus*. The specimens were captured on stony soils, at the old channel of the Río San Pedro. El Chaguaral is the only locality where this species has been collected in Jujuy, and is located in the Chacoan region.

Ctenomys opimus Wagner, 1848
Highland Tuco-tuco

Ctenomys opimus Wagner, 1848. Archiv fuer Naturgeschichte, 1:75.

Ctenomys opimus luteolus Thomas, 1900

Ctenomys opimus luteolus Thomas, 1900. Annals and Magazine of Natural History, ser. 7, 6:384.

Distribution in Argentina.-- High Andean region in Jujuy and Salta provinces (Cabrera, 1961a).

Specimens Examined (37).--Abra Pampa, 4 (3 CML 1344, 1345, 1346; 1 FMNH 29050); Abra Pampa, 3500 m, 20 (2 CML 188; 708; 2 MACN 20260, 28.162; 16 BMNH 19.8.1.55, 19.8.1.56, 19.8.1.57, 19.8.1.58, 19.8.1.59, 19.8.1.60, 19.8.1.63, 19.8.1.64, 19.8.1.65, 19.8.1.66, 19.8.1.67, 19.8.1.68, 19.8.1.69, 19.8.1.70, 19.8.1.72, 19.94.487); Abrapampa, 3600 m, 2 (BMNH 19.8.1.54, 19.8.1.61); Cordilleras of Jujuy, 1 (BMNH 99.2.22.17 *Ctenomys opimus luteolus* holotype); "Jujuy," 1 (MACN 1.18); La Quiaca, 1 (MLP 8-VII-42-5); La Quiaca, 3000 m, 1 (BMNH 25.3.1.58); Tres Cruces, 4 (2 CML 245, 256; 2 MACN 32.3, 32.6); Tres Cruces FCCN, 3700 m, 1 (FMNH 35235); Tres Cruces, 4000 m, 1 (CML 5559); Yavi

Chico, 1 (MACN 36.407).

Comments.--According to Budin´s notes, this species is rare and the specimens from Abra Pampa were collected in sandy areas. In March at Abra Pampa juveniles were collected. In Curques, 21 km al N de Susques, sobre ruta provincial N° 74; at Salar Cauchari, 31 km al N de Cauchari, sobre ruta provincial N° 70, 3840 m; and at Mina Pan de Azúcar, 8 km al N, we were not able to collect specimen but several burrows and vegetation with tooth marks of *Ctenomys* were observed; we are confident that these burrows belong to C. *opimus* as the area is typical for the distribution of this species. All localities correspond to the Puna, up to 3000 m, in the NE part of the province.

Family Octodontidae

Genus *Octodontomys*

Octodontomys gliroides (Gervais and d'Orbigny, 1844)
Mountain Degu, chozchori

Octodon gliroides Gervais and d'Orbigny, 1844. Nouveau bulletin des sciences par la Société Philomatique, Paris, p. 22.

Distribution in Argentina.--Andean and Subandean areas of the NW, from Jujuy to La Rioja provinces (Mann Fischer, 1945; Cabrera, 1961a; Lucero, 1983; Contreras et al., 1987).

Specimens Examined (63).--11 km al E de Humahuaca, 2 km al E de Pucará, sobre camino a Cianzo, 1 (IADIZA 4477); 11 km east of Humahuaca, 2 km east of Pucará on road to Cianzio, 11,500 ft., 1 (SNOMNH 23476); Alfarcito, 2600 m, 5 (BMNH 21.11.174, 21.11.175, 21.11.176, 21.11.177, 21.11.178); Casa Colorada, app 2 km al N de Alfarcito, 3034 m, 1 (MMD 379); Casabindo, 4000 m, 2 (BMNH 19.8.2.26, 19.8.2.27); Cerro Casabindo, 4500 m, 1 (BMNH 19.8.2.28); Cochinoca, 1 (MLP 11-XII-35-19); Cuesta de Lipán, 15 km al O de Purmamarca, sobre ruta provincial N° 52, 3156 m, 1 (MMD 311); Cuesta del Hurón, 29 km al O de Cieneguillas, sobre ruta provincial N° 64, 3835 m, 7 (MMD 440, 444, 451, 461, 465, 468, 469); Curques, 24 km al N de Susques, sobre ruta provincial N° 74, 1 (MMD 283); El Alfarcito, 2700 m, 1 (CML 371); El Pucará, Tilcara, 3 (MACN 17835, 17836, 17837); "Jujuy," 1 (MACN 32.59); Maimará, 1 (FMNH 41279); Maimará, 2200 m, 2 (CML 369, 370); Maimará, 2230 m, 8 (2 BMNH 12.12.12.42, 12.12.12.43; 1 FMNH 23642; 5 MACN 27.92, 27.93, 27.94, 27.95, 27.96); Maimará, 2500 m, 1 (MACN 31.39); Maimará, 2600, 3 (BMNH 12.12.12.41, 12.12.12.44, 12.12.12.45); Mina Pan de Azúcar, 8 km al N y 5 km al O, camino a Herrana, 3820 m, 4 (MMD 491, 499, 506, 510); Mina Pirquitas, 31 km al SE, Sierra de Quichagua, sobre ruta provincial N° 74 b, 4200 m, 2 (MMD 512, 524); Pucapampa "Chozchoi," 1 (MACN 49.101); Pucará, Tilcara, 3 (MACN 17832, 17833, 17834); Purmamarca, 10 km al O, sobre ruta 52, 1 (CML 3437); Ronqui Angosto, 2 km al O, sobre ruta provincial 16, 3700 m, 1 (IADIZA, not number); Sierra de Zenta, 2 (MACN 32.15, 32.16; see comments under *Localities and maps*); Sierra de Zenta, 4500 m, 2 (MACN 28.207, 32.60; see comments under *Localities and maps*); Tilcara, 1 (MACN 8.17); Tilcara, 2470 m, 1 (BMNH 25.3.1.57); Tres Cruces, 4000 m, 1 (CML 85); Yavi, 1 (CML 2872); Yavi Chico, 2 (MACN 36.476, 41.116).

Additional Records.--A lo largo de ruta 9, en las proximidades de Maimará (Ojeda and Mares, 1989); Altiplano jujeño (Crespo, 1941); Campo Laguna (local residents, personal communication); Humahuaca, 16 km al E, camino a Cianzio (J. K. Braun, personal communication); Miyuyoc, 3750 m (M. M. Díaz, personal observation); Laguna de Pozuelos (Massoia, 1993); Sierra de Zenta, 2 km al N del cruce del camino a Miyuyoc and ruta provincial N° 13 (M. M. Díaz, personal observation).

Comments.--A typical species of dry areas of the Prepuna and Puna; they live among rocks, with scattered vegetation, scrubs and cactus. It is diurnal but may remain active during the first hours of darkness. At Sierra de Zenta, 2 km al N del cruce del camino a Miyuyoc and ruta provincial N° 13, we observed a specimen during the morning crossing the road. In Jujuy, this species was captured with *Akodon albiventer*, *Andinomys edax*, *Galea musteloides*, *Phyllotis xanthopygus*, and *Thylamys pallidior.* In February, we recorded 1 female with a closed vagina, 1 lactating female with 6 mammae (2 axillar, 2 abdominal, and 2 inguinal), 1 lactating female, and 1 female with 2 fetuses. In March, females with closed vaginas were captured. Males with abdominal testes were recorded in February and March, and males with scrotal testes in December. Juveniles were captured in February and November, and births were recorded in February and March, so juveniles of different ages were in the population at the same time of the year in the same place. Molting was observed in specimens captured in February, March, June, and December.

Family Abrocomidae

Genus *Abrocoma*

Abrocoma cinerea Thomas, 1919
Ashy Chinchilla Rat

Abrocoma cinerea Thomas, 1919. Annals and Magazine of Natural History, ser. 94:132.
Distribution in Argentina.--In the High Andean region of Jujuy, Salta, and Tucumán provinces, from 3500 to 5000 m (Braun and Mares, 2002).

Specimens Examined (3).--Cerro Casabindo, 4800 m, 1 (BMNH 19.8.2.29, *Abrocoma cinerea* holotype); Sierra de Zenta, 4500 m, 2 (BMNH 21.11.1.79, 21.11.1.80; see comments under *Localities and maps*).

Additional Records.--Sierra de Zenta, 4000 m (Thomas, 1921c; see comments under *Localities and maps*).

Comments.--This species lives on montane slopes in the Puna. Its pelt usually is marketed as chinchilla (Mares et al., 1989). Mr. Budin wrote in the holotype tag, that the specimen was captured among stones in a small narrow valley; he also wrote for the specimens from Tilcara, that this lived in volcanoes, and was rare and difficult to catch because it cohabited with other rodent that activated traps.

Family Echimyidae
Subfamily Myocastorinae

Genus *Myocastor*

Myocastor coypus (Molina, 1782)
Nutria

Mus coypus Molina, 1782. Saggio sulla storia naturale del Chili. S. Tommaso d'Aquino, Bologna, p. 287.

Distribution in Argentina.--It is found almost in all country from Jujuy Province to Tierra del Fuego (Woods et al., 1992), except in Catamarca, San Juan, and La Rioja provinces (Alvarez and Martinez, in press.)

Specimens Examined (1).--"Jujuy," 1 (MACN 26.181).

Additional Records.--Aguas Negras, 600 m (Heinonen and Bosso, 1994).

Comments.-- The only specific locality known for the distribution of this species in the province, Aguas Negras, is in the Yungas forests.

Order Lagomorpha
Family Leporidae

Genus *Sylvilagus*

Sylvilagus brasiliensis (Linnaeus, 1758)
Tapeti

Lepus brasiliensis Linnaeus, 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:58.

Distribution in Argentina--In Misiones, Formosa, Chaco, and Santiago del Estero, and eastern Tucumán, Salta, and Jujuy provinces (Cabrera, 1961a; Crespo, 1982)

Specimens Examined (12).--Alto Calilegua, El Duraznillo, 3000 m, 1 (CML 1721); "Jujuy" (Matschie, 1984 as *Lepus brasiliensis*); Laguna La Brea, 25 km antes de Palma Sola, 1 (CML 2257); Ledesma, 1 (CML 243); San Francisco, 60 km de Ledesma camino a Valle Grande, 1 (CML 163); San Rafael, Sierra Santa Bárbara, 1000 m, 2 (BMNH 21.1.1.76, 21.1.1.77); Villa Carolina, Río Lavallén, 500 m, 1 (BMNH 20.1.7.33); Yuto, 5 (4 AMNH 179898, 184657, 184658, 186953; 1 CML 388).

Additional Records.--Abra de Cañas, 1700 m (Heinonen and Bosso, 1994); Agua Salada (local residents, personal communication); Cerro Calilegua (Olrog, 1979); El Simbolar, 25 km al SO de Palma Sola, 1000 m (R. M. Barquez, personal observation); Lagunas de Yala (local residents, personal communication); Mesada de las Colmenas, 1150 m

(Heinonen and Bosso, 1994); Río Las Capillas, 15 km al N de Las Capillas, sobre ruta provincial N° 20 (R. M. Barquez, personal observation).

Comments.--Inhabits forests, transitional forests, and grasslands of the Chaco; most records from Jujuy are from the Yungas, although some specimens are from the Chaco.

In Laguna La Brea, in June, 2 individuals were observed. One, a pregnant female with 2 relatively well-developed fetuses, was collected; the stomach contained plant material. In Yuto, 2 litters and a juvenile in November and a juvenile in May were collected.

DISCUSSION

Changes in Faunal Composition

Ongoing studies in Jujuy Province have allowed us to document 143 species of mammals, represented by 9 didelphimorphs, 10 edentates, 36 bats, 2 primates, 20 carnivores, 1 perissodactyl, 8 artiodactyls, 56 rodents, and 1 lagomorph. One of the species was described as new for science, 4 are new for Argentina, 2 are new for NW Argentina, and 14 are new for the province. Based on information from localities adjacent to Jujuy Province, 7 species probably occur in Jujuy but have not been documented; these are 1 xenarthran, 1 bat, 2 artiodactyls, and 3 rodents. Two artiodactyls are known only by historical records so we consider them as probable for the province. Some specimens of *Thylamys*, *Oligoryzomys*, and *Artibeus* could not be allocated to any known species, and likely represent new taxa.

The Didelphimorphia are more richly represented in Jujuy than in any other province of NW Argentina. In recent years a new species of *Cryptonanus* was documented for NW Argentina (Díaz et al., 2002; Voss et al. 2005), and a new species of *Thylamys* was described but not named (Flores et al., 2000). Additionally, we follow Flores et al. (2000) in considering *Thylamys cinderella* and *T. sponsorius* as full species.

Dasypus novemcinctus was added to the fauna of the Province by Díaz and Barquez (1999). Matschie (1894) cited *Zaedyus pichiy* for Jujuy (as *Euphractus minutus*), but we also obtained a record of this species (MACN 35.351) for "Jujuy." It is possible that there is a mistake in the locality at the MACN, because this species is known only from the central and western part of the country, from San Luis, Mendoza, and Buenos Aires provinces, S to the Strait of Magellan (Cabrera, 1958; Vizcaíno et al., 1995).

Dasypus is a complex and diverse genus in need of revision, including specimens from all areas of the distribution of the species. The last reviews were those of Wetzel and Mondolfi (1979) and Wetzel (1985), and later by Vizcaíno (1995).

Eight new species of Chiroptera have been added to the province of Jujuy; these include 6 Vespertilionidae (*Histiotus velatus*, *Lasiurus cinereus*, *Myotis albescens*, *M. keaysi*, *M. levis*, and *M. riparius*) and 2 Molossidae (*Eumops patagonicus* and *Nyctinomops laticaudatus*). Additionally, the distribution of *Histiotus velatus* was extended from NE Argentina to include the NW part of the country (Díaz and Barquez, 1999; Barquez and Díaz, 2001).

Only 1 species of primate was known for Jujuy province (*Cebus apella*, Cebidae) (Cabrera, 1958; Olrog and Lucero, 1981; Honacki et al., 1982; Arditi et al., 1989; Groves, 1993). However, we have found a specimen of *Aotus azarae* deposited at the CML, indicating that this species inhabited the province (Díaz and Barquez, 1999). This species was cited for Paraguay and Bolivia, and in Argentina was known only from the NE, in Formosa and Chaco provinces (Arditi et al., 1989; Crespo, 1974; Zunino et al., 1986). The distribution of this species has been greatly reduced by hunting pressure and habitat alteration.

The majority of argentine Carnivora also are found in Jujuy. We have been able to detect the presence of 1 canid (*Pseudalopex griseus*) and 1 felid (*Leopardus tigrinus*) not previously cited for the province, as well as to confirm the presence of *L. pardalis* and *O. jacobita*. *Pseudalopex griseus* typically occurs is arid zones, but we have documented it in the Yungas Phytogeographic Province.

The order Perissodactyla is represented by *Tapirus terrestris*, which remains abundant in some areas of the province. In the order Artiodactyla, *Tayassu pecari* and *Pecari tajacu* (Family Tayassuidae) were confirmed. The Camelidae is represented by 2 wild species, *Vicugna vicugna* and *Lama guanicoe*, and 1 domestic species, *L. glama*. Within the Cervidae we document the presence of *Hippocamelus antisensis*, *Mazama gouazoupira*, and *M. americana*.

The most diverse order of mammals in the province is Rodentia, containing 56 species in 31 genera and 11 families. We added 8 species of this order to the province, 4 of which are new for Argentina. The greatest diversity within the order corresponds to Cricetidae (subfamily Sigmodontinae), represented by 17 genera and 40 species, including the polytypic *Akodon*, *Calomys*, *Oligoryzomys*, and *Phyllotis*. Two new species of *Akodon* (*A. fumeus* and *A. lutescens*) were added for Argentina, and *A. tartareus* is treated as a full species. *Oligoryzomys destructor, Eligmodontia puerulus*, and *Andinomys lineicaudatus* are added to the mammals of the province; the latter was previously considered as a subspecies of *A. edax*, but these 2 taxa were found in symaptry, and are here treated as full species. *Calomys boliviae* and *Phyllotis wolffshoni* are included in Argentina. One species of cavidae, *Dolichotis salinicola,* is added to the province. Lagomorphs are represented by 1 species, the widely distributed *Sylvilagus brasiliensis*. Additionally, the distribution of several species was extended, particularly for those from the highlands, and places with incomplete historical sampling.

Other species of mammals likely also occur in the province based either on literature or on records that were not possible to confirm. Among them, 1 xenarthran, 1 chiropteran, 2 artiodactyls (including 1 domestic species, *Lama pacos*), and 3 rodents (1 cricetid, 1 erethizontid, and 1 chinchillid). In addition, we suspect that the province supports 3 introduced murine rodents (*Mus domesticus*, *Rattus rattus*, and *Rattus norvegicus*) and 1 leporid (*Lepus europaeus*). Five species are excluded because we were not able to confirm their presence in the province (1 xenarthran, 1 cricetid, 1 chinchillid, 1 cavid, and 1 ctenomyid).

Priodontes maximus was cited from Urundel (Salta Province), about 10 km from Yuto and separated from Jujuy Province only by the Río San Francisco (Massoia et al., 1992a); thus, the presence of this species in Jujuy is highly probable. One species of bat (*Pygoderma bilabiatum*) likely is present in the province; although there are no documented records, this species was reported in Elio Massoia's catalog from Calilegua, but we have not examined the specimen. *Catagonus wagneri* was not observed, and no specimens were found in collections from Jujuy, but local residents (personal communication) told us of the presence of this species in Sierra Santa Bárbara, approx. 6 km E El Palmar; additionally, records from Bolivia are close to the border with Jujuy

Province (Anderson, 1997). *Lama pacos* was cited by Cajal (1985a) from "Criadero de Abrapampa". According to Franklin (1982), this species was historically present in Argentina, but is now restricted to Bolivia and Peru. Information offered by park rangers from Monumento Natural Laguna Pozuelos indicate that the species was not observed in the southern parts of the province at the department of Susques. For this reason, we considered this species as probable for Jujuy Province.

For *Necromys lenguarum* there is a record from Ingenio La Esperanza in Elio Massoia's catalog; this record, if confirmed, will represent the first known for the species in the province.

Chinchillula sahamae was mentioned as known only in altiplano of Jujuy, up to 4800 m (Pearson, 1951), but see Galliari et al. (1996) for the exclusion of this species from Argentina. Chébez (1994) gave no records of this species except for "Jujuy". Anderson (1997), Hershkovitz (1962), and Pearson (1951), indicated the distribution of this species for northern Chile and western Bolivia, with the closest records more than 400 km from the argentine border. In addition, during our field research this species was neither observed by us nor mentioned by local residents. However, we consider it probable that this species occurs in the province, primarily because their habitats are quite difficult to access, so they may have simply remained unnoticed by field workers. *Coendou prehensilis* is known in Argentina from only a few records in Salta Province and according to Chébez (1994) probably inhabits eastern Jujuy, in Ledesma Department; no specimens were found in collections.

Chlamyphorus retusus was reported in Jujuy by Cabrera (1958), but its occurrence was not confirmed by local residents, our own field observations, or examination of specimens at several museum. *Abrothrix illuteus* is known in this province only by the specimen cited by Olrog (1979); we have not captured this species, and no specimens were found at the CML or other collections. Because this species is known only from Tucumán and Catamarca provinces, it is possible that the specimen cited by Olrog (1979) was incorrectly identified; thus, we decided excluded it from the province. Also, *Lagostomus maximus* was reported in Jujuy by Matschie (1894), but we have been unable to confirm its presence by surveys, observations, or examination of specimens at several museums. Its preferred habitat is the Chaco Phytogeographic Province, which is not extensive in Jujuy and is strongly disturbed; this could be a reason for the actual absence of this species. However, this species is still abundant in the Chaco of Salta province, near the border with Jujuy.

Although Cabrera (1953) considered *Microcavia shiptoni* as likely to occur in Jujuy, we have been unable to document its presence. Similarly, *Ctenomys saltarius* was cited by Cabrera (1961a) and Mares and Ojeda (1982), but we found no actual records. Therefore, we prefer to exclude these species from the province.

Finally, 2 species of deer, *Ozotocerus bezoarticus* and *Blastocerus dichotomus*, could have lived historically in Jujuy, according to Chébez (1994), but precise records are not known.

Biogeographical Comparisons

In this analysis, only the native species with confirmed presence in the province were included (Table 1). Three species (*B. variegatus*, *D. hybridus*, and *D. novemcinctus*) were excluded because no specific localities are available; we also excluded species known only by historical records. The analyses discriminate between 2 major faunal groupings,

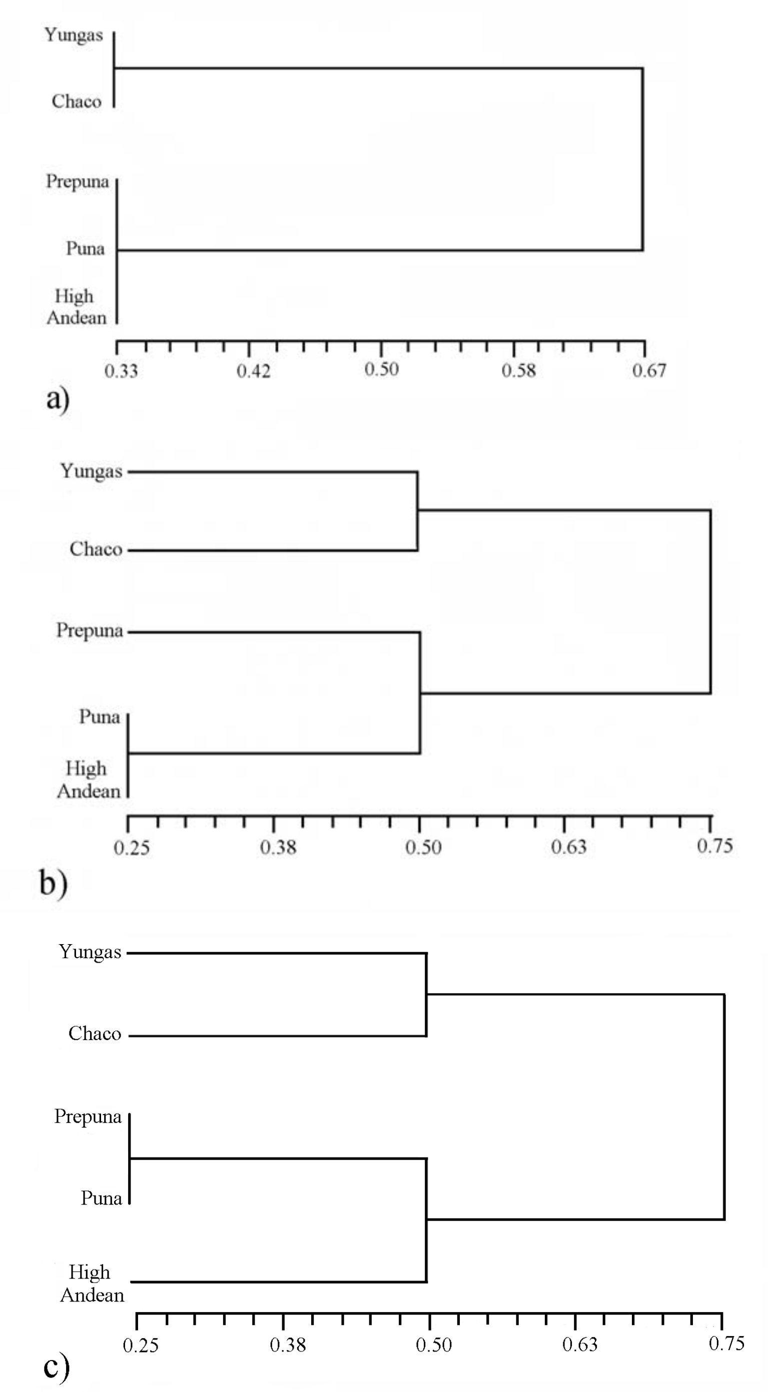

Figure 5. Consensus phenogram of phytogeographic regions in Jujuy Province. Affinities based upon taxonomic similarity of mammals at a) specific level, b) generic level, and c) familial level.

Table 1.--Species of mammals confirmed in Jujuy Province, Argentina, indicating their presence in the Phytogeographic Provinces (indicated by an X).

Order	Family	Species	Yungas	Chaco	Prepuna	Puna	High Andean
Didelphimorphia	Didelphidae	*Didelphis albiventris*	X	X	X		
		Cryptonanus agilis	X	X			
		Cryptonanus ignitus	X				
		Lutreolina crassicaudata	X	X			
		Micoureus constantiae	X				
		Thylamys cinderella	X	X			
		Thylamys pallidior			X	X	X
		Thylamys sp.	X				
		Thylamys sponsorius	X		X		
Xenarthra	Dasypodidae	*Chaetophractus nationi*				X	
		Chaetophractus vellerosus	X	X			
		Dasypus yepesi	X				
		Euphractus sexcinctus	X	X			
		Tolypeutes matacus	X	X			
	Myrmecophagidae	*Myrmecophaga tridactyla*	X				
		Tamandua tetradactyla	X	X			
Chiroptera	Noctilionidae	*Noctilio leporinus*	X				
	Phyllostomidae	*Chrotopterus auritus*	X	X			
		Tonatia bidens	X	X			
		Anoura caudifer	X				
		Glossophaga soricina	X				
		Artibeus planirostris	X	X			
		Artibeus sp.	X				
		Sturnira erythromos	X				
		Sturnira lilium	X	X			
		Sturnira oporaphilum	X				
		Desmodus rotundus	X	X			
		Diaemus youngi	X				

Table 1 (continued).

	Vespertilionidae	*Dasypterus ega*	X				
		Eptesicus diminutus	X	X			
		Eptesicus furinalis	X	X			
		Histiotus laephotis	X	X			
		Histiotus macrotus				X	
		Histiotus velatus	X				
		Lasiurus blossevillii	X				
		Lasiurus cinereus	X	X			
		Myotis albescens	X	X			
		Myotis keaysi	X				
		Myotis levis	X				
		Myotis nigricans	X	X			
		Myotis riparius	X				
	Molossidae	*Cynomops planirotris*	X				
		Eumops glaucinus	X	X			
		Eumops patagonicus		X			
		Eumops perotis	X				
		Molossops temminckii	X	X			
		Molossus rufus	X				
		Molossus molossus	X				
		Nyctinomops laticaudatus		X			
		Nyctinomops macrotis	X				
		Promops nasutus	X				
		Tadarida brasiliensis	X	X			
Primates	Cebidae	*Aotus azarae*	X				
		Cebus apella	X				
Carnivora	Canidae	*Cerdocyon thous*	X	X			
		Pseudalopex culpaeus	X		X	X	X
		Pseudalopex griseus	X			X	
		Pseudalopex gymnocercus	X	X		X	
	Felidae	*Herpailurus yagouarondi*	X	X			
		Leopardus pardalis	X	X			
		Leopardus tigrinus	X				

Table 1 (continued).

		Leopardus wiedii	X				
		Lynchailurus pajeros	X			X	
		Oncifelis geoffroyi	X	X		X	
		Oreailurus jacobita					X
		Puma concolor	X	X	X	X	X
		Panthera onca	X	X			
	Mephitidae	*Conepatus chinga*	X	X	X	X	X
	Mustelidae	*Lontra longicaudis*	X				
		Eira barbara	X	X			
		Galictis cuja	X	X	X	X	
	Procyonidae	*Nasua nasua*	X	X			
		Procyon cancrivorus	X	X		X	
Perissodactyla	Tapiridae	*Tapirus terrestris*	X				
Artiodactyla	Tayassuidae	*Pecari tajacu*	X				
		Tayassu pecari	X				
	Camelidae	*Lama guanicoe*				X	X
		Vicugna vicugna				X	X
	Cervidae	*Hippocamelus antisensis*	X		X	X	
		Mazama americana	X	X			
		Mazama gouazoupira	X	X			
Rodentia	Sciuridae	*Sciurus ignitus*	X				
	Cricetidae	*Abrothrix andinus*				X	X
		Akodon albiventer			X	X	X
		Akodon alterus				X	
		Akodon budini	X				
		Akodon caenosus	X				
		Akodon fumeus	X				
		Akodon lutescens	X		X		
		Akodon simulator	X	X			
		Akodon spegazzinii	X				
		Akodon sylvanus	X				
		Akodon tartareus	X	X			
		Akodon toba	X	X			
		Necromys lactens	X		X		
		Chroeomys jelskii					X

Table 1 (continued).

		Oxymycterus akodontius	X				
		Oxymycterus paramensis	X		X		
		Holochilus chacarius	X	X			
		Oligoryzomys chacoensis	X	X	X		
		Oligoryzomys destructor	X	X	X		
		Oligoryzomys flavescens	X	X	X		
		Oligoryzomys sp.	X				
		Oryzomys legatus	X	X			
		Andinomys edax			X	X	X
		Andinomys lineicaudatus	X		X		
		Auliscomys sublimis			X		X
		Calomys boliviae	X	X			
		Calomys lepidus				X	
		Calomys musculinus	X		X	X	X
		Calomys venustus	X	X			
		Eligmodontia hirtipes				X	
		Eligmodontia puerulus				X	X
		Graomys domorum	X	X	X		
		Graomys griseoflavus	X	X		X	
		Neotomys ebriosus					X
		Phyllotis caprinus			X	X	X
		Phyllotis osilae	X		X	X	
		Phyllotis wolffshoni			X	X	
		Phyllotis xanthopygus	X		X	X	X
		Reithrodon auritus				X	
		Rhipidomys austrinus	X				
	Erethizontidae	*Coendou bicolor*	X				
	Chinchilliidae	*Chinchilla brevicaudata*				X	X
		Lagidium viscacia	X		X	X	X
	Caviidae	*Cavia tschudii*	X				
		Galea musteloides	X	X	X	X	X
		Microcavia australis				X	
		Dolichotis salinicola		X			

Table 1 (continued).

	Hydrochaeridae	*Hydrochoerus hydrochaeris*	X	X			
	Agutidae	*Dasyprocta punctata*	X	X			
	Ctenomyidae	*Ctenomys frater*	X				X
		Ctenomys juris		X			
		Ctenomys opimus				X	
	Octodontidae	*Octodontomys gliroides*			X	X	X
	Abrocomidae	*Abrocoma cinerea*					X
	Echimyidae	*Myocastor coypus*	X				
Lagomorpha	Leporidae	*Sylvilagus brasiliensis*	X	X			

consisting of highlands (High Andean, Puna, Prepuna) and lower elevations (Yungas and Chaco) (Fig. 5, Table 2). The greatest similarity was observed among the Yungas and Chaco, followed by the Puna and High Andean. Within the highland, the Simple Matching Coefficient yielded a greater similarity between Prepuna and High Andean than did Jaccard's coefficient, because the former consider the shared absences (Table 2). The Cophenetic correlation coefficient was relatively high in all analyses (all r > 0.88), indicating little distortion in each phenogram (Table 2).

At the generic level Jaccard's coefficient yielded similar results to the species level, but analyses using the Simple Matching coefficient show greater similarity between High Andean and Puna regions than between Prepuna and the High Andean (Fig. 5). This difference occurs because the High Andean and Puna regions share 17 genera while another 59 species occur in only 1 region; comparable numbers for the High Andean and Prepuna regions are 12 and 60 species, respectively. In the consensus phenogram the highlands cluster showed greater similarity between the Puna and High Andean region, with the Prepuna forming its own subcluster. At family level Jaccard's coefficient grouped the Prepuna and Puna, which then clustered with High Andean. With analyses using the Simple Matching coefficient we obtained 2 trees, 1 with Prepuna and High Andean clustering and then with Puna (similar to the species-level analysis) and another with Prepuna and Puna clustering and then with High Andean. In the consensus phenogram the Puna and Prepuna clustered together before joining with the High Andean, unlike the generic-level analysis.

The Yungas and Chaco share 52 species, 47 genera, and 18 families. At higher taxonomic levels the number of shared groups is higher among arid areas of NW Argentina; for example, although the Chaco and Puna shares only 8 species, they share 14 genera and 12 families. The cophenetic correlation coefficients in the generic and family analyses were all greater than 0.83 (Table 2).

The region with the greatest number of exclusive genera and species in Jujuy is the Yungas, with 23 exclusive genera and 44 exclusive species; this is followed distantly by the Puna, with 2 genera and 8 exclusive species. The High Andean region has 4 exclusive genera, and the Chaco has only 1 exclusive genus. At the species level, the Chaco and the High Andean have 4 exclusive species, while the Prepuna has none.

Table 2. Cophenetic matrix and cophenetic correlation coefficients for mammalian representation in the principal phytogeographic regions of Jujuy Province, Argentina. Jaccard's coefficient is presented above the principal diagonal and Simple Matching Coefficient below it; r_J = cophenetic correlation coefficient for Jaccard Coefficient, r_{SM} = cophenetic correlation coefficient for Simple Matching Coefficient. Analyses are presented for a) species, b) genera, and c) families.

a)

	Yungas	Chaco	Prepuna	Puna	High Andean
Yungas	1	0.4561404	0.1709402	0.1240310	0.0640000
Chaco	0.5507246	1	0.1216216	0.0963855	0.0394737
Prepuna	0.2971014	0.5289855	1	0.3478261	0.3513514
Puna	0.1811594	0.4565217	0.7826087	1	0.4146341
High Andean	0.1521739	0.4710145	0.8260870	0.8260870	1

r_J: 0.97474; r_{SM}: 0.87736

b)

	Yungas	Chaco	Prepuna	Puna	High Andean
Yungas	1	0.6025641	0.2405063	0.2235294	0.1250000
Chaco	0.6593407	1	0.2321429	0.2321429	0.1290323
Prepuna	0.3406593	0.5274725	1	0.4117647	0.3870968
Puna	0.2747253	0.4835165	0.7802198	1	0.5312500
High Andean	0.1538462	0.4065934	0.7912088	0.8351648	1

r_J: 0.96861; r_{SM}: 0.89946

c)

	Yungas	Chaco	Prepuna	Puna	High Andean
Yungas	1	0.6923077	0.3333333	0.4642857	0.2758621
Chaco	0.7241379	1	0.4000000	0.5714286	0.3181818
Prepuna	0.3793103	0.5862069	1	0.6666667	0.6153846
Puna	0.4827586	0.6896552	0.8275862	1	0.6250000
High Andean	0.2758621	0.4827586	0.8275862	0.7931034	1

r_J: 0.85383; r_{SM}: 0.82968

Some species, only recorded in the Yungas in Jujuy, are also present in the Chaco in other provinces; this may reflect the small percentage of land occupied by the Chaco in Jujuy, as well as its disturbed status. At the family level, the Yungas has 7 exclusive families and the High Andean only 1.

CONCLUSIONS

After several years of extensive and intensive field surveys in Jujuy, we have shown that the province, in spite of its limited area, possesses a diverse mammal fauna. The lack of published information on mammals of Jujuy, combined with the limited collecting and therefore poor representation in established collections, made the initial phases of this study difficult. To solve many of our doubts concerning species recognition, we adopted a conventional approach, trying to identify our samples within the bounds of previously documented and relatively well known species in neighboring provinces. With increased familiarity and knowledge of the species we were capturing, including morphological and morphometric studies and comparison with specimens in several museums (both national and international), and especially through comparison with type specimens, we have concluded that the diversity was even higher and more complex than originally believed. We believe that further studies are needed in this province, but we are concerned that the advance of human colonization is both rapid and devastating there.

The influence of technology on the wildlands is affecting the composition of species in each region, with some habitats threatened with disappearing; the Chaco and the biologically rich Yungas exemplify this threat. Studies such as this are inherently a race with development. If we can obtain sufficient knowledge on the needs and distribution of these species, we may have the opportunity to develop conservation and management plans. If "development" sweeps through the region first, however, this list of species will provide only a glimpse of what the region once supported.

Data reported herein reflects extensive field efforts in areas that often are very difficult to access, including both high mountains and lowlands that are subject to flooding. In many parts of Jujuy the climate is challenging as well. Work to date has emphasized small terrestrial and flying mammals, in part reflecting methodologies, and larger species have been studied with less intensity; we intend to rectify this in the future. Jujuy still supports large mammals, but they are in urgent need of investigation.

Jujuy Province is notably diverse, with a variety of habitats that cumulatively support 37% of the argentine mammal fauna. In spite of a long history of field investigations and of our more recent efforts, much remains to be learned with respect to taxonomy, natural history, and ecology. We hope that this summary of the current state of knowledge will promote the understanding of this fauna, and inspire others to pursue investigations within these groups. We also hope that these studies will be helpful to managers in delimiting areas for conservation needs.

APPENDIX

Localities mentioned in text, listed in alphabetical order. Departments are given in parenthesis, followed by the geographic coordinates.

10 km west of Purmamarca on highway 52 (Tumbaya) 23° 42′ S, 65° 37′ W
11 km al E de Humahuaca, 2 km al E de Pucará sobre camino a Cianzo (Humahuaca) 23° 12′ S, 65° 16′ W
11 km al E de Humahuaca, 2 km al E de Pucará sobre camino a Cianzo, 11,500 ft. (Humahuaca) 23° 12′ S, 65° 16′ W
11 km east of Humahuaca, 2 km east of Pucará on road to Cianzo (Humahuaca) 23° 12′ S, 65° 16′ W
11 km east of Humahuaca, 2 km east of Pucará on road to Cianzo, 11,500 ft. (Humahuaca) 23° 12′ S, 65° 16′ W
11-16 km E of Humahuaca, 2 km E of Pucará, on road to Cianzo (Humahuaca) 23° 12′ S, 65° 16′ W
2.5 km W El Bananal (Ledesma) 23° 33´ S, 64° 32´ W
4 km W jct Hwys 34 & 3, along Hwy 3 (Ledesma) 23° 48′ S, 64° 48′ W
4 km W jct Hwys 34 and 3, along Hwy 3, Valle Grande Rd (Ledesma) 23° 48′ S, 64° 48′ W
6 km W jct Hwys 34 and 3, along Hwy 3, Valle Grande Rd (Ledesma) 23° 48′ S, 64° 49′ W
9 km NW Bárcena (Tumbaya) 23° 57′ S, 65° 30′ W
A 12 km cruce con ruta 40, sobre ruta 52, 3700 m (Tumbaya) 23° 34′ S, 65° 54′ W
A 2.5 km del Río Santa Rita, sobre camino al Fuerte (Santa Bárbara) 24° 15′ S, 64° 25′ W
A lo largo de ruta 9, en las proximidades de Maimará (Tilcara) 23° 37′ S, 65° 28′ W
Abra Blanca (Dr. Manuel Belgrano) 24° 05′ S, 65° 34′ W
Abra de Cañas (=El Monolito) (Valle Grande) 23° 40′ S, 64° 54′ W
Abra de Cañas (Valle Grande) 23° 40′ S, 64° 54′ W
Abra de Cañas, 1700 m (Valle Grande) 23° 40′ S, 64° 54′ W
Abra de Cañas, 1710 m (Valle Grande) 23° 40′ S, 64° 54′ W
Abra de Cañas, 1730 m (Valle Grande) 23° 40′ S, 64° 54′ W
Abra de Cañas, approx 30 km NW of Calilegua on Valle Grande Rd (Valle Grande) 23° 40′ S, 64° 54′ W
Abra de Cañas, approx 30 km NW of Calilegua on Valle Grande Rd, 1700 m (Valle Grande) 23° 40′ S, 64° 54′ W
Abra de Cañas, El Monolito (Valle Grande) 23° 40′ S, 64° 54′ W
Abra de Cañas, El Monolito, 1700 m (Valle Grande) 23° 40′ S, 64° 54′ W
Abra de Fundición, 20 km al O de Rinconada y app 50 km al O de Pozuelos (Rinconada) 22° 33′ S, 66° 19′ W
Abra de Santa Laura, límite entre Salta y Jujuy, sobre ruta nacional N° 9, 1397 m (El Carmen) 24° 30′ S, 65° 19′ W
Abra Pampa (Cochinoca) 22° 43′ S, 65° 42′ W
Abra Pampa estación INTA (Instituto Nacional de Tecnología Agropecuaria) (Cochinoca) 22° 43′ S, 65° 42′ W
Abra Pampa, 13 km al NO, sobre ruta provincial N° 7 (Cochinoca) 22° 41′ S, 65° 44′ W
Abra Pampa, 13 km al O sobre ruta provincial N° 71 (Cochinoca) 22° 44′ S, 65° 49′ W
Abra Pampa, 20 km al O sobre ruta provincial N° 71 (Cochinoca) 22° 44′ S, 65° 52′ W
Abra Pampa, 21 km al NO, sobre ruta provincial N° 7 (Cochinoca) 22° 39′ S, 65° 47′ W

Abra Pampa, 29 km al NO, sobre ruta provincial N° 7 (Cochinoca) 22° 36′ S, 65° 50′ W
Abra Pampa, 32 km al NO, sobre ruta provincial N° 7 (Cochinoca) 22° 35′ S, 65° 51′ W
Abra Pampa, 3480 m (Cochinoca) 22° 43′ S, 65° 42′ W
Abra Pampa, 3500 m (Cochinoca) 22° 43′ S, 65° 42′ W
Abra Pampa, 3800 m (Cochinoca) 22° 43′ S, 65° 42′ W
Abra Pampa, 4 km al O sobre ruta provincial N° 71 (Cochinoca) 22° 43′ S, 65° 43′ W
Abra Pampa, 9 km al O sobre ruta provincial N° 71 (Cochinoca) 22° 43′ S, 65° 45′ W
Abra Pampa, Criadero (Cochinoca) 22° 43′ S, 65° 42′ W
Abrapampa, 3500 m (Cochinoca) 22° 43′ S, 65° 42′ W
Abrapampa, 3600 m (Cochinoca) 22° 43′ S, 65° 42′ W
Agua Caliente (Santa Bárbara) 23° 43′ S, 64° 32′ W
Agua Salada (Santa Bárbara) 23° 57′ S, 64° 38′ W
Agua Salada, app 15 km al SE de Agua Caliente, del lado oriental del Río San Francisco (Santa Bárbara) 23° 57′ S, 64° 38′ W
Aguas Blancas, 14 km al E de Santa Clara (Santa Bárbara) 24° 18′ S, 64° 28′ W
Aguas Blancas, 14 km al E de Santa Clara, 900 m (Santa Bárbara) 24° 18′ S, 64° 28′ W
Aguas Calientes, Finca Los Melados (El Carmen) 24° 36′ S, 64° 52′ W
Aguas Calientes, Finca Santa Victoria (El Carmen) 24° 36′ S, 64° 52′ W
Aguas Negras (Ledesma) 23° 45′ S, 64° 56′ W
Aguas Negras, 1400 m (Ledesma) 23° 45′ S, 64° 56′ W
Aguas Negras, 500 m (Ledesma) 23° 45′ S, 64° 56′ W
Aguas Negras, 600 m (Ledesma) 23° 45′ S, 64° 56′ W
Aguas Negras, 650 m (Ledesma) 23° 45′ S, 64° 56′ W
Aguas Negras, Camping (Ledesma) 23° 45′ S, 64° 56′ W
Aguas Negras, Camping, Parque Nacional Calilegua (Ledesma) 23° 45′ S, 64° 56′ W
Aguas Negras, Cerro Calilegua (Ledesma) 23° 45′ S, 64° 56′ W
Aival (=Aibal) (Ledesma) 24° 01′ S, 65° 01′ W
Al E de la Laguna Vilama (Rinconada) 22° 36′ S, 66° 51′ W
Al E de Yuto, cruzando el Río San Francisco (Santa Bárbara) 23° 40′ S, 64° 27′ W
Al N de la Laguna Vilama (Rinconada) 22° 32′ S, 66° 51′ W
Al NE de la Laguna Vilama (Rinconada) 22° 33′ S, 66° 51′ W
Alfarcito (Tilcara) 23° 37′ S, 65° 23′ W
Alfarcito, 2600 m (Tilcara) 23° 37′ S, 65° 23′ W
Along Hwy 9 at border with Salta Province, 4600 ft. (El Carmen) 24° 28′ S, 65° 21′ W
Alrededores de la Capital (Dr. Manuel Belgrano) 24° 12′ S, 65° 19′ W
Alrededores de la ciudad (Dr. Manuel Belgrano) 24° 12′ S, 65° 19′ W
Alto Calilegua (Valle Grande) 23° 28′ S, 64° 55′ W
Alto Calilegua, 3000 m (Valle Grande) 23° 28′ S, 64° 55′ W
Alto Calilegua, El Duraznillo, 3000 m (Valle Grande) 23° 28′ S, 64° 55′ W
Alto de Yoscaba, 10 km al S, camino a Rinconada (Rinconada) 22° 20′ S, 66° 12′ W
Alto de Yoscaba, 12 km al S, camino a Rinconada (Rinconada) 22° 21′ S, 66° 12′ W
Alto de Yoscaba, 3 km al S, camino a Rinconada (Rinconada) 22° 17′ S, 66° 11′ W
Alto de Yoscaba, 4320 m (Rinconada) 22° 16′ S, 66° 11′ W
Alto de Yoscaba, 7 km al S, camino a Rinconada (Rinconada) 22° 19′ S, 66° 11′ W
Alto Laguna (Susques) 23° 04′ S, 66° 29′ W
Angosto El Duraznal, 15 Km al S, Palma Sola, 1225 m (Santa Bárbara) 24° 10′ S, 64° 20′ W
Arroyito Negro, Parque Nacional Calilegua (Ledesma) 23° 46′ S, 64° 47′ W

Arroyo Colorado, cerca de Santa Clara (Santa Bárbara) 24° 18′ S, 64° 41′ W
Arroyo del Medio, Parque Nacional Calilegua (Ledesma) 23° 45′ S, 64° 42′ W
Arroyo El Cano, 7 km al N de Río Saladillo (El Carmen) 24° 32′ S, 64° 52′ W
Arroyo El Sauzalito (Ledesma) 23° 40′ S, 64° 37′ W
Arroyo La Horqueta, 3 km al SE de Lagunas de Yala, 2100 m (Dr. Manuel Belgrano) 24° 07′ S, 65° 27′ W
Arroyo La Horqueta, 6 km al SE de Lagunas de Yala, 2100 m (Dr. Manuel Belgrano) 24° 07′ S, 65° 25′ W
Arroyo La Urbana, 45 km E y 5.4 km N de San Salvador de Jujuy, 620 m (San Pedro) 24° 20′ S, 64° 55′ W
Arroyo Negrito, Parque Nacional Calilegua (Ledesma) 23° 46′ S, 64° 47′ W
Arroyo Pedregoso, 1250 m (San Pedro) 24° 34′ S, 64° 38′ W
Arroyo Sauzalito (Ledesma) 23° 40′ S, 64° 37′ W
Arroyo Yuto, 13 km al SO de Yuto (Ledesma) 23° 38′ S, 64° 32′ W
Arroyo Zanjón Seco, 20 a 30 km al N de Libertador General San Martín (Ledesma) 23° 41′ S, 64° 37′ W
Bomba YPF en márgenes del Arroyo Sauzalito (Ledesma) 23° 40′ S, 64° 37′ W
Bordo La Isla, Finca La Nación (El Carmen) 24° 24′ S, 65° 42′ W
Cafatales (=Cafetales) (Ledesma) 23° 33′ S, 64° 42′ W
Caimancito (Ledesma) 23° 44′ S, 64° 36′ W
Caimancito FCCNA, 700 m (Ledesma) 23° 44′ S, 64° 36′ W
Caimancito, 400 m (Ledesma) 23° 44′ S, 64° 36′ W
Caimancito, 550 m (Ledesma) 23° 44′ S, 64° 36′ W
Caimancito, 600 m (Ledesma) 23° 44′ S, 64° 36′ W
Caimancito, 700 m (Ledesma) 23° 44′ S, 64° 36′ W
Caimancito, El Arroyo, 600 m, Parque Nacional Calilegua (Ledesma) 23° 44′ S, 64° 36′ W
Caimancito, FCCNA (Ledesma) 23° 44′ S, 64° 36′ W
Caimancito, near Yuto (Ledesma) 23° 44′ S, 64° 36′ W
Caimancito, pozos petroleros 38 y 39 (Ledesma) 23° 44′ S, 64° 36′ W
Calilegua (Ledesma) 23° 46′ S, 64° 47′ W
Calilegua, 470 m (Ledesma) 23° 46′ S, 64° 47′ W
Calilegua, El Monolito (Valle Grande) 23° 40′ S, 64° 54′ W
Calilegua, Mesada de las Colmenas, 1150 m (Ledesma) 23° 42′ S, 64° 52′ W
Camino a Las Capillas, 2 km de la intersección de las rutas 56 y 20, por ruta provincial N° 20 (Dr. Manuel Belgrano) 24° 09′ S, 65° 12′ W
Camino a Santa Catalina, 500 m al N del cruce de las rutas provinciales 64 y 65, sobre ruta provincial N° 65 (Santa Catalina) 22° 05′ S, 66° 07′ W
Camino a Santa Catalina, 8 km al N del cruce de las rutas provinciales 64 y 65, sobre ruta provincial N° 65 (Santa Catalina) 22° 01′ S, 66° 05′ W
Camino a Vinalito, entre Las Siete Aguas y Vinalito (Santa Bárbara) 23° 45′ S, 64° 28′ W
Camino a Yuto, cerca del Río Francisco (Ledesma) 23° 39′ S, 64° 27′ W
Camino al Río San Francisco, 12 km al O de la ruta provincial N° 1, entre Sauzalito y El Palmar (Santa Bárbara) 23° 55′ S, 64° 37′ W
Camino de Cornisa, 10 km al O de Dique La Ciénaga (El Carmen) 24° 29′ S, 65° 22′ W
Camino de San Francisco al Duraznillo (Valle Grande) 23° 33′ S, 64° 56′ W
Campo Laguna (Tilcara) 23° 35′ S, 65° 12′ W

Campo Morro (= Cerro Morro) (Rinconada) 22° 42′ S, 66° 40′ W
Capillas, 25 km N von Jujuy (Dr. Manuel Belgrano) 24° 05′ S, 65° 10 ‘ W
Casa Colorada, app 2 km al N de Alfarcito, 3034 m (Tilcara) 23° 35′ S, 65° 21′ W
Casabindo (Cochinoca) 22° 58′ S, 66° 05′ W
Casabindo, 4000 m (Cochinoca) 22° 58′ S, 66° 05′ W
Casabindo, 4000-4500 m (Cochinoca) 22° 58′ S, 66° 05′ W
Casabindo, 4000-5000 m (Cochinoca) 22° 58′ S, 66° 05′ W
Casabindo, 4500 m (Cochinoca) 22° 58′ S, 66° 05′ W
Catamontaña (El Carmen) 24° 26′ S, 65° 18′ W
Cercania de la ciudad de San Pedro, sobre ruta nacional N° 34 (San Pedro) 24° 14′ S, 64° 52′ W
Cercanías de El Simbolar (Santa Bárbara) 24° 11′ S, 64° 28′ W
Cercanías de San Pedro (San Pedro) 24° 14′ S, 64° 52′ W
Cerrito Leones, near the mine of Pan de Azúcar, Man and Biophere Reserve of Laguna de Pozuelos (Rinconada) 22° 26′ S, 66° 00′ W
Cerro Calilegua (Valle Grande) 23° 35′ S, 64° 54′ W
Cerro Calilegua, 1300 m (Valle Grande) 23° 35′ S, 64° 54′ W
Cerro Calilegua, 1400 m (Valle Grande) 23° 35′ S, 64° 54′ W
Cerro Calilegua, 1500 m (Valle Grande) 23° 35′ S, 64° 54′ W
Cerro Calilegua, 1700 m (Valle Grande) 23° 35′ S, 64° 54′ W
Cerro Calilegua, 2000 m (Valle Grande) 23° 35′ S, 64° 54′ W
Cerro Calilegua, 2300-2600 m (Valle Grande) 23° 35′ S, 64° 54′ W
Cerro Calilegua, El Duraznillo (Valle Grande) 23° 28′ S, 64° 55′ W
Cerro Calilegua, El Duraznillo, 2600 m (Valle Grande) 23° 28′ S, 64° 55′ W
Cerro Calilegua, El Duraznillo, 3000 m (Valle Grande) 23° 28′ S, 64° 55′ W
Cerro Casabindo, 4000-4800 m (Cochinoca) 22° 56′ S, 66° 07′ W
Cerro Casabindo, 4500 m (Cochinoca) 22° 56′ S, 66° 07′ W
Cerro Casabindo, 4800 m (Cochinoca) 22° 56′ S, 66° 07′ W
Cerro de la Lagunita (Tilcara) 23° 35′ S, 65° 12′ W
Cerro de la Lagunita al Este de Maimará, 4500 m (Tilcara) 23° 35′ S, 65° 12′ W
Cerro de la Lagunita, 4500 m (Tilcara) 23° 35′ S, 65° 12′ W
Cerro de la Lagunita, Maimará, 4500 m (Tilcara) 23° 35′ S, 65° 12′ W
Cerro de Lagunita al Este de Maimará, 4500 m (Tilcara) 23° 35′ S, 65° 12′ W
Cerro de Lagunita, 4500 m (Tilcara) 23° 35′ S, 65° 12′ W
Cerro de Lagunita, E de Maimará, 4500 m (Tilcara) 23° 35′ S, 65° 12′ W
Cerro de Tilcara (Tilcara) 23° 35′ S, 65° 12′ W
Cerro El Morado (San Antonio) 24° 19′ S, 65° 24′ W
Cerro El Morado, 11 km al NO de San Antonio, sobre Río El Morado (San Antonio) 24° 19′ S, 65° 24′ W
Cerro Guadalupe, 4100 m (Rinconada) 22° 41′ S, 66° 19′ W
Cerro Guadalupe, 4300 m (Rinconada) 22° 41′ S, 66° 19′ W
Cerro Hermoso (cercanías), 2800 m (Ledesma) 23° 35′ S, 64° 53′ W
Cerro Hermoso (Ledesma) 23° 35′ S, 64° 53′ W
Cerro Lagunita, Maimará, 4500 m (Tilcara) 23° 35′ S, 65° 12′ W
Cerro Negro (San Antonio) 24° 21′ S, 65° 36′ W
Cerro Santa Bárbara, 1800 m (Santa Bárbara) 24° 06′ S, 64° 27′ W
Chalicán (Ledesma) 24° 04′ S, 64° 48′ W
Chanchillos (Palpalá) 24° 17′ S, 65° 07′ W

Chijra (Dr. Manuel Belgrano) 24° 10′ S, 65° 17′ W
Chilcayoc (Tumbaya) 23° 57′ S, 65° 26′ W
Cienegüillas, 25 km al O, sobre ruta provincial N° 64 (Santa Catalina) 22° 05′ S, 66° 05′ W
Cienegüillas, 4 km al E sobre ruta provincial N° 5 (Santa Catalina) 22° 05′ S, 65° 51′ W
Cienegüillas, 6 km al E sobre ruta provincial N° 5 (Santa Catalina) 22° 05′ S, 65° 50′ W
Cochinoca (Cochinoca) 22° 44′ S, 65° 54′ W
Cochinoca, 11 km al NO sobre ruta provincial N° 71 (Cochinoca) 22° 41′ S, 65° 58′ W
Cochinoca, 16 km al NO sobre ruta provincial N° 71 (Rinconada) 22° 37′ S, 66° 00′ W
Cochinoca, 2 km al NO sobre ruta provincial N° 71 (Cochinoca) 22° 43′ S, 65° 56′ W
Cochinoca, 3500 m (Cochinoca) 22° 44′ S, 65° 54′ W
Cochinoca, 8 km al NO sobre ruta provincial N° 71 (Cochinoca) 22° 42′ S, 65° 54′ W
Coranzulí (Susques) 23° 01′ S, 66° 23′ W
Coranzulí, 10 km al SO sobre ruta provincial N° 74 (Susques) 23° 03′ S, 66° 29′ W
Coranzulí, 18 km al SO sobre ruta provincial N° 74 (Susques) 23° 03′ S, 66° 34′ W
Coranzulí, 7 km al SO sobre ruta provincial N° 74 (Susques) 23° 03′ S, 66° 28′ W
Criadero Nacional (Cochinoca) 22° 43′ S, 65° 42′ W
Cruce camino a Puesto Viejo y Ruta 34, 4 km al E, sobre camino a Puesto Viejo (El Carmen) 24° 29′ S, 64° 59′ W
Cruce camino a Rinconada y Oros, 4 km al S, sobre camino a Rinconada (Rinconada) 22° 14′ S, 66° 11′ W
Cruce Coranzulí-Rachayte, 2 km al S, sobre ruta provincial N° 74 (Rinconada) 22° 59′ S, 66° 23′ W
Cruce de las rutas 34 y la que se dirige a Vinalito (Ledesma) 23° 39′ S, 64° 27′ W
Cruce de las rutas nacional 34 y provincial 43, camino a Monterrico, km 1160 (El Carmen) 24° 29′ S, 65° 09′ W
Cruce de las rutas provinciales 64 y 65, 5 km al S, sobre ruta provincial N° 65 (Santa Catalina) 22° 07′ S, 66° 08′ W
Cruce de las rutas provinciales 70 y 71, 5 km al O sobre ruta provincial N° 70 (Rinconada) 22° 32′ S, 66° 09′ W
Cruce de las rutas provinciales 70 y 71, 7 km al O sobre ruta provincial N° 70 (Rinconada) 22° 33′ S, 66° 10′ W
Cucho (Dr. Manuel Belgrano) 24° 04′ S, 65° 15′ W
Cucho, San Salvador de Jujuy (Dr. Manuel Belgrano) 24° 04′ S, 65° 15′ W
Cuesta de Lipán, 15 km al O de Purmamarca, sobre ruta 52, 3156 m (Tumbaya) 23° 40′ S, 65° 35′ W
Cuesta del Hurón, 29 km al O de Cienegüillas sobre ruta provincial N° 64, 3835 m (Santa Catalina) 22° 06′ S, 66° 03′ W
Cuesta del Hurón, 4 km al O sobre ruta provincial N° 64 (Santa Catalina) 22° 06′ S, 66° 00′ W
Cueva del Tigre, 74 Km al N Pampa Blanca, 700 m (Ledesma) 23° 57′ S, 64° 47′ W
Cueva del Tigre, El Milagro (El Carmen) 24° 22′ S, 65° 02′ W
Curques, 21 km al N de Susques, sobre ruta 74 (Susques) 23° 13′ S, 66° 23′ W
Curques, 24 km al N de Susques, sobre ruta 74, 4100 m (Susques) 23° 14′ S, 66° 23′ W
Curques, 3 km al N sobre ruta provincial N° 74 (Susques) 23° 12′ S, 66° 23′ W
Cuyaya (Dr. Manuel Belgrano) 24° 13′ S, 65° 20′ W
Dique La Ciénaga, 13 km al SSO de San Salvador de Jujuy (El Carmen) 24° 25′ S, 65° 17′ W

Dique La Ciénaga, casa del club náutico, 30 Km SSW San Salvador de Jujuy, 1000 m (El Carmen) 24° 25′ S, 65° 17′ W
Dique Las Maderas (El Carmen) 24° 27′ S, 65° 25′ W
Dique Las Maderas, 42 Km de San Salvador de Jujuy, 920 m (El Carmen) 24° 27′ S, 65° 25′ W
Duraznillar, 2500 m (Valle Grande) 23° 28′ S, 64° 55′ W
E of El Palmar, Sierra de Santa Bárbara (Santa Bárbara) 24° 05′ S, 64° 35′ W
El Alfarcito, 2700 m (Tilcara) 23° 37′ S, 65° 23′ W
El Alto, Río Caulario, 1200 m (Ledesma) 23° 55′ S, 65° 05′ W
El Arenal (Santa Bárbara) 24° 19′ S, 64° 41′ W
El Bananal, Urundel (Ledesma) 23° 33′ S, 64° 32′ W
El Carmen (El Carmen) 24° 24′ S, 65° 15′ W
El Caulario, Río Caulario, 940 m (Ledesma) 23° 55′ S, 65° 05′ W
El Chaguaral, 500 m (San Pedro) 24° 15′ S, 64° 46′ W
El Chaguaral, entre San Pedro y Villa Carolina, 500 m (San Pedro) 24° 15′ S, 64° 46′ W
El Cuarteadero, km 1177, sobre ruta nacional N° 34 (San Pedro) 24° 23′ S, 64° 58′ W
El Duraznal, Santa Bárbara, 1800 m (Santa Bárbara) 24° 10′ S, 64° 20′ W
El Duraznillo, 3000 m, Cerro Calilegua (Valle Grande) 23° 28′ S, 64° 55′ W
El Jordán, camino a Calilegua, 1700 m (Valle Grande) 23° 38′ S, 64° 56′ W
El Monolito (Valle Grande) 23° 40′ S, 64° 54′ W
El Palmar del Río San Francisco (Santa Bárbara) 24° 05′ S, 64° 35′ W
El Palmar, 1.6 km al E, Sierra de Santa Bárbara (Santa Bárbara) 24° 05′ S, 64° 35′ W
El Palmar, 2.9 km al E, Sierra de Santa Bárbara (Santa Bárbara) 24° 05′ S, 64° 36′ W
El Palmar, 5.9 km al E, Sierra de Santa Bárbara (Santa Bárbara) 24° 05′ S, 64° 38′ W
El Palmar, 8.4 km al E, Sierra de Santa Bárbara (Santa Bárbara) 24° 05′ S, 64° 39′ W
El Perchel (Tilcara) 23° 29′ S, 65° 22′ W
El Pongo (Palpalá) 24° 21′ S, 65° 04′ W
El Pucará (Tilcara) 23° 34′ S, 65° 23′ W
El Simbolar, 25 km al SO de Palma Sola (Santa Bárbara) 24° 11′ S, 64° 28′ W
El Simbolar, 25 km al SO de Palma Sola, 1000 m (Santa Bárbara) 24° 11′ S, 64° 28′ W
El Simbolar, 25 km SW de Palma Sola (Santa Bárbara) 24° 11′ S, 64° 28′ W
El Simbolar, a 2 km (Santa Bárbara) 24° 11′ S, 64° 28′ W
El Sunchal, Sierra de Santa Bárbara, 1200 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
El Sunchal, Sierra de Santa Bárbara, 1400 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
El Toro, 50 km al O de Susques (Susques) 23° 11′ S, 66° 50′ W
El Toro, 55 km O de Susques (Susques) 23° 11′ S, 66° 50′ W
Empalme rutas 40 y 52 (Tumbaya) 23° 36′ S, 65° 48′ W
Entre el empalme con ruta 40 y Quera (Cochinoca) 23° 12′ S, 65° 46′ W
Entre el SE de la Laguna Vilama y Laguna Palar (Rinconada) 22° 41′ S, 66° 51′ W
Entre la casa del Guardaparque y Lagunillas (Rinconada) 22° 25′ S, 66° 07′ W
Entre Laguna Chica y Culi Culi (Rinconada) 22° 35′ S, 66° 33′ W
Entre Mina Campanario y Ojo Catal (Rinconada) 22° 42′ S, 66° 42′ W
Entre Pozo Colorado y el cruce con ruta 52 (Tumbaya) 23° 31′ S, 65° 37′ W
Entre Santo Domingo y la casa del Guardaparque (Rinconada) 22° 38′ S, 66° 13′ W
Estación Experimental de Abra Pampa (Cochinoca) 22° 43′ S, 65° 42′ W
Finca Catamontaña, 33 Km al SSE San Salvador de Jujuy, 925 m (El Carmen) 24° 26′ S, 65° 18′ W
Finca El Olvido, 15 Km al E de Palma Sola (Santa Bárbara) 24° 05′ S, 64° 10′ W

Finca El Pongo, 45 km al E de San Salvador de Jujuy (Palpalá) 24° 21′ S, 65° 04′ W
Finca El Pongo, Estación Perico (Palpalá) 24° 21′ S, 65° 04′ W
Finca El Remate, 24 km al SE de San Salvador de Jujuy, 740 m (Palpalá) 24° 17′ S, 65° 06′ W
Finca La Carolina, Los Perales, San Salvador de Jujuy, 1310 m (Dr. Manuel Belgrano) 24° 11′ S, 65° 19′ W
Finca La Mauricia, 5-10 km al E de Caimancito, 500 m (Ledesma) 23° 44′ S, 64° 34′ W
Finca La Realidad, Río San Francisco, 5 km al E de Caimancito, 440 m (Ledesma) 23° 44′ S, 64° 34′ W
Finca La Toma, 25 Km al SO de San Salvador de Jujuy (San Antonio) 24° 20′ S, 65° 21′ W
Finca Quema Azupera, Palma Sola, 135 km de San Salvador de Jujuy (Santa Bárbara) 24° 00′ S, 64° 19′ W
Fraile Pintado, 12 km al SO, sobre Río Ledesma (Ledesma) 23° 57′ S, 64° 55′ W
Garrapatal, 150 km N von Jujuy (Valle Grande) 23° 33′ S, 64° 57′ W
Higuerilla (Valle Grande) 23° 36′ S, 65° 05′ W
Higuerilla, 2000 m (Valle Grande) 23° 36′ S, 65° 05′ W
Humahuaca (Humahuaca) 23° 12′ S, 65° 21′ W
Humahuaca, 16 km al E, camino a Cianzio (Humahuaca) 23° 14′ S, 65° 08′ W
Humahuaca, 2355 m (Humahuaca) 23° 12′ S, 65° 21′ W
Inca Cueva 5 site (Humahuaca) 23° 00′ S, 65° 27′ W
Ingenio La Esperanza (San Pedro) 24° 14′ S, 64° 52′ W
Ingenio Ledesma (Ledesma) 23° 50′ S, 64° 47′ W
Jujuy, 1000 m (Dr. Manuel Belgrano) 24° 12′ S, 65° 19′ W
Jujuy, 1250 m (Dr. Manuel Belgrano) 24° 12′ S, 65° 19′ W
Jujuy, 1258 m (Dr. Manuel Belgrano) 24° 12′ S, 65° 19′ W
Jujuy, 900 m (Dr. Manuel Belgrano) 24° 12′ S, 65° 19′ W
Jujuy, ciudad (Dr. Manuel Belgrano) 24° 12′ S, 65° 19′ W
Juntas (Santa Bárbara) 23° 54′ S, 64° 38′ W
La Brea (Santa Bárbara) 23° 56′ S, 64° 28′ W
La Ciénaga (Cochinoca) 22° 43′ S, 65° 42′ W
La Ciénaga, 3700 m (Cochinoca) 22° 43′ S, 65° 42′ W
La Ciénaga, Abra Pampa (Cochinoca) 22° 43′ S, 65° 42′ W
La Ciénaga, Tres Cruces (Humahuaca) 22° 55′ S, 65° 35′ W
La cueva site (Yavi) 22° 07′ S, 65° 26′ W
La Laguna (Tilcara) 23° 35′ S, 65° 12′ W
La Laguna 4500 m, Sa de Tilcara, E. de Maimará (Tilcara) 23° 35′ S, 65° 12′ W
La Laguna 4500 m, Sierra de Tilcara, E de Maimará (Tilcara) 23° 35′ S, 65° 12′ W
La Laguna, Sierra de Zenta, 4500 m (Tilcara) 23° 35′ S, 65° 12′ W
La Lagunita (Tilcara) 23° 35′ S, 65° 12′ W
La Lagunita, 4500 m (Tilcara) 23° 35′ S, 65° 12′ W
La Lagunita, Maimará (Tilcara) 23° 35′ S, 65° 12′ W
La Lagunita, Maimará, 4300 m (Tilcara) 23° 35′ S, 65° 12′ W
La Mendieta (San Pedro) 24° 19′ S, 64° 58′ W
La Quiaca (Yavi) 22° 07′ S, 65° 36′ W
La Quiaca, 17 km al O y 3 km al S, sobre ruta provincial N° 5, 3711 m (Yavi) 22° 09′ S, 65° 44′ W
La Quiaca, 3000 m (Yavi) 22° 07′ S, 65° 36′ W

La Quiaca, alrededores (Yavi) 22° 07′ S, 65° 36′ W
Laguna Colorada (Tilcara) 23° 47′ S, 65° 17′ W
Laguna de Leandro, 4455 m (Humahuaca) 23° 02′ S, 65° 13′ W
Laguna de Pozuelos, acceso sur (Rinconada) 22° 26′ S, 66° 00′ W
Laguna Isla Chica, 3,5 km antes (Rinconada) 22° 34′ S, 66° 31′ W
Laguna La Brea (Santa Bárbara) 23° 56′ S, 64° 28′ W
Laguna La Brea, 25 km al O de Palma Sola (Santa Bárbara) 23° 56′ S, 64° 28′ W
Laguna La Brea, 25 km antes de Palma Sola (Ruta 1) (Santa Bárbara) 23° 56′ S, 64° 28′ W
Laguna La Brea, 25 km antes de Palma Sola (Santa Bárbara) 23° 56′ S, 64° 28′ W
Laguna La Brea, 25 km antes de Palma Sola, Ruta 1 (Santa Bárbara) 23° 56′ S, 64° 28′ W
Laguna La Brea, 25 km antes de Palma Sola, sobre ruta 1 (Santa Bárbara) 23° 56′ S, 64° 28′ W
Laguna La Brea, ruta 1, km 134 (Santa Bárbara) 23° 56′ S, 64° 28′ W
Laguna, Durazno, 4500 m (Tilcara) 23° 35′ S, 65° 12′ W
Lagunas de Yala (Dr. Manuel Belgrano) 24° 07′ S, 65° 28′ W
Lagunillas (Rinconada) 22° 25′ S, 66° 07′ W
Lagunita (Tilcara) 23° 35′ S, 65° 12′ W
Las Animas, Fraile Pintado (Ledesma) 23° 57′ S, 64° 46′ W
Las Escaleras (Palpalá) 24° 07′ S, 65° 17′ W
Las Lajitas (Palpalá) 24° 21′ S, 65° 03′ W
Ledesma (Ledesma) 23° 51′ S, 64° 46′ W
León (Dr. Manuel Belgrano) 24° 02′ S, 65° 26′ W
León 1 mi al O, 5800 pies (Dr. Manuel Belgrano) 24° 02′ S, 65° 26′ W
León, 1.6 km al O, 1770 m (Dr. Manuel Belgrano) 24° 02′ S, 65° 26′ W
León, 1200 m (Dr. Manuel Belgrano) 24° 02′ S, 65° 26′ W
León, 1500 m (Dr. Manuel Belgrano) 24° 02′ S, 65° 26′ W
Libertador General San Martín (Ledesma) 23° 49′ S, 64° 47′ W
Libertador Gral. San Martín, límite del Parque Nacional Calilegua (Ledesma) 23° 49′ S, 64° 47′ W
Lipán, 10 km al O de Purmamarca (Tumbaya) 23° 42′ S, 65° 37′ W
Los Perales, San Salvador de Jujuy (Dr. Manuel Belgrano) 24° 11′ S, 65° 19′ W
Maimará (Tilcara) 23° 37′ S, 65° 28′ W
Maimará, 2200 m (Tilcara) 23° 37′ S, 65° 28′ W
Maimara, 2230 m (Tilcara) 23° 37′ S, 65° 28′ W
Maimará, 2300 m (Tilcara) 23° 37′ S, 65° 28′ W
Maimará, 2328 m (Tilcara) 23° 37′ S, 65° 28′ W
Maimará, 2500 m (Tilcara) 23° 37′ S, 65° 28′ W
Maimará, 2600 m (Tilcara) 23° 37′ S, 65° 28′ W
Maimará, 3000 m (Tilcara) 23° 37′ S, 65° 28′ W
Maíz Gordo (=Port. del Maíz Gordo) (Santa Bárbara) 24° 22′ S, 64° 17′ W
Mesada de las Colmenas (Ledesma) 23° 42′ S, 64° 52′ W
Mesada de las Colmenas, 1550 m (Ledesma) 23° 42′ S, 64° 52′ W
Mina El Porvenir (Susques) 23° 53′ S, 66° 53′ W
Mina El Porvenir, 23 km al N, cerca del camino al Paso de Jama (Susques) 23° 41′ S, 66° 49′ W
Mina El Porvenir, 29 km al NE, camino a Susques (Susques) 23° 36′ S, 66° 49′ W

Mina Pan de Azúcar, 10 km al N, 1 km al N del Río Colquimayo (Rinconada) 22° 29′ S, 66° 07′ W
Mina Pan de Azúcar, 11 km al N, 2 km al N del Río Colquimayo (Rinconada) 22° 29′ S, 66° 07′ W
Mina Pan de Azúcar, 13 km al S, sobre Río Cincel (Cochinoca) 22° 42′ S, 66° 04′ W
Mina Pan de Azúcar, 2 km al NE sobre ruta provincial N° 71 (Rinconada) 22° 34′ S, 66° 01′ W
Mina Pan de Azúcar, 2 km al S, sobre ruta provincial N° 71 (Rinconada) 22° 37′ S, 65° 59′ W
Mina Pan de Azúcar, 6 km al NO camino a Rinconada (Rinconada) 22° 33′ S, 66° 04′ W
Mina Pan de Azúcar, 8 km al N (Rinconada) 22° 32′ S, 66° 04′ W
Mina Pan de Azúcar, 8 km al N y 1 km al O (Rinconada) 22° 32′ S, 66° 04′ W
Mina Pan de Azúcar, 8 km al N y 3 km al O (Rinconada) 22° 32′ S, 66° 03′ W
Mina Pan de Azúcar, 8 km al N y 5 km al O camino a Herrana, 3820 m (Rinconada) 22° 34′ S, 66° 06′ W
Mina Pan de Azúcar, 9 km al N (Rinconada) 22° 32′ S, 66° 04′ W
Mina Pirquitas, 10 km al SE sobre ruta provincial N° 74b (Rinconada) 22° 43′ S, 66° 25′ W
Mina Pirquitas, 15 km al SE sobre ruta provincial N° 74b (Rinconada) 22° 44′ S, 66° 23′ W
Mina Pirquitas, 19 km al SE sobre ruta provincial N° 74b (Cochinoca) 22° 46′ S, 66° 22′ W
Mina Pirquitas, 22 km al SE sobre ruta provincial N° 74b (Cochinoca) 22° 49′ S, 66° 20′ W
Mina Pirquitas, 28 km al SE sobre ruta provincial N° 74b (Rinconada) 22° 52′ S, 66° 19′ W
Mina Pirquitas, 31 km al SE, Sierra de Quichagua, sobre ruta provincial N° 74b, 4200 m (Rinconada) 22° 54′ S, 66° 19′ W
Mina Pirquitas, 4 km al E, sobre ruta provincial N° 70 (Cochinoca) 22° 32′ S, 66° 27′ W
Miniaio, 2 km al E sobre ruta provincial N° 71 (Cochinoca) 22° 43′ S, 66° 02′ W
Miniaio, 5 km al E sobre ruta provincial N° 71 (Cochinoca) 22° 43′ S, 66° 00′ W
Miyuyoc, 3750 m (Humahuaca) 22° 51′ S, 65° 18′ W
Normenta (Ledesma) 23° 50′ S, 65° 07′ W
Norte de Lizoite (Yavi) 22° 14′ S, 64° 24′ W
Ocloyas (Dr. Manuel Belgrano) 23° 56′ S, 65° 13′ W
On highway 29 (E off of hwy 9), 10 km W of Tiraxi, 5800 ft. (Dr. Manuel Belgrano) 23° 59′ S, 65° 23′ W
On highway 29 (east off of hwy 9), 10 km west of Tiraxi (Dr. Manuel Belgrano) 23° 59′ S, 65° 23′ W
On highway 9 at border with Salta, at campground on the way to El Carmen (El Carmen) 24° 28′ S, 65° 21′ W
On highway 9 at border with Salta, at campground on the way to El Carmen, 4600 ft. (El Carmen) 24° 28′ S, 65° 21′ W
On Valle Grande Rd, 2 km de Abra de Cañas (Valle Grande) 23° 40′ S, 64° 54′ W
On Valle Grande Rd, about 20 km NW Calilegua (Valle Grande) 23° 33′ S, 65° 00′ W
Orosmayo, 11 km al NE sobre ruta provincial N° 70 (Rinconada) 22° 33′ S, 66° 15′ W
Orosmayo, 9 km al NE sobre ruta provincial N° 70 (Rinconada) 22° 33′ S, 66° 16′ W

Ovejería (Tilcara) 23° 32′ S, 65° 19′ W
Oyeros, 3 km al N, camino entre las rutas 61 y 43 (El Carmen) 24° 30′ S, 65° 00′ W
Palma Sola (Santa Bárbara) 24° 00′ S, 64° 19′ W
Palma Sola, 18 km al S, (Santa Bárbara) 24° 04′ S, 64° 20′ W
Palma Sola, 550 m (Santa Bárbara) 24° 00′ S, 64° 19′ W
Palma Sola, Mina de Azufre (Santa Bárbara) 24° 00′ S, 64° 19′ W
Palos a pique (Santa Bárbara) 24° 05′ S, 64° 24 ′ W
Palpalá (Palpalá) 24° 16′ S, 65° 10′ W
Palpalá, 1 km al E, entre rutas 66 y 1 (Palpalá) 24° 16′ S, 65° 10′ W
Pampa Blanca (El Carmen) 24° 33′ S, 65° 04′ W
Paraje Palo Blanco, Parque Nacional Calilegua (Ledesma) 23° 54′ S, 64° 50′ W
Parque Nacional Calilegua, Aguas Negras, camping (Ledesma) 23° 45′ S, 64° 56′ W
Parque Nacional Calilegua, Arroyo Sauzalito (Ledesma) 23° 40′ S, 64° 37′ W
Paso de Jama, inmediaciones (Susques) 23° 19′ S, 67° 02′ W
Perico (El Carmen) 24° 23′ S, 65° 07′ W
Perico, 4000 ft. (El Carmen) 24° 23′ S, 65° 07′ W
Pirquita, 10 km antes de la mina (Rinconada) 22° 41′ S, 66° 31′ W
Pirquita, 20 km NO de Coranzulí (Rinconada) 22° 52′ S, 66° 19′ W
Planta Caimancito, Parque Nacional Calilegua (Ledesma) 23° 44′ S, 64° 36′ W
Pucapampa “Chozchoi” (Santa Catalina) 22° 23′ S, 66° 11′ W
Pucará (Tilcara) 23° 34′ S, 65° 23′ W
Puente sobre el Arroyo Sapagua y ruta nacional N° 9, 3500 m (Humahuaca) 23° 03′ S, 65° 23′ W
Puente sobre el Arroyo Sapagua, ruta nacional N° 9, entre Humahuaca y desvío a Iruya (Humahuaca) 23° 03′ S, 65° 23′ W
Puente sobre el Río San Francisco, cruce entre Ruta 1 y el Río San Francisco (Santa Bárbara) 23° 43′ S, 64° 32′ W
Puesto Viejo, 16 km al N de General Güemes, Río Las Pavas (El Carmen) 24° 30′ S, 65° 08′ W
Purmamarca, 10 km al O, sobre ruta 62 (Tumbaya) 23° 42′ S, 65° 37′ W
Reserva Olaroz-Cauchari, 3903 m (Susques) 23° 19′ S, 66° 35′ W
Reserva Provincial Olaroz-Cauchari, 30 km al O de Susques, sobre ruta provincial N° 70 (Susques) 23° 19′ S, 66° 35′ W
Reserva Provincial Olaroz-Cauchari, 35 km al O de Susques, sobre ruta provincial N° 70 (Susques) 23° 19′ S, 66° 37′ W
Reyes (Dr. Manuel Belgrano) 24° 11′ S, 65° 23′ W
Rinconada, 13 km al N, camino a Timón Cruz (Rinconada) 22° 23′ S, 66° 12′ W
Rinconada, 20 km al SE sobre ruta provincial N° 7 (Rinconada) 22° 27′ S, 66° 00′ W
Rinconada, 22 km al SE sobre ruta provincial N° 7 (Rinconada) 22° 27′ S, 65° 59′ W
Rinconada, 23 km al SE sobre ruta provincial N° 7 (Rinconada) 22° 27′ S, 65° 59′ W
Rinconada, 25 km al SE sobre ruta provincial N° 7 (Rinconada) 22° 30′ S, 65° 56′ W
Rinconada, 28 km al SE sobre ruta provincial N° 7 (Rinconada) 22° 31′ S, 65° 55′ W
Rinconada, 3 km al E sobre ruta provincial N° 7 (Rinconada) 22° 26′ S, 66° 10′ W
Rinconada, 30 km al SE sobre ruta provincial N° 7 (Rinconada) 22° 32′ S, 65° 54′ W
Rinconada, 32 km al SE sobre ruta provincial N° 7 (Rinconada) 22° 33′ S, 65° 53′ W
Rinconada, 6 km al N, camino a Timón Cruz, 4286 m (Rinconada) 22° 25′ S, 66° 12′ W
Río Ajedrez (Rinconada) 22° 40′ S, 66° 28′ W
Río Blanco (Palpalá) 24° 14′ S, 65° 14′ W

Río Blanco, 9 km SW San Antonio, 1495 m (San Antonio) 24° 25′ S, 65° 23′ W
Río Cincel, 2 km al N de Miniaio, sobre ruta provincial N° 71 (Cochinoca) 22° 42′ S, 66° 04′ W
Río Colorado, Parque Nacional Calilegua (Ledesma) 23° 56′ S, 64° 56′ W
Río Coyaguima (Rinconada) 22° 44′ S, 66° 29′ W
Río Coyaguima, 4000 m (Rinconada) 22° 44′ S, 66° 29′ W
Río de Zora, en cruce con ruta 34 (Ledesma) 23° 44′ S, 64° 41′ W
Río Grande de Jujuy bei Aival (Ledesma) 24° 01′ S, 65° 01′ W
Río Jordán (Valle Grande) 23° 38′ S, 64° 56′ W
Río Las Capillas, 15 km al N de Las Capillas, por ruta provincial N° 20 (Dr. Manuel Belgrano) 24° 02′ S, 65° 07′ W
Río Lavayén, 4 km al E, sobre ruta provincial N° 1 (San Pedro) 24° 16′ S, 64° 50′ W
Río Lavayén, app 1 km al N de Santa Rita (San Pedro) 24° 28′ S, 64° 48′ W
Río Lavayén, sobre ruta 6 al N de Santa Clara (San Pedro) 24° 10′ S, 64° 45′ W
Río Ledesma, app 14 km al S, de Pueblo Ledesma, sobre ruta 34 (Ledesma) 23° 56′ S, 64° 47′ W
Río Orosmayo (Rinconada) 22° 37′ S, 66° 26′ W
Río Orosmayo, Peñas Blancas (Rinconada) 22° 37′ S, 66° 26′ W
Río San Francisco, altura de Yuto, 500 m (Ledesma) 23° 39′ S, 64° 27′ W
Río Tesorero, 4 km al N de Tiraxi, sobre ruta provincial N° 29 (Dr. Manuel Belgrano) 23° 59′ S, 65° 18′ W
Río Tiraxi, 1.5 km al E de Tiraxi, sobre ruta provincial N° 29 (Dr. Manuel Belgrano) 23° 59′ S, 65° 19′ W
Río Tiraxi, app 5 km al S, de Tiraxi, sobre ruta provincial N° 29 (Dr. Manuel Belgrano) 23° 55′ S, 65° 21′ W
Río Yacoraite, 7 km al N de Huacalera y 3 km al O de ruta 9, 2740 m (Humahuaca) 23° 22′ S, 65° 20′ W
Ronqui Angosto, 2 km al O, sobre ruta provincial 16, 3700 m (Tumbaya) 23° 42′ S, 65° 42′ W
Ruinas de Tilcara (Tilcara) 23° 33′ S, 65° 20′ W
Rumi Cruz (Cochinoca) 22° 46′ S, 65° 32′ W
Ruta 83, camino a Valle Grande, 9 km al N de San Francisco, 1200 m (Valle Grande) 23° 35′ S, 64° 58′ W
Ruta nacional N° 34, cerca de Pampa Blanca (El Carmen) 24° 33′ S, 65° 04′ W
Ruta nacional N° 34, entre Ciudad Perico y San Pedro de Jujuy, app 10 km de Ciudad Perico (El Carmen) 24° 23′ S, 65° 06′ W
Salar Cauchari, 13 km al N de Cauchari, sobre ruta provincial N° 70 (Susques) 23° 58′ S, 66° 47′ W
Salar Cauchari, 31 km al N de Cauchari, sobre ruta provincial N° 70 (Susques) 23° 50′ S, 66° 47′ W
Salar Cauchari, 31 km al N de Cauchari, sobre ruta provincial N° 70, 3840 m (Susques) 23° 50′ S, 66° 47′ W
Salinas Grandes, 15 km al E de Tres Pozos sobre ruta provincial N° 16 (Tumbaya) 23° 37′ S, 65° 47′ W
Salinas Grandes, 2 km al E de Tres Pozos sobre ruta provincial N° 52 (Cochinoca) 23° 32′ S, 65° 55′ W
Salinas Grandes, al O de Tilcara, 2400 m (Tumbaya) 23° 34′ S, 65° 51′ W
Salinas Grandes, sobre ruta 52 (Tumbaya) 23° 34′ S, 65° 51′ W

San Antonio (San Antonio) 24° 22’ S, 65° 20’ W
San Francisco (Valle Grande) 23° 37’ S, 64° 57’ W
San Francisco, 1400 m (Valle Grande) 23° 37’ S, 64° 57’ W
San Francisco, 1500 m (Valle Grande) 23° 37’ S, 64° 57’ W
San Francisco, 1550 m (Valle Grande) 23° 37’ S, 64° 57’ W
San Francisco, 60 km de Ledesma camino a Valle Grande (Valle Grande) 23° 37’ S, 64° 57’ W
San Francisco, 60 km de Ledesma camino a Valle Grande, 1800 m (Valle Grande) 23° 37’ S, 64° 57’ W
San Francisco, aproximadamente dos km, pasando el pueblo, camino a Valle Grande (Valle Grande) 23° 37’ S, 64° 57’ W
San Francisco, Calilegua (Valle Grande) 23° 37’ S, 64° 57’ W
San Francisco, Macizo de Calilegua (Valle Grande) 23° 37’ S, 64° 57’ W
San Juancito (El Carmen) 24° 23’ S, 65° 03’ W
San Lorenzo (Ledesma) 23° 33’ S, 64° 40’ W
San Pedro (San Pedro) 24° 14’ S, 64° 52’ W
San Rafael, 1000 m (Santa Bárbara) 24° 07’ S, 64° 24’ W
San Rafael, Sierra Santa Bárbara, 1000 m (Santa Bárbara) 24° 07’ S, 64° 24’ W
San Salvador de Jujuy (Dr. Manuel Belgrano) 24° 12’ S, 65° 19’ W
Santa Bárbara (Santa Bárbara) 24° 17’ S, 64° 24’ W
Santa Bárbara (Valle Grande) 23° 36’ S, 65° 04’ W
Santa Catalina (Santa Catalina) 21° 57’ S, 66° 03’ W
Santa Catalina, 4500 m (Santa Catalina) 21° 57’ S, 66° 03’ W
Santa Catalina, 7 km al S, sobre ruta provincial N° 65, 3845 m (Santa Catalina) 21° 59’ S, 66° 03’ W
Santa Catalina, 8 km al S, por ruta provincial N° 65 (Santa Catalina) 21° 59’ S, 66° 03’ W
Santa Clara (Santa Bárbara) 24° 18’ S, 64° 41’ W
Santa Laura, camino de cornisa (El Carmen) 24° 30’ S, 65° 19’ W
Santa Rita, 2 km al NO, sobre ruta provincial N° 1 (San Pedro) 24° 28’ S, 64° 50’ W
Santa Rita, 4 km al NO, sobre ruta provincial N° 1 (San Pedro) 24° 27’ S, 64° 50’ W

Santa Rita, app 5 km al NO, sobre ruta provincial N° 1 (San Pedro) 24° 27’ S, 64° 50’ W
Santo Domingo (Rinconada) 22° 36’ S, 66° 13’ W
Sierra de Tilcara, 4500 m (Tilcara) 23° 35’ S, 65° 12’ W
Sierra de Tilcara, 4500 m, E de Maimará (Tilcara) 23° 35’ S, 65° 12’ W
Sierra de Zenta (Tilcara) 23° 35’ S, 65° 12’ W
Sierra de Zenta, 2 km al N del cruce del camino a Miyuyoc y ruta provincial N° 13 (Humahuaca) 22° 58’ S, 65° 21’ W
Sierra de Zenta, 4000 m (Tilcara) 23° 35’ S, 65° 12’ W
Sierra de Zenta, 4500 m, E de Maimará (Tilcara) 23° 35’ S, 65° 12’ W
Sierra de Zenta, entre Iturbe y Chaupe Rodeo, sobre ruta provincial N° 13 (Humahuaca) 22° 37’ S, 65° 20’ W
Sierra de Zenta, ruta provincial N° 13, entre Chaupe Rodeo e Iruya, 12 km al N de Chaupe Rodeo (Humahuaca) 22° 53’ S, 65° 15’ W
Sierra de Tilcara (Tilcara) 23° 35’ S, 65° 12’ W
Sierra Santa Bárbara, app 6 km al E de El Palmar (Santa Bárbara) 24° 05’ S, 64° 38’ W

Sierra Santa Bárbara, El Sunchal, 1200 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sobre ruta 40, 29 km al N del empalme con ruta 52 (Tumbaya) 23° 24′ S, 65° 46′ W
Sobre ruta 9 en el limite con al provincia de Salta, camino a El Carmen (El Carmen) 24° 28′ S, 65° 21′ W
Sobre ruta 9 en el límite con Salta, sobre camino a El Carmen (El Carmen) 24° 28′ S, 65° 21′ W
Sobre ruta nacional 52, 10 km al O de Ronqui Angosto (Tumbaya) 23° 40′ S, 65° 46′ W
Sunchal, 1000 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, 1500 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, 1600 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Santa Bárbara, 1200 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Santa Bárbara, 1200-1500 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Santa Bárbara, 1400 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Santa Bárbara, 1500 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Santa Bárbara, 1600 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Sierra de Santa Bárbara (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Sierra de Santa Bárbara, 1200 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Sierra de Santa Bárbara, 1300 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Sierra de Santa Bárbara, 1500 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Sierra de Santa Bárbara, 1600 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Sierra de Santa Bárbara, 1800 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Sierra Santa Bárbara, 1200 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Sierra Santa Bárbara, 1300 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Sierra Santa Bárbara, 1400 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Sierra Santa Bárbara, 1500 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Sunchal, Sierra Santa Bárbara, 1600 m (Santa Bárbara) 24° 14′ S, 64° 27′ W
Susques (Susques) 23° 36′ S, 66° 29′ W
Susques, 1 km al N sobre ruta provincial N° 74 (Susques) 23° 25′ S, 66° 29′ W
Susques, 10 km al N sobre ruta provincial N° 74 (Susques) 23° 21′ S, 66° 30′ W
Susques, 21 km al O, sobre ruta provincial N° 16 (Susques) 23° 24′ S, 66° 39′ W
Susques, 26 km al O, sobre ruta provincial N° 16 (Susques) 23° 24′ S, 66° 42′ W
Susques, 27 km al O, sobre ruta provincial N° 16 (Susques) 23° 24′ S, 66° 42′ W
Susques, 28 km al O, sobre ruta provincial N° 16 (Susques) 23° 25′ S, 66° 43′ W
Susques, 30 km al O, sobre ruta provincial N° 16 (Susques) 23° 25′ S, 66° 44′ W
Tafna, 7 km al O sobre ruta provincial N° 5 (Yavi) 22° 06′ S, 65° 48′ W
Tanques (Susques) 23° 13′ S, 66° 34′ W
Tanques, 1 km al N, sobre ruta provincial N° 74 (Susques) 23° 12′ S, 66° 35′ W
Tanques, 1 km al S, sobre ruta provincial N° 74 (Susques) 23° 14′ S, 66° 34′ W
Tanques, 2 km al N, sobre ruta provincial N° 74 (Susques) 23° 11′ S, 66° 35′ W
Tanques, 6 km al N, sobre ruta provincial N° 74 (Susques) 23° 05′ S, 66° 35′ W
Tanques, 7 km al SE, sobre Ruta provincial N° 74 (Susques) 23° 17′ S, 66° 31′ W
Tanques, 8 km al N, sobre ruta provincial N° 74 (Susques) 23° 08′ S, 66° 35′ W
Tilcara (Tilcara) 23° 33′ S, 65° 20′ W
Tilcara, 0.8 Km al E, 2600 m (Tilcara) 23° 33′ S, 65° 20′ W
Tilcara, 0.8 km al N (Tilcara) 23° 33′ S, 65° 20′ W
Tilcara, 2330 m (Tilcara) 23° 33′ S, 65° 20′ W
Tilcara, 2350 m (Tilcara) 23° 33′ S, 65° 20′ W
Tilcara, 2400 m (Tilcara) 23° 33′ S, 65° 20′ W

Tilcara, 2470 m (Tilcara) 23° 33′ S, 65° 20′ W
Tilcara, 2600 m (Tilcara) 23° 33′ S, 65° 20′ W
Tilcara, 8000 ft. (Tilcara) 23° 33′ S, 65° 20′ W
Tilquiza (Dr. Manuel Belgrano) 24° 05′ S, 65° 16′ W
Timón Cruz, 1 km al S, camino a Rinconada (Santa Catalina) 22° 10′ S, 66° 09′ W
Tocomar (Susques) 24° 10′ S, 66° 36′ W
Tocomar, 3 km al NO, sobre ruta nacional N° 51 (Susques) 24° 10′ S, 66° 37′ W
Tres Cruces (Humahuaca) 22° 55′ S, 65° 35′ W
Tres Cruces FCCN, 3700 m (Humahuaca) 22° 55′ S, 65° 35′ W
Tres Cruces, 3700 m (Humahuaca) 22° 55′ S, 65° 35′ W
Tres Cruces, 4000 m (Humahuaca) 22° 55′ S, 65° 35′ W
Tres Cruces, 8 km S, al lado de ruta 9 (Humahuaca) 22° 59′ S, 65° 35′ W
Tres Cruces, Mina Aguilar (Humahuaca) 22° 55′ S, 65° 35′ W
Tres Pozos, 10 km al E, km 15 sobre ruta provincial N° 16 (Tumbaya) 23° 34′ S, 65° 51′ W
Tres Pozos, 10 km al O del empalme de las rutas 40 y 52 (Cochinoca) 23° 33′ S, 65° 56′ W
Tres Pozos, 5 km al O, sobre ruta provincial N° 16 (Cochinoca) 23° 32′ S, 65° 58′ W
Tres Pozos, 6 km al E, sobre ruta provincial N° 16 (Cochinoca) 23° 34′ S, 65° 53′ W
Tumbaya (Tumbaya, Jujuy) 23° 51´ S, 65° 28´ W
Urundel (Ledesma) 23° 43′ S, 64° 46′ W
Valle Grande (Valle Grande) 23° 28′ S, 64° 58′ W
Valle Morado (Ledesma) 23° 31′ S, 64° 35′ W
Vega entre Laguna Caití y Laguna Isla Grande (Rinconada) 22° 36′ S, 66° 39′ W
Villa Carolina, 1258 m (San Pedro) 24° 16′ S, 64° 43′ W
Villa Carolina, 500 m (San Pedro) 24° 16′ S, 64° 43′ W
Villa Carolina, Río Lavallén, 500 m (San Pedro) 24° 16′ S, 64° 43′ W
Villa Carolina, Río Lavayén, 500 m (San Pedro) 24° 16′ S, 64° 43′ W
Vinalito, 2 km al SE, al borde del 2° canal (Santa Bárbara) 23° 40′ S, 64° 25′ W
Vinalito, Yuto (Santa Bárbara) 23° 40′ S, 64° 27′ W
Yavi (Yavi) 22° 07′ S, 65° 27′ W
Yavi Chico (Yavi) 22° 05′ S, 65° 28′ W
Yavi Chico, 3600 m (Yavi) 22° 05′ S, 65° 28′ W
Yavi Chico, El Habal (Yavi) 22° 05′ S, 65° 28′ W
Yavi, 3600 m (Yavi) 22° 07′ S, 65° 27′ W
Yavi, 3640 m (Yavi) 22° 07′ S, 65° 27′ W
Yavi, 6.8 km al SE de Suripujies, sobre ruta provincial N° 5, 3991 m (Yavi) 22° 13′ S, 65° 16′ W
Yoscaba, 5 km al NE (Santa Catalina) 22° 09′ S, 65° 58′ W
Yuchán (San Pedro) 24° 12′ S, 64° 51′ W
Yuto (Ledesma) 23° 38′ S, 64° 28′ W
Yuto, 700 m (Ledesma) 23° 38′ S, 64° 28′ W
Yuto, Río San Francisco (Ledesma) 23° 39′ S, 64° 27′ W
Zapla (Palpalá) 24° 15′ S, 65° 08′ W

LOCALITIES NOT PRECISELY LOCATED

“Jujuy”
Algunos kilómetros al WNW de Cerro Casabindo (Cochinoca)
Along Yala Laguna Rd, ? km W jct it and Hwy 9 (Dr. Manuel Belgrano)
Altiplano jujeño
Cordillera de Jujuy
Cordilleras of Jujuy
Departamento Ledesma
Departamento Ledesma, E de Jujuy
Departamento Santa Bárbara
Departamento Valle Grande
Finca El Palmar (Santa Bárbara)
Franja E del departamento Santa Bárbara (Santa Bárbara)
Laguna de Pozuelos (Santa Catalina, Rinconada y Yavi)
Laguna de Pozuelos, 3700 m (Santa Catalina, Rinconada y Yavi)
Laguna de Vilama (Rinconada)
Laguna de Vilama, 4500 m (Rinconada)
Lagunita
Mountains W of Yala (Dr. Manuel Belgrano)
Mountains W of Yala 10000 ft. (Dr. Manuel Belgrano)
Mountains W of Yala, 12000 ft. (Dr. Manuel Belgrano)
Parque Nacional Calilegua (Ledesma y Valle Grande)
Parque Provincial de Yala (Dr. Manuel Belgrano)
Quera, Pozuelos (Yavi)
Ramal de Perico a Embarcación
Río Grande de Jujuy
Río Las Pavas (El Carmen)
Río Salitre (Rinconada)
Río San Francisco
Rio San Francisco Valley
Ruta a Las Lagunas de Yala, al O de la unión con ruta 9 (Dr. Manuel Belgrano)
San Pablo
Sierra de Aguilar, 3800 m (Humahuaca y Cochinoca)
Sierra de Cochinoca (Cochinoca)
Sierra de Santa Bárbara, E de Jujuy (Santa Bárbara)
Sierra de Santa Victoria, 3000-5000 m (Yavi)
Sierra de Zenta (Humahuaca)
Sierra El Centinela (Santa Bárbara)
Sierra Santa Bárbara, 1200 m (Santa Bárbara)
Sobre ruta 34, Colonia Libertad
Sudeste de Jujuy
Vecindades del Parque Nacional Calilegua (Ledesma)
W of Yala (Dr. Manuel Belgrano)

LITERATURE CITED

Aceñolaza, E. M. de

1991 El Carpincho. Serie Monográfica y Didáctica Nro. 11. Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán. 26 pp.

Allen, J. A.

1901 New South American Muridae and new *Metachirus*. Bulletin of the American Museum of Natural History 14:405-412.

Alvarez, M. R.

2002 Manejo Sustentable del Carpincho (*Hydrochoerus hydrochaeris*, Linnaeus 1766) en Argentina: Un Aporte al Conocimiento de la Biología de la Especie Desde la Cría en Cautiverio. Tesis Doctoral. Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires. 210 pp.

Alvarez, M. R., and R. A. Martinez

In press Orden Rodentia. Suborden Histricognathi (in part). In Los Mamíferos de Argentina: Sistemática y Distribución (Barquez, R. M., M. M. Díaz, and R. A. Ojeda, eds.). SAREM (Sociedad Argentina para el Estudio de los Mamíferos), Mendoza, Argentina.

Ameghino, F.

1889 Contribución al conocimiento de los mamíferos fósiles de la República Argentina. Actas de la Academia Nacional de Ciencias en Córdoba 6: 1-1027 y Atlas: 98 pls.

Anderson, S.

1993 Los Mamíferos Bolivianos: Notas de Distribución y Claves de Identificación. Publicación Especial del Instituto de Ecología (Colección Boliviana de Fauna), 159 pp.

1997 Mammals of Bolivia: taxonomy and distribution. Bulletin of the American Museum of Natural History 231:1-652.

Anonymous

1996 Revista Nuestra. ADEC. Año 3, N° 110, 22 pp.

Arditi, S., I., M. D. Mudry, and A. Brown

1989 Estado actual del desarrollo de la Primatología en Argentina. Boletín Primatológico Latinoamericano 1:43-66.

Arra, M. A.

1974 Distribución de *Leo onca* (L) en Argentina. Neotrópica 2:156-158.

Baker, R. J., J. C. Patton, H. H. Genoways, and J. W. Bickham
1988 Genic studies of *Lasiurus* (Chiroptera:Vespertilionidae). Occasional Papers, The Museum, Texas Tech University 117:1-15.

Barlow, J. C.
1965 Land Mammals from Uruguay: Ecology and Zoogeography. Ph.D. Dissertation, University of Kansas, Lawrence, Kansas, USA. 346 pp.

Barquez, R. M.
1983 La distribución de *Neotomys ebriosus* (Thomas) en la Argentina y su presencia en la provincia de San Juan (Mammalia, Rodentia, Cricetidae). Historia Natural 3:189-191.

1984 Significativa extensión del rango de distribución de *Diaemus youngi* (Jentink, 1893) (Mammalia, Chiroptera, Phyllostomidae). Historia Natural 4:67-68.

1987 Los Murciélagos de Argentina. Ph.D. Dissertation, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad de Tucumán, Argentina. 525 pp.

In press Orden Chiroptera. In Los Mamíferos de Argentina: Sistemática y Distribución (Barquez, R. M., M. M. Díaz, and R. A. Ojeda, eds). SAREM (Sociedad Argentina para el Estudio de los Mamíferos), Mendoza, Argentina.

Barquez, R. M., and M. M. Díaz
2001 Bat of the Argentine Yungas: A systematic and distributional analysis. Acta Zoológica Mexicana 82:1-81.

Barquez, R. M., N. P. Giannini, and M. A. Mares
1993 Guía de Murciélagos de Argentina. Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma, USA. 119 pp.

Barquez, R. M., and S., C. Lougheed
1990 New distributional records of some argentine bat species. Journal of Mammalogy 71:261-263.

Barquez, R. M., M. A. Mares, and J. K. Braun
1999 The bats of Argentina. Special Publications, Museum of Texas Tech University 4:1-275.

Barquez, R. M., M. A. Mares, and R. A. Ojeda
1991 Mamíferos de Tucumán. Oklahoma Museum of Natural History. University of Oklahoma, Norman, Oklahoma, USA. 282 pp.

Barquez, R. M., and R. A. Ojeda
1992 The bats (Mammalia: Chiroptera) of the Argentine Chaco. Annals of Carnegie Museum 61:239-261.

Barquez, R. M., D. F. Williams, M. M. Mares, and H. H. Genoways
1980 Karyology and morphometrics of three species *Akodon* (Mammalia: Muridae) from northwestern Argentina. Annals of Carnegie Museum 49:379-403.

Berta, A.
1988 Quaternary evolution and biogeography of the large South American Canidae. Mammalia: Carnivora. University of California Publications in Geological Sciences 132:1-149.

Bininda-Emonds, O. R. P., J. L., Gittleman, and A. Purvis
1999 Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). Biological Reviews 74:143-175.

Blaustein, S., A., R. C. Liascovich, L. I. Alfelbaum, L. Dalefe, R. M. Barquez and O. A. Reig
1992 Correlates of systematic differentiation between two closely related allopatric population of the *Akodon boliviensis* group from NW Argentina (Rodentia: Cricetidae). Zeitschrift für Säugetierkunde 57:1-13.

Braun, J. K.
1993 Systematic relationships of the Tribe Phyllotini (Muridae:Sigmodontinae) of South American. Oklahoma Museum of Natural History, Special Publications. 50 pp.

Braun, J. K., and M. A. Mares
2002 Systematics of the *Abrocoma cinerea* species complex (Rodentia: Abrocomidae), with a description of a new species of abrocoma. Journal of Mammalogy 83:1–19.

Brown, A. D.
1995 Las selvas de montaña del noroeste de Argentina: problemas ambientales e importancia de su conservación. Pp. 9-18 in Investigación, Conservación y Desarrollo en Selvas Subtropicales de Montaña (Brown, A. D., and H. R. Grau, eds.). Laboratorio de Investigaciones Ecológicas de las Yungas, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina. 270 pp.

Budin, E.
1931 Lista y notas sobre aves del N. O. Argentino (Provincia de Jujuy). El Hornero 4:401-410.

Cabrera, A.

1953 Los Roedores Argentinos de la Familia "Caviidae." Escuela de Veterinaria. Facultad de Agronomía y Veterinaria, Universidad Nacional de Buenos Aires, Argentina. 93 pp.

1958 Catálogo de los mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciencias Zoológicas 4:1-307.

1961a Catálogo de los mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciencias Zoológicas 4:309-732.

1961b Los félidos vivientes de la República Argentina. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciencias Zoológicas 6:151-247.

1976 Regiones fitogeográficas Argentinas. Enciclopedia Argentina de Agricultura y Jardinería 2(2):1-85.

Cabrera, A. L.

1977 Flora de la Provincia de Jujuy. República Argentina. Colección Científica del INTA (Instituto Nacional de Tecnología Agropecuaria), parte II. 275 pp.

Cabrera, A. L., and A. Willink

1973 Biogeografía de América Latina. Secretaría General de la organización de los Estados Americanos. Serie de Biología, Monografía 13. 122 pp.

Cajal, J. L.

1985a Comportamiento. Pp. 87-99 in Estado Actual de las Investigaciones Sobre Camélidos en la República Argentina (Cajal, J. L., and J. N. Amaya, eds.). Ministerio de Educación y Justicia, Secretaria de Ciencia y Técnica, Programa Nacional de Recursos Naturales Renovables, Buenos Aires, Argentina. 388 pp.

1985b Manejo de Camélidos. Pp. 179-198 in Estado Actual de las Investigaciones Sobre Camélidos en la República Argentina (Cajal, J. L., and J. N. Amaya, eds.). Ministerio de Educación y Justicia, Secretaria de Ciencia y Técnica, Programa Nacional de Recursos Naturales Renovables, Buenos Aires, Argentina. 388 pp.

Cajal, J. L., and S. M. Bonaventura
1998 Densidad, biomasa y diversidad de mamíferos en al Puna y Cordillera Frontal. Pp. 191-213 in Bases Para la Conservación y Manejo de la Puna y Cordillera Frontal de Argentina. El rol de las Reservas de la Biósfera (Cajal, J. L., J. L. G. Fernández and R. Tecchi, eds.). FUCEMA (Fundación para la Conservación de las Especies y el Medio Ambiente), Buenos Aires, Argentina. 336 pp.

Capllonch, P., A. G. Autino, M. Díaz, R. M. Barquez, and M. Goytia
1997 Los mamíferos del Parque Biológico Sierra de San Javier, Tucumán, Argentina: observaciones sobre su sistemática y distribución. Mastozoología Neotropical 4:49-71.

Carleton, M. D., and G. G. Musser
1989 Systematic studies of Oryzomyine rodents (Muridae, Sigmodotinae): A synopsis of *Microryzomys*. Bulletin of the American Museum of Natural History 191:1-83.

Cerqueira, R.
1984 Reproduction de *Didelphis albiventris* dans le nord-est du Brésil (Polyprodontia, Didelphidae). Mammalia 48:95-104.

1985 The distribution of *Didelphis* in South America (Polyprodontia, Didelphidae). Journal of Biogeography 12:135-145.

Chébez, J. C.
1994 Los Que se Van. Especies Argentinas en Peligro. Editorial Albatros, Buenos Aires, Argentina. 604 pp.

Cirignoli, S.,, D. H. Podestá, and U. F. J. Pardiñas
2001 Diet of the short-eared owl in Northwestern Argentina. The Raptor Research Foundation 35:68-69.

Clutton-Brock, J., C.B. Corbet, and M. Hills
1976 A review of the family Canidae, with a classification by numerical methods. Bulletin of the British Museum (Natural History), Zoology series 29:117-199.

Contreras, J. R.
1982 Mamíferos de Corrientes I. Nota preliminar sobre la distribución de algunas especies. Historia Natural 2:71-72.

1984 Notas sobre el género *Marmosa* en el noreste argentino (Marsupialia, Didelphidae). Historia Natural 4:11-12.

Contreras, J. R., and L. M. Berry

1983 Notas acerca de los roedores del Género *Oligoryzomys* de la provincia de Chaco, República Argentina (Rodentia, Cricetidae). Historia Natural 3:145-148.

Contreras, J. R., and M. I. Rosi

1980 Una nueva subespecie del ratón colilargo para la provincia de Mendoza: *Oligoryzomys flavescens occidentalis* (Mammalia, Rodentia, Cricetidae). Historia Natural 1:157-160.

Contreras, L. R., J. C. Torres-Murua, and J. L. Yañez

1987 Biogeography of octodontid rodents: An eco-evolutionary hypothesis. Fieldiana: Zoology, new series 39:401-411.

Corbet, G. B.

1978 The Mammals of the Palaeartic Region: A Taxonomic Review. British Museum of Natural History, London, UK. 314 pp.

Corbet, G. B., and J. E. Hill

1986 A World List of Mammalian Species. British Museum of Natural History, London, UK. 254 pp.

Crespo, J. A.

1941 Datos referidos a la fauna del altiplano jujeño. Revista Argentina de Zoogeografía 1:17-25.

1944 Contribución al conocimiento de la ecología de algunos dasipódidos (Edentata) argentinos. Revista Argentina de Zoogeografía 4:7-39.

1950 Nota sobre mamíferos de Misiones nuevos para la Argentina. Comunicaciones del Instituto Nacional de Investigaciones de las Ciencias Naturales anexas al Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" 1:1-14.

1958 Nuevas especies y localidades de quirópteros para Argentina (Mammalia: Chiroptera). Neotrópica 4:26-32.

1974 Comentarios sobre nuevas localidades para mamíferos de la Argentina y Bolivia. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciencias Zoológicas 11:1-31.

1982 Ecología de las comunidades de mamíferos del Parque Nacional Iguazú, Misiones. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ecología 3:45-162.

Dalby, P. L., and M. A. Mares

1974 Notes on the distribution of the Coney rat, *Reithrodon auritus*, in Northwestern Argentina. American Midland Naturalist 92:205-206.

Davis, W. B.

1973 Geographic variation in the fishing bat, *Noctilio leporinus*. Journal of Mammalogy 54:862-864.

D'Elía, G.

2003 Phylogenetics of Sigmodontinae (Rodentia, Muroidea, Cricetidae), with special reference to the akodont group, and with additional comments on historical biogeography. Cladistic 19:307-323.

Del Ponte, E.

1944 *Basilia romañai nobis* (Diptera, Nycteribiidae) de la Argentina. Anales del Instituto de Medicina Regional de la Universidad Nacional de Tucumán 1(1):117-128.

de Oliveira, T. G.

1998a *Herpailurus yagouarondi*. Mammalian Species 578:1-6.

1998b *Leopardus wiedii*. Mammalian Species 579:1-6.

Díaz, G. B., and R. A. Ojeda (editors)

2000 Libro Rojo de Mamíferos Amenazados de la Argentina. Sociedad Argentina para el Estudio de los Mamíferos, Mendoza. 106 pp.

Díaz, M. M.

2000 Key to Mammals of Jujuy Province, Argentina. Occasional Papers, Oklahoma Museum of Natural History 7:1-29.

Díaz, M. M., and R. M. Barquez

1999 Contributions to the knowledge of the mammals of Jujuy Province, Argentina. Southwestern Naturalist 44:324-333.

2002 Los Mamíferos de Jujuy, Argentina. L.O.L.A. (Literature of Latin America), Buenos Aires, Argentina. 326 pp.

Díaz, M. M., R. M. Barquez, J. K. Braun, and M. A. Mares

1999 A new species of *Akodon* (Muridae: Sigmodontinae) from northwestern Argentina. Journal of Mammalogy 80:786-798.

Díaz, M. M., J. K. Braun, M. A. Mares, and R. M. Barquez

1997 Key to mammals of Salta Province, Argentina. Occasional Papers of the Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma 2:1-10.

2000 An update of the taxonomy, systematics, and distribution of the mammals of Salta Province, Argentina. Occasional Papers, Oklahoma Museum of Natural History 10:1-52.

Díaz, M. M., D. A. Flores, and R. M. Barquez
1998 Instrucciones para la preparación y conservación de mamíferos. Publicaciones Especiales PIDBA (Programa de Investigaciones de Biodiversidad Argentina) 1:1-44.

2002 A new species of gracile mouse opossum, genus *Gracilinanus* (Didelphimorphia: Didelphidae), from Jujuy Province, Argentina. Journal of Mammalogy 83:824-833.

Díaz, M. M., and M. Lucherini
In Press Orden Carnivora. Familia Canidae, Mustelidae, Mephitidae, Procyonidae. In Los Mamíferos de Argentina: Sistemática y Distribución (Barquez, R. M., M. M. Díaz, and R. A. Ojeda, eds). SAREM (Sociedad Argentina para el Estudio de los Mamíferos), Mendoza, Argentina.

Dolan, P.
1989 Systematics of Middle American mastiff bats of the genus *Molossus*. Special Publications, The Museum, Texas Tech University 29:1-71.

Dragoo, J. W., and R. L. Honeycutt
1997 Systematics of mustelid-like carnivores. Journal of Mammalogy 78:426-443.

Dragoo, J. W., J. Salazar-Bravo, L. J. Layne, and T. L. Yates.
2002 Relationships within the *Calomys callosus* species group based on amplified fragment length polymorphisms. Biochemical Systematics and Ecology 31:703-713.

Eger, J. L.
1977 Systematics of the Genus *Eumops* (Chiroptera: Molossidae). Life Sciences Contributions, Royal Ontario Museum 110:1-69.

Eisenberg, J. F., and K. H. Redford.
1999 Mammals of the Neotropics. Vol. 3. The Central Neotropics: Ecuador, Peru, Bolivia, Brasil. University of Chicago Press, Chicago, Illinois, USA. 610 pp.

Espinosa, M. B., and O. A. Reig
1991 Cytogenetics and karyosystematics of South American oryzomine rodents (Cricetidae, Sigmodontinae) III. Banding karyotypes of Argentinian *Oligoryzomys*. Zeitschrift für Säugetierkunde 56:306-317.

Flores, D. A.
2003 Estudio Taxonómico y Zoogeográfico de los Marsupiales de Argentina. Ph.D. Dissertation, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina. 325 pp.

Flores, D. A., and M. M. Díaz
2002 Extensión austral de la distribución conocida de *Micoureus constantiae* (Didelphimorphia, Didelphidae). Acta Zoológica Mexicana 86:239-242.

Flores, D. A., M. M. Díaz, and R. M. Barquez.
2000 Mouse opossums (Didelphimorphia, Didelphidae) of northwestern Argentina: systematics and distribution. Zeitschrift für Säugetierkunde 65:321-339.

Fornes, A., E. Massoia, and G. E. Forrest
1967 *Tonatia sylvicola* (d'Orbigny) nuevo género y especie para la República Argentina (Chiroptera: Phyllotomidae). Physis 27:149-152.

Franklin, W. L.
1982 Biology, ecology, and relationship to man of the South American camelids. Pp. 457-489 in Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, Special Publication Series, 6. University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

Galliari, C. A., and U. F. J. Pardiñas
2000 Taxonomy and distribution of the sigmodontine rodents of the genus *Necromys* in central Argentina and Uruguay. Acta Theriologica 45:211-232.

Galliari, C. A., U. F. J. Pardiñas, and F. J. Goin
1996 Lista comentada de los mamíferos argentinos. Mastozoología Neotropical 3:36-61.

García-Perea, R.
1994 The pampas cat group (Genus *Lynchailurus* Severtzov, 1858) (Carnivora: Felidae), a systematic and biogegraphic review. American Museum Novitates 3096:1-35.

2002 Andean mountain cat *Oreailurus jacobita*: morphological description and comparison with other felines from the Altiplano. Journal of Mammalogy 83:110-124.

Gardner, A. L.
1993 Order Didelphimorphia. Pp. 15-27 in Mammal Species of the World: A Taxonomic and Geographic Reference. Second edition (Wilson, D. E., and D. M. Reeder eds.). Smithsonian Institution Press, Washington, D.C., USA.

Gardner, A. L., and J. L. Patton
1976 Karyotypic variation in oryzomine rodents (Cricetinae) with comments on chromosomal evolution in the Neotropical cricetine complex. Occasional Papers, Museum of Zoology, Louisiana State University 49:1-48.

Gompper, M.E., and D. M. Decker
1998 *Nasua nasua*. Mammalian Species 580:1-9.

Goodwin, G. G.
1960 The status of *Vespertilio auripendulus* Shaw, 1800, and *Molossus ater* Geoffroy, 1805. American Museum Novitates 1994:1-6.

Groves, C. P.
1993 Order Primates. Pp. 243-277 in Mammal Species of the World: A Taxonomic and Geographic Reference. Second edition (Wilson, D. E., and D. M. Reeder eds.). Smithsonian Institute Press, Washington, D.C., USA.

Gyldenstolpe, N.
1932 A manual of Neotropical sigmodont rodents. Kunglia Svenska Vetenskapsakademiens Handlingar, Stockholm, Band 11, 3:1-164 pp. + 18 plates

Hall, E. R.
1981 The Mammals of North America. 2 vols. John Wiley & Sons, New York, New York, USA. xv + 1181 + 90 pp.

Hamlett, G. W. D.
1939 Identity of *Dasypus septemcinctus* Linnaeus, with notes on some related species. Journal of Mammalogy 20:328-336.

Heinonen, S., and A. Bosso
1994 Nuevos aportes para el conocimiento de la mastofauna del Parque Nacional Calilegua (Provincia de Jujuy, Argentina). Mastozoología Neotropical 1:51-60.

Heinonen Fortabat, S., and J. C. Chébez
1997 Los mamíferos de los Parques Nacionales de la Argentina. Monografía Especial L.O.L.A. (Literature of Latin America), Buenos Aires 14:1-70.

Hershkovitz, P.
1955 South American Marsh Rats, Genus *Holochilus*, with a summary of sigmodont Rodents. Fieldiana: Zoology, 37:639-673.

1962 Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana: Zoology, 46:1-524.

1994 The description of a new species of South American hocicudo, or long-nosed mouse, genus *Oxymycterus* (Sigmodontinae, Muroidea), with a critical review of the generic content. Fieldiana: Zoology, new series 19:1-74.

Hill, J. E., and D. L. Harrison

1987 The baculum in the Vespertilioninae (Chiroptera:Vespertilionidae) with a systematic review, a synopsis of *Pipistrellus* and *Eptesicus*, and the description of a new genus and subgenus. Bulletin of the British Museum (Natural History), Zoology series 52:225-305.

Honacki, J. H., K. E. Kinman, and J. W. Koeppl (eds.)

1982 Mammals Species of the World: A Taxonomic and Geographic Reference. Allen Press, Inc. and The Association of Systematics Collections, Lawrence, Kansas, USA. 694 pp.

Husson, A. M.

1962 The bats of Suriname. Zoölogische Monographieën van het Rijksmuseum van Natuurlijke Historie te Leiden 58:1-222.

1978 The mammals of Suriname. Zoölogische Monographieën van het Rijksmuseum van Natuurlijke Historie 2:1-569.

Iudica, C. A.

1995 Frugivoría en murciélagos: el frutero común (*Sturnira lilium*) en las Yungas de Jujuy, Argentina. Pp. 123-128 in Investigación, Conservación y Desarrollo en Selvas Subtropicales de Montaña (Brown, A. D., and H. R. Grau, eds.). Laboratorio de Investigaciones Ecológicas de las Yungas, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina.

Jaccard, P.

1908 Nouvelles aecherches sur la distribution florale. Bulletin Society Vaud. Science Natural 44:223-270.

Jayat, J. P., R. M. Barquez, M. M. Díaz, and P. J. Martinez

1999 Aportes al conocimiento de la distribución de los carnívoros del noroeste de Argentina. Mastozoología Neotropical 6:15-30.

Johnson W. E., J. P. Slattery, E. Eizirik, J. H. Kim, M. M. Raymond, C. Bonacic, R. Cambre, P. Crawshaw, A. Nunes, H. N. Seuanez, M. A. Moreira, K. L. Seymour, F. Simon, W. Swanson, and S. J. O'Brien

1999 Disparate phylogeographic patterns of molecular genetic variation in four closely related South American small cat species. Molecular Ecology 8:S79-S94.

Jones, J. K., D. C. Carter, H. H. Genoways, R. S. Hoffmann, D. W. Rice, and C. Jones
1986 Revised checklist of North American mammals north of Mexico, 1986. Occasional Papers, The Museum, Texas Tech University 107:1-22.

Keegan, R. A., and J. M. Keegan
1993 Atlas de la República Argentina. Agrupación de diarios del Interior, S. A., Buenos Aires, published by Editorial Antártica, Santiago, Chile.

Kelt, D. A., R. E. Palma, M. H. Gallardo, and J. A. Cook.
1991 Chromosomal multiformity in *Eligmodontia* (Muridae: Sigmodontinae), and verification of the status of *Eligmodontia morgani*. Zeitschrift für Säugetierkunde 56:352-358

Koopman, K. F.
1993 Order Chiroptera. Pp. 134-232 in Mammal Species of the World: A Taxonomic and Geographic Reference. Second ed. (Wilson, D. E., and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C., USA.

Kraglievich, L.
1930 Craneometría y clasificación de los cánidos sudamericanos, especialmente los argentinos actuales y fósiles. Physis 10:35-73.

Kramer, K. M., J. A. Monjeau, E. C. Birney, and R. S. Sikes.
1999 *Phyllotis xanthopygus*. Mammalian Species 617:1-7.

La Val, R. K.
1973 A revision of the neotropical bats of the Genus *Myotis*. Bulletin of the Natural History Museum of Los Angeles County 15:1-54.

Langguth, A.
1975 Ecology and evolution in the South American canids. Pp 192-206 in The Wild Canids. Their Systematics, Behavioral Ecology, and Evolution (Fox, M. W., ed.), Van Nostrand and Reibhold Co., New York, New York, USA.

Liascovich, R. C.
1991 Cariosistemática y Evolución Cromosómica en Cricétidos Akodontinos (Rodentia, Muroidea). Ph.D. Dissertation. Universidad de Buenos Aires, Buenos Aires, Argentina. 183 pp.

López González, C., and S. Presley.
2001 Taxonomic status of *Molossus bondae* J. A. Allen, 1904 (Chiroptera: Molossidae), with description of a new subspecies. Journal of Mammalogy 82:760-774.

Lucero, M. M.

1983 Lista y distribución de aves y mamíferos de la provincia de Tucumán. Miscelánea 75, Fundación Miguel Lillo 75:1-61

1987 Sobre la presencia de dos taxa de *Coendu* en el norte argentino (Mammalia: Erethizontidae). Acta Zoológica Lilloana 39:37-42.

Mann Fischer, G.

1945 Mamíferos de Tarapaca: observaciones realizadas durante una expedición al alto norte de Chile. Biológica 2:23-141.

1978 Los pequeños mamíferos de Chile (marsupiales, quirópteros, edentados y roedores). Gayana, Zoología 40:1-342.

Mares, M. A.

1973 Climates, Mammalian Communities, and Desert Rodent Adaptations: An investigation into evolutionary convergence. Ph.D. Dissertation, University of Texas, Austin, Texas, USA. 345 pp.

Mares, M. A., R. M. Barquez, and J. K. Braun

1995 Distribution and ecology of some argentine bats. Annals of Carnegie Museum 64:219-237.

Mares, M. A., R. M. Barquez, J. K. Braun, and R. A. Ojeda

1996 Observations on the mammals of Tucumán Province, Argentina. I. Systematics, distribution, and ecology of the Didelphimorphia, Xenarthra, Chiroptera, Primates, Carnivora, Perissodactyla, Artiodactyla, and Lagomorpha. Annals of Carnegie Museum 65:89-152.

Mares, M. A., J. K. Braun, R. M. Barquez, and M. M. Díaz.

2000 Two new genera and species of halophytic desert mammal from isolated salt flats in Argentina. Occasional Papers, The Museum, Texas Tech University 203:1-27.

Mares, M. A., and R. A. Ojeda

1982 Patterns of diversity and adaptation in South American Histricognath Rodents. Pp. 393-432 in Mammalian Biology in South America (Mares, M. A. , and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, Special Publication Series, 6. University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

Mares, M. A., R. A. Ojeda, and R. M. Barquez

1989 Guide to the Mammals of Salta Province, Argentina. University of Oklahoma Press, Norman, Oklahoma, USA. 303 pp.

Mares, M. A., R. A. Ojeda, J. K. Braun, and R. M. Barquez
1997 Systematics, distribution, and ecology of the mammals of Catamarca Province, Argentina. Pp. 89-141 in Life Among the Muses: Papers in Honor of James S. Findley (Yates, T. L., W. L. Gannon, and D. E. Wilson, eds.). Special Publication, The Museum of Southwestern Biology, The University of New Mexico, Albuquerque, New Mexico, USA.

Mares, M. A., R. A. Ojeda, and M. P. Kosco
1981 Observations on the distribution and ecology of the mammals of Salta Province, Argentina. Annals of Carnegie Museum Natural History 50:151-206.

Massoia, E.
1971 Las ratas nutrias argentinas del género *Holochilus* descriptas como *Mus braziliensis* por Waterhouse (Mammalia-Rodentia-Cricetidae). Revista de Investigaciones Agropecuarias, Ser. 4, Patología Animal 8:141-148.

1973 Observaciones sobre el género *Lutreolina* en la República Argentina (Mammalia-Marsupialia-Didelphidae). Revista de Investigaciones Agropecuarias, ser. 1, Biología y Producción animal 10:13-20.

1976 Mammalia. In Fauna de agua dulce de la República Argentina (Ringuelet, R., ed.), FECIC (Fundación para la Educación, la Ciencia y la Cultura), Buenos Aires, 44:128 pp.

1980 El estado sistemático de cuatro especies de cricétidos sudamericanos y comentarios sobre otras especies congenéricas (Mammalia, Rodentia). Ameghiniana 17:280-287.

1981 *Dusicyon inca* (Thomas) nuevo mamífero para la Argentina (Carnivora, Canidae). Investigaciones Agropecuarias 16:307-311.

1982 *Dusicyon gymnocercus lordi*, una nueva subespecie del "zorro gris grande" (Mammalia: Carnivora: Canidae). Neotrópica 28:147-152.

1993 Análisis de regurgitados de *Bubo virginianus* de Laguna de Pozuelos, provincia de Jujuy. Aprona 26:13-16.

Massoia, E., J. C. Chébez, A. Bosso, A. Parra, and M. Masariche
1992a Nuevas localidades de mamíferos amenazados en la Argentina (1° parte). Boletín Científico 21:1-11.

1992b Nuevas localidades de mamíferos amenazados en la Argentina (2° parte). Boletín Científico 22:39-53.

Massoia, E., and A. Fornes
1972 Presencia y rasgos etoecológicos de *Marmosa agilis chacoensis* Tate, en las provincias de Buenos Aires, Entre Ríos y Misiones (Mammalia-Marsupialia-Didelphidae). Revista de Investigaciones Agropecuarias, ser. 1, Biología y Producción animal 9:72-82.

Massoia, E., and U. F. Pardiñas
1993 El estado sistemático de algunos muroideos estudiados por Ameghino en 1889. Revalidación del género *Necromys* (Mammalia, Rodentia, Cricetidae). Ameghiniana 30:407-418.

Massoia, E., O. B. Vaccaro, C. Galliari, and S. Ambrosini
1987 La mastofauna del Río Uruguay - I, provincia de Misiones. Instituto Nacional de Investigaciones de Ciencias Naturales, Zoología 14:111-124.

Matschie, H.
1894 Herr Mastchie besprach die von Herrn Paul Neumann in Argentinien gesammelten und beobachteten Säugethiere. Gesellschaft naturforschender Freude, Berlin 20:57-63.

McKenna, M. C., and S. K. Bell
1997 Classification of Mammals Above the Species Level. Columbia University Press, New York, New York, USA. 631 pp.

Merino, M. L.
In press Orden Artiodactyla. Suborden Ruminantia. Familia Cervidae. In Los Mamíferos de Argentina: Sistemática y Distribución (Barquez, R. M., M. M. Díaz, and R. A. Ojeda, eds). SAREM (Sociedad Argentina para el Estudio de los Mamíferos), Mendoza, Argentina.

Meyer, T.
1963 Estudios sobre la selva tucumana. Opera Lilloana 19:1-140.

Miller, G. S., Jr.
1907 The families and genera of bats. Bulletin of the United States National Museum 57:1-282.

Mones, A., and J. Ojasti.
1986 *Hydrochoerus hydrochaeris*. Mammalian Species 264:1-7.

Morales, J. C., and J. W. Bickham
1995 Molecular systematics of the Genus *Lasiurus* (Chiroptera: Vespertilionidae) based on restriction site maps of mitochondrial ribosomal genes. Journal of Mammalogy 76:730-749.

Morales, J. M., M. Sirombra, and A. D. Brown
1995 Riqueza de árboles en las Yungas argentinas. Pp. 163-170 in Investigación, Conservación y Desarrollo en Selvas Subtropicales de Montaña (Brown, A. D., and H. R. Grau, eds.). Laboratorio de Investigaciones Ecológicas de las Yungas, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina.

Morello, J., and J. Adámoli
1968 La vegetación de la República Argentina. Las grandes unidades de vegetación y de ambientes del Chaco argentino. Primera parte: Objetivos y Metodología. INTA (Instituto Nacional de Tecnología Agropecuaria), Buenos Aires, Serie Fitogeográfica 10:1-125.

Morello, J., and C. Saravia Toledo
1959 El Bosque Chaqueño, II. La ganadería y el bosque en el Oriente de Salta. Revista de Agronomía del Noroeste Argentino 3:209-258.

Murray, J. L., and G. L. Gardner
1997 *Leopardus pardalis*. Mammalian Species 548:1-10.

Musser, G. G., E. M. Brothers, M. D. Carleton, and A. L. Gardner.
1998 Systematic studies of oryzomine rodents (Muridae, Sigmodontinae): diagnoses and distributions of species formerly assigned to *Oryzomys* "*capito*". Bulletin of the American Museum of Natural History 236:1-376.

Musser G. M., and M. D. Carleton
1993 Family Muridae. Pp 501-756 in Mammal Species of the World: A Taxonomic and Geographic Reference. Second ed. (Wilson, D. E., and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C., USA.

Myers, P.
1982 Origins and affinities of the mammal fauna of Paraguay. Pp. 85-93 in Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, Special Publication Series, 6. University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

1989 A preliminary revision of the *varius* group of *Akodon* (*A. dayi*, *dolores*, *molinae*, *neocenus*, *simulator*, *toba*, and *varius*). Pp. 5-54 in Advances in Neotropical mammalogy (Redford, K., and J. Eisenberg, eds.). The Sandhill Crane Press, Inc., Gainesville, Florida, USA.

Myers, P., and M. D. Carleton
1981 The species of *Oryzomys* (*Oligoryzomys*) in Paraguay and the identity of Azara's "Rat sixième au Rat à Tarse Noir". Miscellaneous Publications, Museum of Zoology, University of Michigan 161:1-41.

Myers, P., and J. L. Patton
1989 *Akodon* of Peru-Revision of the *fumeus* group (Rodentia: Sigmodontinae). Occcasional Papers of the Museum of Zoology, University of Michigan 721:1-35.

Myers, P., J. L. Patton, and M. F. Smith
1990 A review of the *boliviensis* group of *Akodon* (Muridae: Sigmodontinae) with emphasis on Perú and Bolivia. Miscellaneous Publications, Museum of Zoology, University of Michigan 177:1-89.

Novaro, A. J.
1997 *Pseudalopex culpaeus*. Mammalian Species 558:1-8

Nowak, R. M., and J. L. Paradiso.
1991 Walker's Mammals of the World. Fifth ed. Johns Hopkins University Press, Baltimore, 1:1-642; 2:643-1629.

Ojeda, R. A., and M. A. Mares
1989 A biogeographic analysis of the mammals of Salta Province, Argentina. Patterns of species assemblage in the Neotropics. Special Publications, The Museum, Texas Tech University 27:1-66.

Olds, N.
1988 A Revision of the Genus *Calomys* (Rodentia:Muridae). Ph.D. Dissertation, City University of New York, New York, USA.

Olds, N., and S. Anderson
1987 Notes on Bolivian mammals 2. Taxonomy and distribution of rice rats of the subgenus *Oligoryzomys*. Fieldiana: Zoology, new series 39:261-281.

Olrog, C. C.
1959 Notas mastozoológicas. II. Sobre la Colección del Instituto Miguel Lillo. Acta Zoológica Lilloana 17:403-419.

1976 Sobre mamíferos del noroeste argentino. Acta Zoológica Lilloana 32:5-12.

1979 Los Mamíferos de la Selva Húmeda, Cerro Calilegua, Jujuy. Acta Zoológica Lilloana 33:9-14.

Olrog, C. C., and M. M. Lucero
1981 Guía de los Mamíferos Argentinos. Fundación Miguel Lillo, Tucumán. Argentina. 151 pp.

Olrog, C. C., R. A. Ojeda, and R. M. Barquez
1976 *Catagonus wagneri* (Rusconi) en el noroeste argentino (Mammalia, Tayassuidae). Neotrópica 22:53-56.

Ortells, M. O., R. A. Reig, R. L. Wainburg, G. E. Hurtado de Catalfo, and T. M. L. Gentile de Fronza

1989 Cytogenetics and karyosystematics of phyllotine rodents (Cricetidae, Sigmodontinae). II. Chromosome multiformity and autosomal polymorphism in *Eligmodontia*. Zeitschrift für Säugetierkunde 54:129-140.

Ortiz Jaureguizar, E., and M. F. López Armengol

1984 Estudio taxonómico numérico de los representantes vivientes de la Familia Tayassuidae (Mammalia, Artiodactyla) de la República Argentina. Contribuciones en Biología. CIPFE-CEDO, Montevideo, República Oriental del Uruguay 2:3-9.

Ortiz, P. E.

2003 Fossil record and distribution of *Cavia tschudii* (Caviidae, Rodentia) in Argentina. Mammalia 67:607-611.

Ortiz, P. E., S. Cirignoli, D. H. Podesta, and U. F. J. Pardiñas

2000 New records of sigmodontine rodents (Mammalia: Muridae) from High-Andean localities of northwestern Argentina. Biogeographica, París 76:133-140.

Osgood, W. H.

1943 The mammals of Chile. Field Museum of Natural History, Zoological series, 30:1-268.

Pallas, P. S.

1766 Miscellanea zoologica, quibus novae imprimis atque obscurae animalium species describuntur et observationibus iconibusque illustrantur. Hagae Comitum (Holland): Petrum van Cleef. 224 pp.

Palma, R. E.

1994 Historical Relationships of South American Mouse Opossums (*Thylamys*, Didelphidae): Evidence from Molecular Systematics and Historical Biogeography. Ph.D. Dissertation, University of New Mexico, Albuquerque, New Mexico, USA. 112 pp.

1995 Range expansion of two South American mouse opossums (*Thylamys*, Didelphidae) and their biogeographic implications. Revista Chilena de Historia Natural 68:515-522.

Palma, R. E., and T. L. Yates

1998 The chromosomes of Bolivian didelphid marsupials. Occasional Papers, The Museum, Texas Tech University 162:1-8.

Pardiñas, U. F. J., G. D'Elía, P. Teta, P. E. Ortiz, P. Jayat, and S. Cirignoli

In press Orden Rodentia. Familia Muridae. Tribu Akodontini. In Los Mamíferos de Argentina (Barquez, R. M., M. M. Díaz, and R. A. Ojeda, eds.). SAREM (Sociedad Argentina para el Estudio de los Mamíferos), Mendoza, Argentina.

Pardiñas, U. F. J., and C. A. Galliari

2001 *Reithrodon auritus*. Mammalian Species 664:1-8.

Pardiñas, U. F. J., and P. E. Ortiz

2001 *Neotomys ebriosus*, an enigmatic South American rodent (Muridae, Sigmodontinae): its fossil record and present distribution in Argentina. Mammalia 65:244-250.

Patton, J. L., M. N. Da Silva, and J. R. Malcolm

2000 Mammals of the Rio Juruá: evolutionary and ecological diversification within Amazonia. Bulletin of the American Museum of Natural History 244:1-306.

Patton, J. L., P. Myers, and M. F. Smith

1989 Electromorphic variation in selected South American akodontine rodents (Muridae: Sigmodontine), with comments on systematic implications. Zeitschrift für Säugetierkunde 54:347-359.

Pearson, O. P.

1951 Mammals in the highlands of southern Peru. Bulletin of the Museum of Comparative Zoology 106:117-174.

1957 Additions to the mammalian fauna of Peru and notes on some other Peruvian mammals. Breviora 73:1-7.

1958 A taxonomic revision of the rodent Genus *Phyllotis*. University of California Publications in Zoology 56:391-496.

Perovic, P. G.

1998 La comunidad de carnívoros en la Reserva de Biosfera Laguna de Pozuelos. Pp. 175-182 in Bases Para la Conservación y Manejo de la Puna y Cordillera Frontal de Argentina. El Rol de las Reservas de la Biósfera (Cajal, J. L., J. L. G. Fernández, and R. Tecchi, eds.). FUCEMA (Fundación para la Conservación de las Especies y el Medio Ambiente), Buenos Aires, Argentina.

Perovic, P. G., and M. Herrán

1998 Distribución del jaguar *Panthera onca* en las provincias de Jujuy y Salta, Noroeste de Argentina. Mastozoología Neotropical 5:47-52.

Pine, R. H.
1982 Current status of South American Mammalogy. Pp. 27-37 in Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, Special Publication Series, 6. University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

Pine, R. H., S. D. Miller, and M. L. Schamberger
1979 Contributions to the mammalogy of Chile. Mammalia 43:339-376.

Prado, D. E.
1995 Selva pedemontana: contexto regional y lista florística de un ecosistema en peligro. Pp. 19-52 in Investigación, Conservación y Desarrollo en Selvas Subtropicales de Montaña (Brown, A. D., and H. R. Grau, eds.). Laboratorio de Investigaciones Ecológicas de las Yungas, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina.

Pujalte, J. C., and A. R. Reca
1985 Vicuñas y guanacos. Distribución y ambientes. Pp. 21-49 in Estado Actual de las Investigaciones Sobre Camélidos en la República Argentina (Cajal, J. L., and J. N. Amaya, eds.). Ministerio de Educacuón y Justicia, Secretaria de Ciencia y Técnica, Programa Nacional de Recursos Naturales Renovables, Buenos Aires, Argentina.

Ragonese, A. E., and J. C. Castiglione
1970 La vegetación del Parque Chaqueño. Boletín de la Sociedad Argentina de Botánica (Suplemento) 11:133-160.

Redford, K. H., and J. F. Eisenberg
1992 Mammals of the Neotropics. Vol. 2, The Southern Cone: Chile, Argentina, Uruguay, Paraguay. The University of Chicago Press, Chicago, Illinois., USA. 430 pp.

Reig, O. A.
1978 Roedores cricétidos del Plioceno superior de la provincia de Buenos Aires (Argentina). Publicaciones del Museo Nacional de Ciencias Naturales de Mar de Plata "Lorenzo Scaglia" 2:164-190.

1987 An assessment of the systematics and evolution of the Akodontini, with the description of new fossil species of *Akodon* (Cricetidae: Sigmodontinae). Pp. 347-399 in Studies in Neotropical Mammalogy. Essays in Honor of Philip Hershkovitz (Patterson, B. D., and R. M. Timm, eds.). Fieldiana: Zoology, new series 39:1-506.

Rivas, R., O. R. Vidal, and N. I. Barros
1977 Los cromosomas del género *Holochilus*. II. El cariotipo de *H. brasiliensis vulpinus*. Physis 36:215-218.

Rohlf, F. J.
1993 NTSYS-pc. Numerical taxonomy system of multivariate analysis system. Version 1.80. Exeter Software, New York, New York, USA.

Romaña, C., and J. W. Avalos
1950 Lista de quirópteros de la colección del Instituto de Medicina Regional, y sus parásitos. Anales del Instituto de Medicina Regional 3:111-117.

Ruthsatz, B., and C. P. Movia
1975 Relevamiento de las Estepas Andinas del Noreste de la Provincia de Jujuy, República Argentina. Fundación para la Educación, la Ciencia y la Cultura. 127 pp.

Salazar-Bravo, J., J. W. Dragoo, D. S. Tinnin, and T. L. Yates
2001 Phylogeny and evolution of the Neotropical rodent genus *Calomys*: inferences from mitochondrial DNA sequence data. Molecular Phylogenetics and Evolution 20:173-184.

Scrocchi, G. J., and S. P. Halloy
1986 Notas sistemáticas, ecológicas, etológicas y biogeográficas sobre el gato Andino *Felis jacobita* Cornalia (Felidae, Carnivora). Acta Zoológica Lilloana 23:157-170.

Simmons, N. B., and R. S. Voss
1998 The mammals of Paracou, French Guiana: A neotropical lowland rainforest fauna, Part 1. Bats. Bulletin of the American Museum of Natural History, 237:1-219.

Smith, M. F., and J. L. Patton
1991 Variation in mitochrondrial cytocrome *b* sequence en natural populations of South American akodontine rodents (Muridae: Sigmodontinae). Molecular Biology and Evolution 8:85-103.

1993 The diversification of South American murid rodents: evidence form mitochondrial DNA sequence data for the akodontine tribe. Biological Journal of the Linnean Society 50:149-177.

1999 Phylogenetic relationships and the radiation of sigomodontine rodents in South America: Evidence from cytocrome *b*. Journal of Mammalian Evolution 6:89-128.

Sneath, P. H. A.
1957 Some thoughts on bacterial classification. Journal of Genetic Microbiology 17:184-200.

Sneath, P. H. A., and R. R. Sokal
1973 Numerical Taxonomy. The Principles and Practice of Numerical Classification. Freeman, San Francisco, California, USA. 573 pp.

Sokal, P. H., and C. D. Michener
1958 A statistical method for evaluating systematic relationships. University of Kansas Sciences Bulletin 38:1409-1438.

Sokal, R. R., and F. J. Rohlf
1962 Biometry. W. H. Freeman, San Francisco, California, USA. 776 pp.

Sowls, L. K.
1984 The Peccaries. The University of Arizona Press, Tucson, Arizona, USA. 251 pp

Steppan, S. J.
1993 Phylogenetic relationships among the Phyllotini (Rodentia: Sigmodontinae) using morphological characters. Journal of Mammalian Evolution 1:187-214.

1995 Revision of the Tribe Phyllotini (Rodentia: Sigmodontinae), with a phylogenetic hypothesis for the Sigmodontinae. Fieldiana: Zoology, new series 8:1-112.

1998 Phylogenetic relationships and species limits within *Phyllotis* (Rodentia: Sigmodontinae): concordance between mtDNA sequence and morphology. Journal of Mammalogy 79:575-593.

Steppan, S. J., O. Ramirez, J. Banbury, D. Huchon, V. Pacheco, L. Walker, and A. O. Spotorno (This volume)
A molecular reappraisal of the systematics of the leaf-eared mice *Phyllotis* and their relatives. Pp. 799-826 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

Tate, G. H. H.
1933 A systematics revision of the marsupial Genus *Marmosa*. Bulletin of the American Museum of Natural History 66:1-250.

1942 Results of the Archbold Expeditions, N° 47. Review of the Vespertilionidae bats, with special attention to the genera and species of the Archbold collections. Bulletin of the American Museum of Natural History 80:221-297.

Tedford, R. H., B. E. Taylor, and X. Wang
1995 Phylogeny of the canine (Carnivora: Canidae): the living taxa. American Museum Novitates 3146:1-33.

Thomas, O.
1897 On some small mammals from Salta, N. Argentina. Annals and Magazine of Natural History, ser. 6, 20:214-218.

1898 On the small mammals collected by Dr. Borelli in Bolivia and northern Argentina. Bulletino dei Musei di Zoologia ed Anatomia comparata della Universita di Torino 13:1-4

1901 New tropical mammals, with note on the species *Reithrodon*. Annals and Magazine of Natural History, ser. 7, 8:246-255.

1902 On mammals from Cochabamba, Bolivia, and the region north of that place. Annals and Magazine of Natural History, ser. 7, 9:125-143.

1903 Notes on Neotropical Mammals of the Genera *Felis*, *Hapale*, *Oryzomys*, *Akodon*, and *Ctenomys*, with descriptions of new species. Annals and Magazine of Natural History, ser. 7, 12:234-243.

1913 On small mammals collected in Jujuy by Señor E. Budin. Annals and Magazine of Natural History, ser. 8, 11:136-143.

1916a On the grouping of the South-American Muridae that have been referred to *Phyllotis*, *Euneomys*, and *Eligmodontia*. Annals and Magazine of Natural History, ser. 8, 17:139-143.

1916b Notes on the bats of the genus *Histiotus*. Annals and Magazine of Natural History, ser. 8, 17:272-276.

1916c Two new species of *Akodon* from Argentina. Annals and Magazine of Natural History, ser. 8, 18:334-336.

1918 On small mammals from Salta and Jujuy collected by Mr. E. Budin. Annals and Magazine of Natural History, ser. 9, 1:186-193.

1919a On some small Mammals from Catamarca. Annals and Magazine of Natural History, ser. 9, 3:115-118.

1919b List of mammals from the Highlands of Jujuy, North Argentina, collected by Mr. E. Budin. Annals and Magazine of Natural History, ser. 9, 4:128-135.

1919c Two new rodents from Tartagal, Salta, N. Argentina. Annals and Magazine of Natural History, ser. 9, 4:154-156.

1920a A further collection of mammals from Jujuy. Annals and Magazine of Natural History, ser. 9, 5:188-196.

1920b New species of *Reithrodon*, *Abrocoma*, and *Scapteromys* from Argentina. Annals and Magazine of Natural History, ser. 9, 5:473-478.

1921a New *Rhipidomys*, *Akodon*, *Ctenomys*, and *Marmosa* from the Sierra Santa Bárbara, SE Jujuy. Annals and Magazine of Natural History, ser. 9, 7:183-187.

1921b New foxes of the Genera *Cerdocyon* and *Pseudalopex* from Northern Argentina. Annals and Magazine of Natural History, ser. 9, 7:381-385.

1921c On a further collection of mammals from Jujuy obtained by Mr. E. Budin. Annals and Magazine of Natural History, ser. 9, 8:608-617.

1926a The Spedan Lewis South American Exploration. III. On mammals collected by Sr. Budin in the Province of Tucumán. Annals and Magazine of Natural History, ser. 9, 17:602-609.

1926b The Spedan Lewis South American Exploration. IV. List of mammals obtained by Sr. Budin on the boundary between Jujuy and Bolivia. Annals and Magazine of Natural History, ser. 9, 18:193-195.

Tiranti Paz, S. I., and M. P. Torres Martínez
1998 Observations on bats of Córdoba and La Pampa Provinces, Argentina. Occasional Papers, The Museum, Texas Tech University 175:1-13.

Tognelli, M. F., C. M. Campos, and R. A. Ojeda
2001 *Microcavia autralis*. Mammalian Species 648:1-4.

Troll, C.
1959 Die Tropischen Gebirge. Ihre dreidimensionale Klimatiche und pflanzengeographische Zonierung. Bonner Geographic Abhandlung 25:1-93.

Trouessart, E. L.
1897-1905 Catalogus mammalium tam viventium quam fossilium. Quinquennale supplementum anno 1904. [Tomus 1-1897; Tomus 2-1898; Quinquennale supplementum, fascic. 1&2-1904, fascic. 3&4 -1905.]. R. Friedländer and Sohn, Berlin, 1&2:1469 pp., Quin supp:929 pp.

Van Gelder, R.G.
1968 The genus *Conepatus* (Mammalia, Mustelidae): variation within a population. American Museum Novitates 2322:1-37.

1978 A review of canid classification. American Museum Novitates 2646:1-10.

van Zyll de Jong, C. G.
1987 A phylogenetic study of the Lutrinae (Carnivora; Mustelidae) using morphological data. Canadian Journal of Zoology 65:2536-2544.

Vervoorst, F.
1982 Noroeste. Conservación de la Vegetación Natural de la República Argentina. Serie Conservación de la Naturaleza. Simposio XVIII Jornadas Argentinas de Botánica 2:9-24.

Vidal, O. R., R. Rivas, and N. I. Barros
1976 Los cromosomas del género *Holochilus*. I. Polimorfismo en *H. chacarius* Thomas (1906). Physis 35:75-85.

Villa-R., B., and M. Villa-C.
1971 Observaciones acerca de algunos murciélagos del norte de Argentina, especialmente de la biología del vampiro *Desmodus r. rotundus*. Anales del Instituto Biológico, México, Serie Zoológica 42:107-148.

Vitullo, A. D., M. B. Espinosa, and M. S. Merani
1990 Cytogenetics of vesper mice, *Calomys* (Rodentia; Cricetidae): Robersonian variation between *Calomys callidus* and *Calomys venustus*. Zeitschrift für Säugetiekunde 55:99-105.

Vitullo, A. D., M. S. Merani, O. A. Reig, A. E. Kajon, O. Scaglia, M. B. Espinosa, and A. Pérez-Zapata
1986 Cytogenetics of South American akodont rodents (Cricetidae): New karyotypes and chromosomal banding patterns of Argentinian and Uruguayan forms. Journal of Mammalogy 67:69-80.

Vizcaíno, S., F.
1995 Identificación específica de las “mulitas”, Género *Dasypus* L. (Mammalia, Dasypodidae), del noroeste argentino. Descripción de una nueva especie. Mastozoología Neotropical 2:5-13.

Vizcaíno, S. F., A. M. Abba, and C. M. García Esponda
In press Orden Xenarthra. In Los Mamíferos de Argentina: Sistemática y Distribución (Barquez, R. M., M. M. Díaz, and R. A. Ojeda, eds.). SAREM (Sociedad Argentina para el Estudio de los Mamíferos), Mendoza, Argentina.

Vizcaíno, S. F., U. F. Pardiñas, and M. S. Bargo
1995 Distribución de los armadillos (Mammalia, Dasypodidae) en la región pampeana (República Argentina) durante el holoceno. Interpretación paleoambiental. Mastozoología Neotropical 2:149-166.

Voss, R. S., and M. D. Carleton
1993 A new genus for *Hesperomys molitor* Winge and *Holochilus magnus* Hershkovitz (Mammalia, Muridae) with an analysis of its phylogenetic relationships. American Museum Novitates 3085:1-39.

Voss, R. S., D. P. Lunde, and S. Jansa
2005 On the contents of *Gracilinanus* Gardner and Creighton, 1989, with the description of a previously unrecognized clade of small didelphid marsupials. American Museum Novitates 3482:1-34.

Wayne, R. K., E. Geffen, D. J. Girman, K. P. Koepfli, L. M. Lau, and C. R. Marshall
1997 Molecular systematics of the Canidae. Systematic Biology 46:622-653.

Wetzel, R. M.
1975 The species of *Tamandua* Gray (Edentata, Myrmecophagidae). Proceedings of the Biological Society of Washington 88:95-112.

1977 The chacoan peccary *Catagonus wagneri* (Rusconi). Bulletin of Carnegie Museum of Natural History 3:1-36.

1982 Systematics, distribution, ecology, and conservation of South American edentates. Pp. 345-376 in Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, Special Publication Series, 6. University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

1985 Taxonomy and distribution of armadillos, Dasypodidae. Pp. 23-46 in The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas (Montgomery, G. G., ed.). Smithsonian Institution Press, Washington, D. C., USA.

Wetzel, R. M., and J. W. Lovett
1974 A collection of mammals from the Chaco of Paraguay. University of Connecticut Occasional Papers, Biology Science Series 2:203-216.

Wetzel, R. M., and E. Mondolfi
1979 The subgenera and species of long-nosed armadillos genus *Dasypus* L. Pp. 43-63 in Vertebrate Ecology in the Northern Neotropics (Eisenberg, J. F., ed.). Smithsonian Institution Press, Washington, D.C., USA.

Williams, D. F., and M. A. Mares
1978a A new genus and species of phyllotine rodent (Mammalia: Muridae) from northwestern Argentina. Annals of Carnegie Museum 47:192-221.

1978b Karyologic affinities of the South American big-eared bat, *Histiotus montanus* (Chiroptera, Vespertilionidae). Journal of Mammalogy 59:844-846.

Wilson, D. E., and D. M. Reeder (eds.)
1993 Mammal Species of the World: A Taxonomic and Geographic Reference. Second ed. Smithsonian Institution Press, Washington, D.C., USA. 1206 pp.

Woods, C. A.
1993 Suborder Histricognathi. Pp. 771-805 in Mammal Species of the World: A Taxonomic and Geographic Reference. Second ed. (Wilson, D. E., and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C., USA.

Woods, C. A., L. Contreras, G. Willer-Chapman, and H. P. Whidden
1992 *Myocastor coypus*. Mammalian Species 398:1-8.

Wozencraft, W. C.
1993 Order Carnivora. Pp. 279-344 in Mammal Species of the World: A Taxonomic and Geographic Reference. Second ed. (Wilson, D. E., and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C., USA.

Ximénez, A.
1975 *Felis geoffroyi*. Mammalian Species 54:1-4.

Yensen, E., and K. L. Seymour
2000 *Oreailurus jacobita*. Mammalian Species 644:1-4.

Yensen, E., and T. Tarifa
2003 *Galictis cuja*. Mammalian Species 728:1-8.

Yepes, J. V.
1929 Notas sobre algunos de los mamíferos descriptos por Molina, con distribución geográfica en Chile y Argentina. Revista Chilena de Historia Natural 33:469-472.

1930 Los roedores octodóntinos con distribución en la zona cordillerana de Chile y Argentina. Revista Chilena de Historia Natural 34:321-331.

1933a Nuevos roedores para la fauna Argentina. Revista Chilena de Historia Natural 37:46-49.

1933b Una nueva especie de “mulita” (Dasypodidae) para el norte argentino. Physis 11:225-232.

1935a Consideraciones sobre el Género *Andinomys* (Cricetinae) y descripción de una forma nueva. Anales del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” 38:333-348.

1935b Epístome de la sistemática de los roedores argentinos. Revista del Instituto Bacteriológico 7:213-269.

1942 Capacidad defensiva de la fauna agreste. Revista Argentina de Zoogeografía 2:95-99.

1944 Comentarios sobre cien localidades nuevas para mamíferos sudamericanos. Revista Argentina de Zoogeografía 4:59-71.

Zunino, G. E., C. A. Galliari, and O. J. Colillas

1986 Distribución y conservación del Mirikina (*Aotus azarae*) en Argentina: Resultados preliminares. Pp. 305-316 In A Primatologia no Brasil 2. (Thiago de Mello M., ed.). Anais do 2° Congreso Brasileiro de Primatologia, Campinas, Minas Gerais, Brazil.

Zunino, G. E., O. B. Vaccaro, M. Canevari, and A. L. Gardner.

1995 Taxonomy of the Genus *Lycalopex* (Carnivora, Canidae) in Argentina. Proceedings of the Biological Society of Washington 108:729-747.

SYSTEMATICS AND DISTRIBUTION OF MARSUPIALS IN ARGENTINA: A REVIEW

UNA REVISIÓN DE LA SISTEMÁTICA Y DISTRIBUCIÓN DE LOS MARSUPIALES DE ARGENTINA

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ABSTRACT

We present systematic, distributional, and natural history information about the marsupials of Argentina. Four families are recorded, Caluromyidae, Didelphidae, Microbiotheriidae, and Caenolestidae, including a total of 27 species. The Species Accounts contain data on taxonomy, synonymy, specimens examined, and additional records from the literature, recent distribution, and information about reproduction, habitat, and general comments about natural history. We present new taxonomic arrangements for some controversial, polytypic genera (e.g. *Thylamys*, *Cryptonanus*, and *Monodelphis*), as well as an update of the distribution of all Argentine species. However, extensive areas in the country still need to be sampled, particularly those regions where the limits of some species overlap, where some species are potentially present and where specimens are needed to resolve taxonomic conflicts. We discuss some aspects of species diversity in relation to environment and latitude.

Key words: Marsupials, Didelphidae, Caenolestidae, Microbiotheriidae, taxonomy, systematic, distribution, natural history, Argentina

RESUMEN

Se presenta la sistemática, distribución e información acerca de la historia natural de los marsupiales de Argentina. Se registraron cuatro familias, Caluromyidae, Didelphidae, Microbiotheriidae, y Caenolestidae, las cuales incluyen 27 especies. En el tratamiento de las especies se ofrecen datos sobre taxonomía, sinonimia, especimenes examinados, registros adicionales de la literatura, distribución actualizada e información sobre reproducción, hábitat e historia natural de cada especie. Se ofrecen nuevos reordenamientos taxonómicos para algunos géneros politípicos conflictivos (e.g., *Thylamys*, *Cryptonanus*, y *Monodelphis*), así como una actualización de la distribución

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de las especies argentinas. Sin embargo, extensas áreas del país necesitan aún ser muestreadas, particularmente aquellas regiones donde los límites de algunas especies se superponen, aquellas zonas donde potencialmente pueden habitar algunas especies y áreas donde los especimenes necesitan resolución de conflictos taxonómicos. Se discuten algunos aspectos de la diversidad de especies en relación con los ambientes y la latitud.

Palabras claves: Marsupiales, Didelphidae, Caenolestidae, Microbiotheriidae, taxonomía, sistemática, distribución, historia natural, Argentina.

INTRODUCTION

Argentina is situated in the southernmost portion of the South American continent, occupying over 2,800,000 km^2 not including the Antarctic territory (Fig. 1). Climatically, the country ranges from subtropical areas (21° 46′ S) to subantarctic regions (55° 03′ S), and extends latitudinally over about 4000 km. In addition to this latitudinal range, the country possesses significant altitudinal variation (sea level to over 6,000 m), as well as two gradients of physical variability, extending in north-south and east-west directions. Owing to these features, Argentina presents a wide range of climates and soil types, and is one of the countries with greatest diversity in biogeographic regions (Cabrera and Willink, 1973).

The number of recognized biogeographic regions in Argentina varies from 12 (Cabrera and Willink, 1973) to 18 (Burkart et al., 1999). Following Burkart et al. (1999) (Fig. 2), we considered the country to have 15 large ecoregions, plus 2 marine ones and the Antarctic sector. These ecoregions are: High Andean, Puna, Monte of Mountains and Isolated Valleys, Yungas Forests, Dry Chaco, Humid Chaco, Paranaense Forests, Iberá Swamps, Fields and Weedlands, Delta and Islands of the Paraná River System, Espinal, Pampas, Monte of Plains and Steppes, Andean-Patagonian temperate rainforests, Patagonian Steppes, South Atlantic Islands, Argentine Sea, and Antarctic (not shown in the map). Five regions are almost exclusive to Argentina and of the southern portion of South America: the Pampas (shared with Uruguay), the Espinal, two types of Monte and the Patagonian Steppes (a small portion of the latter extends to Chile). In addition, three of the most diverse habitats of South America have their southern limits in Argentina: the Yungas, the Paranaense Forests (Brown and Grau, 1993), and the Chaco (Noss et al., 2002), >45% of which occur in the country. Other remarkable and rich environments are the Delta and the Islands of the Paraná River and the Andean-Patagonian temperate rainforest (endemic to the Southern Cone and shared only with the neighboring countries) (Bertonatti and Corcuera, 2001).

Some of the first contributions on the systematics of South American marsupials that included species of Argentina were the publications of Thomas (1888) and Tate (1933). The extensive revision by Tate (1933) on the genus *Marmosa* was also an important contribution to the knowledge of the species and subspecies of the small didelphids, and their distributions. Later, Cabrera (1957) published a systematic and distributional revision of the mammals of South America, including a list of species and subspecies of marsupials from Argentina. Although recent publications have included lists and field guides to Argentine marsupials (Galliari et al., 1996; Mares and Braun, 2000; Massoia et al., 2000) and keys to some species (Díaz, 2000), none of these

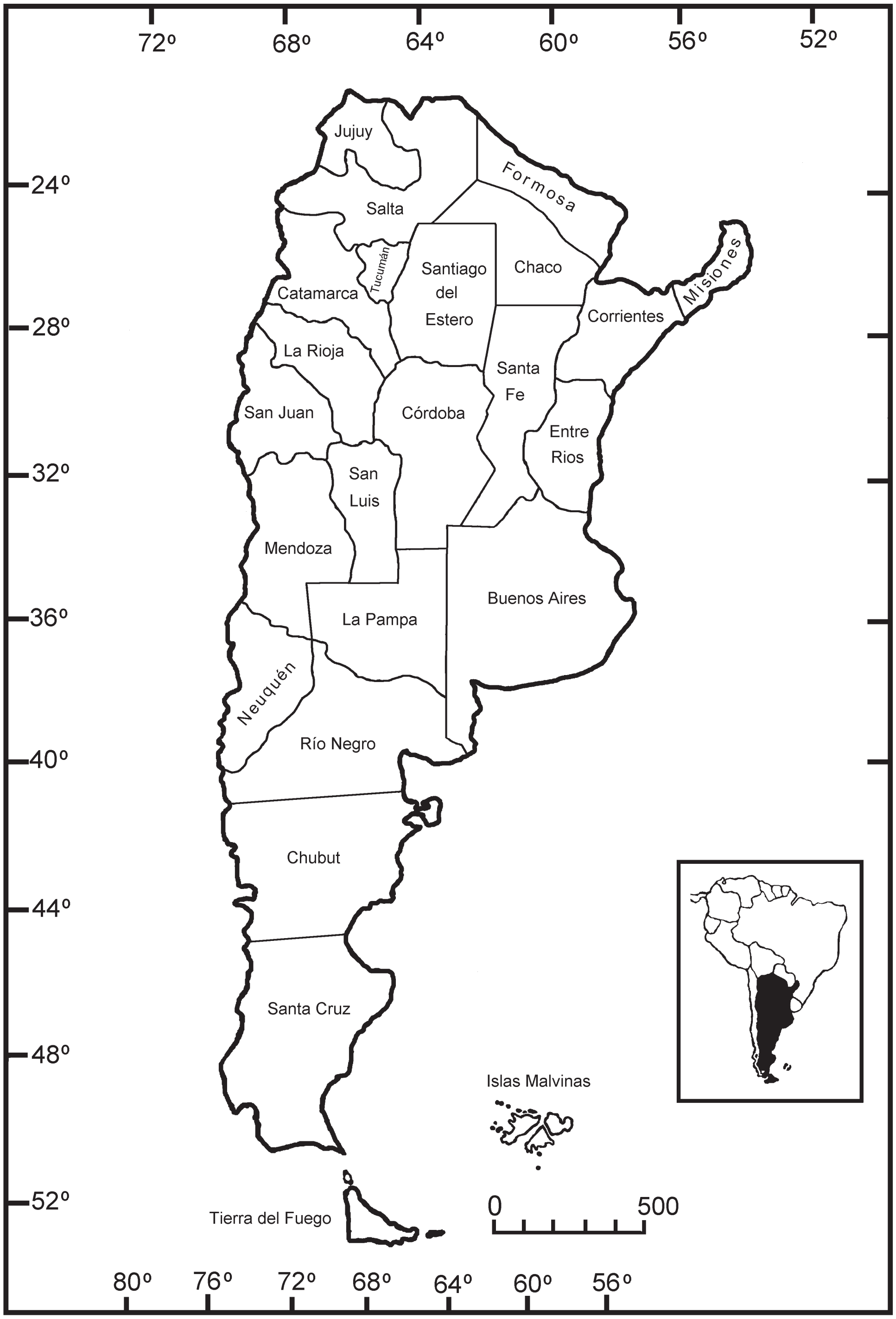

Figure 1. Map of Argentina and its provinces.

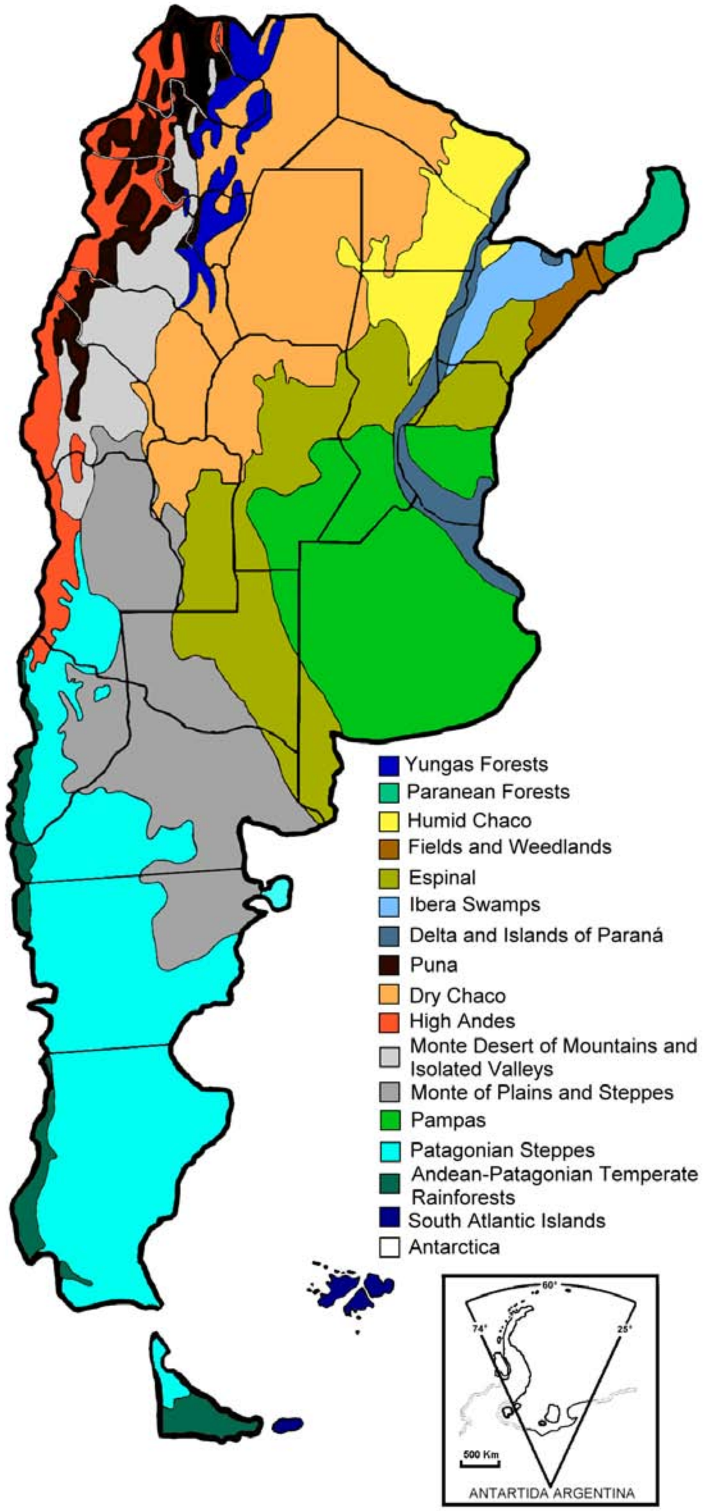
Yungas Forests
Paranean Forests
Humid Chaco
Fields and Weedlands
Espinal
Ibera Swamps
Delta and Islands of Paraná
Puna
Dry Chaco
High Andes
Monte Desert of Mountains and Isolated Valleys
Monte of Plains and Steppes
Pampas
Patagonian Steppes
Andean-Patagonian Temperate Rainforests
South Atlantic Islands
Antarctica
60°
74°
25°
500 Km
ANTARTIDA ARGENTINA

Figure 2 (facing page). Ecoregions of Argentina, modified from Burkart et al. (1999). Antarctica is not shown in the map.

provides an updated compilation of all species.

Flores et al. (2000), recently revised the mouse opossums of northwestern Argentina, and Díaz et al. (2002) described a new species of *Gracilinanus* from northwestern Argentina (now included in *Cryptonanus* by Voss et al., 2005). In addition, Birney et al. (1996b) reported the presence of a new order in the marsupial fauna of Argentina (*Rhyncholestes raphanurus*, Order Paucituberculata), and recently, Brown (2004) published an "Atlas of New World Marsupials." Systematic studies are needed for this and for other groups of mammals in Argentina and the southern cone of South America. The new taxa of mammals from Argentina that have been described (Williams and Mares, 1978; Braun and Mares, 1995; Mares and Braun, 1996; Díaz et al., 1999; Mares et al., 2000; Díaz et al., 2002; Voss et al., 2004), or that are in the process of formal description, reflect the lack of systematic studies and biotic surveys in the country. In this work, we provide an update on the systematics, taxonomy, distribution, and natural history information about the marsupials of Argentina.

MATERIALS AND METHODS

We examined 1049 specimens of four families from field surveys and the following systematic collections (acronyms in parentheses): American Museum of Natural History, New York (AMNH); British Museum (Natural History), London (BMNH); Colección del Centro de Investigaciones Ecológicas Subtropicales, Misiones, Argentina (CIES); Colección Elio Massoia, Buenos Aires, Argentina (CEM); Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (CM); Colección Mamíferos Lillo, Universidad Nacional de Tucumán, Argentina (CML); Colección Rusconi, Tucumán, Argentina (CR); Field Museum of Natural History, Chicago (FMNH); Instituto Argentino de Investigaciones en Zonas Áridas, Mendoza, Argentina (IADIZA); Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina (MACN); Museo de La Plata, Buenos Aires, Argentina (MLP); Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Argentina (MMP); Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma (SNOMNH); National Museum of Natural History, Washington (USNM); University of Wisconsin Zoological Field Museum, Madison, Wisconsin (UWZM). Specimens lacking collection numbers are indicated with the initials of the collector or the program of investigations to which they temporarily belong: ARG, Catalog of Argentine specimens at the Sam Noble Oklahoma Museum of Natural History; MMD, M. Mónica Díaz; PIDBA, Programa de Investigaciones de Biodiversidad Argentina, Tucumán, Argentina; and RMB, Rubén M. Barquez.

Species Accounts.--The taxonomic treatment of each species includes the scientific name, author, synonymy, type locality, specimens examined, additional records, distribution within the Neotropics, habitat, natural history, and comments. Additional records include literature citations, specimens from museums not examined, interviews with local residents, and observations. Available information about taxonomy and general biology is summarized under comments.

We recorded 646 localities obtained from personal field trips, specimens examined in systematic collections, and literature citations. The localities were located with maps from the Military Geographical Institute of Argentina (1957-1960), the Automóvil Club Argentino, Keegan and Keegan (1993), Paynter (1985), and the geographic coordinates of the sampled areas were obtained using a Global Positioning System (GPS). All localities are ordered alphabetically in Appendix 1. Some localities were not mapped, because the citations were imprecise or information was insufficient. Each locality is expressed as in the original label, literature, or the indicated source of information.

SPECIES ACCOUNTS

Order Didelphimorphia Gill, 1872

Family Caluromyidae Kirsch, 1977

The members of this family have the following morphological characters in common: the presence of wide supraorbital processes, reduced palatine vacuities, reduced P1, and lower molars with trigonids longer than wide. Three genera are known in the Neotropics, *Caluromys*, *Caluromysiops,* and *Glironia*, of which only *Caluromys* is represented in Argentina.

Reig (1955) included *Caluromys*, *Caluromysiops,* and *Glironia* within the microbiotherines based on osteological evidence. Using serological characters, Kirsch (1977) demonstrated that Caluromyines are not microbiotherids, but rather they represent a distinct lineage in the evolution of didelphoids, creating the subfamily Caluromyinae. Reig et al. (1985, 1987) also treated these as members of the Caluromyinae. Other studies, using spermatic morphology (Biggers and DeLamater, 1965) and structure of the urogenital tract (Hill and Fraser, 1925; Biggers, 1966) support the separation of caluromyines and didelphines. Several authors (Hershkovitz, 1992a, 1992b; Kirsch and Palma, 1995; Kirsch et al., 1996; Flores, 2003) indicated that morphology and genetics also support treatment of this group as distinct from Didelphidae.

Genus *Caluromys* (Allen, 1900)

This genus contains three living species in the Neotropics: *Caluromys philander* in Guyana, Venezuela, and Brazil; *C. lanatus* in northern and central South America, and *C. derbianus* from southern Mexico south to Colombia and Ecuador. Only the second species is found in Argentina, where it is restricted to Misiones Province in the extreme northeastern part of the country.

Caluromys lanatus (Olfers, 1818)

D[*idelphys*] *lanatus* Olfers, 1818. Bemerkingen zu Illiger's Ueberblick der Säugethiere nach ihrer Vertheilung uber die Welttheile, rücksichtlich der Südamerikanischen Arten (species). Abhandlung 10 of Wilhelm Ludwig Eschwege's Journal von Brasilien..., vol. 15, heft 2:192-237, *in* Neue Bibliothek des wichtigsten Reisenbeschreibungen zur Erweiterung der Erdund Volkerkunde...F. T. Bertuch (ed.), Weimar, p. 206.

Caluromys lanatus: Cabrera, 1957. Catálogo de los mamíferos de América del Sur . 4(1):2.

Type Locality.--"Paraguay;" restricted to Caazapá, Caazapá (Cabrera, 1916).

Specimens Examined (1).--MISIONES: Parque Nacional Iguazú, área cataratas, 1 (MACN 20450).

Additional Records.--MISIONES: Departamento Eldorado (Massoia, 1980; Chébez and Massoia, 1996); Departamento Guaraní (Massoia, 1980; Chébez and Massoia, 1996); Departamento Iguazú (Massoia, 1980; Chébez and Massoia, 1996); Departamento Montecarlo (Massoia, 1980; Chébez and Massoia, 1996); Parque Nacional Iguazú (Heinonen Fortabat and Chébez, 1997), Rio Urugua-í (Massoia et al., 1987).

Distribution.--Northern and central Colombia, northwestern and southern Venezuela, eastern Ecuador, eastern Peru, eastern Bolivia, eastern and southern Paraguay, northern Argentina (Misiones Province), and western and southern Brazil (Cabrera, 1957; Olrog and Lucero, 1981; Redford and Eisenberg, 1992).

Habitat.--This species inhabits humid tropical forests associated with arboreal habits; it also uses secondary growth forests, gallery forests, and cultivated areas. In Argentina, this species is only found in the densest parts of the forests in Misiones Province (Olrog and Lucero, 1981; Redford and Eisenberg, 1992).

Natural History.--The natural history of this species is not well known. It lives in tree hollows or branches and is active mainly during the evening, night, or early morning (Nowak, 1991). Some specimens were captured in forests with several plant strata; they are nocturnal, and eat fruits, seeds, leaves, soft vegetation, insects, and small invertebrates. During the dry season, they feed on nectar of flowers and sap (Linares, 1998). Some studies suggest the existence of well-developed parental care behavior (Redford and Eisenberg, 1992; Emmons and Feer, 1997).

Family Didelphidae Gray, 1821
Subfamily Didelphinae Gray, 1821
Tribe Didelphini Gray, 1821

Genus *Chironectes* Illiger, 1811

Chironectes minimus (Zimmermann, 1780)

Lutra minima Zimmermann, 1780. Geographische Geschichte des Menschen, und der allgemein verbreiteten vierfüssigen Thiere nebst einer gehörigen zoologischen Weltkarte, *in* Der Weygandschen buchhandlung, Leipzig. Vol. 2, p. 317..

Chironectess minimus: Lydekker, 1837. Catalogue of Fossil Mammals in the British Museum, p. 329.

Type Locality.--“Gujana;” restricted to Cayenne, French Guiana (Cabrera, 1957:44).

Specimens Examined (15).--MISIONES: Bonpland, 1 (BMNH 25.3.1.25); Guayaberá, 1 (CML 1542); Piñalitos, 1 (MACN 13053); Pto. Piray, km 18, 7 (MACN 51173, 51174, 51175, 51176, 52.69, 52.71, 52.72); Río Paranaí, 1 (MACN 48297); Río Uruguaí, km 10, 3 (MACN 13548, 13549); San Javier, 1 (MACN 48265).

Additional Records.--MISIONES: Arroyo Garupa (Massoia et al., 1987); Arroyo Piray Guazú (Massoia et al., 1987); Arroyo Tacuara, Cerro Azul (Massoia et al., 1987); Cuarto Rio Victoria, Rt. 14, Km.265 (Massoia, 1976); Departamento Cainguás (Massoia, 1980; Chébez and Massoia, 1996); Departamento Candelaria (Chébez and Massoia, 1996); Departamento Eldorado (Massoia, 1980; Chébez and Massoia, 1996); Departamento General Belgrano (Massoia, 1980; Chébez and Massoia, 1996); Departamento Guaraní (Massoia, 1980; Chébez and Massoia, 1996); Departamento Iguazú (Massoia, 1980; Chébez and Massoia, 1996); Departamento Leandro N. Alem (Massoia, 1980; Chébez and Massoia, 1996); Departamento Libertador General San Martín (Chébez and Massoia, 1996); Departamento Montecarlo (Massoia, 1980; Chébez and Massoia, 1996); Departamento San Javier (Massoia, 1980; Chébez and Massoia, 1996); Departamento 25 de Mayo (Chébez and Massoia, 1996); Parque Nacional Iguazú (Heinonen Fortabat and Chébez, 1997); Piñalitos (Crespo, 1974); Pto. Piray, km 18 (Crespo, 1974); en el Río Paranaí-Guazú, a unos 15 km de la costa del Paraná (Crespo, 1950); Río Uruguaí (Crespo, 1974); San Javier (Crespo, 1950).

Distribution.--From southern Mexico, south through Central America, northern Colombia, western Venezuela and Ecuador, and eastern Peru. Mainly in the Amazon region, from the Guyanas, Orinoco, and Amazon Basins, to eastern Paraguay and northeastern Argentina (in Misiones Province) (Cabrera, 1957; Marshall, 1978b; Massoia, 1980; Olrog and Lucero, 1981; Redford and Eisenberg, 1992; Gardner, 1993; Emmons and Feer, 1997). A recent record included this species in Uruguay (González and Fregueiro, 1998).

Habitat.--Water opossums are mostly confined to tropical and subtropical habitats, where they frequent freshwater streams and lakes; in some areas they are found at considerable elevations along montane rivers (Nowak, 1991). They generally are associated with dense forests (Mondolfi and Medina Padilla, 1957; Hunsaker, 1977; Marshall, 1978b; Redford and Eisenberg, 1992; Emmons and Feer, 1997).

Natural History.--This species is the only Neotropical marsupial adapted for a semi-aquatic life; they are excellent swimmers and divers (Nowak, 1991) and have water-repellent fur, webbed feet, a water-proof pouch, and a streamlined body (Marshall, 1978b). The den usually is reached through a hole in a stream bank just above water level (Marshall, 1978b). They also use ground nests of leaves or grasses. *Chironectes* is nocturnal, but has been reported active during the day (Oliver, 1976). Feeds on small fishes, insects, other invertebrates, and aquatic vegetation (Mondolfi and Medina Padilla, 1957; Marshall, 1978b; Redford and Eisenberg, 1992).

Comments.--In captivity, it has been observed that the young start to become independent from their mother after 48 days, so the young have a much shorter development period than other didelphids (Rosenthal, 1975).

Both sexes have a well-developed marsupium; in males, the scrotum is retracted into the pouch when the animal is in the water (Marshall, 1978b). Females have 4 or 5 mammae (Mondolfi and Medina Padilla, 1958; Brack, 1962). Litter of 2 and 3 young are most common, but the largest reported is 5 young (Mondolfi and Medina Padilla, 1957; Enders, 1966). Oliver (1976) reported that this is species is polyestrous.

Genus *Didelphis* Linnaeus, 1758

The systematic history of this genus is controversial. Traditionally, most part of the medium- and large-sized American marsupials were allocated to the genus *Didelphis*. Pioneer contributions clarifying the systematics of the genus were those by Thomas (1888, 1901), Allen (1900a, 1900b, 1901, 1902), and Rebin (1901), and later by Hershkovitz (1951, 1969). Allen (1901, 1902) provided a detailed revision of the genus, recognizing two groups in South America, the *paraguayensis* (=*albiventris*) and *marsupialis* groups. One of the most important contributions was Gardner's (1973) taxonomic study of North and Central American *Didelphis*.

Six living species (*D. albiventris, D. aurita, D. imperfecta, D. marsupialis, D. pernigra,* and *D. virginiana*) currently are recognized (Gardner, 2005), although some discrepancy exists between different authors. In a biogeographic analysis, Cerqueira (1985) argued that *D. aurita*, previously treated as a disjunct population of *D. marsupialis* and inhabiting southern Brazil, southeastern Paraguay, and northeastern Argentina, should be treated as a distinct species; this criterion was followed by Gardner (1993). On the other hand, taking into account the extreme ecological variability among regions where *D. albiventris* occurs, Cerqueira (1982, 1985) interpreted this to be a composite taxon, including two forms ranked as "semispecies" -- *D. albiventris albiventris* and *D. a. pernigra*. Subsequently, Gardner (1993) placed all the white-eared opossums in *D. albiventris*. More recently, Voss and Emmons (1996) considered populations of "*albiventris*" from Guiana to be a different species, *D. imperfecta.* Finally, Lemos and Cerqueira (2002) reported morphological and morphometric differences between the three groups, previously recognized as populations of *albiventris,* and suggested these should be treated as full species (*albiventris*, *pernigra*, and *imperfecta*). On the other hand, the variation observed between *aurita* and *marsupialis* is less than that between *albiventris, imperfecta* and *pernigra*, yet they are treated as different species (Lemos and Cerqueira, 2002). It is clear that further work is required to define species and species limits within this group.

Didelphis albiventris (Temminck, 1825)

Didelphis azarae Temmink, 1825. Monographies Mammalia 1:30.

Didelphis albiventris: Lund, 1840. Konigelige Danske Videnskabernes Selskabs Naturvidenskabelige Mathemmatiske Afhandlinger, Kjöbenhavn, p. 20 [preprint of Lund, 1841]

Type Locality.--Brazil, Minas Gerais, "Rio das Velhas," Lagoa Santa.

Specimens Examined (213).--BUENOS AIRES**:** 4 de Noviembre, Estancia Miraflores, 1 (MLP 17.II.71.1); 4 km NE de Azul, 1 (USNM 331055); Adrogué, 1 (MACN 19); Azul Benson Farm, 1 (USNM 331054); Carmen de Areco, 1 (MACN 37.90); Isla de Tigre, 1 (MACN 14); Junín, Estancia Agustina, 2 (MLP 8.V.59.2, 8.V.59.3); La Isolina, Ruta 200 km 63, 1 (MACN 17807); La Plata, 4 (MLP 6929, 9-VIII-39.1, 21-X-39.1, 16-VIII-40.1); Los Yngleses, Ajo, 5 (BMNH 20.2.7.39, 9.12.1.51, 9.12.1.52, 9.12.1.54, 9.12.1.55); Madariaga, Laguna Salada Grande, 1 (MLP 26.V.99.1); Magdalena, 1 (MLP 1692); Pehuajó, 1 (MACN 26.82); Playa Chapadmalal, 2 (MMP 88003, 88018); Punta Lara, 1 (CML 1354); 4 de Noviembre, 2 (MLP 17.II.71.2, 17.II.71.3); Quiroga km 300, 1 (MACN 17257); Roberto Payró, 1 (MACN 43.12); San Vicente, 1 (MLP 27.X.97.05); South of Mar del Plata, 1 (USNM 172780). CATAMARCA: Cañuelas, km 58, 1 (MACN 17259); Ipizca, 1 (CML 5481); La Merced 1 (MACN 17263). CHACO: 10 km S Puerto Bermejo, 1 (USNM 536826); Las Palmas, 20 mi N. of Corrientes, 1 (BMNH 6.5.5.6); Puesto El Zapallar, 1 (CML 20). CORDOBA: Ballesteros, 2 (MACN 39718, 39719); Bell Ville, 1 (MACN 13067); Bialet Massé, 3 (MACN 39197, 39199, 39200); Estancia La Magdalena, Barreto, 1 (MLP 18.XI.41.9); La Delfina, Barreto, 1 (MLP 1609); La Toma, Soto, 1 (MACN 39203); Noetinger, F.C.C.A., 100 m, 5 (BMNH 17.1.25.56, 17.1.25.57, 17.1.25.58, 17.1.25.59, 17.1.25.60, 17.1.25.61); San José, 1 (MACN 39198); Tela Cruz, 3 (MACN 29344, 39347, 39349). CORRIENTES: Estancia El Ceibo, 2 (MLP 28.IV.50.2, 28.IV.50.3); Goya, 600 m, 3 (BMNH 98.8.19.2, 98.3.19.4, 98.8.19.5); Goya, on Río Paraná, 2 (AMNH 18983, 18984); San Cayetano, CAPRIM, 7 (MLP 6-IX-95.1, 6-IX-95.2, 6-IX-95.3, 6-IX-95.4, 6-IX-95.5, 6-IX-95.6, 6-IX-95.7); Sauce Viejo, 1 (MLP 679); 20 km SE of Centro Argentino de Primates, 5 (USNM 539383, 539384, 539385, 539386, 539387). ENTRE RÍOS: Colonia Hocker, 2 (MLP 5.V.99.2, 5.V.99.6); Gualeguaychú, 1 (MACN 27.11); Nueva Escocia, 3 (MACN 48102, 48119, 48125). FORMOSA: Comandante Fontana, 1 (MACN 29848); Laguna Blanca, 20 km al SE sobre Ruta Nacional 86, 1 (PIDBA 535). JUJUY: Caimancito, 1 (MACN 30.348); "Jujuy," 4 (MACN 31.14, 36.102, 36.103, 36.104); Maimará, 2230 m, 2 (MACN 27.97, 27.98); Palpalá, 1 km al Este entre rutas 66 y 1, 2 (MMD 404, 405); Parque Nacional Calilegua, Aguas Negras, 1 (CML 4067); Río Las Capillas, sobre ruta provincial 20, 1 (MMD 340); San Salvador de Jujuy, 1 (CML 1639); Yuchán, 1 (MACN 34.586); Yuto, 4 (AMNH 179892, 179893, 179894, 185206). LA PAMPA: Santa Rosa, 1 (MACN 425). LA RIOJA: Villa Unión, 1 (MACN 34561). MENDOZA: Cerro de La Gloria, 1 (IADIZA s/n.); San Martín, 3 (MLP 1644, 1645, 1646); San Martín, Distrito Buen Orden, 4 (MLP 12.VIII.40.1, 12.VIII.40.2, 12.VIII.40.3, 12.VIII.40.4). MISIONES: 10 km W Aristóbulo del Valle by road along Río Cunapirú, 1 (CML 3172); Cuña Pirú, 1 (MLP 3.VIII.99.14); Deseado, 1 (MACN 15432); Loreto, 1 (MACN 35.13); Río Aguaraí Guazú (sup), 3 (MACN 48298, 48299, 48300); Río Iguazú, 60 km al sur de Puerto Iguazú, 3 (MACN 51.56, 51.65, 51.69). SALTA: 3.9 km N Potrerillos along Ruta Provincial 6, 1 (ARG 4511); Agua Linda, 1 (MACN 36753); Aguaray, 11 (MACN 36192, 36195, 36196, 36655, 36668, 36669, 36670, 36671, 36673, 36676, 36678); Campo Quijano, 1 (MACN 17262); Dragones, 1 (MACN 36489); El Quebrachal, 18 (MACN 36299, 36300, 36301, 36302, 36303, 36304, 36305, 36306, 36307, 36729, 36730, 36731, 36732, 36734, 36735, 36737, 36757, 36808); Lumbreras, 1 (MACN 36679); Rosario de Lerma, 27 km SSW Salta, Valle de Lerma, 3 (AMNH 41535, 41536, 41537); Ruiz de los Llanos, 2 (CML 651, 652). SAN LUIS: Villa Mercedes, 1 (MACN 549). SANTA FE: Esperanza, 1 (MACN 16546); Florencia, 1 (MACN 31227); Las Rosas, 2 (MACN 30.27, 30.28); Maciel, 2 (MACN

19193, 19194); María Eugenia, 1 (MACN 29799); Rosario, 1 (MLP 31-VIII-41.1); Ruinas de Santa Fe La Vieja, Cayastá, 2 (IADIZA 1418, 3418). SANTIAGO DEL ESTERO: El Rincón, 1 (MACN 17265); Termas de Río Hondo, 1 (CML 5482). TUCUMAN: 1.3 km S Benjamín Paz along Ruta 9, 1 (ARG 4506); 2 km al W de Reserva Experimental Horco Molle, 1 (CML 5976); At km marker 42, on highway 364, south of San Pedro de Colalao, 1 (CML 3174); Biological Reserve at Horco Molle, behind dining area of residencia, 1 (CML 3173); Concepción, 1 (FMNH 35016); Choromoro, 1 (MACN 30100); El Cajón, 1 (CML 445); El Corte, 1 (CML 4832); El Mollar, 1 (PIDBA 837); Horco Molle, 1 (PIDBA 645); Instituto Miguel Lillo, 1 (CML 440); km 42 al Sur de San Pedro de Colalao, 1 (CML 3174); Las Arcas, 1 (MACN 17266); Los Romanos, 1 (CML 437); Los Vallistos, Ruta 9 km 1285, 2 (CML 2858, 3199); Monteros, 1 (MACN 30222); Río Salí, 1 (CML 506); Sarmiento, 2 (AMNH 41538, 41539); San Fernando, 1 (CML 1559); San Pedro del Colalao, 13 (CML 447, 463, 469, 471; 472, 473, 474, 476, 480, 519, 1075, 1181, 1182, 1559); San Pedro de Colalao, Las Mesadas, 1 (CML 1075); San Miguel de Tucumán, 3 (CML 506, 4652, PIDBA 414); Tucumán, 450 m, 1 (BMNH 0.7.9.19); Yerba Buena, 2 (CML 3173, 5971).

Additional Records.--BUENOS AIRES: 25 de Mayo (Yepes, 1944); Arroyo Brusquitas (Reig, 1964); Arroyo Brusquitas-Miramar (Wainberg and Hurtado, 1973); Arroyo Chapadmalal (Reig, 1964); Baliza Caniu (Reig, 1964); Ciudad de Mar del Plata (Reig, 1964); Laguna Chasico (Contreras, 1973); Laguna de Los Padres (Reig, 1964); La Plata Punta Lara (Reig et al., 1977); Los Yngleses (Thomas, 1910); Mar del Sur (Reig, 1964); Miramar (Reig, 1964; Fornes and Massoia, 1965); Rivera de Punta Lara (Wainberg and Hurtado, 1973); Reserva Natural estricta Otamendi (Heinonen Fortabat and Chébez, 1997). CATAMARCA: 2 km S, 1 km W Choya (Mares et al., 1997); along Hwy 65, between Andalgalá and San Miguel de Tucumán, ca. 7 km S of the Tucumán-Catamarca border, ca. 2000 ft. (Mares, 1973); Andalgalá (Mares, 1973); Choya, 13 km NNW of Andalgalá, 4000 ft. (Mares et al., 1997). CHACO: Chaco near Asunción (Allen, 1902); Parque Nacional Chaco (Heinonen Fortabat and Chébez, 1997). CORDOBA: Cruz del Eje (Thomas, 1902); La Paz (Yepes, 1936b). CORRIENTES: Goya (Allen, 1902); Parque Nacional Mburucuyá (Heinonen Fortabat and Chébez, 1997). ENTRE RÍOS: Parque Nacional Diamante (Heinonen Fortabat and Chébez, 1997); Parque Nacional el Palmar (Crespo, 1982b; Heinonen Fortabat and Chébez, 1997). FORMOSA: El Colorado (Massoia, 1970); Laguna Blanca (Massoia, 1970); La Urbana, Rio Pilcomayo (Krumbiegel, 1941a); Las Lomitas (Yepes, 1944); Parque Nacional Pilcomayo (Heinonen Fortabat and Chébez, 1997); Reserva Natural Formosa (Heinonen Fortabat and Chébez, 1997). JUJUY: Calilegua (CEM, not examined); Cercanías de El Simbolar (census); Cerro Calilegua (Olrog, 1979); Cueval (Ojeda y Mares, 1989); El Arenal (Yepes, 1944); Puente sobre el río San Francisco, cruce entre ruta 1 y el Río San Francisco (M.M. Díaz, personal observation); Río Blanco (Yepes, 1944). LA RIOJA: Proximidades de Villa Castelli (Yepes, 1936a). MENDOZA: 27 km S Tunuyán (Mares and Braun, 2000); 60 km N Tunuyán, along Hwy 40 (Mares and Braun, 2000); La Paz (Yepes, 1936b); "Mendoza" (Yepes, 1936b; Roig, 1965); Reserva Ecológica de Ñacuñan (Contreras, 1979); Rivadavia (Yepes, 1936b, 1944; Roig, 1965); San Carlos (Yepes, 1936b, 1944; Roig, 1965); San Rafael (Yepes, 1936b, 1944; Roig, 1965). MISIONES: Arroyo Viña (Brazo del Arroyo Garupá), Rio Urugua-i (Massoia et al., 1987); Departamento Cainguás (Chébez and Massoia, 1996); Departamento Candelaria (Massoia, 1972, 1980; Chébez and Massoia, 1996); Departamento Capital (Massoia, 1980; Chébez and Massoia, 1996); Departamento Eldorado (Massoia, 1980; Chébez and Massoia, 1996); Departamento General Belgrano (Chébez and Massoia, 1996); Departamento Guaraní (Massoia, 1980; Chébez and Massoia, 1996); Departamento Iguazú (Massoia, 1980; Chébez and Massoia, 1996); Departamento Leonardo N. Alem (Massoia, 1980; Chébez and Massoia, 1996); Departamento Montecarlo (Massoia, 1980; Chébez and Massoia, 1996); Departamento San Ignacio (Chébez and Massoia, 1996); Departamento San Pedro (Chébez and Massoia, 1996); Departamento 25 de Mayo (Chébez and Massoia, 1996); Eldorado (Mares and Braun, 2000); Parque Nacional Iguazú (Crespo, 1982a; Heinonen Fortabat and Chébez, 1997); Puerto Península (D. Flores, personal Observation); Puerto Iguazú (D. Flores, personal observation); Puerto Schwelm (Wainberg and Hurtado, 1973). SALTA: 6 km SW of Santa Victoria at "El Breal", extreme NE of Salta Province (Mares et al., 1981); Aguaray (Yepes, 1944); Cafayate (Yepes, 1944); Dragones (Yepes, 1944); El Quebrachal (Yepes, 1944); Lumbreras (Yepes, 1944); Metán (M. M. Díaz, personal observation); Parque Nacional Baritú (Heinonen Fortabat and Chébez, 1997); Parque Nacional El Rey (Heinonen Fortabat and Chébez, 1997); Tabacal (Yepes, 1944); Zuviría (Yepes, 1944). SAN LUIS**:** Manuel Solá (Mares and Braun, 2000); Rincón (Yepes, 1936b); San Francisco del Monte de Oro, 1480 ft. (Mares and Braun, 2000). SANTA FE: Estancia la Germania (Krumbiegel, 1941a); Malabrigo (Yepes, 1944); Santa Fe (Krieg, 1924); Villa Ana (Yepes, 1944). SANTIAGO DEL ESTERO: Estancia la Geraldina (Krumbiegel, 1941a); Santo Domingo (Mares and Braun, 2000). TUCUMAN: 4 km al oeste de la unión de la Ruta Provincial 338 y el camino a Horco Molle, sobre camino a San Javier (Capllonch et al., 1996); 4 km W of junction 338 and road to Horco Molle, on road to San Javier (Mares and Braun, 2000); Aconquija, Concepción (Mares and Braun, 2000); Aguas Chiquitas (Cajal, 1976, 1981); Cerro del Campo, 800 m. (Mares and Braun, 2000); Cerro Medici (Cajal, 1981); Cerro San Javier (Capllonch et al., 1996); Camino de acceso al Parque Biológico (Capllonch et al., 1996); Dique Escaba (Mares et al., 1996); El Cadillal Dike, 35 km NW San Miguel de Tucumán (Mares and Braun, 2000); foot of Cerro del campo, Burruyacú, 800 m (Thomas, 1926); Mala Mala (Mares et al., 1996); Piedra Tendida, 12 km WNW Burruyacú along Río El Cajón, 2500 ft. (Mares and Braun, 2000); Pozo Hondo (Mares and Braun, 2000); Reserva Experimental de Flora y Fauna de Horco Molle (Capllonch et al., 1996); Río Las Cañas, Horco Molle (Capllonch et al., 1996); Santa Rosa de Leales (Massoia and Fornes, 1967); Tafí del Valle (Mares and Braun, 2000); "Tucumán" (Allen, 1902).

Distribution.--This species has a wide distribution in South America, being present in Colombia, Guyana, southern Venezuela, southwestern Surinam, northern Brazil, Ecuador, Peru, Bolivia, and all of northern Argentina south to the province of Mendoza. Along the eastern side of the continent it is present in Brazil, Paraguay, Uruguay, and all the Pampas and Subtropical regions of Argentina, south to the province of Río Negro in Argentina (ca. 40° S latitude).

Habitat.--Inhabits a wide range of environments, being frequent in disturbed areas under human influence. It is not known from severe desert areas or from the High Andes. Although it seems to be rare in dense forests, one adult specimen was captured in Yungas Forests at Río Las Capillas, Jujuy.

Natural History.--Crepuscular and nocturnal, mainly terrestrial, they use tree holes as shelter during the day; solitary; good climbers. They are generalist foragers, consuming insects, small mammals, eggs, worms, leaves, and fruits. Fertility of females is coincident with the rainy season in the Chacoan region. Litter size is variable; a female carrying 8 young individuals in her pouch was collected in Tucumán in October, and another with 9 pouched young was observed at Puerto Península (Misiones) in November.

Comments.--This species is considered a pest because of the damage that it causes to crops and poultry; however, it plays an important role in the natural regulation of populations of small mammals that can be detrimental to humans (Mares et al., 1989). In Argentina, it is included in the list of harmful species for agriculture; for this reason it is persecuted, and the skin is used for leather (Mares et al., 1989). Abdala et al. (2001) studied the morphological variation in an ontogenetic series.

Didelphis aurita Wied-Neuwied, 1826

Didelphys aurita Wied-Neuwied, 1826. Beiträge zur Naturgeschichte von Brasilien. Band 2. Verzeichniss der Amphibien, Säugethiere und Vögel,…. Abt. 2, Mammalia. Landes-Industrie-Comptoirs, Weimar, p. 395,

Didelphis aurita: Cerqueira, 1985. Journal of Biogeography, 12:135-45.

Type Locality.--Brazil, Bahia, "Villa Viçosa am Flusse Paruhype."

Specimens examined (1).--MISIONES: jct. Hwy 21 and Arroyo Oveja Negra (approx.) 2 km W Parque Provincial Mocona, 1 (SNOMNH, 23495).

Additional Records.--MISIONES: Departamento El Dorado (Massoia, 1980; Chébez, 1996); Departamento General Belgrano (Massoia, 1980; Chébez, 1996); Departamento Guarani (Massoia, 1980; Chébez, 1996); Departamento Iguazu (Massoia, 1980; Chébez, 1996); Departamento 25 de mayo (Chébez, 1996); Deseado (Crespo, 1974); Parque Nacional Iguazu (Crespo, 1982a; Heinonen Fortabat and Chébez, 1997); Puerto Iguazu (Wainberg and Hurtado, 1973); Puerto Shwelm (Wainberg and Hurtado, 1973); Reserva natural Estricta san Antonio (Heinonen Fortabat and Chébez, 1997); Rio Iguazu, 60 Km al Este de Puerto Iguazu (Crespo, 1974); 1 km W of jct. Hwy 14 and 2 de Mayo Road (Mares and Braun, 2000).

Distribution.--This species has a wide distribution, from southeastern Brazil and southern Paraguay to northeastern Argentina, in Misiones Province (Cerqueira, 1985; Gardner, 1993).

Habitat.--In Argentina this species is restricted to the forested areas of Misiones Province, where it may be more sensitive to human disturbance than *D. albiventris*, although in other zones of their wide distribution it tolerates a variety of habitats. According to Cerqueira (1985), the distribution of *D. aurita* is limited by low humidity.

Natural History.--Nocturnal, arboreal, and terrestrial. Usually solitary, although during the breeding season two or more individuals may be found together. Females build nests of leaves in tree cavities or burrows (Redford and Eisenberg, 1992). Often climbs when threatened or when searching for food. An opportunistic feeder that eats insects, worms, and small vertebrates, as well as fruits and nectar; it also consumes other marsupials of smaller size. In Misiones, one animal's stomach contained muscular tissue of a medium-sized vertebrate, remains of insects, a nematode parasite, a piece of Heteroptera, and remains of plant material (Crespo, 1982a).

Comments--This species exhibits marked color variation. The coloration can be variable across ages. Populations living in southeastern Brazil, eastern Paraguay, and northeastern Argentina were considered as subspecies of *D. marsupialis* (*D. m. aurita*), but we treat this taxon as a distinct species based on morphological characters and biogeographic patterns (Cerqueira, 1985; Cerqueira and Lemos, 2000). In the recent phylogeographic study of Patton and Costa (2003) *auritus* and *marsupialis* are reciprocally monophyletic. Thus, the molecular results indicate concordance with the conclusions of Cerqueira (1985) and Cerqueira and Lemos (2000). Brown (2004) erroneously cited this species from Villa Castelli (La Rioja Province); this is an arid region, however, and this species does not occur in arid parts of Argentina. The other congeneric species (*D. albiventris*) was cited by Yepes (1936a) for this locality (see above).

Genus *Lutreolina* Thomas, 1910

The only species recognized for this genus occupies a variety of environments throughout much of South America, as well as some isolated populations.

Lutreolina crassicaudata (Desmarest, 1804)

Didelphis crassicaudata Desmarest, 1804. Tableau Méthodique des mammiferes, *in* Nouveau dictionnaire d`histoire naturelle, appliquée aux arts, principalement à l'agriculture et à l'économie rurale et domestique: par une société de naturalistes et d'agriculteurs: avec des figures tirées des trois règnes de la nature…. Ch. Deterville, Paris 24:19.

Lutreolina crassicaudata crassicaudata: Thomas, 1923. Annals and. Magazine of Natural History, 9° ser. 11:584.

Type Locality.--Paraguay, Asunción, by subsequent restriction (Cabrera, 1957:39).

Specimens Examined (161)**.**--BUENOS AIRES: Algarrobo, 1 (MACN 32233); Arroyo Brusquitas, 1 (MMP 152); Arroyo Pereyra, 2 (AMNH 254511, 254512); Arroyo Tapalqué, 1 (MACN 17.63); Belgrano, 3 (BMNH 85.11.26.9, 85.11.26.10, 85.11.26.11); Bella Vista, 1 (MACN 43.73); Berisso, Arroyo El Pescado, 1 (MLP 19.VI.97.2); Berisso-La Balandra, 1 (MLP 4.IV.00.9); Bonefacio (=Bonifacio), 1 (BMNH 31.7.4.5); Buenos Aires, 4 (AMNH 838, 36923, 36924, 36925); Castelar, 1 (MACN 50477); Chapadmalal, 2 (MACN 13066, 13069); Chascomús, 1 (MACN 15365); Chascomús, Los Libres del Sur, 2 (MACN 49213, 52.76); Dock Sur, 2 (MACN 92, 93); Escobar, 3 (MACN 30404, 30405, 30406); Estancia El Tuyú, 1 (MLP 9.VIII.71.16); Estancia Los Lobos, 6 (MMP 88009, 88034, 88040, 88049, 88050, 88051); General Belgrano, 10 (MLP 1569, 1570, 1571, 1591, 17.V.44.7, 17.VI.44.10, 17.VI.44.8, 17.VI.44.9, 25.XI.41.1, 25.XI.41.2); General Lavalle, 7 (MLP 1676, 20.I.41.3,

6.VII.40.3, 6.VII.40.4, 6.VIII.40.1, 6.VIII.40.2, 6.VIII.40.5); INTA (Instituto Nacional de Tecnología Agropecuaria), Delta, 1 (MACN 19202); Isla Ella, Delta del Parana, 2 (BMNH 17.6.1.36, 17.6.1.37); Isla Ella, Paran, 1 (BMNH 25.5.6.14); Isla Talavera, 1 (MLP 10.V.87.10); Jardín Zoológico de La Plata, 1 (MLP 10.XII.37.1); La Plata, 12 (10 MLP 10.VI.44.4, 11.VI.42.1, 17.V.44.9, 17.VI.44.2, 17.VI.44.3, 17.VI.44.4, 17.VI.44.5, 17.VI.44.6, 21.X.35.2, 620; 2 BMNH 97.1.1.2, 39,4221); La Plata- Villa Elisa, 3 (MLP 21.X.35.1, 21.X.35.4, 21.X.35.5); Las Flores, 2 (MACN 31258, 52.79); Los Yngleses, Ajo, 1 (BMNH 9.12.1.56); Los Yngleses, Ajo SL, 3 (BMNH 20.2.7.42, 20.2.7.43, 20.2.7.44); Magdalena-Estancia San Isidro, 1 (MLP 5.IX.4.9); Mar de Ajó, 2 (MACN 18.12, 18.13); Matheu, 1 (MACN 34547); Moreno, 1 (BMNH 88.5.16.2); Morón, 1 (MACN 13.70); Paraje Talavera, 1 (MMP 607); Pergamino, 3 (MACN 18735, 19190, 19191); Pigüe Cura Malal Chico, 1 (MLP 21.X.35.6); Pta Indio, Estancia San Isidro, 2 (MLP 22.VI.41.1, 22.VII.41.2); Punta Lara, 2 (AMNH 254513, MACN 17267); Quilmes, 1 (MACN 30248); Quiroga, 1 (MMP 579); Ramallo, 4 (CML 4114, 4115, 4116, 4117); Roberto Payró, 1 (MACN 42108); Rojas, 1 (MACN 18196); Ruta 188 km 116, 3 (MLP 22.III.72.2, 22.III.72.3, 22.III.72.4); San Fernando, 1 (MACN 33282); San Nicolás, 1 (MLP 20.IX.49.16); Tres Arroyos, 1 (MACN 24160); Urdampilleta (=La Torrecita), 1 (FMNH 24375); Villa Gesell, 2 (IADIZA 3301, 3745); Zelaya, 1 (MACN 31297). CHACO: Las Palmas, 1 (MACN 39466); Las Palmas, 20 mi N. of Corrientes, 1 (BMNH 6.5.5.7); Río de Oro, 1 (MACN 14343); Villa Ana, 1 (MLP 707). CORDOBA: Barreto, 1 (MLP 7.XI.41.1); Leones, 2 (MACN 49.37, 49242); Noetinger, F.C.C.A., 7 (BMNH 17.1.25.62, 17.1.25.63, 17.1.25.64, 17.1.25.66, 17.1.25.67, 17.1.25.68, 17.1.25.69); Río Cuarto, Puente Olmos, 3 (MLP 1509, 1.VII.37.1, 1.VII.37.2). CORRIENTES: 8 km N El Palmar, 1 (IADIZA 3303); Estancia El Ceibo, 1 (MLP 28.IV.50.2); Goya, N. Argentine, 1 (BMNH 95.4.17.1); Ituzaingó, Pto. Valle, 1 (IADIZA 3435); Laguna Grande, 1 (MLP 28.IV.50.1); Las Lomas, Laguna Paiva, 7 (IADIZA 3304, 3305, 3427, 3428, 3430, 3743, 3744); Manantiales, 1 (MACN 13713); Mercedes, Isleta Cabo Estancia, 1 (USNM 331053); Paso de la Patria, 1 (MACN 40161); Pirayuí, 8 (IADIZA 3296, 3297, 3298, 3299, 3300, 3302, 3429, S/N); SE Corrientes, at Centro Argentino de Primates, 9 (USNM 536827, 536828, 536829, 536830, 536831, 536832, 536833, 536834, 536835). ENTRE RÍOS*:* Brazo Largo, 1 (MLP 22.I.44.1); Concordia, 1 (MACN 48282); Estancia Paranacito, 1 (MMP 1015); María Grande, 1 (MACN 14904); Pronunciamiento, 1 (MACN 31269). FORMOSA: Parque Nacional Pilcomayo, Brazo Norte, 1 (MACN 20809). JUJUY*:* Abra de Cañas, El Monolito, 1707m, 1 (CML 1759); El Duraznal, 1800m, 2 (CML 1596, 1597); "Jujuy," 1 (MACN not numbered). LA PAMPA*:* 5 km E General Acha, 1 (IADIZA S/N); Fco. Pampa, 2 (MLP 21.X.35.7, 21.X.35.8). MENDOZA*:* Santa Rosa, 1 (MLP 1688). MISIONES: Arroyo Agrupa, 1 (MACN 17270); Posadas, 1 (MACN 17923). SALTA*:* Aguas Blancas, 1 (MACN 17269). SANTA FE*:* Colonia Mascias, 1 (MACN 43.21); Las Rosas, 100 m, 5 (BMNH 17.5.2.19, 17.5.2.20, 17.5.2.21, 17.5.2.22 holotipe of *L. crassicaudata paranalis*, 17.5.2.23); Malabrigo, 6 (MACN 36104, 36882, 36884, 36886, 36888, 36889); Rufino, 2 (MLP 1694, 22.VII.41.3); Santo Tomé, 2 (MLP 669, 703); Tostado, 1 (MACN 45101); Villa Guillermina, 1 (MACN 33175). TUCUMAN*:* Aconquija, 1 (BMNH 26.5.9.25); Cerro San Javier, 1 (CML 1357); Dique San Ignacio, 1 (CML 2895); Horco Molle, 650 m, 1 (CML, not number); Oeste Sierra San Javier, 1 (BMNH 26.11.13.1); Raco, 1 (CML 465); Raco, Sierra de San Javier, 1 (BMNH 26.11.13.2).

Additional Records.--BUENOS AIRES: Arroyo Brusquitas (Reig, 1964); Arroyo Corrientes (Reig, 1964), Arroyo La Matanza (Wainberg and de Fronza, 1969); Arroyo

Pereyra (Ximénez, 1967); Bañado de San Jorge, Parque Pereyra Iraola (Reig et al., 1977); Belgrano (Waterhouse, 1846); Buenos Aires Zoological Gardens (Brown, 2004); Delta del Paraná (Wainberg and de Fronza, 1969); González Catán (Ximénez, 1967); Hurlingam (Thomas, 1923; Ximénez, 1967); La Plata (Waterhouse, 1846); Los Yngleses (Thomas, 1910, 1917); Mar del Sur (Reig, 1964; Ximénez, 1967); Moreno (Waterhouse, 1846); Miramar (Fornes and Massoia, 1965; Wainberg and de Fronza, 1969); Paraje Talavera (Ximénez, 1967); Quiroga (Ximénez, 1967); Reserva Natural Estricta Otamendi (Heinonen Fortabat and Chébez, 1997); Zárate (Ximénez, 1967); Urdampilleta (Brown, 2004). CHACO: Parque Nacional Chaco (Heinonen Fortabat and Chébez, 1997); Palm Swamp, 12 km ESE of Resistencia (Brown, 2004); Río de Oro (Cirignoli et al. 2000). CORRIENTES: Left bank of Rio Parana (Brown, 2004); Parque Nacional Mburucuyá (Heinonen Fortabat and Chébez, 1997). ENTRE RIOS: Las Cuevas (Brown, 2004); Parque Nacional El Palmar (Crespo, 1982b). FORMOSA: El Colorado (Massoia, 1970); Laguna Blanca (Massoia, 1970); Parque Nacional Pilcomayo (Heinonen Fortabat and Chébez, 1997); San Jose (Krumbiegel, 1941b). JUJUY: Abra de Cañas, 1700 m (Olrog, 1976); Aguas Negras (Heinonen and Bosso, 1994); Caimancito, Arroyo Sauzalito (D. Flores, personal observation); Cerro Calilegua (Olrog, 1979); Cerro Santa Bárbara, 1800 m (Olrog, 1976); Parque Nacional Calilegua (Heinonen Fortabat and Chébez, 1997). MISIONES: Departamento Apóstoles (Chébez and Massoia, 1996); Departamento Candelaria (Chébez and Massoia, 1996); Departamento Capital (Massoia, 1980; Chébez and Massoia, 1996); Departamento Iguazú (Chébez and Massoia, 1996); Departamento Oberá (Chébez and Massoia, 1996); Parque Nacional Iguazú (Heinonen Fortabat and Chébez, 1997); Santa Teresa, 30 km W of San Ignacio (Brown, 2004). SALTA: 24 km N of Aguas Blancas (Mares and Braun, 2000); a lo largo del alto Río Bermejo (Aguas Blancas, Departamento Orán) (Olrog, 1976); Parque Nacional El Rey (Heinonen Fortabat and Chébez, 1997). SANTA FE: Galvez (Krumbiegel, 1941b); Goya (Thomas, 1923); Las Rosas (Thomas, 1923); Malabrigo (Yepes, 1944); Santa Fe (Krieg, 1924; Brown, 2004). TUCUMAN: 25 km NW San Miguel de Tucumán (Mares et al., 1996); Aguas Chiquitas (Cajal, 1981); Arroyo El Saltón, Reserva Provincial Santa Ana (R. M. Barquez, personal observation); Cerro San Javier (Capllonch et al., 1996); Dique San Ignacio (R. M. Barquez, personal observation); El Indio, Ruta 307 (R. M. Barquez, personal observation); Piedras Coloradas (Mares et al., 1996); Quebrada de Lules, 11 km SW de San Pablo (Mares and Braun, 2000); Raco, 1000 m (Olrog, 1976); Raco, Sierra de San Javier (Capllonch et al., 1996); Río Pueblo Viejo, Reserva Provincial La Florida (R. M. Barquez, personal observation); San Pablo, 11 km NW (Mares and Braun, 2000); Sierras de Medina, Aguas Chiquitas, El Cadillal (Mares et al., 1996); Tafí Viejo (Capllonch et al., 1996).

Distribution.--This species is distributed from northern South America south to the Pampean region in Argentina, being more abundant in the southern portion of its range (Cabrera, 1957; Ximénez, 1967; Marshall, 1978a; Barquez et al., 1991; Redford and Eisenberg, 1992). Additional records from the literature indicate a distribution from southern Brazil south to Chubut Province in Argentina, including eastern Paraguay, Uruguay, and southern Bolivia. The populations from northwestern Argentina seem to be isolated from those of the rest of the country by the wide Chacoan region, and they comprise different subspecies (Cabrera, 1957; Ximénez, 1967; Massoia, 1973; Olrog, 1976; Marshall, 1978a; Gardner, 1993).

Habitat.--Frequently found near permanent watercourses, and associated with forests in northwestern Argentina. In the coasts of Buenos Aires Province, it has been captured in grasses, and in the eastern part of the province in gallery forests and swampy areas (Hunsaker, 1977; Marshall, 1978a; Mares et al., 1989; Ojeda and Mares, 1989; Barquez et al., 1991; Redford and Eisenberg, 1992).

Natural History.--Crepuscular and nocturnal; the muscles and morphology of the mandible are well adapted to carnivorous habits, as is its behavior (Mares et al., 1989; Flores et al., 2003). Feeds on small mammals, invertebrates, fishes, bird eggs, and fruits. It is a good climber, agile on the ground, and an excellent swimmer. In captivity, it behaves as an excellent predator, and its night activity is sporadic. Its biology is still poorly known (Olrog, 1976; Marshall, 1978a; Redford and Eisenberg, 1992).

Comments.--The systematic status of the subspecies of *Lutreolina crassicaudata* is still unclear, probably as a consequence of the lack of records in some areas, and also because of the individual variation in size within a population (Thomas, 1888). Some authors have reported variation in color of captive specimens, postulating that a relation exists between color and diet and the environment where the animal resides (Cabrera, 1957; Ximénez, 1967). Museum specimens can be discolored if exposed to sunlight (Ximénez, 1967; Pérez Hernández, 1985).

Along the wide distributional range of this species 5 subspecies are currently recognized. *L. c. turneri* occurs in British Guiana and was treated by Thomas (1923) and Cabrera (1957) as a subspecies due to its small size. *L. c. crassicaudata* was reported from Paraguay by Thomas (1923) based on specimens from "the Chaco west of Asunción," but these probably correspond to Formosa or Chaco provinces, Argentina; this subspecies is distributed in Paraguay, northeastern Argentina, and southwestern Brazil (Cabrera, 1957; Marshall, 1978a). Thomas (1923) described *L. c. lutrilla* including specimens from Rio Grande do Sul in Brazil and Uruguay; in the same paper, he described *L. c. paranalis* from Santa Fe, Argentina, extending to the Delta of the Paraná River and eastward to Montevideo, Uruguay. Later, Cabrera (1957) extended the distribution of this subspecies to Corrientes and south to southern Buenos Aires and westward to La Rioja and San Juan provinces. Finally, *L. c. bonaria* was described by Thomas (1923) from Buenos Aires, but treated by Cabrera (1957) as a synonym of *paranalis.* Ximénez (1967) did not recognize *L. c. lutrilla*, considering it to be a synonym of *L. c. paranalis,* the subspecies that inhabits Uruguay, northeastern Argentina, and Río Grande, Paraná, Santa Catarina, São Paulo, and Mato Grosso in northern Brazil.

None of these authors has included *Lutreolina crassicaudata* in northwestern Argentina, although there are records from Raco, Tucumán Province since 1903 at the CML. Later, Massoia (1973) suggested that specimens from northwestern Argentina could be assigned to *L. c. crassicaudata.*

The specimens from northwestern Argentina can be assigned to *L. c. crassicaudata*, because its size is coincident with the measurements offered by Massoia (1973) for specimens from Misiones, although some differences can be seen in the drawing of the skulls published by the author. Anderson (1997) considered *L. c. crassicaudata* as the subspecies present in Bolivia, and the measurements of his specimens are very similar to those from northwestern Argentina and Misiones Province.

Although Marshall (1978a) recognized only one subspecies for southern South America (*L. c. crassicaudata*), there are great differences in body size and skulls between specimens from the Pampean region versus those of northern Argentina, so the existence of at least two subspecies is highly probable in these parts of South America (*L. c. paranalis* and *L. c. crassicaudata*). Even though differences in the structure of the molars and the basicranium were not observed (D. A. Flores, unpubl. data), some morphometrical differences are evident between *L. c. crassicaudata* and *L. c. paranalis* (Graipel et al., 1996).

Brown (2004) listed a series of localities for this species in Argentina, which actually correspond to fossil records. For example, the author cited the localities of "Rio Lujan," "Chapadmalal Formation," "Monte Hermoso Formation" (all in Buenos Aires Province), and "Corral Quemado Formation" (Catamarca Province). All of these localities correspond to fossil records from the Pliocene and Pleistocene (Marshall, 1978a). On the other hand, *L. crassicaudata* is not found in Catamarca Province (Mares et al., 1997).

Genus *Philander* Tiedemann, 1808

This genus has a wide distribution from Tamaulipas, Mexico, to northern Argentina. The common name "Four-Eyed Opossum" is due to the pale spots they have above each eye. Thomas (1888) included all the current species of the genus *Philander* within the subgenus *Metachirus* (genus *Didelphys*). *Philander* was elevated to generic level by Hershkovitz (1949). The nomenclatorial status of *Philander* has been discussed by several authors (Hershkovitz, 1949, 1976, 1981, 1997; Pine, 1973; Husson, 1978; Gardner, 1981), but the number of species and their distributional ranges remain unclear (Patton and da Silva, 1997; Patton and Costa, 2003). Simpson (1972) and Pine (1973) suggested that *Philander* could be treated as a subgenus of *Didelphis*, but Reig et al. (1987), considered this group of species to be well differentiated in anatomy as well as ecology. Traditionally, it was considered as a monotypic genus, with a single species (*P. frenata*). Later, Gardner and Patton (1972) described *Philander mcilhennyi* from the Peruvian Amazon, based on size and chromatic characters of the skin, and reported siympatry with *P. frenata*. Hershkovitz (1997) reviewed the genus, using morphological characters as well as anatomy, geographical distribution and behavior.

Recent genetic studies allowed a phylogeographic analysis that derived in-depth modifications of the systematics and taxonomy of the group (Patton and da Silva, 1997; Patton and Costa, 2003). These studies confered specific status to *P. frenata* (synonym with *P. o. quica* Temminck), from the Atlantic forests of southeastern Brazil. They also considered *Philander andersoni* and *P. mcilhennyi* to be valid species, in contrast to Gardner (1993) and Hershkovitz (1997), who treated these as subspecies. Recently, Castro-Arellano et al. (2000) recognized just *P. frenata, P. andersoni*, and *P. mcilhennyi* as full species. The species *andersoni* and *mcilhennyi* have a similar dark coloration pattern, but they are very different genetically (Patton and da Silva, 1997; Patton and Costa, 2003). Two new species (*P. mondolfii* and *P. deltae*) were described by Lew et al. (2006) from Colombia and Venezuela.

Philander frenatus (Olfers, 1818)

Didelphys frenata Olfers, 1818. Abhanddlungen, *en* W.L. Eschwege, Journal von Brasilien, Neue Bibliothek der wichtigstern Reisebeschreibungen zur Erweiterung der Erd-und Volkerkinde), K. T. Bertuch, Weimar, Germany, 15:204.

Philander frenatus: Patton and da Silva, 1997. Journal of Mammalogy, 78:97.

Type Locality.--"Südamerica"; restricted to Bahia, Brasil by Wagner (1843).

Specimens Examined (32).--CHACO: 10 km S de Puerto Bermejo, 7 (USNM 536836, 536837, 536838, 536839, 536840, 536841, 536842); Parque Nacional Chaco, camping sobre Río Negro, 2 (MACN 20866, 20868); Río de Oro, 1 (MACN 14342). FORMOSA: about 13 km S of Clorinda, 1 (AMNH 256980); Parque Nacional Pilcomayo, Abadie Cue, 1 (MACN 20743); Parque Nacional Pilcomayo, Estero Poi, 3 (MACN 20736, 20735, 20734); Parque Nacional Pilcomayo, Lata Cue, 4 (MACN 20740, 20739, 20737, 20738); Parque Nacional Pilcomayo, Paso Pomelo, 2 (MACN 20742, 20741); Ruta 11, 13 km S de Clorinda, 2 (CML 2065, 2083). MISIONES: Arroyo Piray Guazú, 1 (CML 1811); Arroyo Urugua-í, curso medio, 3 (MACN 49307, 49376, 49465); Arroyo Urugua-í, km 10, 2 (MACN 51127, 51133); Fracrán, 1 (MACN 52.19); Parque Nacional Iguazú, Acceso a Cataratas, 1 (CIES-PNI M-92); Río Urugua-í, a 30 km al N de Puerto Bemberg, 1 (MACN 51.18).

Additional Records.--CHACO: Chaco (Thomas, 1888); Parque Nacional Chaco (Heinonen Fortabat and Chébez, 1997); Río de Oro (Crespo, 1974; Hershkovitz, 1997). CORRIENTES: Estancia La Blanca, 10 km al N de Santo Tomé, sobre Río Uruguay (P. Capllonch, pers. comm.). FORMOSA: Estancia Linda Vista (Brown, 2004); Laguna Blanca (Massoia, 1970); NNE Formosa (Brown, 2004); Parque Nacional Pilcomayo (Heinonen Fortabat and Chébez, 1997). MISIONES: Departamento Cainguás (Massoia, 1980; Chébez and Massoia, 1996); Departamento Eldorado (Massoia, 1980; Chébez and Massoia, 1996); Departamento General Belgrano (Chébez and Massoia, 1996); Departamento Guaraní (Massoia, 1980; Chébez and Massoia, 1996); Departamento Iguazú (Massoia, 1980; Chébez and Massoia, 1996); Departamento San Pedro (Massoia, 1980; Chébez and Massoia, 1996); Fracrán (Crespo, 1974; Hershkovitz, 1997) Parque Nacional Iguazú (Crespo, 1982a; Heinonen Fortabat and Chébez, 1997); Río Urugua-í, a 30 km al Norte de Puerto Bemberg (Crespo, 1950; Hershkovitz, 1997); San Pedro (Kantis, 1963).

Distribution.-- From southeastern Brazil, from Goias to Parana; adjacent southeastern Paraguay, and northeastern Argentina. In Argentina, it is known only from the Paranaense region and adjacent Chacoan environments related to gallery forests, in the provinces of Formosa, Chaco, Corrientes, and Misiones (Castro-Arellano et al., 2000; Brown, 2004; Gardner, 2005).

Habitat.--Particularly associated with primary and secondary forests, and savannas, either at ground level or at low heights in trees. In Argentina, they are found mainly in gallery forests, and all captures are from or near watercourses (Olrog and Lucero, 1981; Redford and Eisenberg, 1992; Emmons and Feer, 1997; Castro-Arellano et al., 2000 as *Philander opossum*).

Natural History.--Nocturnal, arboreal, and terrestrial, with a remarkable capacity to swim. The diet consists primarily of invertebrates and small vertebrates, with some flowers, fruits, and seeds. The food is eaten on the ground or in trees. Solitary, although the home range for one individual has a wide overlapping area with that of another.

Some groups have been observed only during the reproductive season. In Argentina, it is reproductively active from August through February. It builds nests of leaves in hollow trees, tree forks, fallen logs, and in burrows.

The offspring stay with the mother for about 60 days and remain in contact for about 8 to 10 additional days; later on the young become independent and contacts between them are less frequent (Crespo, 1982a; Charles-Dominique, 1983; Emmons and Feer, 1997 as *Philander opossum*). The number of young per litter varies from 1 to 7; in northeastern Argentina, 4 to 6 young per litter have been reported (Redford and Eisenberg, 1992 as *Philander opossum*).

Comments.-- Cabrera (1958) recognized to *P. opossum azaricus* for northeastern Argentina and Paraguay. Hershkovitz (1997) recognized in the genus only 2 species (*P. opossum* and *P. andersoni*), including the populations of northeastern Argentina in the subspecies *P. o. quica*; and the same author mentioned that there is a high degree of morphological uniformity in the populations from eastern Brazil, northern Argentina, Paraguay, lower parts of Bolivia, eastern Peru, and Ecuador. Finally, 6 subspecies were recognized by Patton and da Silva (1997) for *P. opossum*, but specimens from Bolivia, Paraguay, and Argentina were not included in their analysis. Specimens from northeastern Argentina (Formosa and Misiones provinces) do not differ morphologically with those from southeastern Brazil and Paraguay. Recently, Castro-Arellano et al. (2000) recognized *P. opossum frenatus* for northeastern Argentina, and according to Patton and Pires Costa (2003), and Gardner (2005) this species is valid and different than *P. opossum*.

We used the name *frenatus* instead *frenata* following Patton and Pires Costa (2003), Gardner (2005), and the Article 31.2 of the International Code of Zoological Nomenclature).

Tribe Metachirini Reig, Kirsch, and Marshall, 1985

Genus *Metachirus* Burmeister, 1854.

Metachirus nudicaudatus (Desmarest, 1817)

Didelphis nudicaudatus Desmarest, 1817. Tableau Méthodique des mammiferes, *in* Nouveau dictionnaire d`histoire naturelle, appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à la médicine, etc. Par une société de naturalistes et d'agriculteurs. Nouveau édition, presqú entièrement refondue et consideerablement augmentée. Ch. Deterville, Paris 9:424

Metachirus nudicaudatus: Allen, 1900. Bulletin of the American Museum of Natural History 13:197.

Type Locality.--French Guiana, "Cayenne."

Specimens Examined (4).--MISIONES: Parque Nacional Iguazú, acceso a Cataratas, 1 (CIES-PNI-M 78); Puerto Península, 1 (RMB 1586); Río Uruguaí, curso medio, 2 (MACN 49455, 49466).

Additional Records.--MISIONES: Departamento General Belgrano (Chébez and Massoia, 1996); Departamento Iguazú (Massoia, 1980; Chébez and Massoia, 1996); Departamento Montecarlo (Massoia, 1980; Chébez and Massoia, 1996); Parque Nacional Iguazú (Heinonen Fortabat and Chébez, 1997); Río Urugua-í, a 30 km al Norte de Puerto Bemberg (Crespo, 1950).

Distribution.--This species is widely distributed from southern Nicaragua south to Paraguay and northeastern Argentina (in Misiones Province) (Crespo, 1950; Cabrera, 1957; Massoia, 1980).

Habitat.--Mainly tropical forest with scarce underbrush, although it has also been captured in areas of dense underbrush, disturbed areas, and secondary forests (Emmons and Feer, 1997). In Argentina, it has been found only in undisturbed areas.

Natural History.--Nocturnal, largely terrestrial, it travels on the ground and runs rather than climbs when in danger (Reid, 1997). The diet includes fruits, insects (termites, beetles, and cicadas), mollusks, amphibians, reptiles, birds, eggs, and small mammals, taken from the ground or trees. Emmons and Feer (1997) mentioned several aspects about the natural history.

Nests of leaves or twigs are built in the branches of the trees, and sometimes under logs or rocks, depressions, under palm fronds, or close to the ground (Nowak, 1991; Reid, 1997). *Metachirus* may damage fruit crops in some areas (Nowak, 1991).

Comments.-- *Metachirus* contains only 1 species which is widely distributed in South America. It is similar in shape, external aspect, and body size to species of the genus *Philander*, but the hind feet are larger, giving this genus a tendency towards a more bipedal posture (Hildebrand, 1961); additionally, there are numerous differences in cranial and dental anatomy (Flores, 2003) and karyotype (Reig et al., 1977). The 8 subspecies considered by Cabrera (1957) are questionable given the lack of detailed taxonomic revision. Cabrera (1957) considered the subspecies from northeastern Argentina to be *M. nudicaudatus modestus*. Crespo (1950) included this species in Argentina.

Brown (2004) cited the locality of "La Urbana, Rio Pilcomayo" in Formosa Province for this species based in a report of Krumbeigel (1941b). *M. nudicaudatus* not was reported for Formosa Province; in Argentina it is only known in Misiones Province. The Krumbeigel report probably corresponds to *Philander*, which is common in Formosa Province, and is similar externally to *Metachirus*.

Subfamily Marmosinae Reig, Kirsch, and Marshall, 1985

Tribe Marmosini Reig, Kirsch, and Marshall, 1985

Genus *Chacodelphys* Voss, Gardner, and Jansa, 2004

Chacodelphys formosa (Shamel, 1930)

Marmosa muscula Shamel, 1930. Journal of the Washington Academy of Sciences 20: 83. Original description.

Marmosa formosa: Shamel, 1930. Journal of Mammalogy 11:311. Replacement name.

Chacodelphys formosa: Voss, Gardner, and Jansa, 2004. American Museum Novitates 3442:2.

Type Locality.-- Argentina, Formosa, Kilometro 182 Riacho Pilaga, 10 mi. NW.
Specimens examined.--None.

Additional Records.-- Argentina, Formosa, kilometro 182, Riacho Pilaga, 10 mi. NW. (Voss et al., 2004).

Distribution.--Known only from the type locality.

Habitat.--The only available information about the habitat of this species was recorded by the collector of the holotype. Wetmore (1926) described the landscape as a Chacoan forest with savannas, and gallery forests (Voss et al., 2004).

Natural History.--Nothing is known about the natural history, but their carnassial dentition indicates an almost exclusive diet of insects and other arthropods (Voss et al., 2004).

Comments.--This taxon was originally described as *Marmosa muscula* by Shamel (1930a), but he promptly (Shamel, 1930b) proposed the replacement name *M. formosa* to avoid homonymy with *muscula* (a synonym of *M. murina*). Tate (1933) recognized it as a valid species in his "*elegans* Group" of *Marmosa*. Later, Cabrera (1957) considered it as a juvenile form of a subspecies of *Marmosa velutina*, in the subgenus *Thylamys*. On the other hand, Gardner and Creighton (1989) placed *formosa* in *Gracilinanus*, as a synonym of *G. agilis*, which was followed in Hershkovitz's (1992a) revision of *Gracilinanus*. Recently, Voss et al. (2004) examined the type specimen of "*Marmosa formosa*" and found it to exhibit a particular combination of characters that do not fit with *Thylamys* or *Gracilinanus*, or any other currently recognized supraspecific taxon. *Chacodelphys formosa* perhaps is the smallest living didelphid, and can be distinguished from other close taxa by several qualitative morphological characters (Voss et al., 2004).

Genus *Cryptonanus* Voss, Lunde, and Jansa, 2005

Recently described by Voss at al. (2005), this genus includes 2 species from Argentina (*C. chacoensis* and *C. ignitus*) that were previously treated as genus *Gracilinanus*.

Cryptonanus chacoensis (Tate, 1931)

Marmosa agilis chacoensis Tate, 1931. American Museum Novitates 493:10.

Gracilinanus agilis: Gardner and Creighton, 1989. Proceedings of the Biological Society of Washington 102:7.

Cryptonanus chacoensis: Voss, Lunde, and Jansa, 2005. American Museum Novitates 3482:14.

Type Locality.--Sapucay, Paraguay.

Specimens Examined (41).--BUENOS AIRES*:* A° Ñacurutú-Isla El Roble, 4 (MLP 23.X.50.1, 23.X.50.2, 23.X.50.4, 23.X.50.5); Arroyo Ñacurutú, 1 (MACN 49.35); Delta, Canal 6, 1 (CML 1810); Isla Talavera, 1 (MLP 5.VIII.98.9); Reserva Natural Punta Lara, 2 (MLP 9.IX.97.3, 9.IX.97.4). CHACO; Las Palmas, 1 (USNM 236329). ENTRE RÍOS*:* Villa Elisa-A° Perucho Verna, 1 (MLP 30.VI.98.1). MISIONES*:* Escuela 51 a 4 km de Loreto, 1 (MLP S/N); Puerto San Juan Candelaria, 1 (MLP 17.VII.96.4); Río Urugua-í, a 30 km al Norte de Puerto Bemberg, 1 (MACN 49325); San Ignacio, Desembocadura Arroyo Yabebiry, 2 (MLP 30.X.95.16, 4.VIII.98.12). JUJUY: Ingenio La Esperanza, 24° 14′ S 64° 52′ W, 1 (CEM 4691); Santa Bárbara, 1 (AMNH, 185270); Yuto, 1 (AMNH 167851). SALTA*:* Ingenio Tabacal, 2 (IADIZA 6201, 6203); Ingenio Tabacal, Lote Milagros, 19 (CML 2700, 2701, 5910, 5911, 5912, 5913, 5914, 5915, 5916, 5917, 5918, 5919, 5920, 5921, 5922, 5923, 5924, 5925, 5926). We also examined the type of *Marmosa agilis chacoensis* from Sapucay, Paraguay (BMNH 4.1.5.48).

Additional Records.--BUENOS AIRES: Campana (Hershkovitz, 1992a); Isla Roble, Delta del Paraná (Hershkovitz, 1992a); Reserva Natural Estricta Otamendi (Heinonen Fortabat and Chébez, 1997); Zárate, Arroyo Ñacurutú (Hershkovitz, 1992a). CHACO: Las Palmas (Voss et al., 2005); Parque Nacional Chaco (Contreras, 1984; Heinonen Fortabat and Chébez, 1997); Río de Oro (Cirignoli 2000). CORRIENTES: en las cercanías de Laguna González, Santa Ana, Departamento San Cosme (Contreras, 1982); Cañada Pirayuí (Contreras, 1984). ENTRE RÍOS: Brazo largo, Delta del Paraná (Hershkovitz, 1992a). FORMOSA: Ingeniero Juárez (Olrog, 1959; Hershkovitz, 1992a); Pago del Tigre, Patiño (Hershkovitz, 1992a); Pozo del Tigre (Massoia and Fornes, 1972); Riacho Pilagá, 10 mi NW of kilómetro 182 (Tate, 1933; Hershkovitz, 1992a; Mares and Braun, 2000). MISIONES: Departamento Apóstoles (Massoia, 1980; Chébez and Massoia, 1996); Departamento Candelaria (Chébez and Massoia, 1996); Departamento Capital (Chébez and Massoia, 1996); Departamento General Belgrano (Chébez and Massoia, 1996); Departamento Guaraní (Massoia, 1980; Chébez and Massoia, 1996); Departamento Iguazú (Chébez and Massoia, 1996); Departamento L. N. Alem (Chébez and Massoia, 1996); Departamento Montecarlo (Chébez and Massoia, 1996); Departamento Oberá (Chébez and Massoia, 1996); Departamento San Ignacio (Chébez and Massoia, 1996); Puerto Libertad-Iguazú, Río Urugua-í (Hershkovitz, 1992a); Reserva Natural Estricta San Antonio (Heinonen Fortabat and Chébez, 1997).

Distribution.--Argentina, Paraguay, and probably Bolivia. In Argentina, in the provinces of Misiones, Corrientes, Formosa, Chaco, Entre Ríos, and Buenos Aires (Cabrera, 1957; Massoia and Fornes, 1972; Hershkovitz, 1992a; Redford and Eisenberg, 1992; Gardner, 1993) and recently added to the northwest in the provinces of Salta and Jujuy (Flores et al., 2000).

Habitat.--In Argentina, this species usually inhabits gallery forests, although it may be found in other habitats (Olrog and Lucero, 1981; Redford and Eisenberg, 1992; Emmons and Feer, 1997), such as cultivated areas (Massoia and Fornes, 1972). Two of the localities, Ingenio La Esperanza and Ingenio Tabacal, listed in *Specimens Examined* are from areas where sugar cane is cultivated (Flores et al., 2000).

Natural History.--Nocturnal, arboreal, and terrestrial (Massoia and Fornes, 1972; Redford and Eisenberg, 1992).This species feeds on insects and small fruits, and probably also eats sap (Linares, 1998).

Comments.--This species was previously considered as a subspecies of *Gracilinanus agilis*. Flores et al. (2000) treated the populations from Argentina as *Gracilinanus agilis chacoensis*. In the more recent scheme, the populations from Paraguay, Argentina, and probably Bolivia are included in *Cryptonanus*, and the forms from Brazil, Peru, and probably Paraguay are retained in *Gracilinanus agilis*.

Cryptonanus ignitus (Díaz, Flores, and Barquez, 2002)

Gracilinanus ignitus Díaz, Flores, and Barquez, 2002. Journal of Mammalogy 83:824.

Cryptonanus ignitus: Voss, Lunde, and Jansa, 2005. American Museum Novitates 3482:16.

Type Locality.--Yuto, Departamento Ledesma, Jujuy, Argentina.

Specimens Examined (1).--JUJUY*:* Yuto, 1 (AMNH 167852, holotype).

Distribution.--Known only from the type locality.

Habitat.--The type locality is in the province phytogeographic of Yungas. At present, the habitat is highly disturbed. Extensive areas for cultivation of sugar cane and fruits have been established in the region during the last several decades. The habitat is an ecotone between transitional and montane forest (Díaz et al., 2002).

Natural History.--Nothing is known about the natural history of this species.

Comments.--Description of this species was based on a specimen deposited at the American Museum of Natural History (New York), collected by F. Contino in 1962, when Jujuy Province was less disturbed by agricultural development. The holotype is the only specimen known for this species.

Genus *Gracilinanus* Gardner and Creighton, 1989

Gardner and Creighton (1989) proposed the name *Gracilinanus* for the species included in the *microtarsus* group of Tate (1933). *Gracilinanus* includes 6 species widely distributed across the forests and woodlands of the Neotropics (Voss et al., 2005). Previously, 2 species were known for Argentina, *G. agilis* and *G. microtarsus* (Massoia and Fornes, 1972; Massoia, 1980; Olrog and Lucero, 1981; Contreras, 1982, 1984; Redford and Eisenberg, 1992; Chébez and Massoia, 1996; Heinonen Fortabat and Chébez, 1997); with the former taxon transferred to *Cryptonanus* (Voss et al. 2005, and see above), only 1 species of *Gracilinanus* now inhabits the country.

Gracilinanus microtarsus (Wagner, 1842)

Didelphis microtarsus Wagner, 1842. Archiv für Naturgeschichte, Jahrgang 8, Bd. 1:359.

Gracilinanus microtarsus: Gardner and Creighton, 1989. Proceedings of the Biological Society of Washington 102:7.

Type Locality.--Brazil, São Paulo, "Ypanema."

Specimens Examined.--None.

Additional Records.--MISIONES: Departamento Cainguás (Massoia, 1980; Chébez and Massoia, 1996); Departamento Candelaria (Chébez and Massoia, 1996); Departamento Oberá (Chébez and Massoia, 1996).

Distribution.--The distribution of this species is restricted to the southern portion of Brazil, from Rio de Janeiro to Rio Grande do Sul, and probably Misiones Province in Argentina (Tate, 1933; Cabrera, 1957; Massoia, 1980; Hershkovitz, 1992a; Gardner, 1993; Redford and Eisenberg, 1992; Emmons and Feer, 1997).

Habitat.--Found in humid primary forests, and less frequently captured in secondary forests (Olrog and Lucero, 1981; Redford and Eisenberg, 1992; Emmons and Feer, 1997).

Natural History.--Nocturnal; captured on the ground as well as in trees. Arboreal habits are well developed (Davis, 1947; Redford and Eisenberg, 1992).

Comments.--The occurrence of this species (and genus) in Argentina is not documented by specimens in collections.

Genus *Lestodelphys* Tate, 1934
Lestodelphys halli (Thomas, 1921)

Notodelphis halli Thomas, 1921. Annals and Magazine of Natural History, 9° ser., 8:137.

Lestodelphys halli: Tate, 1934. Journal of Mammalogy 15:154.

Type Locality.--Argentina, Santa Cruz, "Cabo Tres Puntas, S.E. Patagonia, 47° S"; subsequently emended to "Estancia Madujada, not far from Puerto Deseado" (Thomas, 1929:45).

Specimens Examined (15).--CHUBUT: Comodoro Rivadavia, 1 (BMNH 34.11.8.1); Estancia Los Manantiales, Languiñeo, 1 (CML 1032); Pico de Salamanca, 3 (MACN 47.24, 47.25, 47.26); Pico Salamanca, 5 (BMNH 28.12.11.205, 28.12.11.206, 28.12.11.207, 28.12.11.208). RIO NEGRO: 10 km by road E Clemente Onelli, 1 (UWZM 22422); 15 km SE de Los Menucos, 1 (MMP 945); Choele Choel, 1 (MACN 31236); "Río Negro," 1 (MMP 88037). SANTA CRUZ: near Cape Tres Puntas, Patagonia, 1 (BMNH 21.6.7.19 *Notodelphis halli* holotype).

Additional Records.--CHUBUT: 30 km N Pampa de Agnia, 43° 28.78′ S, 69° 49.09′ W (Birney et al., 1996a); 30 km NW Pampa de Agnia, 43° 28.78′ S, 69° 49.09′ W (Birney et al., 1996b); Arroyo Mayoco N° 1, 797 m, 42° 45′ 06″ S, 70° 52′ 12″ O (Martín, 2003); Arroyo Mayoco N° 2, 915 m, 42° 47′ 00″ S, 70° 49′ 00″ O (Martín, 2003); Arroyo Mayoco N° 3, 744 m, 42° 43′ 00″ S, 70° 50′ 00″ O (Martín, 2003); Boquete Nahuel Pan, 765 m, 42° 57′ 56″ S, 71° 09′ 24″ O (Martín, 2003); Cabaña Arroyo Pescado, 593 m; 43° 04′ 11″ S, 70° 54′ 46″ O (Martín, 2003); Cueva Watkins, 837 m, 42° 45′ 01″ S, 70° 52′ 25″ O (Martín, 2003); Estancia Los Manantiales, near Languiñeo (Reig, 1959); Estancia Los Manantiales near Languiñeo, approximately 43° 18´ S, 69° 50´ W (Birney et al., 1996a); Nahuel Pan, 842 m, 42° 59′ 15″ S, 70° 10′ 59″ O (Martín, 2003); Pico Salamanca, approximately 45° 30´ S, 68° 30´ W (Birney et al., 1996a); Piedra Parada, 420 m, 43° 39′ 32″ S, 70° 06′ 34″ O (Martín, 2003); Río Gualjaina, 1000 m al Oeste del cruce entre las rutas provinciales 25 y 14, 574 m, 43° 01′ 00″S, 70° 47′ 48″ O (Martín, 2003); Sarmiento (Reig, 1959); Valle del Rio Chico (Reig, 1959). LA PAMPA: Lihuel Calel, approximately 45° 30´ S, 68° 30´ W (Birney et al., 1996a); Parque Nacional Lihuel Calel (Heinonen Fortabat and Chébez, 1997). MENDOZA: Chacras de Coria, Departamento Godoy Cruz, approximately 32° 45´ S, 69° 00´ W (Birney et al., 1996a). NEUQUEN: Cueva Traful (Pearson and Pearson, 1982); Estancia Tehuel Malal, 6 km NW Nahuel Huapi, approximately 41° 02´ S, 71° 10´ W (Birney et al., 1996a). RÍO NEGRO: 8-10 km WSW Comallo, approximately 41° 04´ S, 70° 20´ W (Birney et al., 1996a); 9 km E (by road) Clemente Onelli (Birney et al., 1996a); 10 km (by road) Clemente Onelli, approximately 41° 10´ S, 70° 10´ W (Birney et al., 1996a); 15 km SE Los Menucos, approximately 40° 55´ S, 68° 05´ W (Birney et al., 1996a); Cerro Leones, 16 km ENE Bariloche, approximately 41° 04´ S, 71° 08´ W (Birney et al., 1996a). SANTA CRUZ: Cabo Tres Puntas (Thomas, 1921); Estancia La Madrugada, not far from Puerto Deseado (Thomas, 1929, originally cited as Cabo Tres Puntas by Thomas, 1921); Estancia La Madrugada, not far from Puerto Deseado, 47° 06´ S, 66° 29´ W (Birney et al., 1996a); Meseta El Pedrero, 46° 46.37´ S, 69° 38.49´ W (Birney et al., 1996a).

Distribution.--This species is endemic to central and southern Argentina, reaching the extreme south of the Golfo de San Jorge, which is the southernmost point known for the distribution of a living marsupial. It seems that the distribution of this species is wider that thought, although records are scarce. It has been captured in the provinces of Santa Cruz, Chubut, Río Negro, La Pampa, Mendoza, and Neuquén.

Habitat.--The habitat of this species is not well known. The known records are from arid regions and rocky areas in southern Argentina, Patagonian and Monte shrublands, dense shrub microhabitats, dense steppe grasslands, associated with watercourses and meadows. One specimen was captured inside a house (S. Saba, personal communication, 1994). The records cited by Martin (2003) extend the distribution of this species to the ecotonal area between Andean-Patagonian temperate rainforest and Patagonian Steppe.

Natural History.--Judging by their habitat and the morphology of their teeth, this species should be a skilled predator, as has been observed in captivity (Birney et al., 1996a). Because of the harsh weather in its distributional range it is possible that this species may undergo periods of torpor, similar to *Thylamys elegans* in southern Chile (Thomas, 1929; Marshall, 1977; Redford and Eisenberg, 1992). This species is probably more terrestrial than other murine opossums (Marshall, 1977).

Comments.--The records cited by Martin (2003) were based on owl pellets from *Tyto alba* and *Bubo magellanicus*. Nahuel Pan is one of the most western records of this species (Martin, 2003).

Genus *Micoureus* Lesson, 1842

This genus has a wide distribution from southern Belize to northern Argentina. *Micoureus* was originally considered a subgenus of *Didelphys* (Thomas, 1888), but later included in *Marmosa* (Tate, 1933; Cabrera, 1957); recent reviews consider it to be a valid genus (Marshall, 1981; Reig et al., 1985, 1987; Gardner and Creighton, 1989; Gardner, 1993). Reig et al. (1985, 1987) included the following species: *M. cinereus* (with *alstoni* and *demerarae* as subspecies), *M. constantiae*, *M. dominus*, *M. mapirensis*, *M. rapposus*, *M. germanus*, *M. reginus*, and *M. phaeus*, which correspond perfectly with the species of the "*cinereus* group" of Tate (1933). Gardner and Creighton (1989) and Gardner (1993) only recognized *M. cinereus*, *M. constantiae*, *M. regina*, and *M. alstoni*. However, there are some discrepancies with Emmons and Feer (1997), who recognized five species (*M. alstoi*, *M. constantiae*, *M. demerarae*, *M. phaea*, and *M. regina*). In a recent phylogeographic study, Patton and Costa (2003) proposed that another name should apply to the southern Atlantic Forest population (currently known as *M. demerarae*). For the moment, they use *M. travossi* Miranda Riveiro.

Two species are found in the forests of northern Argentina, *M. constantiae* in the northwest, and *M. demararae* (= *travossi* Miranda Riveiro) in the northeast (Cabrera, 1957; Massoia, 1972; Gardner, 1993; Flores et al., 2000). While some authors treat these as a single species (Emmons and Feer, 1997) other authors consider them to be distinct (Gardner and Creighton, 1989; Gardner, 1993).

Micoureus constantiae (Thomas, 1904)

Marmosa constantiae Thomas, 1903 [1904]. Proceedings of the Zoological Society of London, 2:243.

Micoureus constantiae: Reig, Kirsch and Marshall, 1987. P. 7 in Possums and Opossums: Studies in Evolution.

Type Locality.--Brazil, Mato Grosso, "Chapada."

Specimens Examined (14).--JUJUY: Aguas Negras, 5 (CML 2921, 5688; MACN 19425, 19426, 19427); Caimancito, 1 (MACN 30297); Calilegua, 1 (CEM 4886); Río San Francisco, altura de Yuto, 500 m, 1 (BMNH 20.1.7.134 holotype of *Marmosa budini*). SALTA: 43.7 km al NO del cruce de las rutas 50 y 18, camino a Isla de Cañas, 1 (PIDBA 790); Orán, 1 (CML 2); Parque Nacional Baritú, desembocadura Arroyo Santelmita, 700 m, 2 (CML 5497, MACN 20704); Parque Nacional El Rey, 1 (IADIZA 6117). TUCUMAN: Cerro de Vipos, 1 (MACN 32.29).

Additional Records.--JUJUY: Altura de Yuto, Río San Francisco, 500m (Thomas, 1920b; Tate, 1933); Mesada de las Colmenas, 1150 m (Heinonen and Bosso, 1994); Parque Nacional Calilegua (Heinonen Fortabat and Chébez, 1997). SALTA: Parque Nacional Baritú (Heinonen Fortabat and Chébez, 1997).

Distribution. --In the Mato Grosso of Brazil and eastern Bolivia, south to northwestern Argentina, in Salta, Jujuy, and Tucumán provinces (Cabrera, 1957; Olrog and Lucero, 1981; Redford and Eisenberg, 1992; Flores et al., 2000; Flores and Díaz, 2002). Recently reported for Tucumán Province (Flores and Díaz, 2002), about 350 km south of the southernmost known locality in Salta Province.

Habitat.--In Argentina, known from humid and transitional forests of the Yungas phytogeographic province (Mares et al., 1989); the records correspond to protected areas in the northwest (Parque Nacional Baritú, Salta, and Parque Nacional Calilegua, Jujuy) or nearby areas (Flores et al., 2000).

Natural History.--Nocturnal and mainly arboreal. The biology of this species is not well known, but feeding habits are omnivorous according to Mares et al. (1989). At Aguas Negras, Jujuy Province, a lactating female was captured in June. In the same locality, we found hemipterans and plants in the stomach of one specimen, and a young was registered in August (Flores et al., 2000; Díaz and Barquez, this volume). The specimen from Tucumán was a sub-adult with the third premolars and fourth molars erupting, collected in July 1931.

Comments.--Thomas (1904, 1920b) treated *constantiae* and *budini* as full species of *Marmosa*. These were later considered as subspecies of *Marmosa constantiae* (Tate, 1933; Cabrera, 1957). Tate (1933) treated the specimens from Bolivia and Brazil as *Marmosa c. constantiae*, and the type from Jujuy province as *Marmosa constantiae budini*. Cabrera (1957) followed the same systematic treatment but recognized the populations from Bolivia and Argentina as belonging to the subspecies *budini*. Our analysis of the morphology of specimens from Bolivia and northwestern Argentina, supports the opinion of Cabrera (1957). However, Anderson (1997) recognized two subspecies for Bolivia, restricting *constantiae* to the north, and *budini* to the southern part of the country. Patton and Costa (2003) proposed, in a phylogeographic context, that populations of *M. demerarae* from southwestern Brazil should be included in *M. constantiae.*

Micoureus demerarae (Thomas, 1905)

Marmosa cinerea demerarae Thomas, 1905. Annals and Magazine of Natural History, ser. 7, 16:313.

Micoureus demerarae: Gardner, 1993. P. 20 in Mammal Species of the World.

Type Locality.--Guyana, East Demerara-West Coast Berbice, "Comackka, 80 miles up Demerara River."

Specimens Examined (2).--MISIONES: Parque Nacional Iguazú, 1 (PIDBA 486); Parque Nacional Iguazú, Cataratas, 1 (CML 2867).

Additional Records.--MISIONES: Arroyo Viña (brazo del Arroyo Garupá), Departamento Apóstoles (Chébez and Massoia, 1996); Departamento Cainguás (Massoia, 1980; Chébez and Massoia, 1996); Departamento Candelaria (Massoia, 1972, 1980; Chébez and Massoia, 1996); Departamento Dos de Mayo (Massoia, 1972); Departamento

General Belgrano (Chébez and Massoia, 1996); Departamento Iguazú (Chébez and Massoia, 1996); Departamento Oberá (Chébez and Massoia, 1996); Departamento San Ignacio (Chébez and Massoia, 1996).
Distribution.--South America in almost all of Brazil, eastern Paraguay and northeast Argentina, in the provinces of Misiones and Formosa (Tate, 1933; Cabrera, 1957; Massoia, 1972, 1980; Contreras, 1984; González et al., 1997).

Habitat.--Found mainly in humid forests, but has been captured in thorn forests in eastern Paraguay, as well as in brush and forested habitats in Brazil (Massoia, 1972; Redford and Eisenberg, 1992).

Natural History.--Nocturnal; forages both arboreally and on the ground, mainly for insects. It builds nests in trees, and in captivity it has been observed transporting nesting materials in the mouth (Beach, 1939; Massoia, 1972; Redford and Eisenberg, 1992).

Comments.--Both *M. cinereus* and *M. demerarae* were recognized as different species (Tate, 1933), but some authors considered them to both same species (Thomas, 1905; Cabrera, 1957). Gardner (1993) replaced the name *cinereus* with *demerarae* because it was preoccupied by *Didelphis cinereus*. Cabrera (1957) considered *demerarae* as a subspecies of *cinerea*. Among the various names used as synonyms of *M. demerarae* (*sensu* Gardner, 1993), Tate (1933) recognized several as full species. *Micoureus demerarae* is taxonomically complex and needs revision (Voss et al., 2001). Recently, Patton and Costa (2003) proposed the name *travossi* Miranda Riveiro for peopulations of the Atlantic Forests of Brazil, and probably for those of northeastern Argentina and eastern Paraguay. However, *paraguayana* Tate, with its type locality in eastern Paraguay, might prove to be the oldest name available for this taxon (Patton and Costa, 2003; Voss and Jansa, 2003).

Genus *Thylamys* Gray, 1843

This genus includes several species distributed in South America. All share characters that maintain them as a group with a well-supported monophyly (Flores, 2003). From the studies of Tate (1933) and Cabrera (1957), to those of Hershkovitz (1992a, 1992b) and Kirsch et al. (1996), the species were grouped together, but in different taxonomic ranks, either as subgenera, subfamilies, or tribes. Among the most outstanding characters that define this group are the parallel and non-inflated structure of the nasal bones, the large size of the bullae, the highly compressed protocone, the annular disposition of the caudal scales, the presence of pectoral, abdominal, and inguinal mammae, the pattern of the fur in patches, and the accumulation of fat in the tail.

Palma (1995) and Palma and Yates (1998) studied the phylogeny of the species based on allozymic and chromosomal information. Some aspects of the historical biogeography of this group were also studied by Palma (1995). In contrast to most marmosines, which inhabit humid forests, the genus *Thylamys* prefers open arid and semiarid areas (Palma, 1995; Palma and Yates, 1998; Flores et al., 2000).

Currently, five species are recognized: *Thylamys elegans*, *T. pusillus*, *T. macrura*, *T. pallidior*, and *T. velutinus* (Gardner, 1993). However, some authors consider populations of *T. elegans* from northwestern Argentina and southern Bolivia to be a sixth species, *T.*

venustus (Tate, 1933; Heinonen and Bosso, 1994; Palma, 1995; Galliari et al., 1996; Díaz et al., 1997), restricting *T. elegans* to Chile. The taxonomy of this genus in northwestern Argentina was reviewed by Flores et al. (2000), and they considered *cinderella*, *sponsorius,* and *venustus* to be valid species, well differentiated by morphology, although some authors (e.g., Mares and Braun, 2000; Solari, 2003; Brown, 2004) do not follow this taxonomic arrangement. In other areas (Bolivia, Chile, Paraguay, and eastern Brazil) the identity of species and subspecies is not clear. González et al. (2000) included the genus in Uruguay based on a skull that may belong to an undescribed species. Recently, Solari (2003) studied the diversity and distribution of *Thylamys* in South America, with emphasis on species from the western side of the Andes; he considered *T. tatei* as a full species endemic to the western side of the Andes in central Peru.

In a recent revision of the distribution of New World Marsupials, Brown (2004) erroneously included *T. macrura* for northeastern Argentina, but this species inhabits only southeastern Paraguay (Solari, 2003). The locality refered to by Brown (2004) for this species in Argentina is Goya, Corrientes Province, based on Thomas (1894) who refered to this specimen as *Marmosa marmota*; this was later synonymized with *Marmosa* (=*Thylamys*) *pusillus* (Tate, 1933; Cabrera, 1957).

Thylamys cinderella (Thomas, 1902)

Marmosa elegans cinderella Thomas, 1902. Annals and Magazine of Natural History, ser. 7, 10:159.

Thylamys cinderella: Matschie, 1916. Sitzungsberichte Gesellschaft Naturforschunde Freunde, 271.

Marmosa venusta cinderella: Tate, 1933. Bulletin American Museum Natural History, 66:226.

Type Locality.--Argentina, "Tucuman, 450 m."

Specimens Examined (69)**.**--JUJUY: 4 km W jct Hwys 34 & 3, along Hwy 3, 1 (CM 42779); Caimancito, 400 m, 1 (BMNH 21.1.2.17); Caimancito, 600 m, 1 (FMNH 41266); Caimancito, 700 m, 1 (MACN 30.299); Cruce camino a Puesto Viejo y Ruta 34, 4 km al Este, sobre camino a Puesto Viejo, 5 (MMD 102, 106, 107, 108, 1 released); Jujuy, 1258 m, 5 (BMNH 20.1.7.135, 20.1.7.136, 20.1.7.137, 20.1.7.138, 20.1.7.139); Laguna La Brea, 1 (MMD 49); Laguna La Brea, 25 km antes de Palma Sola (Ruta 1), 1 (SNOMNH 19580); León, 1500 m, 5 (BMNH 18.1.1.47, 18.1.1.48, 18.1.1.49, 18.1.1.50, 18.1.1.51); On highway 9 at border with Salta, at campground on the way to El Carmen, 4600 ft., 4 (ARG 2496, 2516, 2598, 2623); Oyeros, 3 km al Norte, camino entre rutas 61 y 43, 1 (MMD 210); Santa Rita, 2 km al NW sobre ruta provincial 1, 2 (MMD 216, 217); Santa Rita, 4 km al NW sobre ruta provincial 1, 3 (MMD 215); Sobre ruta 9 en el límite con Salta, sobre camino a El Carmen, 12 (CML 3175, 3176, 3177, 3178, 3179, 3180; IADIZA 4642, 4646, 4648, 4649, 4652, 4657); Villa Carolina, Río Lavallén, 500 m, 3 (BMNH 20.1.7.140, 20.1.7.141, 20.1.7.142); Yuto, 4 (AMNH 167853, 185271, 186948; CML 486). SALTA: Aguaray, 700 m, 4 (MACN 30292, 30293, 30295, 30296); Güemes, ruta 34, km 1383, 1 (MACN 17276); 6 km W of Piquirenda Viejo, 1 (SNOMNH 19578); Laguna de las Catas, Tartagal, 1 (CML 2344); Playa Ancha, 1 (CML 327); Río Mojotoro, puente del Ferrocarril

Belgrano, 1 (MMD 4); San Ramón de la Nueva Orán, 1 (CML 742). TUCUMAN: Cerro del Campo, 2 (BMNH 26.2.13.169, 26.2.13.170); Finca el Jagüel, 4,5 km al Oeste de la Ruta Provincial 304, sobre camino a Requelme, 1 (PIDBA 413); Ñorco, Vipos, 2500 m, 2 (BMNH 26.2.13.176, 26.2.13.177); Raco, 1000 m, 1 (MACN 27.54), Tucumán, 450 m, 1 (BMNH 0.7.9.20, *Marmosa elegans cinderella* holotype); Villa Nougés, 1200 m, 2 (BMNH 2.1.5.16, 2.1.5.17).

Additional Records.--TUCUMAN: Cerro de Raco (Flores et al., 2000); Cerro de Tafí Viejo (Flores et al., 2000); Concepción (Tate, 1933, as *Marmosa venusta cinderella*); Ñorco-Vipos (cited as Norreo-Vipos, Tate, 1933, as *Marmosa venusta cinderella*); Villa Nougués, San Pablo (Tate, 1933, as *Marmosa venusta cinderella*).

Distribution.--From the mountains of northwestern Argentina, in the provinces of Catamarca, Tucumán, Salta, and Jujuy, north to northern Bolivia. In some localities along their distributional ranges in northwestern Argentina, *cinderella* and *sponsorius* can be found in sympatry (Tate, 1933; Flores et al., 2000).

Habitat.--The records of this species correspond mostly to the Chaco, and some are located in transitional areas near the Chaco or in arid zones (Díaz, 1999; Flores et al., 2000).

Natural History.--Nocturnal; arboreal habits well developed. It feeds on fruits and insects. Reproductive activity takes place mainly in summer; in Salta, a lactating female was captured in February, and young individuals were obtained in April and May (Flores et al., 2000).

Comments.--*Thylamys cinderella* was traditionally considered a subspecies of either *venustus* or *elegans*, but Flores et al. (2000) elevated the taxon to the species level. In a recent molecular study, Braun et al. (2005) also recognized *T. cinderella* as separate from *T. venustus*, but they included *T. sponsorius* as a synonym. Tate (1933) considered the two taxa as subspecies of *T. venustus*, in spite of showing sympatry between *T. cinderella* and *T. sponsorius*. However, in his specimens examined, some of the same individuals were listed for both taxa. For example, he cited León and Carmencito (=Caimancito) for *T. venusta cinderella* and also for *T. v. sponsorius*, but in both cases he referenced the same specimens (Flores et al., 2000).

The specimens from "Serra de Tucuman" at the AMNH that Tate (1933) identified as *cinderella* are here reidentified as *sponsorius*.

Thylamys pallidior (Thomas, 1902)

Marmosa elegans pallidior Thomas, 1902. Annals and Magazine of Natural History, ser. 7, 10:161.

Thylamys pallidior: Matschie, 1916. Sitzungsberichte Gesellschaft Naturforschunde Freunde 1916:271.

Marmosa pallidior: Tate, 1933. Bulletin of the American Museum of Natutal History 66:229.

Type locality.--Bolivia, Oruro, “Chapallata”, al este del lago Poopó.

Specimens Examined (190).--BUENOS AIRES: Abra de la Ventana, 1 (MACN 14955, 14962); Laguna Chasicó, 7 (MLP 2.I.73.4, 21.V.74.1, 24.V.74.5, 27.X.95.11, 27.X.95.12, 27.X.95.12, 27.X.95.9); Sierra de la Ventana, 3 (MACN 16283, 18656, 18657). CATAMARCA: Chumbicha, 1.5 km E of Hwy 38 along Hwy 60, 1 (CML 3187); La Toma de Andalgalá, 1 (CML 4713). CHUBUT: Puerto Madryn, Cañadón Cerro Avezado, 1 (CML 1766). CORDOBA: La Paz, 1 (MACN 29.54); Leones, 1 (MACN 13159); Tala Cañada, 1 (MACN 14750). JUJUY: 9 km NW Bárcena, 2 (ARG 4603, 4627); 11 km East of Humahuaca, 2 km East of Pucará, on road to Cianzo, 1 (ARG 2690); Abra Pampa, 4 (CML 1028, 1030, 1031; MACN 15602); Abrapampa, 3500 m, 1 (BMNH 19.8.1); Alfarcito, 2600 m, 1 (BMNH 21.11.1.105); Casabindo, 4000 m, 6 (BMNH 19.8.2.35, 19.8.2.36, 19.8.2.40, 19.8.2.41, 19.8.2.42, 19.8.2.44); Cerro Casabindo, 4500 m, 2 (BMNH 19.8.2.39, 19.8.2.43); Cuesta del Hurón, 29 km al Oeste de Cieneguillas sobre ruta provincial 64, 3835 m, 3 (MMD 441, 463, 466); Curques, 24 km al Norte de Susques, sobre ruta 74, 4100 m, 1 (MMD 286); La Quiaca, 17 km al Oeste, sobre ruta provincial Nro 5 y 3 km al S de la misma ruta, 1 (MMD 418); Laguna de Pozuelos, 2 (MACN 19413, 31.40); Maimará, 2230 m, 3 (2 BMNH 12.12.12.53, 12.12.12.54; 1 MACN 31.108); Maimará, 2500 m, 2 (MACN 31.40, 31.41); Mina Pan de Azúcar, 13 km al S, sobre Río Cincel, 1 (MMD 535); Mina Pirquitas, 31 km al SE, sobre ruta 74b, Sierra de Quichagua, 4200 m, 2 (MMD 528, 529); Miyuyoc, 1 (MMD 399); Salar Cauchari, 31 km al Norte de Cauchari, sobre ruta 70, 3840 m, 1 (MMD 313); Sierra de Zenta, 1 (MACN 31107; the correct locality is Sierra de Tilcara). LA RIOJA: Cerro Famatina, 3200 m, 1 (CML 777); Patquía, 1 (MACN 28205); Potrerillo, 1 (MACN 20273). MENDOZA: 10.5 km al W de la vieja ruta a lo largo de Laguna Diamante, 2, (IADIZA 2175, 2181); 2 km S Puesto Punta de Agua, 2 (CML 3574; IADIZA 5469); 25 de Mayo, 34.7 km W a lo largo de ruta 150, 1 (IADIZA 2157); 35 km S Pareditas, by Hwy 40, and 3 km E, 1, (IADIZA 4666); 37 km N along Villavicencio Hwy, 4, (IADIZA 2124, 2127, 2128, 2129); 7 km S Uspallata, 4 (CML 4479, 4493, 4494, 4497); Luján, 2 (MACN 17272, 17274); Malargüe, 4,8 km El Peralito, 1, (IADIZA 1990); Malargüe, P° El Peralito, 120 km E Malargüe, 1, (IADIZA 2092); Ñacuñán, 71 (IADIZA 1170, 1209, 1258, 1399, 1401, 1409, 1410, 1432, 1447, 1739, 1740, 1741, 1760, 1761, 1765, 1769, 1772, 1893, 1957, 2024, 2027, 2098, 2146, 2236, 2261, 2330, 2338, 2353, 2363, 2368, 2369, 2568, 2618, 2691, 2698, 2701, 2709, 2713, 2730, 2731, 2732, 2733, 2767, 2768, 2769, 2860, 2867, 2963, 2964, 2977, 3820, 3854, 3855, 3856, 3891, 3921, 3923, 3932, 3949, 3979, 3985, 3986, 3987, 3988, 6077, 6120, 6121, 6122, 6123, 6124, 6170); Pto. Lima, 1 (MACN 17273); Salinas de Diamante, 3 (CML 3188, 3189; IADIZA 4668); Villavicencio, 1, (IADIZA 6119). NEUQUEN: Las Coloradas, Campo Grande, 4 (MACN 13495, 13496, 13543, 17280). RÍO NEGRO: Choele-Choel, 3 (MACN 28127, 28128, 28129). SAN JUAN: 9 km W Complejo Astronómico El Leoncito, 1 (CML 3190); Agua de la Peña, Ischigualasto, 1 (CML 1199); Estancia Leoncito, 2 km E Observatorio Astronómico, 1 (CML 3191); Quebrada de Las Flores, 4 km E, 5 km N Guayamas 2200 ft, 1 (CML 3575); Quebrada de Las Flores, 4 km E, 5 km N Guayamas, 1 (IADIZA 5470); Tudcum nacedero, 2 (CML 3192; IADIZA 4680). SALTA: Inca Mayo, 1 (BMNH 34.11.4.186); M. Solá, 4 (34.11.4.180, 34.11.4.181, 34.11.4.182, 34.11.4.183). SAN LUIS: 1 km N Paso del Rey along Arroyo de la Cañada Honda, 3 (CML 3193, 3194; IADIZA 4684); Merlo, Villa Elena, 2 (IADIZA 6093, 6094); Quebrada de López, San Francisco del Monte de Oro, 2 (CML 3196, 3197). Salinas de Bebedero, 15 km SE, 2 (CML 3195, 4463); Sierras de las Quijadas, 2 (IADIZA 3857, 3858). TUCUMAN: Pichao, primeras estribaciones Sierras de Quilmes, 1 (CML 636); Tafi del Valle, 7 (5 AMNH 41723, 41724, 41725, 41726, 41727; 2 FMNH 41397, 41398). Also de type specimen of *Marmosa elegans pallidior* from Bolivia, Challapata, 3800 m, was examined (BMNH 2.2.2.116).

Additional Records.--CATAMARCA: Belén (Mares et al., 1997; Mares and Braun, 2000); Chumbicha (Thomas, 1919a); Chumbicha, 0.5 km E of Hwy 38 along Hwy 60 (Mares et al., 1997; Mares and Braun, 2000); Chumbicha, 600 m (Thomas, 1919a). Hualfín (Tate, 1933); Inmed. N Andalgalá, Río Andalgalá (Mares et al., 1997; Mares and Braun, 2000); Minas Capillitas, 3200 m (Mares et al., 1997; Mares and Braun, 2000); Off Hwy 62, 8 km E Jct. Hwy 1 and 62 (Mares et al., 1997; Mares and Braun, 2000); Otro cerro (Tate, 1933); Quirós (Mares et al., 1997; Mares and Braun, 2000); Río Andalgalá, 3 km N Andalgalá (Mares et al., 1997). CHUBUT: 3 km S Punta Norte, Peninsula Valdes (Mares and Braun, 2000); Approximately 200 km W Dolavon (Birney et al., 1996b); Approximately 280 km W Dolavon (Birney et al., 1996b); Isla de los Pájaros, en el borde norte del itsmo de entrada a la Península de Valdés (Crespo, 1974); Itsmo Ameghino (Birney et al., 1996b); Puerto Lobos (Birney et al., 1996b); Puerto Pirámide (Birney et al., 1996b). JUJUY: Abra Pampa, 3500 m (Thomas, 1919b; Olrog, 1959); Casabindo (Tate, 1933); Humahuaca (Thomas, 1918). LA PAMPA: Parque Nacional Lihuel Calel (Heinonen Fortabat and Chébez, 1997). LA RIOJA: Cerro Famatina, 3200 m (Olrog, 1959); La Invernada (Thomas, 1920a); La Invernada, Famatina Range, 3800 m (Tate, 1933); Patquía (Yepes, 1936a); Pagancillo (Yepes, 1936a); Potrerillo (Thomas, 1920a); Potrerillo, Famatina range (Tate, 1933). MENDOZA: 10.5 km al W de la vieja ruta a lo largo de Laguna Diamante (Mares and Braun, 2000); 12.8 km E Malargüe (Mares and Braun, 2000); 2 km N Valle Grande Dike along Hwy 173 (Mares and Braun, 2000); 2 km S Puesto Punta de Agua (Mares and Braun, 2000); 23 km W Tunuyán (Mares, 1973); 3 km N Salinas de Diamante R. R. Station (Mares and Braun, 2000); 3 km W Refugio Militar General Alvarado (Mares and Braun, 2000); 31 km W Tunuyán (Mares and Braun, 2000); 32 km W Tunuyán (Mares and Braun, 2000); 33 km W Tunuyán (Mares, 1973); 35 km S Pareditas, by Hwy 40, and 3 km E (Mares and Braun, 2000); 37 km N along Villavicencio Hwy (Mares and Braun, 2000); 40.2 km W of 25 de Mayo along Rt. 150 (Mares and Braun, 2000); 50 km W Tunuyán (Mares and Braun, 2000); 8 km NW El Sosneado (Mares and Braun, 2000); Cacheuta (Roig, 1965); Callao (Yepes, 1936b); Challao (Roig, 1965); Colonia Alvear, Río Atuel (Tate, 1933); Desaguadero (Roig, 1965); La Paz (Roig, 1965); Las Heras (Roig, 1965); Loncocava (Roig, 1965); Luján de Cuyo (Yepes, 1936b); Ñacuñán (Contreras, 1979); Punta del Agua (Roig, 1965); Santa Rosa (Roig, 1965); Tupungato (Tate, 1933; Roig, 1965). NEUQUEN: Chos Malal (Tate, 1933); Chos Malal, 805 m (Thomas and St. Leger, 1926); Collon Cura (Tate, 1933); Las Lajas (Tate, 1933); Las Lajas, 640 m (Thomas and St. Leger, 1926); Parque Nacional Laguna Blanca (Heinonen Fortabat and Chébez, 1997); Zapala, 1062 m (Thomas and St. Leger, 1926). RIO NEGRO: Estancia María Sofía (Birney et al., 1996b); General Roca (Tate, 1933). SALTA: 30 km Este de Cachi, 2600 m (Mares and Braun, 2000; Flores et al., 2000). SAN JUAN: 17 km ESE Jose Marti (by road) on road to Chañar Seco 31°53.70', 68°02.77', 1241 ft. (Mares and Braun, 2000); 2 km E Complejo Astronómico El Leoncito (Mares and Braun, 2000); 4 km W Complejo Astronómico El Leoncito (Mares and Braun, 2000); 6 km N km 514 of Hwy 20 (Mares and Braun, 2000); 8 km W Complejo Astronómico El Leoncito (Mares and Braun, 2000); 9 km NW Villa Nueva (Mares and Braun, 2000); Castaño Nuevo, 9 km of Villa Nueva, 5040 ft. (Mares and Braun, 2000); Reserva Natural Estricta El Leoncito (Heinonen Fortabat and Chébez, 1997). SAN LUIS: 12 km N Varela (by road), 2200 ft. (Mares and Braun, 2000); 15 km N Paso del Rey, 4700 ft. (Mares and Braun, 2000); 3 km W Hualtaran, Parque Provincial Sierra de las Quijadas (Mares and Braun, 2000); Alto Pencoso (Tate, 1933); Parque Nacional Sierra de las Quijadas (Heinonen Fortabat and Chébez, 1997); Río Gómez, 7 km E of downtown San Francisco del Monte de Oro, 2800 ft. (Mares and Braun, 2000). TUCUMAN: Near Amaicha del Valle (Flores et al., 2000); Tafí del Valle (Tate, 1933).

Distribution.--This species inhabits the high mountains of southwestern Bolivia, northern Chile, and northwestern Argentina. In Argentina, it is found also in lower elevations in the Monte and the northern parts of the Patagonian Regions from the provinces of Jujuy to Chubut near the shores of the Atlantic Ocean (Palma, 1995; Flores et al., 2000). The distribution considered by Solari (2004, fig. 5) does not include the Monte phytogeographic province and northern Patagonia, which are biomes where this species is found.

Habitat.--Mainly in rocky hills in the mountains up to 3000 m. In lower zones, it inhabits arid lands, such as the Patagonian steppes and the Monte region. The majority of the specimens were collected in rocky areas with scarce vegetation, but always associated with watercourses (Flores et al., 2000).

Natural History.--Nocturnal and insectivorous. Its habits are not well known in Argentina. A lactating female with open vagina was captured in the Puna in February, and young individuals were captured in this area in February, March, and April.

Comments.--*T. pallidior* was described as a subspecies of *T. elegans* and included as a subspecies of *T. pusillus* (Cabrera, 1957; Olrog, 1979), but currently is treated as a valid species (Gardner, 1993). Mares and Braun (2000) mentioned the locality "Villa Valeria", as located in San Luis Province following Tate (1933), but in fact this locality is in Córdoba Province; on the other hand, Tate (1933) did not cite any locality for *T. pallidior* in Córdoba or San Luis provinces.

Brown (2004) cited the locality of "Isla de los Pájaros" in Santa Cruz Province. However, this locality is located in Chubut Province. On the other hand, the same author cited the locality of "Laguna Chasicó" in Chubut Province, but this is actually located in Buenos Aires Province.

Thylamys pusillus (Desmarest, 1804)

Didelphis pusilla Desmarest, 1804. Tableau Méthodique des mammiferes, *in* Nouveau dictionnaire d`histoire naturelle, appliquée aux arts, principalement à l'agriculture et à l'économie rurale et domestique: par une société de naturalistes et d'agriculteurs: avec des figures tirées des trois règnes de la nature…. Ch. Deterville, Paris, 24:19.

Marmosa pusilla: Bertoni, 1914. P. 69 in Fauna Paraguaya.

Thylamys pusilla: Kirsch and Calaby, 1977. P. 14 in The Biology of Marsupials.

Type Locality.--Not established; restricted to Paraguay, Misiones, "San Ignacio," by Tate (1933).

Specimens Examined (39)**.**--CHACO: 20 km N and NW by road and 11 km NE by road to El Mangrullo, 1 (CML 3946); Avia Terai, 1 (BMNH 34.11.4.184). ENTRE RÍOS: A orillas del Río Gualeguaychú, 1 (CML 1455). La Picada a 20 km de Paraná, 1 (MLP 3.VIII.99.13); Pronunciamiento, 2 (MACN 16262, 16266). FORMOSA: Ingeniero Juárez, 2 (CML 726, 730); Parque Nacional Pilcomayo, Pto. El Quebrachal, 2 (MACN 20779, 20780); Puesto Divisadero, 35 km S Ingeniero Juárez, 1 (IADIZA 5463); Puesto Divisadero, 35 km S 5 km E Ing. Guillermo N. Juárez, 1(CML 3573). SANTIAGO DEL ESTERO: 15 km antes de Picada de Olmos, sobre ruta 16, W de Los Pirpintos, 2 (CML 2081, 2082); Lavalle, 2 (AMNH 41721, 41722); Lago Muyo, 2 (CML 1033, 1034); San Antonio, 2 (MACN 17278, 17279); Virgen del Valle Picnic area on Highway 64 between Santa Catalina and La Puerta Chiquita, 1 (CML 3198). SALTA: Finca Abra Grande, Quebrada de Tartagal, 1 (AMNH 256979); Hickman, 1 (CML 896); Los Colorados, 17 km al Este de Santo Domingo, 7 (CML 3060, 3061, 5181, 5182, 5183, 5203, 5229); Puesto Campo Grande, 17 km al Este de Santo Domingo, 1 (CML 3059); Salta, 1 (MACN 17277). TUCUMAN: Cerros de Vipos, 1 (CML 324); El Bracho, 400 m, 2 (CML 386, 390); El Cadillal, 2 (CML 43, 520); Las Mesadas, 1 (CML 1070). San Pedro de Colalao, 1 (CML 1509).

*Additional Records***.**--CORRIENTES: Estancia Coropa, Goya (Tate, 1933); Goya (Tate, 1933); Goya, 600 m (Thomas, 1912). ENTRE RÍOS: La Paz (Tate, 1933). FORMOSA: Parque Nacional Río Pilcomayo (Heinonen Fortabat and Chébez, 1997). SALTA: 5 km S Tolloche, on Vinalito rd. (Mares at al., 1981; Ojeda and Mares, 1989; Díaz et al., 2000); 6 km W of Piquirenda Viejo (Mares and Braun, 2000); 90 km NNW of Tucumán (Tate, 1933); Dragones (Flores et al., 2000). SANTIAGO DEL ESTERO: 6 km S, 2 km E Pampa de los Guanacos (Mares and Braun, 2000); Estancia Guampacha (Flores et al., 2000); Lavalle (Tate, 1933; Flores et al., 2000); Robles (Cabrera, 1934); Villa La Punta (Massoia and Latorraca, 1992). TUCUMAN: Cerro Medici (Cajal, 1981); Estación Vipos (Tate, 1933; Flores et al., 2000); Tapia (Tate, 1933; Flores et al., 2000).

Distribution.--Found in a wide portion of the Chacoan region, in central and southern Brazil, Paraguay, southeastern Bolivia, and north-central Argentina in the provinces of Formosa, Chaco, Salta, Santiago de Estero, Entre Ríos, and Tucumán. Probably its distributional overlaps with *T. pallidior* in ecotonal zones such as Monte-Chaco in northern and central Argentina (Flores et al., 2000). Solari (2003, fig. 5) misinterpreted the distribution of this species in Argentina, since he did not include the western Chaco phytogeographic province, or extend the distribution to northern Patagonia.

*Habitat***.**--Mainly in Chacoan forests, but it can be also found in areas with higher humidity such as the transitional forests of the Yungas in the northwest, and gallery forests in northeastern Argentina. According to Palma (1995) and Palma et al. (2002), this species can be found only in the Monte and Chacoan Regions, but Flores et al. (2000) concluded that the species that lives in the Monte is *T. pallidior*.

Natural History.--Arboreal and nocturnal; feeds mainly on insects. It is common to find it using abandoned nests of ovenbirds, such as the "rufous hornero" (*Furnarius rufus*).

Comments.--Some authors consider this species to be conspecific with *T. pallidior*, probably because of their external similarity, but the cranial and dental differences are very clear between the two species (Flores, 2003); furthermore, they live in different environments.

Brown (2004), following Mares and Braun (2000), cited the localities of "Esteros," "Lago Muyo," and "La Valle (=Lavalle)," all in Santiago del Estero Province, for *Thylamys pallidior* and *T. pusillus*. All of these localities are located in the Chaco phytogeographic province, typical of *T. pusillus*, and the specimens which are deposited at CML and AMNH were identified as *T. pusillus* (Flores et al., 2000). Mares and Braun (2000) cited this species at "6 km W of Piquirenda Viejo," corresponding to Yungas forest. It is improbable that this species would inhabit this area; and this record probably corresponds to the same specimen that is cited above as *T. cinderella*.

Thylamys sponsorius (Thomas, 1921).

Marmosa elegans sponsoria Thomas, 1921. Annals and Magazine of Natural History, ser. 9, 7:186.

Marmosa venusta sponsoria: Tate, 1933. Bulletin of the American Museum of Natutal History 66:228.

Thylamys sponsoria: Flores, Díaz, and Barquez, 2000. Zeitschrift für Säugetierkunde 65:321.

Type Locality.--Argentina, Jujuy, "Sunchal, 1200 m."

Specimens Examined (160)**.**--JUJUY: 2.5 km W El Bananal, 1 (PIDBA 892); 9 km NW Bárcena, 2 (ARG 4609, 4620); Abra de Cañas, 2 (MACN 19434, 19435); Abra de Cañas, El Monolito, 1700 m, 1 (CML 1781); Abra de Cañas, El Monolito, 1700 m, 6 (CML 1781, 1782, 1785, 1786, 1787, 1788). Aguas Negras, 2 (MACN 19428, 19429); Arroyo La Horqueta, 3 km SE de Laguna de Yala, 2100 m, 2 (MMD 182); Arroyo La Horqueta, 6 km SE de Laguna de Yala, 2100 m, 1 (MMD 191); Arroyo Yuto, 13 km al SO de Yuto, 2 (MMD 68, 69); Calilegua, 2 (1 CEM 4885; 1 FMNH 22353); Cerro Hermoso, 3 (MACN 19431, 19432, 19433); El Simbolar, 25 km al SO de Palma Sola, 3 (2 CM 42780, 42783; 1 SNOMNH 19579, RMB 565); Higuerilla, 2000 m, 6 (BMNH 21.11.1.99, 21.11.1.100, 21.11.1.101, 21.11.1.102, 21.11.1.103, 21.11.1.104); Mesada de Las Colmenas, 5 (MACN 19436, 19437, 19438, 20280, 20281); Mountains W of Yala, 1 (FMNH 22354); On highway 29 (east off of hwy 9), 10 km west of Tiraxi, 1 (ARG 2659); Palma Sola, 1 (AMNH 183307); Parque Nacional Calilegua, Aguas Negras, camping, 3 (CML 5695, 5696, 5697); Parque Nacional Calilegua, Arroyo Sauzalito, 1 (CML 5698); Río Blanco, 9 km SW San Antonio, 1495 m, 2 (PIDBA 622, 623); Río Tesorero, 4 km al Norte de Tiraxi, sobre ruta provincial N° 29, 2 (MMD 192, 200); Río Tiraxi, 1,5 km al Este de Tiraxi, sobre ruta 29, 1 (PIDBA 671); Sunchal, Sierra Santa Bárbara, 1200 m, 9 (BMNH 21.1.1.82, 21.1.1.83, 21.1.1.84, 21.1.1.85 *Marmosa elegans sponsoria* holotype; 21.1.1.86, 21.1.1.87, 21.1.1.88, 21.1.1.89, 21.1.1.90); Sunchal, Sierra Santa Bárbara, 1400 m, 1 (BMNH 21.1.1.81); Tumbaya, 1 (IADIZA 4641); Yuto, 1 (AMNH 185323). SALTA: 23 km al NW de intersección de rutas 50 y 18, camino a Isla de Cañas, 2 (781, 784); 3.9 km N Potrerillos, along provincial road 6, 1 (ARG 4527); 43.7 km al NW de intersección de rutas 50 y 18, camino a Isla de Cañas, 4 (PIDBA 780, 788, 789, 791); 7 km N Potrerillos, along provincial road 6, 1 (ARG 4531); Apolinario Saravia, 1 (PIDBA 627); Río de las Conchas, 2 km N y 6 km W de Metán, 1 (PIDBA 710); Río Santa María, 1 (MACN 51.159); San Javier, Pozo largo 19 km SE J. V. González, 1 (IADIZA 3001); Vado de Arrazayal, 20 km al NO de Aguas Blancas, 2 (CML 912, 1867). TUCUMAN: Aconquija, 3000 m, 1 (MACN 29718); Alrededores de Dique El Cajón, 4 (PIDBA 845, 856, 857, 858); Biological reserve at Horco Molle, near Residencia, 9 (CML 3181, 3182, 3183, 3184, 3185, 3186; IADIZA 4009, 4012, 4014); Cerro San Javier, 6 (CML 789, 1727, 6130, 6131, 6132, 6133); Concepción, 20 (CML 345; MACN 29705, 29706, 29707, 29708, 29709, 29710, 29712, 29713, 29714, 29715, 29716, 29717, 29719, 29720, 29721, 29722, 29723, 29724, 29727); Cumbres del Taficillo, La Agüita, 1 (CML 3992); Dique El Cadillal, 1 (IADIZA 3761); Horco Molle, 650 m, 6 (CML 2838, 2839, 2840, 2841, 2842, 2843); Los Chorrillos, 13 km N limite Norte de Estancia Los Chorrillos, 4 (ARG 4384, 4467, 4436, 4425); On Hwy 308, 5 km N of Las Higuerillas, 1 (IADIZA 4019); Parque Provincial El Cochuna, sobre Ruta 48, 1 (CML 2902); Piedra Tendida, 8 km W Dique El Cajón, 2 (PIDBA 422, 427); Reserva Natural La Florida, 7 km W de Ibatín, sobre Río Pueblo Viejo, 11 (ARG 4073, 4103, 4117, 4150, 4156, 4181, 4182, 4184, 4193, 4208, 4211); San Ignacio, 1 (CML 5586); Sierra de Tucuman, 16 (AMNH 41702, 41703, 41704, 41706, 41707, 41708, 41710, 41711, 41712, 41713, 41714, 41715, 41716, 41717, 41718, 41719); Villa Nougués, 1 (CML 5175).

Additional Records.--JUJUY: Caimancito, 500 m (Heinonen and Bosso, 1994; Flores et al., 2000). TUCUMAN: San Javier, Estación Biológica R. Schreiter (Flores et al., 2000); San Miguel de Tucumán (Flores et al., 2000).

Distribution.--Forests of northwestern Argentina, in the provinces of Tucumán, Salta, and Jujuy, north to central Bolivia. As mentioned under "distribution" of *T. cinderella*, it is possible that this species may be partially sympatric with *venustus* and *cinderella* (Tate, 1933; Anderson, 1997; Flores et al., 2000). Previously this species was known in Argentina only in the province of Jujuy; Flores et al. (2000) extended the distribution to Salta and Tucumán provinces.

Habitat.--Found in the humid montane forests of northwestern Argentina and central and southern Bolivia. It can be also found in transitional forests near the Chacoan region (Díaz, 1999; Flores et al., 2000). The majority of the specimen records are from the Yungas. In Jujuy Province, at the locality of 9 km NW Bárcena, an ecotonal area between Yungas and Prepuna, this species was captured in the same trapline and habitat with *T. pallidior,* which is typical of the Puna in this province.

Natural History.--Nocturnal; arboreal; feeds on insects and fruits. Breeding season is in summer; lactating females and young individuals were captured in northwestern Argentina from December to March (Flores et al., 2000). A female with a juvenile attached to a nipple was captured in December and a lactating female was captured in February in Jujuy Province. Young were captured in Tucumán Province in January, February, and March, and in Jujuy Province in July.

Specimens with incrassate tails were collected in Jujuy, in May, June, and July.

Comments.--*Thylamys sponsorius* was considered a subspecies of *venustus* or *elegans* (Tate, 1933; Cabrera, 1957), but Flores et al. (2000) elevated this form to the species level based on morphological differences and sympatry with *cinderella*.

Thylamys venustus (Thomas, 1902)

Marmosa elegans venusta Thomas, 1902. Annals and Magazine of Natural History, ser. 7, 10:159.

Thylamys venusta: Matschie, 1916. Sitzungsberichte Gesellschaft Naturforschunde Freunde 1916:271.

Marmosa venusta: Tate, 1933. Bulletin of the American Museum of Natural History 66:225.

Type Locality.--Bolivia, "Paratani, W. of Cochabamba, 2800 m."

Specimens Examined (8)**.--**SALTA: 27 km Oeste de Aguas Blancas, 1 (MACN 17275); Parque Nacional Baritú, Arroyo Santelmita, 1 (MACN 20732); Parque Nacional Baritú, Cerro Chaguar, 1 (MACN 20733); Parque Nacional Baritú, Finca Yakulica, Angosto del Río Pescado, 650 m, 2 (CML 5527, 5537); Río Pescado Chico, 2 (CML 31, 2188). Also the type specimen of *Marmosa elegans venusta*, from Bolivia, Paratani, 2800 m, was examined (BMNH 2.1.1.120).

*Distribution***.**--In mountains and forests of southwestern Bolivia and the extreme northern part of Argentina in Salta Province (Cabrera, 1957; Flores et al., 2000).

*Habitat***.**--The records from Argentina correspond to humid forests located near Natural Protected Areas.

Natural History.--Little is known about the natural history of this species. Nocturnal and arboreal; feeds on insects and fruits.

*Comments***.**--The species *cinderella* and *sponsorius* were included as subspecies of *T. venustus* by Cabrera (1957) and Tate (1933); both taxa were elevated to species status by Flores et al. (2000).

Tribe Monodelphini Goin, 1995

Genus *Monodelphis* Brunett, 1830

The genus *Monodelphis* includes 17 species widely distributed in America, from Panama to the Pampas in Argentina (Gardner, 1993; Lew and Pérez-Hernández; 2004; Solari, 2004). The main external character differentiating this group from other marsupials is the length of the tail, which is about half as long as the head and body combined.

The diploid number of this genus is different from all of the other didelphids (2n=18). The coloration is variable and ranges from gray to strong red. They are among the members of the Didelphidae most poorly adapted to arboreal life (Nowak, 1991). Nests of *Monodelphis* are usually built in hollow logs, fallen tree trunks that bridge streams, or among rocks. Most species of *Monodelphis* are thought to be nocturnal. Their food consists of small rodents, insects, carrion, seeds, and fruits.

Cabrera (1957) recognized two subgenera, *Monodelphis* and *Minuania*, the latter containing one species, *Monodelphis* (*Minuania*) *dimidiata*. However, the interpretation of the subgenera is different in Nowak (1991). The Tribe Monodelphini (*sensu* Goin, 1995) includes this genus and the fossil *Thylateridium*. Hershkovitz (1992a, 1992b) considered this genus as a separate subfamily (Monodelphinae) within the Family Marmosidae.

Monodelphis dimidiata (Wagner, 1847)

Didelphis dimidiata Wagner, 1847. Abhandlungen der Mathematisch-Physikalischen Klasse der Königlich Bayerischen Akademie del Wissenschaften (München) 5:151, footnote

Monodelphis dimidiata: Matschie, 1916. Sitzungsberichte Gesellschaft Naturforschunde Freunde 1916:259.

Monodelphis fosteri: Thomas, 1924. Annals and Magazine of Natural History, 9° ser., 13:586.

Monodelphis henseli: Cabrera and Yepes, 1940. P. 32 in Mamíferos Sudamericanos.

Type Locality.--Uruguay, Maldonado

Specimens Examined (55).--BUENOS AIRES: Abra de la Ventana, 4 (MACN 14954, 14961, 15718, 15719); Arroyo Brusquitas, 1 (MLP 27.X.95.7); Balneario Sierra Grande, 8 km E Monte Hermoso, 4 (.MMP 8526, 8528, 8535, 8538); General Alvarado, 1 (MLP 7.VI.96.1); Miramar, 1 (MLP 27.X.95.8); Miramar, Arroyo Brusquitas, 3 (MACN 17281, 17282, 17283); Parque Provincial E. Tornquist, 2 (MLP 14.IX.99.65, 14.IX.99.69); Pergamino, 13 (CML 4122, MMP 154, 155, 156, 157, 158, 159, 160, 161, 162, 163; MACN 18734, 18998); Pergamino, Curva de Pena, Ruta 188, 1 (FMNH 122698); Rojas, 2 (CML 4118, 4120); Santa Clara del Mar, 3 (MMP 241, 317, 2277); Sierra de la Ventana, 4 (2 MACN 18658, 18659; 2 MLP 5.II.96.39, MMP s/n); Sierras de Curamalal Abra del Hinojo, 2 (TTU 64313, 64314); Tambo Nuevo, 2 (MACN 17285, 17286). CORDOBA*:* Calamuchita, Yacanto, 1150 m, 7 (MACN 14751, 14752, 14753, 14754, 14755, 14756, 14798); Río Ceballos, 1 (BMNH 27.3.25.6). LA PAMPA: Caleufú, 1 (BMNH 24.4.5.1 *Monodelphis fosteri* holotype). MISIONES: "Misiones," 1 (BMNH 26.2.11.20). SANTA FE*:* Máximo Paz, 1 (CML 4123). TUCUMAN: Concepción, 1 (BMNH 27.3.25.5).

Additional Records.--BUENOS AIRES: Arroyo Brusquitas (Reig, 1964; Reig and Bianchi, 1969); Arroyo Brusquitas, Miramar (Reig et al., 1977); Arroyo Chocorí (Reig, 1964); Arroyo del Pescado (Reig, 1964); Baliza caniú (Reig, 1964); Baliza San Andrés (Reig, 1964); Corvetto Field, ca. 6 km N Balcarce (Balcarce 37° 51´ S, 58° 16´ W), 100 m (Pine et al., 1985); ditch along INTA (Instituto Nacional de Tecnología Agropecuaria) side along Ruta 226 km 68 (Pine et al., 1985); ditch along Ruta 226 (Pine et al., 1985); Hill Plot, 150m (Pine et al., 1985); ditches along Ruta 226 between km 65-75 (Pine et al., 1985); in ditch along Ruta 226, approx. km 78 (Pine et al., 1985); INTA (Instituto Nacional de Tecnología Agropecuaria) área, Ruta 226, ditch (Pine et al., 1985); INTA (Instituto Nacional de Tecnología Agropecuaria)property in overgrown pasture (Pine et al., 1985); INTA (Instituto Nacional de Tecnología Agropecuaria), in ditch (grass tall) near buildings (Pine et al., 1985); INTA (Instituto Nacional de Tecnología Agropecuaria)/ ditch near buildings (Pine et al., 1985); La Tinta (Pine et al., 1985); Miramar (Wainberg, 1972); near INTA (Instituto Nacional de Tecnología Agropecuaria), Ruta 226 ditch, km 74 (Pine et al., 1985); Partido Balcarce, Estación Experimental del Instituto Nacional de Tecnología Agropecuaria (INTA), ca. 15 k NW Balcarce (Balcarce at 37° 51′ S, 58° 16′ W) and nearby, ca. 100-150 m (Pine et al., 1985); Partido de Pergamino, Estación Tambo Nuevo y Ruta 188, km 60 (Massoia and Fornes, 1967); Partido de Tandil, proximidades de la ciudad homónima (Masoia and Fornes, 1967); Pergamino (33° 53′ S, 60° 36′ W), Pergamino (Wainberg, 1972); Río Ceballos (Pine et al., 1985); Ruta 188, Curva de Peña (Pine et al., 1985); Ruta 226 ditch, 1 km W of INTA (Instituto Nacional de Tecnología Agropecuaria)gate (Pine et al., 1985); Santa Clara del Mar (Reig, 1964); Sierra de La Peregrina (Reig, 1964); Sierra de La Tinta (Holmberg, 1898; Pine et al., 1985); Terrenos del INTA (Instituto Nacional de Tecnología Agropecuaria) (Massoia and Fornes, 1967). CORDOBA: Yacanto, 1150 m (Crespo, 1964). MISIONES: Arroyo Zaimán, Departamento Capital (Massoia, 1980); Departamento Apóstoles (Chébez and Massoia, 1996); Departamento Capital (Chébez and Massoia, 1996); El Cruce, Departamento Apóstoles (Massoia, 1980). SALTA: Tartagal (Crespo, 1964).

Distribution.--From southern Brazil south to Uruguay and to the Pampean region of Argentina. The distribution in Argentina is broad, including isolated records from the provinces of Buenos Aires, Córdoba, La Pampa**,** Santa Fe, Misiones, Salta, and Tucumán (Reig, 1964; Olrog and Lucero, 1981; Pine et al., 1985; Mares et al., 1989; Ojeda and Mares, 1989; Barquez et al., 1991; Redford and Eisenberg, 1992).

*Habitat***.**--This species seems to be restricted to grasslands and marshy areas, but it has also been captured in cultivated fields, always near water. In northwestern Argentina, it was captured in secondary-growth forests (Pine et al., 1985; Mares et al., 1989; Barquez et al., 1991).

Natural History.--Differing from the well known nocturnal habits of the didelphids in general, this species apparently has significant diurnal activity, mainly in late afternoon. Its feeding habits are omnivorous but predation on rodents has been reported (Busch and Kravetz, 1992), although Pine et al. (1985) stated that it is not believed to be a major predator of rodents. Pine et al. (1985) reported individuals of this species removing the hairs of caterpillars before eating them; this behavior has not been reported for other opossums. Pine et al. (1985) published an extensive monograph related to ecology, postnatal development, and other aspects of the biology of this species, indicating that apparently is semelparous.

*Comments***.**--*M. fosteri* and *M. henseli* were considered synonyms of this species by Pine et al. (1985). According to Gardner (1993), it is found only in northeast Argentina, however, it is common in the Pampean region (Pine et al., 1985). The locality "Maximo Paz" is the first record for Santa Fe Province.

Monodelphis domestica (Wagner, 1842)

Didelphys domestica Wagner, 1842. Archiv für Naturgeschichte, Jahrgang 8, Bd. 1:359.

Peramys domestica: Heck, 1912. Brehms Tierleben 10:114.

Monodelphis domestica: Matschie, 1916. Sitzungsberichte Gesellschaft Naturforschunde Freunde 1916:271.

Type Locality.--Brazil, Mato Grosso, "Cuyaba."

Specimens Examined (2).--FORMOSA: Ingeniero Juárez, 1 (CML 727); R N Formosa, Paso de los Coyas, Río Bermejito, 1 (MACN 20492).

Additional Records.--FORMOSA: Reserva Natural Formosa (Heinonen Fortabat and Chébez, 1997).

Distribution.--This species is found in most of eastern and southern Brazil, eastern Bolivia, Paraguay, and in Formosa Province in northern Argentina (Cabrera, 1957; Olrog and Lucero, 1981; Redford and Eisenberg, 1992). Although Gardner (1993) does not mention this species for Argentina, it has been reported from Formosa Province.

Habitat.--Apparently not related to humid forest, but rather to secondary and deciduous forests, and cultivated areas. It also exists in areas of scrubby vegetation, and it colonizes clearings caused by human activity within humid forests (Olrog and Lucero, 1981; Streilein, 1982; Emmons and Feer, 1997).

Natural History.--Solitary, both diurnal and nocturnal. Mainly terrestrial; received its name because it is commensal with humans; eats rodents and insects and is an efficient predator, particularly skilled at capturing scorpions (Streilein, 1982; Nowak, 1991; Redford and Eisenberg, 1992).

Comments.--Cabrera (1957) recognized two subspecies (*M. d. domestica* and *M. d. maraxina*), but none was included in Argentina.

Monodelphis iheringi (Thomas)

Didelphis (Peramys) iheringi Thomas, 1888. Annals and Magazine of Natural History, ser. 6, 1:159.

Monodelphis americana: Cabrera and Yepes, 1940. P. 30 in Mamíferos Sudamericanos.

Monodelphis iheringii: Vieira, 1951. Arquivos de Zoologia do Estado de Sao Paulo 7: 357.

Type Locality.--Brazil, Taquara, Rio Grande do Sul as indicated by Thomas (1888).

Specimens Examined.--None.

Additional Records.--MISIONES: cercanías del Río Victoria, Departamento Guaraní (Massoia, 1980); Departamento Guaraní (Massoia, 1980; Chébez and Massoia, 1996); Departamento Iguazú (Chébez and Massoia, 1996); Departamento Oberá (Chébez and

Massoia, 1996); Parque Nacional Iguazú (Heinonen Fortabat and Chébez, 1997).

Distribution.--The distribution of this species includes southeastern Brazil along the Atlantic coast to northeastern Argentina, in Misiones Province (Massoia, 1980; Redford and Eisenberg, 1992; Gardner, 1993; Emmons and Feer, 1997).

Habitat.--Inhabits the Atlantic coastal forests usually near water, and Paranaense forests (Redford and Eisenberg, 1992; Emmons and Feer, 1997).

Natural History.--This species is poorly known due to the scarcity of records. It is probably diurnal and terrestrial. According to Redford and Eisenberg (1992), this species (treated as *M. americana*) was found to make nests in the forks of trees or in bushes. Emmons and Feer (1997) mentioned that this species (as *M. americana*) feeds on insects but in captivity it can voraciously kill and eat small vertebrates.

Comments.--Cabrera (1957) recognized *M. iheringi* as a subspecies of *M. americana*, but Pine (1977) suggested that *M. iheringi* and *M. americana* are different species. He noted that *M. iheringi* is smaller and that its skull has a different shape. Gardner (1993) treated both as distinct species.

Monodelphis kunsi Pine, 1975

Monodelphis kunsi Pine, 1975. Mammalia 38:321.

Type Locality.--La Granja, W bank of Rio Itonamas, 4 km N Magdalena, Itenez Province, Beni Departament, Bolivia, below 200 m.

Specimens Examined.--None.

Additional Records.--SALTA: Finca El Falcón, Depto. San Martin, 3 km al NW del pozo de agua N° 5 (Jayat and Miotti, 2005).

Distribution.--This species is known from Bolivia, Brazil, and Argentina. It is known only from 4 localities in Bolivia, 5 in Brazil, and just 1 in Argentina (Anderson, 1982, 1997; Eisenberg y Redford, 1999; Carvalho et al., 2002; Vargas et al., 2003; Jayat and Miotti, 2005).

Habitat.--The single locality in Argentina is in secondary forest in the lower Yungas phytogeographic province (Jayat and Miotti, 2005).

Natural History.--The habits are not well known. The unique specimen from Argentina was captured on the ground (Jayat and Miotti, 2005).

Monodelphis scalops (Thomas, 1888)

Didelphis (*Peramys*) *scalops* Thomas, 1888. Annals and Magazine of Natural History, ser. 6, 1:158.

Monodelphis scalops: Cabrera and Yepes, 1940. P. 32 in Mamíferos Sudamericanos.

Type Locality.--"Brazil" restricted to Rio de Janeiro, Therezôpolis, by Vieira (1951).

Specimens Examined (1).--MISIONES: Cataratas del Iguazú, sendero Yacaratiá, 1 (CIES-PNI-M 68).

Additional Records.--MISIONES: Departamento Guaraní (Massoia, 1980; Chébez and Massoia, 1996); Departamento Iguazú (Chébez and Massoia, 1996); Departamento Oberá (Chébez and Massoia, 1996); Parque Nacional Iguazú (Heinonen Fortabat and Chébez, 1997).

Distribution.--From the Atlantic forests of southeastern Brazil, to northeastern Argentina in Misiones Province (Olrog and Lucero, 1981; Redford and Eisenberg, 1992; Gardner, 1993; Emmons and Feer, 1997). Gardner (1993) did not mention this species for Argentina, but it has been registered in Misiones Province (Massoia, 1980).

Habitat.--Subtropical humid forests (Emmons and Feer, 1997).

Natural History.--Its habits are not well known but it is considered to be carnivorous, nocturnal, and terrestrial (Massoia et al., 2000). Some comments with respect to the habitat and morphology of this species in Brazil are offered in Pine and Abravaya (1978).

Monodelphis sorex (Hensel, 1872)

Didelphys (Microdelphys) sorex Hensel, 1872. P. 122 in Abhandlungen der Physikalischen Klasse der Königlichen Akademie der Wissenschaften zu Berlin.

Didelphis sorex: Thomas, 1888. P. 362 in Catalogue of Marsupialia and Monotremata in the British Museum

Monodelphis sorex: Cabrera and Yepes, 1940. P. 32 in Mamíferos Sudamericanos.

Type Locality.--Brazil, "Provinz Rio Grande do Sul;" restricted to Brazil, Rio Grande do Sul, Taquara, by Cabrera (1957).

Specimens Examined (18).--MISIONES: Arroyo Urugua-í, 3 (MACN 18882, 52.52, 52.58); Dos de Mayo, 2 (CML 1861, 1862); Eldorado, 2 (CML 913, 1860); "Misiones," 2 (CML 1915, MMP 1201); Parque Nacional Iguazú, Paseo Inferior Cataratas, 1 (CIES-PNI M 79); Parque Nacional Iguazú, Seccional Yacui, 1 (CIES-PNI M 44); Pto. Piray, 2 (MACN 52.70, 51177); Río Paraná, Caraguatay, 3 (FMNH . 29279, 44773, 44774); Río Paraná, Caraguatay, 100 mi S Rio Iguazu, 3 (FMNH 26761, 26762, 26763).

Additional Records.--MISIONES: Departamento Cainguás (Massoia, 1980; Chébez and Massoia, 1996); Departamento Guaraní (Massoia, 1980; Chébez and Massoia, 1996); Departamento Iguazú (Massoia, 1980; Chébez and Massoia, 1996); Departamento General Belgrano (Chébez and Massoia, 1996); Departamento Oberá (Chébez and

Massoia, 1996); Departamento Montecarlo (Chébez and Massoia, 1996); Parque Nacional Iguazú (Heinonen Fortabat and Chébez, 1997); Reserva Natural Estricta San Antonio (Heinonen Fortabat and Chébez, 1997).

Distribution.--From the Atlantic forests of southeastern Brazil and eastern Paraguay to northeastern Argentina in Misiones Province (Redford and Eisenberg, 1992; Emmons and Feer, 1997).

Habitat.--Subtropical humid forests (Emmons and Feer, 1997).

Natural History.--Nothing is known about its natural history.

Order Microbiotheria Ameghino, 1889
Family Microbiotheriidae Ameghino, 1887

Dromiciops gliroides Thomas, 1894

Dromiciops gliroides Thomas, 1894. Annals and Magazine of Natural History, ser. 6, 14:187.

Type Locality.---Chile, Biobio, "Huite, N.E.Chiloe Island."

Specimens Examined (11).--NEUQUEN: Beatriz, 800 m, 1 (BMNH 19.1.1.46); Beatriz, Nahuel Huapi, 800 m, 1 (BMNH 19.1.1.47); Lago Nahuel Huapi, Isla Victoria, 6 (MACN 13308, 19142, 19143, 19144, 19145, 48.26); Puerto Radal, Isla Victoria, 1 (CML 1869). RIO NEGRO: Bariloche, W Rio Negro, 1 (BMNH 28.5.7.1); San Pedro, Bariloche, 1 (IADIZA 2526).

Additional Records.--CHUBUT: Lago Puelo, Parque Nacional Los Alerces (Heinonen Fortabat and Chébez, 1997); Parque Nacional Los Alerces (Heinonen Fortabat and Chébez, 1997); Río Azul, 272 m; 42° 01′ S, 71° 06′ O (Martín, 2003); Villa la Angostura (Hershkovitz, 1999). NEUQUEN: Beatriz, Lago Nahuel Huapi, 800 m. (Hershkovitz, 1999); Huemul, Nahuel Huapi, 767 m. (Hershkovitz, 1999); Lacar, Lago (Hershkovitz, 1999); Nahuel Huapi, National Park (Hershkovitz, 1999), Parque Nacional Lanin (Heinonen Fortabat and Chébez, 1997); Parque Nacional Los Arrayanes (Heinonen Fortabat and Chébez, 1997). RIO NEGRO: 0,5 km S Puerto Blest, Parque Nacional Nahuel Huapi, 770 m (Pearson and Pearson, 1982); 2 km E, 1 km S Co. Catedral (Mares and Braun, 2000); 5 km NW Pampa Linda (44 km W Bariloche), Parque Nacional Nahuel Huapi, 950 m (Pearson and Pearson, 1982); Puerto Blest, Parque nacional Nahuel Huapi, 41° 02.15′ S, 71° 48.54′ W, 780 m (Birney et al., 1996b) (Fig. 3).

Distribution.--South and central Chile, including the Chiloé Island and in Argentina in the austral forests near Lake Lacar and Lake Nahuel Huapi (Cabrera, 1957; Marshall, 1978c; Olrog and Lucero, 1981).

Habitat.--*Dromiciops* inhabits dense, cool, humid *Nothofagus* and *Araucaria* forests intermixed with bamboo (*Chusquea*) thickets in the southern Chilean and Argentine Andes, it is captured from 425 m up to 1000 m (Mann Fisher, 1978; Marshall, 1978c;

Figure 3. *Dromiciops gliroides* on Oliver Pearson's hand. Photo taken by R. M. Barquez in Puerto Blest, Parque Nacional Nahuel Huapi (Bariloche, Río Negro) in March 1977.

Kelt et al., 1999; Hershkovitz, 1999). A study in Chile recorded positive correlation between the abuncance of this species and the altitude (Kelt et al., 1999).

Natural History.--Nocturnal, arboreal habits well developed. Food consists mainly of insects and other invertebrates, as well as leaves and seeds (Mann Fisher, 1978; Hershkovitz, 1999). During the reproductive period, the female builds a spherical nest of vegetation. In the winter, it apparently undergoes periods of torpor, due to the low temperatures in the area (Mann Fisher, 1978; Marshall, 1978c). The dense fur, dark color, and the reduced size of the external ears represent adaptations to cold environments; this species hibernates in winter, preceded by an accumulation of fat in the tail (Marshall, 1978c). *Dromiciops* uses strong and repugnant secretions from cutaneous glands to protect itself from predators (Marshall, 1978c).

Comments.--This species was considered a didelphid for a long time, until Reig (1955) described it as a living microbiotherid, based on the bullae and molar morphology. However, its phylogenetic position is still problematic. Szalay (1982, 1994) stated that it is related to Australasian fauna based on tarsal morphology. In recent studies, *Dromiciops* unambiguously appears more closely related to australidelphian marsupials than to didelphids (Colgan, 1999). On the other hand, there is no agreement on the exact position of the genus. *Dromiciops* either is the sister taxon of all australidelphians (Retief et al., 1995; Rougier et al., 1998; Palma and Spotorno, 1999; Asher et al., 2004) or is placed whithin australidelphians, usually sister to Diprotodontia (Kirsch et al., 1991; Retief et al., 1995; Palma and Spotorno, 1999; Jansa and Voss, 2000; Horovitz and Sánchez-Villagra, 2003). Recently, Giannini et al. (2004) studied the morphological variations in an ontogenetic series, and concluded that most of the developmental trends seen in this species are similar to those found in other didelphids studied. However, other aspects, such as the orbit, bulla, and postcanine toothrow exhibit an ontogenetic pattern probably unique to *Dromiciops.*

Order Paucituberculata Ameghino, 1894
Family Caenolestidae Trouessart, 1898

Rhyncholestes raphanurus Osgood, 1924

Rhyncholestes raphanurus Osgood, 1924. Field Museum of Natural History Publications, Zoological series 14:170.

Type Locality.--Chile, Chiloé, "from forests at mouth of Rio Inio, south end of Chiloé Island. S. Lat. 43° 20′."

Specimens Examined (1).--RIO NEGRO: Puerto Blest, Parque Nacional Nahuel Huapi, 1 (MACN 20625).

Additional Records.--NEUQUEN: Parque Nacional Nahuel Huapi (Heinonen Fortabat and Chébez, 1997). RIO NEGRO: Parque Nacional Nahuel Huapi (Heinonen Fortabat and Chébez, 1997); Puerto Blest, Parque Nacional Nahuel Huapi, 41° 02.15′ S, 71° 48.54′ W, 780 m (Birney et al., 1996b).

Distribution.--Found in south-central Chile and at one locality in adjacent parts of Argentina (Cabrera, 1957; Patterson and Gallardo, 1987; Monjeau et al., 1994).

Habitat.--This species appears to be restricted to temperate rainforests habitats (Meserve et al., 1982; Patterson and Gallardo, 1987), with *Nothofagus* as the dominant tree species and dense understory of bamboo (*Chusquea*), *Podocarpus* and *Saxegothaea* (Mares and Braun, 2000). Specimens have been taken on moist ground, at the bases of trees, alongside moss-covered logs, and in dense cover (Kelt and Martínez, 1989; Meserve et al., 1982, 1988; Birney et al., 1996b). Some captures have been in or near disturbed areas (Pine et al., 1979; Kelt and Martínez, 1989), and also it was captured in isolated forest remnants in regions dominated by agriculture areas and grazing (Kelt, 2000).

Natural History.--Nocturnal (Meserve et al., 1982). Tail incrassated with fat during the winter, in contrast to other caenolestids (Meserve et al., 1982; Kelt and Martínez, 1989; Birney et al., 1996b). Caudal fat storage has been associated with extended torpor (McNab, 1982). However, individuals have been captured during winter in snow (Kelt and Martínez, 1989), suggesting that torpor (if employed) can be interrupted; alternatively, the fact that most individuals that entered in hypothermia died would argue against the use of facultative hypothermia. Mostly insectivorous, but also eats significant amounts of plant material, fungi and other animal material like earthworms (Meserve et al., 1988).

Females were reported to have five mammae (Osgood, 1924), but further observation has determined that seven are present; the seventh is medial in position (Patterson and Gallardo, 1987). A marsupium is absent (Osgood, 1924; Patterson and Gallardo, 1987). Females are reproductively active during the austral summer (Meserve et al., 1982); males likely are active throughout the year (Meserve et al., 1982; Patterson and Gallardo, 1987).

General Comments.--This species was included in Argentina by Monjeau et al. (1994). The locality of "Parque Nacional Nahuel Huapi" cited by Heinonen Fortabat and Chébez (1997) is given for the Province of Neuquen. However, the few known specimens were collected in the sector of Río Negro Province of Puerto Blest (A. Monjeau pers. comm.). Bublitz (1987) and Pearson (1995) considered mainland populations as a different species and used the name *R. continentalis*, restricting *R. raphanurus* to populations of Isla Grande de Chiloé .

DISCUSSION

South America is a continent with a peculiar geological history. In its current position, it has more equatorial land than any other continent. The climatic patterns of the continent are a consequence of its geographic position, oceanic currents, and unique geomorphological features (Cerqueira, 1982; Webb and Marshall, 1982). The presence of the Andes in the west has an important influence on the climate, establishing a real and effective barrier between the east and the west of the mountain chain for many species. This combination of factors: the geographic position, geological characteristics, and oceanic currents, has created an important diversity of habitats and climates, in which the South American marsupials have evolved. In terms of ecological processes, which have determined the limits between habitats, some ecologists agree in the sense that the climate has exerted the greatest influence (Klijn and Udo de Haes, 1994). Monjeau et al. (1997) determined that temperature and precipitation are the most reliable factors in order to predict the composition of communities of small mammals. Tognelli and Kelt (2004) stablished that the variables associated with the productivity (e.g. evapotranspiration, radiation, and Normalized Digital Vegetation Index) were the most important factor to determinate the mammalian species richness, better than habitat or climate. This result contrasted with Ruggiero (1999), who determinated that the productivity is a poor predictor of the mammal richness.

Although marsupials are more diverse in tropical areas at lower latitudes in South America (da Fonseca et al., 2003; Palma, 2003), several species from Argentina are almost exclusive to southern regions, or have their southern limit of distribution in Argentina and Chile. Due to its particular outline, South America has its greatest area at lower latitudes, where the dominant environments are rainforests. At these latitudes, the alpha diversity of marsupials is the highest, and the majority of species are arboreal. At higher latitudes, the continent decreases in area, and arid lands become more common compared with humid environments. Several species of marsupials have their southern distributional limits at mid-latitudes, such as those from the tropical and subtropical humid forests that reach their southern limits in the humid forests of northern Argentina, or southern Bolivia, Paraguay and Brazil.

The humid areas of northern Argentina represent the southern limits for several species of didelphids, such as *Caluromys lanatus*, *Chironectes minimus*, *Metachirus nudicaudatus*, *Didelphis aurita*, *Micoureus demerarae*, *M. constantiae*, *Monodelphis iheringi*, *M. kunsi*, *M. sorex*, *M. scalops*, *Thylamys cinderella*, *T. sponsorius*, and *T. venustus*. There also are an important number of species that reach their southern distributional limits in southern Bolivia, such as *Glironia venusta*, *Gracilinanus aceramarcae*, *Marmosa lepida*, *M. murina*, *Marmosops impavidus*, *M. noctivagus*, and *Micoureus regina* (Anderson, 1997). However, some didelphids tolerate extreme climates and live in arid and seasonally cold environments, such as the Monte, Chaco, Puna, Espinal, Pampas, and Patagonia. *Didelphis albiventris* and *Lutreolina crassicaudata*, opportunistic species of medium to large body size, are capable to living in a wide variety of environments, and range down to 40° S. Other groups of species with smaller size also reach higher latitudes, such as *Monodelphis dimidiata*, which is found in northern and central Argentina, and is typical of the Pampean region in southern Buenos Aires Province; this is a terrestrial species with diurnal activity in the Pampean region (Pine et al., 1985). Other small species that are found at high latitudes have developed physiological adaptations to survive these extreme environments, such as caudal storage of fat. This attribute is distinctive of *Thylamys* and *Lestodelphys*, which live in arid and semiarid environments. *Thylamys pallidior* reaches the southern limits of the Monte Desert and northern Patagonia at ca. 44° S, and is the southern-most member of this genus, *Lestodelphys halli* occupies the southern Monte Desert and the northern portion of the Patagonia region, to about 47° S, being the marsupial with the southernmost distribution in the world. Caudal storage of fat has been documented in *Dromiciops gliroides* (Microbiotheria: Microbiotheriidae) and in *Rhyncholestes raphanurus* (Paucituberculata: Caenolestidae); they live in the Andean-Patagonian temperate rainforest in southern Argentina and Chile, tolerating low temperatures. Recently, Birney and Monjeau (2003) studied the latitudinal patterns of species diversity, habitat use, body size, and tail characteristics in South American marsupials. These authors found a latitudinal gradient of replacement of food habits, from nectar and fruits in tropical latitudes, to insects and meat towards the south. Another pattern found in this work, was the replacement of prehensile tails in the north to fat-filled tails towards the south. With respect to climatic parameters, they found that minimum temperatures seem to be the primary cause of changes in diversity, although differences in precipitation and the shape of the continent also influence this metric.

The present study reports 27 species of marsupials in Argentina, with higher diversity in the Paranaense and Yungas Forests (Table 1); 25 species belong to the Order Didelphimorphia, 1 to Microbiotheria, and 1 to Paucituberculata. Specimens of *Philander frenata*, from Formosa and Misiones provinces in Argentina, are not morphologically different of those from Santa Cruz de la Sierra, in Bolivia. Some authors considered populations of this species from Brazil, northern Argentina, and Bolivia to be the same species (Hershkovitz, 1997; Patton and da Silva, 1997). The populations of Misiones probably correspond to *P. frenatus* recognized by Patton and da Silva (1997) due to their geographic proximity and also because of similarities in their environments. With this proposal, the populations from Argentina and those from central and southern Bolivia could be recognized as *P. frenata*. However, we agree with Patton and Costa (2003), who stated that additional analyses are needed with samples from the Brazilian state of Paraná as well as northeastern Argentina to define the taxonomic position of these populations either as *frenatus* or *canus*. The specimens of *Lutreolina* from northwestern Argentina are considered to be *L. c. crassicaudata*. The measurements from specimes from Misiones Province (Massoia, 1973) are similar to those of the forests of northwestern Argentina, and the size of Bolivian specimens (Anderson, 1997) is close to those of northwestern Argentina and Misiones Province. Important morphometric differences were observed between the populations from

São Paulo, Brazil (*L. c. crassicaudata*), and those of the Pampean region in Argentina (*L. c. paranalis*) (Graipel et al., 1996). Although Marshall (1978a) recognized only one subspecies from southern South America (*L. c. crassicaudata*), clear differences still exist in body and skull size, among the Pampean specimens (*L. c. paranalis*) and those from northern Argentina. The presence of at least two subspecies in southern South America is highly probable.

With respect to the recently described genus *Cryptonanus*, a new species was recently described in the Yungas forests, *Cryptonanus ignitus* (Díaz et al., 2002 as *Gracilinanus ignitus*), based on one specimen deposited at the American Museum of Natural History. Also, a new genus and species, *Chacodelphys formosa* (Voss et al., 2004) were described from the Argentine Chaco.

A new locality for *Micoureus constantiae* was reported, extending the distribution of this species to the southern portion of northwestern Argentina (Flores and Díaz, 2002).

The taxonomy of *Thylamys* from northwestern Argentina was reviewed by Flores et al. (2000), and they consider *cinderella*, *sponsorius*, and *venustus* as valid species, well differentiated by morphological characters. However, in other parts of their distribution (Bolivia, Chile, Paraguay, and eastern Brazil), the taxonomic composition and geographical limitof the species and subspecies of this genus remain controversial. Recently, González et al. (2000) reported *Thylamys* from Uruguay, based on a skull. The species *T. pallidior* and *T. pusillus* live in arid areas of high altitude and latitude. The former has been recorded in the Puna, Monte of Plains and Steppes, and in southern Argentina to northern Patagonia (Monte of Mountains and Isolated Valleys and Patagonian Steppes). The latter is found in the Chacoan area. In the ecotone between Humid Chaco and Monte (Monte of Mountains and Isolated Valleys and Monte of Plains and Steppes) sympatry of this species is highly probable.

Monodelphis kunsi, a rare marsupial, only known from few specimens and localities, was recently found in northern Argentina (Jayat and Miotti, 2005). The presence in Argentina of *Monodelphis unistriata* needs to be confirmed, because the specimen deposited at the MACN, collected by Bocard in April 1899, has a locality that is not clear (“Misiones, alrededores”) (Chébez and Massoia, 1996).

Several marsupial species in Argentina have been listed as threatened on the IUCN red list; these include *Dromiciops gliroides*, *Rhyncholestes raphanurus*, and *Lestodelphys halli* (da Fonseca et al., 2003). The recent described taxa, *Cryptonanus ignitus* (Diaz et al., 2002) and *Chacodelphys formosa* (Voss et al., 2004) are known only at the type locality and by the holotype specimen. Hence these taxa may be extinct at present, in view of the degradation of the native vegetation in forest at northern Argentina (Yungas and Chaco forests). Additionally, 18 of 27 species that inhabit Argentina, live in one biome represented in the country (Table 1).

Finally, in this paper, new taxonomic arrangements for some confusing polytypic genera (e.g. *Thylamys, Monodelphis*), as well as an update of the distribution of all the Argentine species are offered. Extensive areas in the country still need to be sampled, particularly those regions where some species overlap, where some species are potentially present, and where specimens are needed to resolve taxonomic conflicts. New species are likely to be discovered in Argentina, but most of the papers related to the marsupials of South America have focused in areas where the dense tropical forests are present, neglecting the importance of the arid and semiarid zones, and the importance of the latitudinal gradient in the composition of species of this group.

Table 1. Distribution of Argentine marsupials within the currently recognized ecoregions. Abbreviations are as follows: P) Puna; MPS) Monte of Plains and Steppes; YF) Yungas Forest; DC) Dry Chaco; HC) Humid Chaco; PF) Paranaense Forest; IS) Ibera Swamps; FW) Fields and Weedlands; DIP) Delta and Islands of the Parana River Systems; E) Espinal; Pa) Pampas; MMIV) Monte of Mountains and Isolated Valleys; PS) Patagonian Steppes; APTR) Andean-Patagonian Temperate Rainforest.

Genus and Species	P	MPS	YF	DC	HC	PF	IS	FW	DIP	E	Pa	MMIV	PS	APTR
Caluromys lanatus						X								
Didelphis albiventris		X	X	X	X	X	X	X	X	X	X	X	X	
Didelphis aurita						X								
Philander frenata					X	X			X					
Chacodelphys formosa					X									
Chironectes minimus						X								
Lutreolina crassicaudata			X		X	X	X	X	X	X	X			
Metachirus nudicaudatus						X								
Cryptonanus ignitus			X											
Cryptonanus chacoensis			X		X	X		X	X					
Gracilinanus microtarsus						X								
Micoureus constantiae			X											
Micoureus demerarae						X								
Lestodelphys halli		X											X	
Thylamys cinderella			X											
Thylamys pallidior	X	X										X	X	
Thylamys pusillus				X	X									

Table 1 (continued).

Genus and Species	P	MPS	YF	DC	HC	PF	IS	FW	DIP	E	Pa	MMIV	PS	APTR
Thylamys sponsorius			X											
Thylamys venustus			X											
Monodelphis dimidiata			X			X					X			
Monodelphis domestica					X									
Monodelphis iheringi						X								
Monodelphis kunsi			X											
Monodelphis scalops						X								
Monodelphis sorex						X								
Dromiciops gliroides														X
Rhyncholestes raphanurus														X

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APPENDIX

Localities mentioned in text, listed in alphabetical order. Departments and Provinces are given in parentheses, followed by the geographic coordinates.

0,5 km S Puerto Blest, Parque Nacional Nahuel Huapi, 770 m (Bariloche, Río Negro) 41° 02´ S, 71° 49´ W
1 km N Paso del Rey along Arroyo de la Cañada Honda (Pringles, San Luis) 32° 58´ S, 65° 57´ W
1.3 km S Benjamín Paz along Ruta 9 (Trancas, Tucumán) 26° 23´ S, 65° 18´ W
10 km E (by road) Clemente Onelli, approximately 41° 10´ S, 70° 10´ W (25 de Mayo, Río Negro) 41° 10´ S, 70° 10´ W
10 km S Puerto Bermejo (Bermejo, Chaco) 27° 00´ S, 58° 34´ W
10 km W Aristóbulo del Valle by road, along Río Cunapiru (Cainguás, Misiones) 27° 06´ S, 54° 57´ W
10,5 km al W de la vieja ruta a lo largo de Laguna Diamante (San Carlos, Mendoza) 34° 10´ S, 69° 50´ W
11 km East of Humahuaca, 2 km East of Pucará, on road to Cianzo (Humahuaca, Jujuy) 23° 12´ S, 65° 16´ W
12 km N Varela (by road), 2200 ft. (Capital, San Luis) 34° 02´ S, 66° 26´ W
12 km Norte de San Pablo (Lules, Tucumán) 26° 51´ S, 65° 23´ W
12,8 km E Malargüe (Malargüe, Mendoza) 35° 29´ S, 69° 26´ W (*378*)
15 km al sur de Dragones (General San Martín, Salta) 23° 16´ S, 63° 21´ W
15 km antes de Picada de Olmos, sobre ruta 16, W de Los Pirpintos (Copo, Santiago del Estero) 26° 00´ S, 62° 25´ W

15 km E Los Menucos (25 de Mayo, Río Negro) 40° 55′ S, 68° 05′ W
15 km E Salinas del Bebedero (Capital, San Luis) 33° 37′ S, 66° 35′ W
15 km N Paso del Rey, 4700 ft. (Pringles, San Luis) 32° 52′ S, 65° 57′ W
15 km SE Los Menucos, approximately 40° 55′ S, 68° 05′ W (25 de Mayo, Río Negro) 40° 55′ S, 68° 05′ W
17 km ESE Jose Marti (by road) on road to Chañar Seco 1241 ft (25 de Mayo, San Juan) 31° 53.70’ S, 68° 02.77’ W
2 km al W de Reserva Experimental Horco Molle (Yerba Buena, Tucumán) 26° 45′ S, 65° 21′ W
2 km E Complejo Astronómico El Leoncito (Calingasta, San Juan) 31° 48′ S, 69° 22′ W
2 km E, 1 km S, Cerro Catedral (Bariloche, Río Negro) 41° 15′ S, 71° 40′ W
2 km N Valle Grande Dike along Hwy 173 (San Rafael, Mendoza) 34° 49′ S, 68° 30′ W
2 km S Puesto Punta de Agua (San Rafael, Mendoza) 35° 34′ S, 68° 03′ W
2 km S, 1 km W, Choya (Andalgalá, Catamarca) 27° 32′ S, 66° 24′ W
2,5 km W El Bananal (Ledesma, Jujuy) 23° 33′ S, 64° 32′ W
20 km N and NW by road and 11 km NE by road El Mangrullo (General Güemes, Chaco) 26° 03′ S, 61° 15′ W
20 km NE Rio Cuarto (Río Cuarto, Cordoba) 33° 02′ S, 64° 18′ W
20 km SE of Centro Argentino de Primates (Capital, Corrientes) 27° 28′ S, 58° 50′ W
23 km al NW de intersección de rutas 50 y 18, camino a Isla de Cañas (Orán, Salta) 23° 00′ S, 64° 33′ W
23 km W Tunuyán (Tunuyán, Mendoza) 33° 40′ S, 69° 24′ W
24 km N of Aguas Blancas (Iruya-Santa Victoria, Salta) 22° 42’ S, 64° 41’ W
25 de Mayo (25 de Mayo, Buenos Aires) 35° 27′ S, 60° 15′ W
25 de Mayo, 34,7 km W sobre ruta 150 (San Rafael, Mendoza) 34° 30′ S, 68° 57′ W
25 km NW San Miguel de Tucumán (Tafí Viejo, Tucumán) 26° 38′ S, 65° 20′ W
27 km S Tunuyán (Tupungato, Mendoza) 33° 35′ S, 68° 57′ W
3 km N Salinas de Diamante R. R. Station (San Rafael, Mendoza) 34° 55′ S, 69° 00′ W
3 km W Hualtaran, Parque Provincial Sierra de las Quijadas (Belgrano, San Luis) 32° 29′ S, 67° 00′ W
3 km W Refugio Militar General Alvarado (San Carlos, Mendoza) 34° 18′ S, 69° 23′ W
3 km Norte de San Pablo (Lules, Tucumán) 26° 50′ S, 65° 23′ W
3 km S Punta Norte, Peninsula Valdes (Biedma, Chubut) 42° 10’ S, 64° 03’ W
6,9 km N de Potrerillos, along provincial road 6 (Candelaria, Salta) 26° 04′ S, 65° 30′ W
3,9 km N Potrerillos sobre ruta provincial 6 (Candelaria, Salta) 26° 03′ S, 65° 30′ W
30 km Este de Cachi, 2600 m (Cachi, Salta) 25° 09′ S, 66° 00′ W
30 km N Pampa de Agnia, 43° 28,78′ S, 69° 49,09′ W (Languiñeo, Chubut) 43° 28′ S, 69° 49′ W
30 km NW Pampa de Agnia, 43° 28.78′S, 69° 49.09′W (Languiñeo, Chubut) 43° 28′ S, 69° 49′ W
31 km W Tunuyán (Tunuyán, Mendoza) 33° 40′ S, 69° 27′ W
32 km W Tunuyán (Tunuyán, Mendoza) 33° 40′ S, 69° 27′ W
33 km W Tunuyán (Tunuyán, Mendoza) 33° 40′ S, 69° 30′ W
35 km S Pareditas, by Hwy 40, and 3 km E (San Carlos, Mendoza) 34° 38′ S, 69° 10′ W
37 km N along Villavicencio Hwy (Las Heras, Mendoza) 32° 20′ S, 69° 05′ W
4 de Noviembre (Rojas, Buenos Aires) 34° 10′ S, 60° 45′ W
4 de Noviembre, Estancia Miraflores (Rojas, Buenos Aires) 34° 10′ S, 60° 45′ W

4 km NE de Azul (Azul, Buenos Aires) 36° 45’ S, 59° 51’ W
4 km al Oeste de la unión de la Ruta Provincial 338 y el camino a Horco Molle, sobre camino a San Javier (Yerba Buena, Tucumán) 26° 47´ S, 65° 23´ W
4 km al NE de Azul (Azul, Buenos Aires) 36° 47´ S, 59° 51´ W
4 km W Complejo Astronómico El Leoncito (Calingasta, San Juan) 31° 48´ S, 69° 23´ W
4 km W Jct. Hwys 34 and 3, along Hwy 3 (Ledesma, Jujuy) 23° 48´ S, 64° 48´ W
4 km W of junction 338 and road to Horco Molle, on road to San Javier (Yerba Buena, Tucumán) 27° 47´ S, 66° 23´ W
40,2 km W of 25 de Mayo along Rt. 150 (San Rafael, Mendoza) 34° 32´ S, 69° 03´ W
43,7 km al NW de intersección de rutas 50 y 18, camino a Isla de Cañas (Orán, Salta) 22° 57´ S, 64° 33´ W
5 km E General Acha (Utracán, La Pampa) 37° 23´ S, 64° 36´ W
5 km S Tolloche, on Vinalito rd. (Anta, Salta) 25° 30´ S, 63° 32´ W
5 km NW Pampa Linda (44 km W Bariloche), Parque Nacional Nahuel Huapi, 950 m. (Bariloche, Rio Negro) 41° 10’ S, 71° 30’ W
50 km W Tunuyán (Tunuyán, Mendoza) 33° 41´ S, 69° 35´ W
6 km S, 2 km E Pampa de los Guanacos (Alberdi, Santiago del Estero) 26° 17´ S, 62° 01´ W
6 km SW of Santa Victoria at “El Breal”, extreme NE of Salta Province (Rivadavia, Salta) 22° 17´ S, 62° 43´ W
6 km W of Piquirenda Viejo (General San Martín, Salta) 22° 21´ S, 63° 50´ W
60 km N Tunuyán, along Hwy 40 (Luján de Cuyo, Mendoza) 33° 10´ S, 68° 55´ W
7 km S Uspallata (Las Heras, Mendoza) 32° 39´ S, 69° 20´ W
8 km N El Palmar (San Cosme, Corrientes) 27° 22´ S, 58° 31´ W
8 km W Complejo Astronómico El Leoncito (Calingasta, San Juan) 31° 48´ S, 69° 23´ W
8-10 km WSW Comallo, approximately 41° 04´ S, 70° 20´ W (Pilcaniyeu, Río Negro) 41° 04´ S, 70° 20´ W
9 km E (by road) Clemente Onelli (25 de Mayo, Río Negro) 41° 14´ S, 70° 01´ W
9 km NW Barcena (Tumbaya, Jujuy) 23° 57´ S, 65° 30´ W
9 km NW Villa Nueva (Calingasta, San Juan) 31° 02´ S, 69° 32´ W
9 km W Complejo Astronómico El Leoncito (Calingasta, San Juan) 31° 48´ S, 69° 23´ W
A orillas del Río Gualeguaychú (Gualeguaychú, Entre Ríos) 33° 01´ S, 58° 31´ W
Abadie Cue, Parque Nacional Pilcomayo(Pilcomayo, Formosa) 25° 10´ S, 58° 10´ W
Abra de Cañas (Valle Grande, Jujuy) 23° 40´ S, 64° 54´ W
Abra de Cañas, El Monolito, 1700 m (Valle Grande, Jujuy) 23° 40´ S, 64° 54´ W
Abra de Cañas, El Monolito, 1707 m. (Valle Grande, Jujuy) 23° 40´ S, 64° 54´ W
Abra de la Ventana (Tornquist, Buenos Aires) 38° 09´ S, 61° 48´ W
Abra Pampa (Cochinoca, Jujuy) 22° 43´ S, 65° 42´ W
Abra Pampa, 3500 m (Cochinoca, Jujuy) 22° 43´ S, 65° 42´ W
Abrapampa, 3500 m (Cochinoca, Jujuy) 22° 43´ S, 65° 42´ W
Acceso a Cataratas, Parque Nacional Iguazú (Iguazú, Misiones) 25° 39´ S, 54° 20´ W
Aconquija (Chicligasta, Tucumán) 27° 13´ S, 66° 08´ W
Aconquija, Concepción (Chicligasta, Tucumán) 27° 20´ S, 63° 35´ W
Adrogué (Almirante Brown, Buenos Aires) 34° 48´ S, 58° 24´ W
Agua de la Peña, Ischigualasto (Valle Fértil, San Juan) 30° 12´ S, 67° 57´ W

Agua Linda (General San Martín, Salta) 25° 15´ S, 63° --´ W
Aguaray (General San Martín, Salta) 22° 16´ S, 63° 44´ W
Aguaray, 700 m (General San Martín, Salta) 22° 16´ S, 63° 44´ W
Aguas Blancas (Orán, Salta) 22° 45´ S, 64° 22´ W
Aguas Blancas, 27 km al Oeste (Orán, Salta) 22° 29´ S, 64° 39´ W
Aguas Chiquitas (Burruyacú, Tucumán) 26° 37´ S, 65° 12´ W
Aguas Negras (Ledesma, Jujuy) 23° 45´ S, 64° 56´ W
Aguas Negras, Camping (Ledesma, Jujuy) 23° 45´ S, 64° 56´ W
Alfarcito, 2600 m (Tilcara, Jujuy) 23° 37´ S, 65° 23´ W
Algarrobo (Villarino, Buenos Aires) 38° 53´ S, 63° 08´ W
Along Hwy 65, between Andalgalá and San Miguel de Tucumán, ca. 7 km S of the Tucumán-Catamarca border, ca. 2000 ft. (Andalgalá, Catamarca) 27° 25´ S, 66° 00´ W
Along Hwy 9 at border with Salta Province (El Carmen, Jujuy) 24° 28´ S, 65° 21´ W
Alrededores de Dique El Cajón (Burruyacú, Tucumán) 26° 29´ S64° 52´ W
Alto Pencoso (Capital, San Luis) 33° 26´ S, 66° 56´ W
Andalgalá (Andalgalá, Catamarca) 27° 36´ S, 66° 19´ W
Apolinario Saravia (Anta, Salta) 24° 26´ S, 63° 59´ W
Approximately 200 km W Dolavon (Paso de Indios, Chubut) 43° 32´ S, 68° 08´ W
Approximately 280 km W Dolavon (Paso de Indios, Chubut) 43° 45´ S, 68° 57´ W
Área Cataratas, Parque Nacional Iguazú (Iguazú, Misiones) 25° 39´ S, 54° 20´ W
Arroyo Brusquitas (General Alvarado, Buenos Aires) 38° 16´ S, 57° 51´ W
Arroyo Brusquitas, Miramar (General Alvarado, Buenos Aires) 38° 16´ S, 57° 51´ W
Arroyo Brusquitas-Miramar (General Alvarado, Buenos Aires) 38° 16´ S, 57° 51´ W
Arroyo Chapadmalal (General Pueyrredón, Buenos Aires) 38° 14´ S, 57° 48´ W
Arroyo Chocorí (General Alvarado, Buenos Aires) 38° 20´ S, 58° 03´ W
Arroyo del Pescado (Lobería, Buenos Aires) 38° 22´ S, 58° 06´ W
Arroyo El Saltón, Reserva Provincial Santa Ana (Río Chico, Tucumán) 27˚ 26′ S 65˚ 46′ W
Arroyo Garupá (Candelaria, Misiones) 28° 30´ S, 55° 43´ W
Arroyo La Horqueta, 3 km al SE de Laguna de Yala, 2100 m (Dr. Manuel Belgrano, Jujuy) 24° 07´ S, 65° 27´ W
Arroyo La Horqueta, 6 km al SE de Laguna de Yala (Dr. Manuel Belgrano, Jujuy) 24° 07´ S, 65° 27´ W
Arroyo La Horqueta, 6 km al SE de Laguna de Yala, 2100 m (Dr. Manuel Belgrano, Jujuy) 24° 07´ S, 65° 25´ W
Arroyo La Matanza (La Matanza, Buenos Aires) 35° 15´ S, 58° 42´ W
Arroyo Ñacurutú (Zárate, Buenos Aires) 34° 04´ S, 59° 02´ W
Arroyo Ñacurutú-Isla El Roble (Zárate, Buenos Aires) 34° 04´ S, 59° 02´ W
Arroyo Pereyra (Berazategui, Buenos Aires) 34° 50´ S., 58° 06´ W
Arroyo Piray Guazú (Eldorado, Misiones) 26° 30´ S, 54° 30´ W
Arroyo Santelmita, Parque Nacional Baritú (Santa Victoria, Salta) 22° 31´ S, 64° 34´ W
Arroyo Sauzalito, Parque Nacional Calilegua, (Ledesma, Jujuy) 23° 40´ S, 64° 37´ W
Arroyo Tacuara, Cerro Azul (Misiones) 27° 38′ S, 55° 29′ W
Arroyo Tapalqué (Tapalqué, Buenos Aires) 36° 21´ S, 60° 01´ W
Arroyo Uruguaí (Iguazú, Misiones) 25° 54´ S, 54° 36´ W
Arroyo Urugua-í, curso medio (Iguazú, Misiones) 25° 54´ S, 54° 36´ W
Arroyo Urugua-í, km 10 (Iguazú, Misiones) 25° 54´ S, 54° 36´ W

Arroyo Viña (Brazo del Arroyo Garupá) (Candelaria, Misiones) 28° 30´ S, 55° 43´ W
Arroyo Yuto, 13 km al SW de Yuto (Ledesma, Jujuy) 23° 38´ S, 64° 32´ W
At km marker 42, on highway 364, south of San Pedro de Colalao (Trancas, Tucumán) 26° 15´ S, 65° 29´ W
Avia Terai (Independencia, Chaco) 26° 41´ S, 60° 44´ W
Ballesteros (Unión, Cordoba) 32° 33´ S, 62° 59´ W
Balneario Sierra Grande, 8 km E Monte Hermoso (Coronel Dorrego, Buenos Aires) 38° 59´ S, 61° 03´ W
Bañado de San Jorge, Parque Pereyra Iraola (Berazategui, Buenos Aires) 34° 51´ S, 58° 04´ W
Bariloche, W Río Negro (Bariloche, Río Negro) 41° 09´ S, 71° 18´ W
Barreto, (Juárez Celman, Cordoba) 33° 21´ S, 63° 18´ W
Beatriz, Nahuel Huapi (Los Lagos, Neuquén) 40° 57´ S, 71° 30´ W
Belén (Belén, Catamarca) 27° 39´ S, 67° 02´ W
Belgrano (General Belgrano, Buenos Aires) 35° 45´ S, 58° 48´ W (*384*)
Bell Ville (Unión, Cordoba) 32° 38´ S, 62° 40´ W
Bella Vista (San Miguel, Buenos Aires) 34° 33´ S, 58° 41´ W
Berisso, Arroyo El Pescado (Berisso, Buenos Aires) 34° 52´ S, 57° 53´ W
Berisso, La Balandra (Berisso, Buenos Aires) 34° 52´ S, 57° 53´ W
Bielet Massé (Punilla, Cordoba) 31° 20´ S, 64° 30´ W
Biological reserve at Horco Molle, behind dining area of residencia (Yerba Buena, Tucumán) 26° 45´ S, 65° 21´ W
Biological reserve at Horco Molle, near Residencia (Yerba Buena, Tucumán) 26° 45´ S, 65° 21´ W
Bonifacio (Coronel Suárez, Buenos Aires) 36° 49´ S, 62° 13´ W
Bonpland (Candelaria, Misiones) 27° 29´ S, 55° 29´ W
Brazo Largo (Islas del Ibicuy, Entre Ríos) 33° 47´ S, 58° 36´ W
Brazo largo, Delta del Paraná (Islas del Ibicuy, Entre Ríos) 33° 47´ S, 58° 36´ W
Brazo Norte, Parque Nacional Pilcomayo (Pilcomayo, Formosa) 25° 10´ S, 58° 10´ W
Cabo Tres Puntas (Deseado, Santa Cruz) 47° 06´ S, 65° 52´ W
Cacheuta (Luján de Cuyo, Mendoza) 33° 01´ S, 69° 07´ W
Cafayate (Cafayate, Salta) 26° 05´ S, 65° 58´ W
Caimancito (Ledesma, Jujuy) 23° 44´ S, 64° 36´ W
Caimancito, 400 m (Ledesma, Jujuy) 23° 44´ S, 64° 36´ W
Caimancito, 500 m (Ledesma, Jujuy) 23° 44´ S, 64° 36´ W
Caimancito, 600 m (Ledesma, Jujuy) 23° 44´ S, 64° 36´ W
Caimancito, 700 m (Ledesma, Jujuy) 23° 44´ S, 64° 36´ W
Calamuchita, Yacanto, 1150 m (Calamuchita, Cordoba) 32° 03´ S, 65° 03´ W
Caleufú (Rancul, La Pampa) 35° 35´ S, 64° 33´ W
Calilegua (Ledesma, Jujuy) 23° 47’ S, 64° 47’ W
Camino de acceso al Parque Biológico (Yerba Buena, Tucumán) 26° 45´ S, 65° 21´ W
Campana (Campana, Buenos Aires) 34° 10´ S, 58° 57´ W
Campo Quijano (Rosario de Lerma, Salta) 24° 54´ S, 65° 38´ W
Cañada de Pirayuí (Capital, Corrientes) 27° 28´ S, 58° 51´ W
Cañada Pirayuí (Capital, Corrientes) 27° 28´ S, 58° 51´ W
Cañuelas, km 58 (Cañuelas, Buenos Aires) 35° 03´ S, 58° 46´ W
Capital (Capital, Buenos Aires) 34° 36´ S, 58° 27´ W
Carmen de Areco (Carmen de Areco, Buenos Aires) 34° 23´ S, 59° 49´ W

Casabindo (Cochinoca, Jujuy) 22° 58´ S, 66° 05´ W
Casabindo, 4000 m (Cochinoca, Jujuy) 22° 58´ S, 66° 05´ W
Castaño Nuevo, 9 km of Villa Nueva, 5040 ft. (Calingasta, San Juan) 31° 02´ S, 69° 32´ W
Castelar (Morón, Buenos Aires) 34° 39´ S, 58° 37´ W
Cataratas (Iguazú, Misiones) 25° 39´ S, 54° 20´ W
Cercanías de El Simbolar (Santa Bárbara, Jujuy) 24° 11´ S, 64° 28´ W
Cercanías de Río Victoria (Guaraní, Misiones) 26° 58´ S, 54° 30´ W
Cerro Calilegua (Valle Grande, Jujuy) 23° 35´ S, 64° 54´ W
Cerro Casabindo, 4500 m (Cochinoca, Jujuy) 22° 56´ S, 66° 07´ W
Cerro Chaguar, Parque Nacional Baritú (Santa Victoria, Salta) 22° 31´ S, 64° 34´ W
Cerro de La Gloria (Capital, Mendoza) 32° 53´ S, 68° 49´ W
Cerro de Raco (Tafí Viejo, Tucumán) 26° 38´ S, 65° 26´ W
Cerro de Tafí Viejo (Tafí Viejo, Tucumán) 26° 44´ S, 65° 16´ W
Cerro del Campo (Tafí Viejo, Tucumán) 26° 35´ S, 64° 57´ W
Cerro del Campo, 800 m (Burruyacú, Tucumán) 26° 35´ S, 64° 57´ W
Cerro Famatina, 3200 m (Famatina, La Rioja) 28° 54´ S, 67° 31´ W
Cerro Hermoso (Ledesma, Jujuy) 23° 35´ S, 64° 53´ W
Cerro Leones, 16 km ENE Bariloche, approximately 41° 04´ S, 71° 08´ W (Bariloche, Río Negro) 41° 04´ S, 71° 08´ W
Cerro Medici (Trancas, Tucumán) 26° 37´ S, 65° 12´ W
Cerro San Javier (Yerba Buena, Tucumán) 26° 47´ S, 65° 23´ W
Cerro Santa Barbara, 1800 m (Santa Bárbara, Jujuy) 24° 07´ S, 64° 29´ W
Cerro Vipos (Trancas, Tucumán) 26° 29´ S, 65° 22´ W
Cerros de Vipos (Trancas, Tucumán) 26° 29´ S, 65° 22´ W
Chacras de Coria (Godoy Cruz, Mendoza) 33° 00´ S, 68° 52´ W
Chacras de Coria, Departamento Godoy Cruz, approximately 32° 45´ S, 69° 00´ W (Godoy Cruz, Mendoza) 32° 45´ S, 69° 00´ W
Challao (Las Heras, Mendoza) 32° 51´ S, 68° 56´ W
Chapadmalal (General Pueyrredón, Buenos Aires) 38° 14´ S, 57° 48´ W
Chascomus (Chascomús, Buenos Aires) 35° 34´ S, 58° 01´ W
Chascomus, Los Libres del Sur (Chascomús, Buenos Aires) 35° 43´ S, 57° 43´ W
Choele Choel (Avellaneda, Río Negro) 39° 16´ S, 65° 41´ W
Choromoro (Trancas, Tucumán) 26° 25´ S, 65° 20´ W
Chos Malal (Chos Malal, Neuquén) 37° 23´ S, 70° 16´ W
Chos Malal, 805 m (Chos Malal, Neuquén) 37° 23´ S, 70° 16´ W
Choya, 13 km NNW of Andalgalá, 4000 ft. (Andalgalá, Catamarca) 27° 32´ S, 66° 24´ W
Chumbicha (Capayán, Catamarca) 28° 52´ S, 66° 14´ W
Chumbicha, 0,5 km E of Hwy 38 along Hwy 60 (Capayán, Catamarca) 28° 52´ S, 66° 14´ W
Chumbicha, 1, 5 km E of Hwy 38 along Hwy 60 (Capayán, Catamarca) 28° 52´ S, 66° 14´ W
Chumbicha, 600m (Capayán, Catamarca) 28° 52´ S, 66° 14´ W
Ciudad de Mar del Plata (General Pueyrredón, Buenos Aires) 38° 00´ S, 57° 33´ W
Collon Cura (Collon Cura, Neuquén) 40° 07´ S, 70° 44´ W
Colonia Alvear NE bank of Río Atuel (General Alvear, Mendoza) 34° 58´ S, 67° 42´ W
Colonia Alvear, Río Atuel (General Alvear, Mendoza) 34° 58´ S, 67° 42´ W

Colonia Hocker (Colón, Entre Ríos) 32° 07´ S, 58° 20´ W
Colonia Mascias (San Justo, Santa Fe) 30° 48´ S, 60° 01´ W
Comandante Fontana (Patiño, Formosa) 25° 20´ S, 59° 44´ W
Comodoro Rivadavia (Escalante, Chubut) 45° 52´ S, 67° 30´ W
Concepción (Chicligasta, Tucumán) 27° 20´ S, 63° 35´ W
Concordia (Concordia, Entre Ríos) 31° 24´ S, 58° 02´ W
Corvetto Field, ca. 6 km N Balcarce (Balcarce, Buenos Aires) 37° 50´ S, 58° 16´ W
Cruce camino a Puesto Viejo y Ruta 34, 4 km al Este, sobre camino a Puesto Viejo (El Carmen, Jujuy) 24° 29´ S, 64° 59´ W
Cruz del Eje (Cruz del Eje, Cordoba) 30° 44´ S, 64° 48´ W
Cuesta del Hurón, 29 km al Oeste de Cieneguillas sobre ruta provincial 64, 3835 m (Santa Catalina, Jujuy) 22° 06´ S, 66° 03´ W
Cueva Traful (Los Lagos, Neuquén) 40° 43´ S, 71° 05´ W
Cumbres del Taficillo, La Agüita (Tafí Viejo, Tucumán) 26° 42´ S, 65° 22´ W
Cuña Pirú (Libertador General San Martín, Misiones) 27° 05´ S, 55° 03´ W
Curques, 24 km al N de Susques, sobre ruta 74, 4100 m (Susques, Jujuy) 23° 14´ S, 66° 23´ W
Delta del Paraná (Campana, Buenos Aires) 33° 58´ S, 59° 03´ W
Delta, Canal 6 (Campana, Buenos Aires) 33° 58´ S, 59° 03´ W
Desaguadero (La Paz, Mendoza) 33° 25´ S, 67° 11´ W
Deseado (General Belgrano, Misiones) 25° 47´ S, 54° 02´ W
Desembocadura Arroyo Santelmita, 700 m, Parque Nacional Baritú (Santa Victoria, Salta) 22° 31´ S, 64° 34´ W
Dique El Cadillal (Tafí Viejo, Tucumán) 26° 37´ S, 65° 12´ W
Dique Escaba (J. B. Alberdi, Tucumán) 27° 40´ S, 65° 46´ W
Dique San Ignacio (La Cocha, Tucumán) 27° 44´ S, 65° 40´ W
Ditch along INTA (Instituto Nacional de Tecnología Agropecuaria)side along ruta 226 km 68 (Balcarce, Buenos Aires) 37° 50´ S, 58° 20´ W
Ditch along ruta 226 (Balcarce, Buenos Aires) 37° 50´ S, 58° 20´ W
Ditch along Ruta 226, app. km 78 (Balcarce, Buenos Aires) 37° 50´ S, 58° 20´ W
Ditches along ruta 226 between km 65-75 (Balcarce, Buenos Aires) 37° 50´ S, 58° 20´ W
Dock Sur (Capital, Buenos Aires) 34° 36´ S, 58° 27´ W
Dos de Mayo (Guaraní, Misiones) 27° 02´ S, 54° 38´ W
Dragones (General San Martín, Salta) 23° 15´ S, 63° 21´ W
El Arenal (Santa Bárbara, Jujuy) 24° 19´ S, 64° 41´ W
El Bracho, 400 m (Cruz Alta, Tucumán) 26° 59´ S, 65° 11´ W
El Cadillal (Tafí Viejo, Tucumán) 26° 37´ S, 65° 12´ W
El Cadillal Dike, 35 km NW San Miguel de Tucumán (Tafí Viejo, Tucumán) 26° 37´ S, 65° 12´ W
El Cajón (Burruyacú, Tucumán) 26° 30´ S, 64° 52´ W
El Colorado (Pirané, Formosa) 26° 25´ S, 59° 28´ W
El Corte (Yerba Buena, Tucumán) 26° 45´ S, 65° 21´ W
El Duraznal, 1800m (Santa Bárbara, Jujuy) 24° 10´ S, 64° 20´ W
El Duraznillo, Cerro Calilegua, 3000 m (Valle Grande, Jujuy) 23° 28´ S, 64° 55´ W
El Indio, Ruta 307 (Monteros, Tucumán) 27° 02´ S, 65° 40´ W
El Mollar (Tafí del Valle, Tucumán) 26° 52´ S, 65° 41´ W
El Quebrachal (Anta, Salta) 25° 17´ S, 64° 04´ W
El Rincón (Jiménez, Santiago del Estero) 26° 43´ S, 64° 50´ W

El Simbolar, 25 km al SO de Palma Sola (Santa Bárbara, Jujuy) 24° 11´ S, 64° 28´ W
Eldorado (Eldorado, Misiones) 26° 25´ S, 54° 37´ W
En el Río Paranaí-Guazú, a unos 15 km de la costa del Paraná (Montecarlo, Misiones) 26° 46´ S, 54° 43´ W
En las cercanías de Laguna González, Santa Ana (San Cosme, Corrientes) 27° 30´ S, 58° 39´ W
Escobar (Escobar, Buenos Aires) 34° 21´ S, 58° 47´ W
Escuela 51 a 4 km de Loreto (Candelaria, Misiones) 27° 19´ S, 55° 32´ W
Esperanza (Las Colonias, Santa Fe) 31° 28´ S, 60° 55´ W
Estación INTA (Instituto Nacional de Tecnología Agropecuaria)Pellegrini (Pellegrini, Buenos Aires) 36° 18´ S, 63° 07´ W
Estación Vipos (Trancas, Tucumán) 26° 29´ S, 65° 22´ W
Estancia El Ceibo (Santo Tomé, Corrientes) 28° 40´ S, 56° 11´ W
Estancia El Tuyú (La Costa, Buenos Aires) 36° 22´ S, 56° 43´ W
Estancia Guampacha (Guasayán, Santiago del Estero) 27° 59´ S, 64° 45´ W
Estancia La Blanca, 10 km al N de Santo Tomé, sobre Río Uruguay (Corrientes) 28° 28´ S, 56° 05´ W
Estancia La Germania (Santa Fe) 32° 33’ S, 61° 24’ W
Estancia La Madrugada, not far from Puerto Deseado, 47° 06´ S, 66° 29´ W (Deseado, Santa Cruz) 47° 06´ S, 66° 29´ W
Estancia La Magdalena, Barreto (Juárez Celman, Cordoba) 33° 21´ S, 63° 18´ W
Estancia Leoncito, 2 km E Observatorio Astronómico (Calingasta, San Juan) 31° 48´ S, 69° 22´ W
Estancia Linda Vista (Formosa) 25° 13’ S, 57° 47’ W
Estancia Los Lobos (General Pueyrredón, Buenos Aires) 38° 01´ S, 57° 33´ W
Estancia Los Manantiales (Escalante, Chubut) 43° 18´ S, 69° 50´ W
Estancia Los Manantiales near Languiñeo, aproximately 43° 18´ S, 69° 50´ W (Escalante, Chubut) 43° 18´ S, 69° 50´ W
Estancia María Sofía (Pilcaniyeu, Río Negro) 40° 37´ S, 70° 09´ W
Estancia Paranacito (Islas del Ibicuy, Entre Ríos) 33° 47´ S, 59° 00´ W
Estancia Tehuel Malal, 6 km NW Nahuel Huapi, approximately 41° 02´ S, 71° 10´ W (Los Lagos, Neuquén) 41° 02´ S, 71° 10´ W
Estero Poi, Parque Nacional Pilcomayo (Pilcomayo, Formosa) 25° 10´ S, 58° 10´ W
Finca Abra Grande, Quebrada de Tartagal (San Martín, Salta) 22° 40´ S, 63° 41´ W
Finca Finca Falcón, aproximadamente 3 km al NW del pozo de agua N° 5 (San Martin, Salta) 22° 18’ S, 63° 58’ W
Finca El Jagüel, 4,5 km al Oeste de la Ruta Provincial 304, sobre camino a Requelme (Burruyacú, Tucumán) 26° 28´ S, 64° 48´ W
Finca Yakulica, Angosto del Río Pescado, 650 m Parque Nacional Baritú (Santa Victoria, Salta) 22° 31´ S, 64° 34´ W
Florencia (General Obligado, Santa Fe) 28° 02´ S, 59° 15´ W
Foot of Cerro del Campo, Burruyacú, 800m (Burruyacú, Tucumán) 26° 35´ S, 64° 57´ W
Fracrán (Guaraní, Misiones) 26° 46´ S, 54° 16´ W
Galvez (Santa Fe) 32° 02’ S, 61° 13’ W
General Alvarado (General Alvarado, Buenos Aires) 38° 16´ S, 57° 51´ W
General Belgrano (General Belgrano, Buenos Aires) 35° 45´ S, 58° 48´ W
General Lavalle (General Lavalle, Buenos Aires) 36° 24´ S, 56° 58´ W

General Roca (General Roca, Río Negro) 39° 02´ S, 67° 35´ W
González Catán (La Matanza, Buenos Aires) 34° 46´ S, 58° 39´ W
Goya (Goya, Corrientes) 29° 08´ S, 59° 16´ W
Goya, 600 m (Goya, Corrientes) 29° 08´ S, 59° 16´ W
Goya, N. Argentine (Goya, Corrientes) 29° 08´ S, 59° 16´ W
Goya, on Río Paraná (Goya, Corrientes) 29° 08´ S, 59° 16´ W
Gualeguaychú (Gualeguaychú, Entre Ríos) 33° 01´ S, 58° 31´ W
Güemes, Highway 34, km 1383 (General Güemes, Salta) 24° 41´ S, 65° 02´ W
Güemes, ruta 34, km 1383 (General Güemes, Salta) 24° 41´ S, 65° 02´ W
Hickman (General San Martín, Salta) 23° 13´ S, 63° 34´ W
Higuerilla (Valle Grande, Jujuy) 23° 36´ S, 65° 05´ W
Higuerilla, 2000 m (Valle Grande, Jujuy) 23° 36´ S, 65° 05´ W
Horco Molle (Yerba Buena, Tucumán) 26° 45´ S, 65° 21´ W
Horco Molle, 650 m (Yerba Buena, Tucumán) 26° 45´ S, 65° 21´ W
Hualfín (Belén, Catamarca) 27° 14´ S, 66° 50´ W
Humahuaca (Humahuaca, Jujuy) 23° 12´ S, 65° 21´ W
Hurlingam (Morón, Buenos Aires) 34° 36´ S, 58° 38´ W
Inca Mayo (Rosario de Lerma, Salta) 24° 36´ S, 65° 44´ W
Ingeniero Juárez (Matacos, Formosa) 23° 54´ S, 61° 51´ W
Ingenio La Esperanza (San Pedro, Jujuy) 24° 14´ S, 64° 52´ W
Ingenio Tabacal (Orán, Salta) 23° 15´ S, 64° 15´ W
Ingenio Tabacal, Lote Milagros (Orán, Salta) 23° 15´ S, 64° 15´ W
Inmed. N Andalgalá, Río Andalgalá (Andalgalá, Catamarca) 27° 34´ S, 66° 16´ W
Instituto Miguel Lillo (Capital, Tucumán) 26° 49´ S, 65° 11´ W
INTA (Instituto Nacional de Tecnología Agropecuaria), in ditch (grass tall) near buildings (Balcarce, Buenos Aires) 37° 50´ S, 58° 20´ W
INTA (Instituto Nacional de Tecnología Agropecuaria)area, Ruta 226, km 74, ditch (Balcarce, Buenos Aires) 37° 50´ S, 58° 20´ W
INTA (Instituto Nacional de Tecnología Agropecuaria)property in overgrown pasture (Balcarce, Buenos Aires) 37° 50´ S, 58° 20´ W
INTA (Instituto Nacional de Tecnología Agropecuaria) ditch near buildings (Balcarce, Buenos Aires) 37° 50´ S, 58° 20´ W
Ipizca (Ancasti, Catamarca) 28° 50´ S, 65° 30´ W
Isla de los Pájaros, en el borde norte del itsmo de entrada a la Península de Valdés (Viedma, Chubut) 42° 30´ S, 64° 40´ W
Isla de Tigre (Tigre, Buenos Aires) 34° 25´ S, 58° 34´ W
Isla Retama, Delta del Paraná (Campana, Buenos Aires) 33° 58´ S, 59° 03´ W
Isla Roble, Delta del Paraná (Zárate, Buenos Aires) 34° 04´ S, 59° 02´ W
Isla Talavera (Zárate, Buenos Aires) 34° 00´ S, 59° 12´ W
Itsmo Ameghino (Viedma, Chubut) 42° 25´ S, 64° 35´ W
Ituzaingó, Pto. Valle (Capital, Corrientes) 27° 36´ S, 56° 41´ W
Jct. Hwy 21 and Arroyo Oveja Negra (approx.) 2 km W Parque Provincial Mocona (Guaraní, Misiones) 27° 08´ S, 53° 54´ W
Jardín Zoológico La Plata (La Plata, Buenos Aires) 34° 55´ S, 57° 57´ W
Jujuy, 1258 m (Dr. Manuel Belgrano, Jujuy) 24° 12´ S, 65° 19´ W
Junín, Estancia Agustina (Junín, Buenos Aires) 34° 35´ S, 61° 10´ W
km 42 al Sur de San Pedro de Colalao, sobre Ruta 364 (Trancas, Tucumán) 26° 15´ S, 65° 29´ W

La Delfina, Barreto (Juárez Celman, Cordoba) 33° 21´ S, 63° 18´ W
La Higuera (Trancas, Tucumán) 26° 23´ S, 65° 26´ W
La Isolina, R 200 km 63 (Navarro, Buenos Aires) 34° 55´ S, 59° 15´ W
La Merced (Paclín, Catamarca) 28° 10´ S, 65° 41´ W
La Paz (La Paz, Entre Ríos) 30° 45´ S, 59° 39´ W
La Paz (La Paz, Mendoza) 33° 28´ S, 67° 33´ W
La Paz (San Javier, Córdoba) 32° 13´ S, 65° 03´ W
La Picada a 20 km de Paraná (Paraná, Entre Ríos) 31° 44´ S, 60° 18´ W
La Plata (La Plata, Buenos Aires) 34° 55´ S, 57° 57´ W
La Plata, El Bosque (La Plata, Buenos Aires) 34° 55´ S, 57° 57´ W
La Plata, Punta Lara (Ensenada, Buenos Aires) 34° 49´ S, 57° 59´ W
La Plata, Villa Elisa (La Plata, Buenos Aires) 34° 51´ S, 58° 04´ W
La Quiaca, 17 km al Oeste, sobre ruta provincial 5, y 3 km al Sur de la misma ruta (Yavi, Jujuy) 22° 09´ S, 65° 44´ W
La Tinta (Benito Juárez, Buenos Aires) 37° 37´ S, 59° 33´ W
La Toma de Andalgalá (Andalgalá, Catamarca) 27° 36´ S, 66° 20´ W
La Toma, Soto (Cruz del Eje, Cordoba) 30° 51´ S, 65° 01´ W
Lago Muyo (Santiago del Estero) 28° 42’ S, 62° 50’ W
Lago Nahuel Huapi, Isla Victoria (Los Lagos, Neuquén) 40° 57´ S, 71° 30´ W
Lago Puelo, Parque Nacional Los Alerces (Cushamen, Chubut) 42° 03’ S, 71° 15’ W
Laguna Blanca (Pilcomayo, Formosa) 25° 08´ S, 58° 15´ W
Laguna Blanca, 20 km al SE sobre Ruta Nacional 86 (Pilcomayo, Formosa) 25° 08´ S, 58° 15´ W
Laguna Chasicó (Villarino, Buenos Aires) 38° 40´ S, 63° 06´ W
Laguna de las Catas, Tartagal (General San Martín, Salta) 22° 32´ S, 63° 49´ W
Laguna de Los Padres (General Pueyrredón, Buenos Aires) 37° 57´ S, 57° 44´ W
Laguna de Pozuelos (Rinconada, Jujuy) 22° 26´ S, 66° 00´ W
Laguna Grande (Santo Tomé, Corrientes) 28° 43´ S, 56° 27´ W
Laguna La Brea (Santa Bárbara, Jujuy) 23° 56´ S, 64° 28´ W
Laguna La Brea, 25 km W Palma Sola (Santa Bárbara, Jujuy) 23° 56´ S, 64° 28´ W
Las Arcas (Trancas, Tucumán) 26° 12´ S, 65° 15´ W
Las Cuevas (Entre Rios) 32° 21’ S, 60° 29’ W
Las Coloradas, Campo Grande (Catan Lil, Neuquén) 39° 35´ S, 70° 40´ W
Las Flores (Las Flores, Buenos Aires) 36° 03´ S, 59° 07´ W
Las Heras (Las Heras, Mendoza) 32° 51´ S, 68° 49´ W
Las Lajas (Picunches, Neuquén) 38° 31´ S, 70° 22´ W
Las Lajas, 640 m (Picunches, Neuquén) 38° 31´ S, 70° 22´ W
Las Lomas, Laguna Paiva (Capital, Corrientes) 27° 27´ S, 58° 51´ W
Las Lomitas (Patiño, Formosa) 24° 42´ S, 60° 36´ W
Las Palmas (Bermejo, Chaco) 27° 04´ S, 58° 42´ W
Las Palmas, 20 mi N of Corrientes (Bermejo, Chaco) 27° 04´ S, 58° 42´ W
Las Rosas (Belgrano, Santa Fe) 32° 28´ S, 61° 34´ W
Las Rosas, 100 m (Belgrano, Santa Fe) 32° 28´ S, 61° 34´ W
Lata Cue, Parque Nacional Pilcomayo (Pilcomayo, Formosa) 25° 10´ S, 58° 10´ W
La Urbana, Rio Pilcomayo (Formosa) 25° 01’ S, 59° 19’ W
Lavalle (Guasayán, Santiago del Estero) 28° 12´ S, 65° 08´ W
León (Dr. Manuel Belgrano, Jujuy) 24° 02´ S, 65° 26´ W
León, 1500 m (Dr. Manuel Belgrano, Jujuy) 24° 02´ S, 65° 26´ W

Leones (Marcos, Cordoba) 32° 39´ S, 62° 18´ W
Lihuel Calel (Lihuel Calel, La Pampa) 37° 57´ S, 65° 33´ W
Loreto (Candelaria, Misiones) 27° 19´ S, 55° 32´ W
Los Chorrillos, 13 km N limite Norte de Estancia Los Chorrillos (Burruyacú, Tucumán) 26° 15´ S, 64° 59´ W
Los Colorados, 17 km al Este de Santo Domingo (Anta, Salta) 24° 28´ S, 63° 57´ W
Los Romanos (Leales, Tucumán) 27° 24´ S, 65° 08´ W
Los Vallistos, Ruta 9 km 1285 (Cruz Alta, Tucumán) 26° 55´ S, 65° 10´ W
Los Yngleses (General Lavalle, Buenos Aires) 36° 31´ S, 56° 53´ W
Los Ingleses, Ajo (General Lavalle, Buenos Aires) 36° 31´ S, 56° 53´ W
Los Ingleses, Ajo SL (General Lavalle, Buenos Aires) 36° 31´ S, 56° 53´ W
Luján (Luján de Cuyo, Mendoza) 33° 03´ S, 68° 52´ W
Luján de Cuyo (Luján de Cuyo, Mendoza) 33° 03´ S, 68° 53´ W
Lumbreras (Metán, Salta) 25° 12´ S, 64° 55´ W
Maciel (San Jerónimo, Santa Fe) 32° 28´ S, 60° 53´ W
Madariaga, Laguna Salada Grande (General J. Madariaga, Buenos Aires) 36° 57´ S, 57° 05´ W
Magdalena (Magdalena, Buenos Aires) 35° 16´ S, 57° 14´ W
Magdalena, Estancia San Isidro (Magdalena, Buenos Aires) 35° 16´ S, 57° 14´ W
Maimará (Tilcara, Jujuy) 23° 37´ S, 65° 28´ W
Maimará, 2230 m (Tilcara, Jujuy) 23° 37´ S, 65° 28´ W
Malabrigo (General Obligado, Santa Fe) 29° 22´ S, 59° 50´ W
Malargüe, P° El Peralito, 120 km E Malague (Malargüe, Mendoza) 36° 07´ S, 68° 56´ W
Malragüe, 4,8 km El Peralito (Malargüe, Mendoza) 35° 28´ S, 69° 35´ W
Manantiales (Mburucuyá, Corrientes) 27° 57´ S, 58° 08´ W
Manuel Solá (Rosario de Lerma, Salta) 24° 34´ S, 65° 50´ W
M. Solá (Rosario de Lerma, Salta) 24° 34´ S, 65° 50´ W
Mar de Ajó (La Costa, Buenos Aires) 36° 43´ S, 56° 40´ W
Mar del Sur (General Alvarado, Buenos Aires) 38° 18´ S, 58° 00´ W
María Eugenia (Castellanos, Santa Fe) 31° 45´ S, 61° 50´ W
María Grande (Paraná, Entre Ríos) 31° 39´ S, 59° 54´ W
Matheu (Escobar, Buenos Aires) 34° 23´ S, 58° 50´ W
Máximo Paz (Constitución, Santa Fe) 33° 30´ S, 60° 55´ W
Mercedes, Isleta Cabo Estancia (Mercedes, Corrientes) 29° 12´ S, 58° 05´ W
Merlo, Villa Elena (Junín, San Luis) 32° 21´ S, 65° 02´ W
Mesada de Las Colmenas (Ledesma, Jujuy) 23° 42´ S, 64° 52´ W
Mesada de las Colmenas, 1150 m (Ledesma, Jujuy) 23° 42´ S, 64° 52´ W
Meseta El Pedrero, 46°46.37´S, 69°38.49´W (Deseado, Santa Cruz) 46° 46´ S, 69° 38´ W
Metán (Metán, Salta) 25° 30´ S, 64° 58´ W
Mina Pan de Azúcar, 13 km al S, sobre Río Cincel (Cochinoca) 22° 42′ S, 66° 04′ W
Mina Pirquitas, 31 km al SE, sobre ruta 74b, Sierra de Quichagua, 4200 m (Cochinoca, Jujuy) 22° 54´ S, 66° 19´ W
Minas Capillitas, 3200 m (Andalgalá, Catamarca) 27° 20´ S, 66° 25´ W
Miramar (General Alvarado, Buenos Aires) 38° 16´ S, 57° 51´ W
Miramar, Arroyo Brusquitas (General Alvarado, Buenos Aires) 38° 16´ S, 57° 51´ W
Miyuyoc (Humahuaca, Jujuy) 22° 51´ S, 65° 18´ W
Monteros (Monteros, Tucumán) 27° 10´ S, 65° 30´ W

Moreno (Moreno, Buenos Aires) 34° 39´ S, 58° 47´ W
Morón (Morón, Buenos Aires) 34° 39´ S, 58° 37´ W
Nahuel Huapi, National Park (Los Lagos, Neuquén) 40° 57´ S, 71° 30´ W
Near Amaicha del Valle (Tafí del Valle, Tucumán) 26° 36´ S, 65° 55´ W
Near Cape Tres Puntas, Patagonia (Deseado, Santa Cruz) 47° 06´ S, 65° 52´ W
Noetinger, FCCA (Marcos Juárez, Cordoba) 32° 22´ S, 62° 19´ W
Noetinger, F.C.C.A., 100 m (Marcos Juárez, Córdoba) 32° 22´ S, 62° 19´ W
Nueva Escocia (Concordia, Entre Ríos) 31° 39´ S, 58° 01´ W
Ñacuñán (Santa Rosa, Mendoza) 34° 03´ S, 67° 57´ W
Ñorco-Vipos (Trancas, Tucumán) 26° 29´ S, 65° 22´ W
Oeste Sierra de San Javier (Tafí Viejo, Tucumán) 26° 48´ S, 65° 23´ W
Off Hwy 62, 8 km E jct. Hwy 1 and 62 (Andalgalá, Catamarca) 27° 36´ S, 66° 15´ W
On highway 9 at border with Salta, at campground on the way to El Carmen, 4600 ft. (El Carmen, Jujuy) 24° 28´ S, 65° 21´ W
On highway 29 (east off of hwy 9), 10 km west of Tiraxi (Dr. Manuel Belgrano) 23° 59’ S, 65° 23’ W
On Hwy 308, 5 km N of Las Higuerillas (Alberdi, Tucumán) 27° 44´ S, 65° 50´ W
Orán (Orán, Salta) 23° 08´ S, 64° 20´ W
Otro cerro (Capayán, Catamarca) 28° 44´ S, 66° 17´ W
Oyeros, 3 km al N, camino entre rutas 61 y 43 (El Carmen, Jujuy) 24° 30´ S, 65° 00´ W
Pagancillo (Coronel F. Varela, La Rioja) 29° 33´ S, 68° 08´ W
Palma Sola (Santa Bárbara, Jujuy) 24° 00´ S, 64° 19´ W
Palm Swamp, 12 km ESE of Resistencia (Chaco) 27° 27’ S, 58° 59’ W
Palpalá, 1 km al E entre rutas 66 y 1 (Palpalá, Jujuy) 24° 16´ S, 65° 10´ W
Paraje Talavera (Zárate, Buenos Aires) 34° 00´ S, 59° 12´ W
Parque Nacional Baritú (Santa Victoria, Salta) 22° 31´ S, 64° 34´ W
Parque Nacional Calilegua (Ledesma, Jujuy) 23° 37´ S, 64° 48´ W
Parque Nacional Chaco (Presidencia de la Plaza, Chaco) 26° 40´ S, 59° 48´ W
Parque Nacional Chaco, camping sobre Río Negro (Presidencia de la Plaza, Chaco) 26° 40´ S, 59° 48´ W
Parque Nacional Diamante (Diamante, Entre Ríos) 32° 07´ S, 60° 38´ W
Parque Nacional El Palmar (Colón, Entre Ríos) 31° 49´ S, 58° 15´ W
Parque Nacional El Rey (Anta, Salta) 24° 42´ S, 64° 38´ W
Parque Nacional Iguazú (Iguazú, Misiones) 25° 39´ S, 54° 20´ W
Parque Nacional Laguna Blanca (Zapala, Neuquén) 39° 05´ S, 70° 10´ W
Parque Nacional Lanin (Lacar, Neuquén) 40° 05’ S, 71° 10’ W
Parque Nacional Lihuel Calel (Lihuel Calel, La Pampa) 37° 57´ S, 65° 33´ W
Parque Nacional Los Arrayanes (Los Lagos, Neuquén) 40° 57´ S, 71° 30´ W
Parque Nacional Los Alerces (Futalefú, Chubut) 42° 52’ S, 71° 46’ W
Parque Nacional Mburucuyá (Mburucuyá, Corrientes) 28° 01´ S, 58° 01´ W
Parque Nacional Pilcomayo (Pilcomayo, Formosa) 25° 10´ S, 58° 10´ W
Parque Nacional Río Pilcomayo (Pilcomayo, Formosa) 25° 10´ S, 58° 10´ W
Parque Nacional Sierra de las Quijadas (Belgrano, San Luis) 32° 30´ S, 67° 08´ W
Parque Provincial E. Tornquist (Tornquist, Buenos Aires) 38° 06´ S, 62° 14´ W
Parque Provincial El Cochuna, sobre Ruta 48 (Chicligasta, Tucumán) 27° 20´ S, 65° 55´ W
Parque San Martín (Capital, Mendoza) 32° 53´ S, 68° 49´ W

Partido de Balcarce, Estación Experimental del INTA (Instituto Nacional de Tecnología Agropecuaria), ca. 15 km NW de Balcarce (Balcarce, Buenos Aires) 37° 50´ S, 58° 20´ W
Partido de Pergamino, Estación Tambo Nuevo y Ruta 188, km 60 (Pergamino, Buenos Aires) 34° 00´ S, 60° 35´ W
Partido de Tandil, proximidades de la ciudad homónima (Tandil, Buenos Aires) 37° 19´ S, 59° 09´ W
Paseo inferior Cataratas, Parque Nacional Iguazú (Iguazú, Misiones) 25° 39´ S, 54° 20´ W
Paso de la Patria (San Cosme, Corrientes) 27° 19´ S, 58° 35´ W
Paso Pomelo, Parque Nacional Pilcomayo (Pilcomayo, Formosa) 25° 10´ S, 58° 10´ W
Patquía (Independencia, La Rioja) 30° 03´ S, 66° 53´ W
Pehuajó (Pehuajó, Buenos Aires) 35° 48´ S, 61° 54´ W
Pergamino (Pergamino, Buenos Aires) 33° 53´ S, 60° 35´ W
Pergamino, ruta 188, Curva de la Peña (Pergamino, Buenos Aires) 33° 53´ S, 60° 36´ W
Pergamino, Curva de Pena, Ruta 188 (Pergamino, Buenos Aires) 33° 53´ S, 60° 36´ W
Pichao, primeras estribaciones Sierras de Quilmes (Tafí del Valle, Tucumán) 26° 18´ S, 66° 02´ W
Pico de Salamanca (Escalante, Chubut) 45° 30´ S, 68° 30´ W
Pico Salamanca (Escalante, Chubut) 45° 30´ S, 68° 30´ W
Piedra Tendida, 12 km WNW Burruyacú along Río El Cajón, 2500 ft (Burruyacú, Tucumán) 26° 30´ S, 64° 52´ W
Piedra Tendida, 8 km W Dique El Cajón (Burruyacú, Tucumán) 26° 30´ S, 64° 52´ W
Piedras Coloradas (Monteros, Tucumán) 27° 04´ S, 65° 40´ W
Pigüe, Curamalal Chico (Saavedra, Buenos Aires) 37° 28´ S, 62° 06´ W
Piñalitos (General Manuel Belgrano, Misiones) 25° 59´ S, 53° 54´ W
Pirayuí (Capital, Corrientes) 27° 28´ S, 58° 51´ W
Playa Ancha (General San Martín, Salta) 22° 07´ S, 63° 44´ W
Playa Chapadmalal (General Pueyrredón, Buenos Aires) 38° 15´ S, 57° 48´ W
Posadas (Capital, Misiones) 27° 23´ S, 55° 53´ W
Potrerillo (Famatina, La Rioja) 28° 24´ S, 67° 45´ W
Potrerillo, Famatina range (Famatina, La Rioja) 28° 24´ S, 67° 45´ W
Pozo del Tigre (Patiño, Formosa) 24° 54´ S, 60° 19´ W
Pozo Hondo (Graneros, Tucumán) 27° 49´ S, 65° 20´ W
Pronunciamiento (Uruguay, Entre Ríos) 32° 21´ S, 58° 26´ W
Proximidades de Villa Castelli (General La Madrid, La Rioja) 29° 00´ S, 68° 17´ W
Puente sobre el Río San Francisco, cruce entre Ruta 1 y el Río San Francisco (Santa Bárbara, Jujuy) 23° 43´ S, 64° 32´ W
Puerto Blest, Parque Nacional Nahuel Huapi (Bariloche, Río Negro) 41° 02´ S, 71° 49´ W
Puerto Iguazú (Iguazú, Misiones) 25° 36´ S, 54° 35´ W
Puerto Libertad-Iguazú, Río Urugua-í (Iguazú, Misiones) 25° 57´ S, 54° 40´ W
Puerto Lobos (Viedma, Chubut) 42° 04´ S, 65° 09´ W
Puerto Madryn, Cañadón Cerro Avezado (Viedma, Chubut) 42° 47´ S, 65° 02´ W
Puerto Península (Iguazú, Misiones) 25° 38´ S, 54° 30´ W
Puerto Pirámide (Viedma, Chubut) 42° 34´ S, 64° 17´ W
Puerto Piray (Montecarlo, Misiones) 26° 28´ S, 54° 42´ W
Puerto Piray, km 18 (Montecarlo, Misiones) 26° 28´ S, 54° 42´ W

Puerto Radal, Isla Victoria (Los Lagos, Neuquén) 40° 57´ S, 71° 30´ W
Puerto San Juan Candelaria (Candelaria, Misiones) 27° 28´ S, 55° 44´ W
Puesto Campo Grande, 17 km al Este de Santo Domingo (Anta, Salta) 24° 28´ S, 63° 57´ W
Puesto Divisadero, 35 km S Ingeniero Juárez (Bermejo, Formosa) 24° 11´ S, 61° 53´ W
Puesto Divisadero, 35 km S, 5 km E Ing. Guillermo N. Juárez (Bermejo, Formosa) 24° 11´ S, 61° 53´ W
Puesto El Quebrachal, Parque Nacional Pilcomayo (Pilcomayo, Formosa) 25° 10´ S, 58° 10´ W
Puesto El Zapallar (Libertador General San Martín, Chaco) 26° 30´ S, 59° 35´ W
Punta del Agua (San Rafael, Mendoza) 35° 31´ S, 68° 05´ W
Punta Indio, Estancia San Isidro (Magdalena, Buenos Aires) 35° 16´ S, 57° 14´ W
Punta Lara (Ensenada, Buenos Aires) 34° 49´ S, 57° 59´ W
Quebrada de Las Flores, 4 km E, 5 km N Guayamas (Caucete, San Juan) 31° 40´ S, 68° 08´ W
Quebrada de Las Flores, 4 km E, 5 km N Guayamas 2200 ft (Caucete, San Juan) 31° 40´ S, 68° 08´ W
Quebrada de López, San Francisco del Monte de Oro (Ayacucho, San Luis) 32° 36´ S, 66° 07´ W
Quebrada de Lules, 11 km SW de San Pablo (Lules, Tucumán) 26° 52´ S, 65° 25´ W
Quebrada de Lules, 13 km SO de San Pablo (Lules, Tucumán) 26° 53´ S, 65° 26´ W
Quebrada de Lules, 18 km SO de San Pablo (Lules, Tucumán) 26° 54´ S, 65° 27´ W
Quilmes (Quilmes, Buenos Aires) 34° 44´ S, 58° 16´ W
Quiroga (9 de Julio, Buenos Aires) 35° 18´ S, 61° 25´ W
Quiroga, km 300 (9 de Julio, Buenos Aires) 35° 18´ S, 61° 25´ W
Quirós (La Paz, Catamarca) 28° 45´ S, 65° 07´ W
Raco, 1000 m (Tafí Viejo, Tucumán) 26° 38´ S, 65° 26´ W
Raco, Sierra de San Javier (Tafí Viejo, Tucumán) 26° 38´ S, 65° 26´ W
Raco, Sierra de San Javier (Tafí Viejo, Tucumán) 27° 38´ S, 66° 26´ W
Ramallo (Ramallo, Buenos Aires) 33° 18´ S, 60° 01´ W
Reserva Ecologica de Ñacuñán (Santa Rosa, Mendoza) 34° 03´ S, 67° 57´ W
Reserva Experimental Flora y Fauna de Horco Molle (Yerba Buena, Tucumán) 26° 45´ S, 65° 21´ W
Reserva Natural Estricta El Leoncito (Calingasta, San Juan) 31° 48´ S, 69° 22´ W
Reserva Natural Estricta Otamendi (Campana, Buenos Aires) 34° 14´ S, 58° 53´ W
Reserva Natural Estricta San Antonio (General Manuel Belgrano, Misiones) 26° 05´ S, 53° 46´ W
Reserva Natural Formosa (Bermejo, Formosa) 24° 10´ S, 61° 44´ W
Reserva Natural Formosa, Paso de los Coyas, Río Bermejito (Bermejo, Formosa) 24° 11´ S, 61° 44´ W
Reserva Natural La Florida, 7 km al W de Ibatín, sobre Río Pueblo Viejo (Monteros, Tucumán) 27° 11´ S, 65° 40´ W
Reserva Natural Punta Lara (Ensenada, Buenos Aires) 34° 49´ S, 57° 59´ W
Riacho Pilagá, 10 mi NW of km 182 (Patiño, Formosa) 25° 13´ S, 59° 47´ W
Rincón (Junín, San Luis) 32° 21´ S, 64° 59´ W
Río Aguaraí Guazú (sup) (Eldorado, Misiones) 26° 15´ S, 54° 20´ W
Río Andalgalá, 3 km N Andalgalá (Andalgalá, Catamarca) 27° 34´ S, 66° 16´ W
Río Blanco (Palpalá, Jujuy) 24° 14´ S, 65° 14´ W

Río Blanco, 9 km SW San Antonio, 1495 m (San Antonio, Jujuy) 24° 25´ S, 65° 23´ W
Río Ceballos (Colón, Cordoba) 31° 10´ S, 64° 20´ W
Río Cuarto, Puente Olmos (Río Cuarto, Cordoba) 33° 08´ S, 64° 21´ W
Río de las Conchas, 2 km N y 6 km W de Metán (Metán, Salta) 25° 18´ S, 61° 01´ W
Río de Oro (Bermejo, Chaco) 27° 04´ S, 58° 34´ W
Río Gómez, 7 km E of downtown San Francisco del Monte de Oro, 2800 ft. (Ayacucho, San Luis) 32° 36´ S, 66° 03´ W
Río Iguazú, 60 km al sur de Puerto Iguazú (Iguazú, Misiones) 26° 27´ S, 54° 28´ W
Río Las Cañas, Horco Molle (Yerba Buena, Tucumán) 26° 45´ S, 65° 21´ W
Río Las Capillas, sobre ruta provincial 20 (Dr. Manuel Belgrano, Jujuy) 24° 02´ S, 65° 07´ W
Río Mojotoro, puente del Ferrocarril Belgrano (General Güemes, Salta) 24° 40´ S 65° 03´ W
Río Paraná, Caraguatay (Montecarlo, Misiones) 26° 40’ S, 54° 45’ W
Rió Paraná, Caraguatay, 100 mi S Río Iguazú (Montecarlo, Misiones) 26° 40’ S, 54° 45’ W
Río Pescado Chico (Santa Victoria, Salta) 22° 31´ S, 64° 34´ W
Río Pueblo Viejo, Reserva Provincial La Florida (Monteros, Tucumán) 27˚ 13’ S 65˚ 37’ W
Río Salí (Cruz Alta, Tucumán) 26° 50´ S, 65° 10´ W
Río San Francisco, Altura de Yuto, 500m (Ledesma, Jujuy) 23° 38´ S, 64° 28´ W
Río Santa María (Orán, Salta) 23° 17´ S, 64° 14´ W
Río Tesorero, 4 km al Norte de Tiraxi, sobre ruta provincial N° 29 (Dr. Manuel Belgrano, Jujuy) 23° 59´ S, 65° 18´ W
Río Tiraxi, 1,5 km al Este de Tiraxi, sobre ruta 29 (Dr. Manuel Belgrano, Jujuy) 23° 59´ S, 65° 19´ W
Río Uruguaí (Iguazú, Misiones) 25° 54´ S, 54° 36´ W
Río Urugua-í, a 30 km al N de Puerto Bemberg (Iguazú, Misiones) 25° 57´ S, 54° 30´ W
Río Uruguaí, curso medio (Iguazú, Misiones) 25° 54´ S, 54° 36´ W
Río Uruguaí, km 10 (Iguazú, Misiones) 25° 54´ S, 54° 36´ W
Rivadavia (Rivadavia, Mendoza) 33° 11´ S, 68° 28´ W
Rivera de Punta Lara (Ensenada, Buenos Aires) 34° 49´ S, 57° 59´ W
Roadside trapping near INTA (Instituto Nacional de Tecnología Agropecuaria)entrance (Balcarce, Buenos Aires) 37° 50´ S, 58° 20´ W
Roberto Payró (Magdalena, Buenos Aires) 35° 15´ S, 57° 46´ W
Robles (Robles, Santiago del Estero) 27° 55´ S, 64° 08´ W
Rojas (Rojas, Buenos Aires) 34° 12´ S, 60° 44´ W
Rosario (Rosario, Santa Fe) 32° 57´ S, 60° 40´ W
Rufino (General López, Santa Fe) 34° 09´ S, 62° 50´ W
Ruinas de Santa Fe La Vieja, Cayastá (Garay, Santa Fe) 31° 12´ S, 60° 10´ W
Ruiz de los Llanos (Candelaria, Salta) 26° 07´ S, 65° 17´ W
Ruta 11, 13 km al Sur de Clorinda (Pilcomayo, Formosa) 26° 30´ S, 57° 45´ W
Ruta 188 km 116 (Rojas, Buenos Aires) 34° 11´ S, 60° 42´ W
Ruta 226 ditch, km 74 (Balcarce, Buenos Aires) 37° 50´ S, 58° 20´ W
Salar Cauchari, 31 km al Norte de Cauchari, sobre ruta 70, 3,840 m (Susques, Jujuy) 23° 58´ S, 66° 47´ W
Salinas de Bebedero, 15 km SE (Capital, San Luis) 33° 37´ S, 66° 35´ W

Salinas de Diamante (San Rafael, Mendoza) 34° 55´ S, 69° 00´ W
Salta (Capital, Salta) 24° 47´ S, 65° 25´ W
San Antonio (Jiménez, Santiago del Estero) 26° 40´ S, 64° 15´ W
San Carlos (San Carlos, Mendoza) 33° 46´ S, 69° 02´ W
San Cayetano, CAPRIM (Capital, Corrientes) 27° 28´ S, 58° 50´ W
San Fernando (San Fernando, Buenos Aires) 34° 26´ S, 58° 34´ W
San Fernando (Trancas, Tucumán) 26° 22´ S, 65° 27´ W
San Francisco del Monte de Oro, 1480 ft (Ayacucho, San Luis) 32° 36´ S, 66° 08´ W
San Ignacio (La Cocha, Tucumán) 27° 43´ S, 65° 40´ W
San Ignacio, desembocadura de Arroyo Yabebiry (San Ignacio, Misiones) 27° 17´ S, 55° 30´ W
San Javier (San Javier, Misiones) 27° 53´ S, 55° 08´ W
San Javier, Estación Biológica R. Schreiter (Yerba Buena, Tucumán) 26° 47´ S, 65° 23´ W
San Javier, Pozo largo 19 km SE Joaquín V González (Anta, Salta) 25° 00´ S, 65° 13´ W
San José (Tulumba, Córdoba) 30° 22´ S, 63° 56´ W
San José (Formosa) 25° 15’ S, 58° 15’ W
San Martín (San Martín, Mendoza) 33° 04´ S, 68° 28´ W
San Martín, Distrito Buen Orden (San Martín, Mendoza) 33° 04´ S, 68° 28´ W
San Miguel de Tucumán (Capital, Tucumán) 26° 49´ S, 65° 13´ W
San Nicolás (San Nicolás, Buenos Aires) 33° 20´ S, 60° 13´ W
San Pablo, 11 km al NO (Lules, Tucumán) 26° 52´ S, 65° 25´ W
San Pedro (Misiones) 26° 38’ S, 54° 08’ W
San Pedro de Colalao (Trancas, Tucumán) 26° 14´ S, 65° 29´ W
San Rafael (San Rafael, Mendoza) 34° 36´ S, 68° 20´ W
San Salvador de Jujuy (Dr. Manuel Belgrano, Jujuy) 24° 12´ S, 65° 19´ W
San Vicente (San Vicente, Buenos Aires) 35° 05´ S, 58° 30´ W
Santa Bárbara (Santa Bárbara, Jujuy) 24° 17´ S, 64° 24´ W
Santa Clara del Mar (Mar Chiquita, Buenos Aires) 37° 50´ S, 57° 30´ W
Santa Rita, 2 km al NW sobre ruta provincial 1 (San Pedro, Jujuy) 24° 28´ S, 64° 50´ W
Santa Rita, 4 km al NW sobre ruta provincial 1 (San Pedro, Jujuy) 24° 27´ S, 64° 50´ W
Santa Rosa (Capital, La Pampa) 36° 37´ S, 64° 17´ W
Santa Rosa (Santa Rosa, Mendoza) 33° 15´ S, 68° 09´ W
Santa Rosa de Leales (Leales, Tucumán) 27° 09´ S, 65° 15´ W
Santa Teresa, 30 km W of San Ignacio (San Ignacio, Misiones) 27° 16’ S, 55° 32’ W
Santo Domingo (Capital, Santiago del Estero) 28° 07´ S, 64° 13´ W
Santo Tomé (Capital, Santa Fe) 31° 39´ S, 60° 46´ W
Sarmiento (Chubut) 45° 36’ S, 69° 05’ W
Sauce Viejo, Santo Tomé (Santo Tomé, Corrientes) 28° 43´ S, 56° 27´ W
SE Corrientes, at Centro Argentino de Primates (Capital, Corrientes) 27° 28´ S, 58° 50´ W
Seccional Yacui, Parque Nacional Iguazú (Iguazú, Misiones) 25° 39´ S, 54° 20´ W
Sendero Yacaratiá, Parque Nacional Iguazú (Iguazú, Misiones) 25° 39´ S, 54° 20´ W
Sierra de La Tinta (Benito Juárez, Buenos Aires) 37° 37´ S, 59° 33´ W
Sierra de la Ventana (Tornquist, Buenos Aires) 38° 09´ S, 61° 48´ W
Sierra de Tilcara (Tilcara, Jujuy) 23° 35´ S, 65° 12´ W
Sierras de Curamalal, Abra del Hinojo (Saavedra, Buenos Aires) 37° 28´ S, 62° 06´ W
Sierras de las Quijadas (Belgrano, San Luis) 32° 30´ S, 67° 08´ W

Sierras de Medina, Aguas Chiquitas, El Cadillal (Burruyacú, Tucumán) 26° 37′ S, 65° 12′ W
Sobre ruta 9 en el límite con Salta, sobre camino a El Carmen (El Carmen, Jujuy) 24° 28′ S, 65° 21′ W
Sunchal, Sierra de Santa Bárbara (Santa Bárbara, Jujuy) 24° 14′ S, 64° 27′ W
Sunchal, Sierra Santa Bárbara, 1,200 m (Santa Bárbara, Jujuy) 24° 14′ S, 64° 27′ W
Sunchal, Sierra Santa Bárbara, 1,200 m (Santa Bárbara, Jujuy) 24° 14′ S, 64° 27′ W
Tabacal (Orán, Salta) 23° 15′ S, 64° 15′ W
Tafí del Valle (Tafí del Valle, Tucumán) 26° 52′ S, 65° 41′ W
Tafí Viejo (Tafí Viejo, Tucumán) 26° 44′ S, 65° 16′ W
Tambo Nuevo (Pergamino, Buenos Aires) 34° 00′ S, 60° 35′ W
Tapia (Trancas, Tucumán) 26° 36′ S, 65° 18′ W
Tartagal (General San Martín, Salta) 22° 32′ S, 63° 49′ W
Tela Cruz, Río de Los Sauces (Calamuchita, Cordoba) 32° 32′ S, 64° 36′ W
Termas de Río Hondo (Río Hondo, Santiago del Estero) 27° 29′ S, 64° 52′ W
Terrenos del INTA (Instituto Nacional de Tecnología Agropecuaria) (Balcarce, Buenos Aires) 37° 50′ S, 58° 20′ W
Tostado (9 de Julio, Santa Fe) 29° 14′ S, 61° 46′ W
Tres Arroyos (Tres Arroyos, Buenos Aires) 38° 23′ S, 60° 17′ W
Tucumán, 450 m (Capital, Tucumán) 26° 50′ S, 65° 13′ W
Tudcum nacedero (Iglesias, San Juan) 30° 12′ S, 69° 15′ W
Tumbaya (Tumbaya, Jujuy) 23° 51′ S, 65° 28′ W
Tupungato (Tupungato, Mendoza) 33° 22′ S, 69° 08′ W
Urdampilleta (Buenos Aires) 36° 27’ S, 61° 26’ W
Vado de Arrazayal, 20 km al NW de Aguas Blancas (Orán, Salta) 22° 40′ S, 64° 37′ W
Villa Ana (General Obligado, Santa Fe) 28° 29′ S, 59° 37′ W
Villa Carolina, Río Lavayén, 500 m (San Pedro, Jujuy) 24° 16′ S, 64° 43′ W
Villa Elisa (Colón, Entre Ríos) 32° 09′ S, 58° 20′ W
Villa Elisa, Arroyo Perucho Verna (Colón, Entre Ríos) 32° 09′ S, 58° 20′ W
Villa Gesell (Villa Gesell, Buenos Aires) 37° 15′ S, 56° 55′ W
Villa Guillermina (General Obligado, Santa Fe) 28° 20′ S, 59° 32′ W
Villa La Punta (Choya, Santiago del Estero) 28° 23′ S, 64° 45′ W
Villa Mercedes (General Pedernera, San Luis) 33° 40′ S, 65° 28′ W
Villa Nougués (Lules, Tucumán) 26° 51′ S, 65° 23′ W
Villa Nougués, San Pablo (Lules, Tucumán) 26° 51′ S, 65° 23′ W
Villa Unión (Coronel F. Varela, La Rioja) 29° 18′ S, 68° 12′ W
Villavicencio (Las Heras, Mendoza) 32° 31′ S, 69° 01′ W
Virgen del Valle Picnic area on Highway 64 between Santa Catalina and La Puerta Chiquita (Guasayán, Santiago del Estero) 28° 10′ S, 64° 45′ W
Yacanto, 1150 m (Calamuchita, Córdoba) 32° 03′ S, 65° 03′ W
Yerba Buena (Yerba Buena, Tucumán) 26° 45′ S, 65° 21′ W
Yuchán (San Pedro, Jujuy) 24° 12′ S, 64° 51′ W
Yuto (Ledesma, Jujuy) 23° 38′ S, 64° 28′ W
Zapala, 1062 m (Zapala, Neuquén) 38° 54′ S, 70° 04′ W
Zárate (Zárate, Buenos Aires) 34° 06′ S, 59° 02′ W
Zelaya (Luján, Buenos Aires) 34° 21′ S, 58° 52′ W
Zuviría (Chicoana, Salta) 25° 05′ S, 65° 29′ W

LOCALITIES NOT FOUND

1 km W of jct. Hwy 14 and 2 de Mayo Road (Misiones)
6 km N km 514 of Hwy 20, 25 de Mayo (San Juan)
Arroyo Corrientes (Buenos Aires)
Arroyo Zaimán, Capital (Misiones)
Azul Benson Farm (Buenos Aires)
Baliza Caniu, Gral. Pueyrredón (Buenos Aires)
Baliza Caniu, Gral. Pueyrredón (Buenos Aires)
Baliza San Andrés, General Pueyrredón (Buenos Aires)
Cuarto Rio Victoria, Rt. 14, Km.265 (Misiones)
Cueval (Salta)
El Cruce, Apóstoles (Misiones)
El Rincón (Salta)
Estación Guerrero
Estancia Coropa, Goya (Corrientes)
Fco. Pampa (La Pampa)
Gral. Roca (La Rioja)
Guayaberá, Oberá (Misiones)
Hill Plot, 150 m, Balcarce (Buenos Aires)
INTA (Instituto Nacional de Tecnología Agropecuaria), Delta (Buenos Aires)
Isla Ella, Delta del Paraná (Buenos Aires) (For the location of this locality see Pardiñas et al., this volume)
Isla Ella, Paraná (Buenos Aires)
"Jujuy"
La invernada, Famatina (La Rioja)
La Invernada, Famatina Range, 3800 m, Famatina (La Rioja)
Laferrere (Buenos Aires)
Left bank of Rio Parana
Loncocava (Mendoza)
Los Mistoles (Cordoba)
"Mendoza"
"Misiones"
Mountains W of Yala (Jujuy)
NNE Formosa (Formosa)
Oeste Sierra San Javier (Tucumán)
Pto. Lima (Mendoza)
Puerto Schwelm (Misiones)
Río Cetalles (Cordoba)
"Río Negro"
San Pedro, Bariloche (Río Negro)
Sierra de la Peregrina (Buenos Aires)
South of Mar del Plata (Buenos Aires)
Tala Cañada, Pocho (Cordoba)
Totoral (Cordoba)
"Tucumán"
Urdampilleta (=La Torrecita) (Buenos Aires)

Valle del Rio Chico (Chubut)
Villa Ana (Chaco)

LITERATURE CITED

Abdala, F. N., D. A. Flores, and N. P. Giannini
2001 Post-weaning ontogeny of the skull of *Didelphis_albiventris*. Journal of Mammalogy 82:190-200.

Allen, J. A.
1900a Note on the generic names *Didelphis* and *Philander*. Bulletin of the American Museum of Natural History 13:185-190.

1900b Descriptions of new American marsupials. Bulletin of the American Museum of Natural History 13:191-199.

1901 A preliminary study of the North American opossum of the genus *Didelphis*. Bulletin of the American Museum of Natural History 14:149-180.

1902 A preliminary study of the South American opossums of the Genus *Didelphis*. Bulletin of the American Museum of Natural History 16:249-279.

Anderson, S.
1982 *Monodelphis kunsi.* Mammalian Species 190:1-3.

1997 Mammals of Bolivia: Taxonomy and distribution. Bulletin of the American Museum of Natural History 231:1-652.

Asher, J. R., I. Horovitz, and M. Sanchez-Villagra.
2004 First combined cladistic analysis of marsupial mammal interrelationships. Molecular Phylogenetics and Evolution 33:240-250.

Barquez, R. M., M. A. Mares, and R. A. Ojeda
1991 Mamíferos de Tucumán. Oklahoma Museum of Natural History. University of Oklahoma, Norman, Oklahoma, USA. 282 pp.

Beach, F. A.
1939 Maternal behavior of the pouchless marsupial *Marmosa cinerea*. Journal of Mammalogy 20:315-322.

Bertonatti, C., and J. Corcuera (eds.).
2001 Situación Ambiental Argentina 2000. Fundación Vida Silvestre Argentina. Buenos Aires, Argentina. 440 pp.

Biggers, J. D.
1966 Reproduction in male marsupials. Pp. 251-280 in Comparative Biology of Reproduction in Mammals (Roland, I. W., ed.). Academic Press, London, England.

Biggers, J. D., and E. D. DeLamater
1965 Marsupial spermatozoa: pairing in the epididymus. Nature 208:401-404.

Birney, E. C., and A. Monjeau
2003 Latitudinal variation in South American marsupial biology. Pp. 297-317 in Predators with Pouches: The Biology of Carnivorous Marsupials (Jones, M., C. Dickman, and M. Archer, eds.). CSIRO Publishing, Collingwood, Victoria, Australia.

Birney, E. C., J. A. Monjeau, C. J. Phillips, R. S. Sikes, and I. Kim
1996a *Lestodelphys halli*: new information on a poorly known Argentine marsupial. Mastozoología Neotropical 3:171-181.

Birney, E. C., R. S. Sikes, J. A. Monjeau, N. Guthman, and C. J. Phillips
1996b Comments on Patagonian marsupials from Argentina. Pp. 149-154 in Contributions in Mammalogy: A Memorial Volume Honoring Dr. J. Knox Jones, Jr. (Genoways, H. H., and R. J. Baker, eds.). Museum of Texas Tech University, Lubbock, Texas, USA.

Brack, A.
1962 La cuica de agua. Biota (Lima) 4:55-59.

Braun, J. K., and M. A. Mares
1995 A new genus and species of Phyllotine rodent (Muridae: Sigmodontinae: Phyllotini) from South America. Journal of Mammalogy 76:504-521.

Braun, J. K., R. A. Van Den Bussche, P. K. Morton, and M. A. Mares.
2005 Phylogenetic and biogeographic relationships of mouse opossums *Thylamys* (Didelphimorphia, Didelphidae) in southern South America. Journal of Mammalogy 86:147–159.

Brown, A. D., and H. R. Grau
1993 La Naturaleza y el Hombre en las Selvas de Montaña. Colección Nuestros Ecosistemas. Proyecto GTZ, Salta, Argentina. 143 pp.

Brown, B. A.
2004 Atlas of New World marsupials. Fieldiana: Zoology, new series 102:1-308.

Bublitz, J.
1987 Untersuchungen zur Systematik der Rezenten Caenolestidae Trouessart, 1898. Bonner Zoologische Monographien, 23:1-96.

Burkart, R., N. Bárbaro, R. Sánchez, and D. Gómez
1999 Eco-regiones de la Argentina. Parques Nacionales, Programa Desarrollo Institucional Ambiental, Buenos Aires, Argentina.

Busch, M., and F. O. Kravetz
1992 Diet composition of *Monodelphis dimidiata* (Marsupialia: Didelphidae). Mammalia 55:619-621.

Cabrera, A.
1916 El tipo de *Philander laniger* Desm. en el Museo de Ciencias Naturales de Madrid. Boletín de la Real Sociedad Española de Historia Natural 16:514-517.

1934 Dos nuevos micromamíferos del norte argentina. Notas preliminares del Museo de La Plata 3:123-128.

1957 Catálogo de los mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciencias Zoológicas 4:1-307.

Cabrera, A. L., and A. Willink
1973 Biogeografía de América Latina. Secretaría General de la Organización de los Estados Americanos. Serie de Biología, Monografía 13:1-122.

Cajal, J. L.
1976 Una población de *Didelphis albiventris* Lund según el método de Boguslavsky. Physis 35:243-249.

1981 Estudios preliminares sobre el área de acción en marsupiales (Mammalia, Marsupialia). Physis 40:27-37.

Capllonch, P., A. G. Autino, M. M. Díaz, R. M. Barquez, and M. Goytia
1996 Los mamíferos del Parque Biológico Sierra de San Javier, Tucumán, Argentina: observaciones sobre su sistemática y distribución. Mastozoología Neotropical 4:49-71.

Carvalho B., L. F. B. Oliveira, A. P. Nunes, and M. S. Mattevi
2002 Karyotypes of nineteen marsupial species from Brazil. Journal of Mammalogy 83: 58-70.

Castro-Arellano, I., H. Zarza, and R. A. Medellín
2000 *Philander opossum.* Mammalian Species 638:1-8.

Cerqueira, R.
1982 South American landscapes and their mammals, Pp 53-75 in Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, Special Publication Series, 6. University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

1985 The distribution of *Didelphis* in South America (Polyprotodontia, Didelphidae). Journal of Biogeography 12:135-145.

Cerqueira, R., and B. Lemos
2000 Morphometric differentiation between Neotropical black eared opossums, *Didelphis marsupialis*_and *D. aurita* (Didelphimorphia, Didelphidae). Mammalia 64:319-327.

Charles-Dominique, P.
1983 Ecology and social adaptations in didelphid marsupials: comparison with eutherians of similar ecology. Pp. 395-422 in Advances in the Study of Mammalian Behavior (Eisenberg, J. F., and D. G. Kleiman, eds.). Special Publications, American Society of Mammalogists 7.

Chébez, J. C., and E. Massoia
1996 Fauna Misionera. A Systematic and Zoogeographical Catalogue of the Vertebrate Fauna of the Province of Misiones (Argentina). L.O.L.A. (Literature of Latin America), Buenos Aires, Argentina. 320 pp.

Cirignoli, S.; C. A. Galliari, H. Merlo Alvarez; U. F. J. Pardiñas, and D. H. Podestá
2000 Pequeños mamíferos terrestres del Río de Oro (Chaco, Argentina). Resúmenes IX Jornadas Argentinas de Mastozoología, La Plata, Argentina.

Colgan, D. J.
1999 Phylogenetic studies of marsupials based on phosphoglycerate kinase DNA sequences. Molecular Phylogenetics and Evolution 11:13-26.

Contreras, J. R.
1973 La mastofauna de la Laguna Chasico, Provincia de Buenos Aires. Physis 32:215-219.

1979 Lista faunística preliminar de los vertebrados de la Reserva Ecológica Ñacuñan. IADIZA (Mendoza), Cuaderno Técnico, 1-79.

1982 Mamíferos de Corrientes. I. Nota preliminar sobre la distribución de algunas especies. Historia Natural 2:71-72.

1984 Notas sobre el género *Marmosa* en el Noreste Argentino (Marsupialia, Didelphidae). Historia Natural, 4:11-12.

Crespo, J.
1950 Nota sobre mamíferos de Misiones nuevos para la Argentina. Comunicaciones del Instituto Nacional de Investigación de las Ciencias naturales anexo al Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" 1(14):1-14.

1964 Dos mamíferos nuevos para la provincia de Cordoba. Neotrópica 10:62.

1974 Comentarios sobre nuevas localidades para Mamíferos de Argentina y de Bolivia. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," 11:13-31.

1982a Ecología de la comunidad de Mamíferos del Parque Nacional Iguazú, Misiones. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigación de las Ciencias Naturales 3:45-162.

1982b Introduccion a la ecologia de los mamiferos del Parque Nacional El Palmar, Entre Rios. Anales de Parques Nacionales 15:1-33.

da Fonseca, G. A. B., A. Pereira Paglia, J. Sanderson, and R. A. Mittermeier
2003 Marsupials of the New World: Status and conservation. Pp. 399-406 in Predators with Pouches: The Biology of Carnivorous Marsupials (Jones, M., C. Dickman, and M. Archer, eds). CSIRO Publishing, Collingwood, Victoria, Australia.

Davis, D. E.
1947 Notes on the life histories of some Brazilian mammals. Boletin Museu Nacional (Rio de Janeiro) 76:1-8.

Díaz, M. M.
1999 Mamíferos de la Provincia de Jujuy: Sistemática, Distribución y Ecología. Ph.D. Dissertation, Universidad Nacional de Tucumán, Tucumán, Argentina. 640 pp.

2000 Key to mammals of Jujuy Province, Argentina. Occasional Papers, Oklahoma Museum of Natural History 7:1-29.

Díaz, M. M., and R. M. Barquez (This volume)
The wild mammals of Jujuy Province, Argentina: Ssstematics and distribution. Pp. 417-578 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

Díaz, M. M., R. M. Barquez, J. K. Braun, and M. A. Mares
1999 A new species of *Akodon* from Northwestern Argentina. Journal of Mammalogy 80:786-798.

Díaz, M. M., J. K. Braun, M. A. Mares, and R. M. Barquez
1997 Key of mammals of Salta Province, Argentina. Occasional Papers of the Oklahoma Museum of Natural History 2:1-10.

2000 An update of the taxonomy, systematic, and distribution of the mammals of Salta Province, Argentina. Occasional Papers of the Oklahoma Museum of Natural History 10:1-52.

Díaz, M. M., D. A. Flores, and R. M. Barquez
2002 A new species of gracile mouse opossum, genus *Gracilinanus*, from Argentina. Journal of Mammalogy 83:824-833.

Eisenberg, J. F., and K. H. Redford
1999 Mammals of the Neotropics. Vol. 3. The Central Neotropics: Ecuador, Peru, Bolivia, Brasil. University of Chicago Press, Chicago, Illinois, USA. 609 pp.

Emmons, L. H., and F. Feer
1997 Neotropical Rainforest Mammals: A Field guide. University of Chicago Press, Chicago, Illinois, USA. 307 pp.

Enders, R. K.
1966 Attachment, nursing and survival of young in some didelphids. Pp. 195-203 in Comparative Biology of Reproduction in Mammals (Rowlands, I. W., ed.). Academic Press, New York, New York, USA.

Flores, D. A.
2003 Estudio Taxonómico y Zoogeográfico de los Marsupiales de Argentina. Ph.D. Dissertation. Universidad Nacional de Tucumán, Tucumán, Argentina. 325 pp.

Flores, D. A., and M. M. Díaz
2002 Extensión austral a la distribución conocida de *Micoureus constantiae* (Didelphimorphia, Didelphidae). Acta Zoológica Mexicana 86:239-242.

Flores, D. A., M. M. Díaz, and R. M. Barquez
2000 Mouse opossums (Didelphimorphia, Didelphidae) of northwestern Argentina: Systematics and distribution. Zeitschrift für Säugetierkunde 65:1-19.

Flores, D. A., N. P. Giannini, and F.N. Abdala
2003 Comparative cranial ontogeny of *Lutreolina crassicaudata* (Didelphidae). Acta Theriologica 48:1-9.

Fornes, A., and E. Massoia
1965 Micromamiferos (Marsupialia y Rodentia) recolectados en la localidad bonaerense de Miramar. Physis 25:99-108.

Galliari, C. A., U. J. F. Pardiñas, and F. J. Goin
1996 Lista comentada de los Mamíferos de Argentina. Mastozoología Neotropical 3:39-61.

Gardner, A. L.

1973 The systematics of the genus *Didelphis*_(Marsupialia: Didelphidae) in North and Middle America. Special Publications, The Museum, Texas Tech University 4:1-81.

1981 [Review of] The mammals of Suriname. Journal of Mammalogy 62:445-448.

1993 Order Didelphimorphia. Pp. 15-27 in Mammal Species of the World: A Taxonomic and Geographic Reference. Second edition (Wilson, D. E., and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C., USA.

2005 Order Didelphimorphia. Pp. 3-18 in Mammal Species of the World: A Taxonomic and Geographic Reference. Third Edition (Wilson, D. E., and D. M. Reeder, eds.). Johns Hopkins University Press, Baltimore, Maryland. USA

Gardner, A. L., and G. K. Creighton

1989 A new generic names for Tate's (1933) *microtarsus* group of South American Mouse Opossums (Marsupialia, Didelphidae). Proceedings of Biological Society of Washington 102:3-7.

Gardner, A. L., and J. Patton

1972 New species of *Philander* (Marsupialia: Didelphidae) and *Mimon* (Chiroptera: Phyllostomidae) from Perú. Occasional Papers of the Museum of Zoology 43:1-11.

Giannini, N., F. Abdala, and D. A. Flores

2004 Comparative postnatal ontogeny of the skull in *Dromiciops gliroides* (Marsupialia: Microbiotheriidae). American Museum Novitates 3460:1-17.

Goin, F. J.

1995 Los Marsupiales. Pp.162-179 in Evolución Biológica y Climática en la Región Pampeana Durante los Últimos Cinco Millones de Años, un Ensayo de Correlación con el Mediterráneo Occidental. Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciónes Científicas, Madrid, Spain.

González, E., and G. Fregueiro

1998 Primer registro de *Chironectes minimus* para Uruguay. Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo 12(192):1-8.

González, E., A. Saralegui, and G. Fregueiro

2000 The genus *Thylamys* Gray, 1843 (Didelphimorphia, Didelphidae) in Uruguay. Boletín de la Sociedad de Zoología de Uruguay 12:44-45.

González, J. C., R. Vera Marques, and S. M. Pacheco
1997 Ocorrência de *Micoureus cinereus paraguayanus* (Tate), (Mammalia, Didelphidia, Marmosidae), no Rio Grande do Sul, Brasil. Revista Brasileira de Zoologia 14:195-200.

Graipel, M, P. R. M. Miller, and A. Ximenez
1996 Contribuçao a identificaçao das subespecies de *Lutreolina crassicaudata* (Desmarest) (Marsupialia, Mammalia). Revista Brasileira de Zoología 13:781-790.

Heinonen, S., and A. Bosso
1994 Nuevos aportes para el conocimiento de la mastofauna del Parque Nacional Calilegua. Mastozoología Neotropical 1:51-60.

Heinonen Fortabat, S. H., and J. C. Chébez
1997 Los mamíferos de los Parques Nacionales de la Argentina. Monografía Especial, L.O.L.A. (Literature of Latin America), Buenos Aires 14:1-70.

Hershkovitz, P.
1949 Generic names of the four-eyed pouch opossum and the woolly opossum (Didelphidae). Proceedings of the Biological Society of Washington 62:11-12.

1951 Mammals from British Honduras, Mexico, Jamaica and Haiti. Fieldiana: Zoology, 31:547-570.

1969 The evolution of mammals in southern continents. VI. The Recent mammals of the Neotropical Region: zoogeographical and ecological review. Quarterly Review of Biology 44:1-70.

1976 Comments of generic names of four-eyed opossums (Family Didelphidae). Proceedings of the Biological Society of Washington 89:295-304.

1981 *Philander* and four-eyed opossum once again. Proceedings of the Biological Society of Washington, 93:943-946.

1992a The South American gracile mouse opossums, Genus *Gracilinanus* Gardner and Creighton, 1989 (Marmosidae, Marsupialia): A taxonomic review with notes on general mkorphology and relationships. Fieldiana: Zoology, new series 70:1-56.

1992b Ankle bones: the Chilean opossum *Dromiciops gliroides* Thomas, and marsupial phylogeny. Bonner Zoologische Beitrage 43:181-213.

1997 Composition of the Family Didelphidae Gray, 1821 (Didelphimorphia, Marsupialia), with a review of the morphology and behavior of the included four-eyed pouched opossum of the genus *Philander* Tiedemann, 1808. Fieldiana: Zoology, new series 86:1-103.

1999 *Dromiciops gliroides* Thomas, 1894, Last of the Microbiotheria (Marsupialia), with a review of the Family Microbiotheriidae. Fieldiana: Zoology, new series 93:1-60.

Hildebrand, M.
1961 Body proportions of didelphids (and some other) marsupials, with emphasis on variability. American Journal of Anatomy 109:239-249.

Hill, J. P., and E. A. Fraser
1925 Some observations on the female urogenital organs of the Didelphydae. Proceedings of the Zoological Society of London 14:189-219.

Holmberg, E. L.
1898 La fauna de la República Argentina. Pp. 383-602 in Segundo Censo de la República Argentina 10-V-1895. Volumen 1. Territorios, I, parte 6..

Horovitz, I., and M. R. Sanchez-Villagra
2003 A morphological analysis of marsupial mammal higher-level phylogenetic relationships. Cladistics 19:181-212.

Hunsaker II, D.
1977 The ecology of New World marsupials. Pp. 95-153 in The Biology of Marsupials (Hunsaker II, D., ed.). Academic Press, New York and London.

Husson, A. M.
1978 The mammals of Suriname. Zoölogische Monographieën van het Rijksmuseum van Natuurlijke Historie 2:1-569.

Jansa, S. A., and R. S. Voss
2000 Phylogenetic studies on didelphid marsupials. I. Introduction and preliminary results from nuclear IRBP gene sequences. Journal of Mammalian Evolution 7:43-77.

Jayat, P., and D. Miotti
2005 Primer registro de *Monodelphis kunsi* (Didelphimorphia, Didelphidae) para Argentina. Mastozoologia Neotropical 12:253-256.

Kantis, E.
1963 Nueva localidad para marsupiales didelfidos coleccionados en el Chaco. Neotropica 9:54.

Keegan, R. A., and J. M. Keegan
1993 Atlas de la República Argentina. Agrupación de diarios del Interior, S. A., Buenos Aires, published by Editorial Antártica, Chile.

Kelt, D. A.
2000 Small mammal communities in rainforest fragments in central southern Chile. Biological Conservation 92:345-358.

Kelt, D. A., and D. R. Martínez
1989 Notes on distribution and ecology of two marsupials endemic to the Valdivian forests of southern South America. Journal of Mammalogy 70:220-224.

Kelt, D. A., P. L. Meserve, B. D. Patterson, and B. K. Lang
1999 Scale dependence and scale independence in habitat associations of small mammals in southern temperate rainforest. Oikos 85:320-334.

Kirsch, J. A. W.
1977 The classification of marsupials. Pp 1-48 in The Biology of Marsupials (Hunsaker II, D., ed.). Academic Press, New York and London.

Kirsch, J. A. W., A. W. Dickerman, and O. A. Reig
1996 DNA/DNA Hybridization studies of carnivorous marsupials IV. Intergeneric relationships of the opossum (Didelphidae). Marmosiana 1:57-78.

Kirsch, J. A.W., A.W. Dickerman, O.A. Reig, and M. S. Springer
1991 DNA hybridization evidence for the Australian affinity of the American marsupial *Dromiciops australis*. Proceedings of the National Academy of Science (USA) 88:10465-10469.

Kirsch, J. A. W., and R. E. Palma
1995 DNA/DNA hybridization studies of carnivorous marsupials. V. A further estimate of relationships among opossums (Marsupialia, Didelphidae). Mammalia 59:403-425.

Klijn, F., and Udo de Haes
1994 A hierarchical approach to ecosystems and its implications for ecological land classification. Landscape Ecology 9:89-104.

Krieg, H.
1924 Beobachtungen an argentineshen Beutelratten. Zeitchrift für Morphologie und Ökologie der Tiere 1:637-659.

Krumbiegel, I.
1941a Die Säugetiere der Sudamerika Expeditionen Prof. Dr. Kriegs. 10. Opossums (*Didelphys*). Zoologisher Anzeiger 134:29-53.

1941b Die Säugetiere der Sudamerika Expeditionen Prof. Dr. Kriegs. 11. Mittelgross Didelphyiden (*Lutreolina* u *Metachirus*). Zoologisher Anzeiger 134:189-211.

Lemos, B., and R. Cerqueira
2002 Morphological differentiation of the white-eared opossum group (Didelphidae: *Didelphis*). Journal of Mammalogy 83:354-369.

Lew, D., and R. Pérez-Hernández
2004 Nueva especie del género *Monodelphis* (Didelphimorphia: Didelphidae) de la sierra Lema Venezuela. Memoria de la Fundación La Salle de Ciencias Naturales 159-160:7-25

Lew, D, R. Perez Hernandez, and J. Ventura
2006 Two new species of *Philander* (Didelphimorphia, Didelphidae) from Northern South America. Journal of Mammalogy, 87:224-237.

Linares, O. J.
1998 Mamíferos de Venezuela. Sociedad Conservacionista Audubon de Venezuela, Caracas. 691 pp.

Mann Fisher, G.
1978 Los pequeños mamíferos de Chile (marsupiales, quirópteros, edentados y roedores). Gayana, Zoología 40:1-342.

Mares, M. A.
1973 Desert rodent ecology. Review for origin and structure of ecosystems convergent evolution research program. Acta Zoológica Lilloana 30:207-225.

Mares, M. A., R. M. Barquez, J. K. Braun, and R. A. Ojeda
1996 Observations on the mammals of Tucumán Province, Argentina. I. Systematics, distribution, and ecology of the Didelphimorphia, Xenarthra, Chiroptera, Primates, Carnivora, Perissodactyla, Artiodactyla, and Lagomorpha. Annals of Carnegie Museum 65:89-152.

Mares, M. A., and J. K. Braun
1996 A new species of Phyllotine rodent, genus *Andalgalomys* (Muridae: Sigmodontinae), from Argentina. Journal of Mammalogy 77:928-941.

2000 Systematics and natural history of marsupials from Argentina. Pp. 23-47 in Reflections of a Naturalist: Papers Honoring Professor Eugene D. Fleharty (Choate, J. R., ed.). Fort Hays Studies, Special Issue 1.

Mares, M. A., J. K. Braun, R. M. Barquez, and M. M. Díaz
2000 Two new genera and species of halophytic desert mammal from isolated salt flats in Argentina. Occasional Papers, The Museum, Texas Tech University 203:1-27.

Mares, M. A., R. A. Ojeda, and R. M. Barquez

1989 Guide to the Mammals of Salta Province of Argentina. Guía de los Mamíferos de la Provincia de Salta. University of Oklahoma Press, Norman, Oklahoma, USA. 303 pp.

Mares, M. A., R. A. Ojeda, J. K. Braun, and R. M. Barquez

1997 Systematics, distribution, and ecology of the mammals of Catamarca Province, Argentina: Pp. 89-141 in Life Among the Muses: Papers in Honor of James S. Findley (Yates, T. L., W. L. Gannon, and D. E. Wilson, eds.). Special Publication, Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, USA.

Mares, M. A., R. A. Ojeda, and M. P. Kosco

1981 Observations on the distribution and ecology of the mammals of Salta Province, Argentina. Annals of Carnegie Museum 50:151-206.

Marshall, L. G.

1977 *Lestodelphys halli*. Mammalian Species, 81:1-3.

1978a *Lutreolina crassicaudata.* Mammalian Species, 91:1-4.

1978b *Chironectes minimus*. Mammalian Species, 109:1-6.

1978c *Dromiciops australis.* Mammalian Species, 99:1-5.

1981 The families and genera of Marsupialia. Fieldiana:geology, new series 7:1-65.

Martin, G.

2003 Nuevas localidades para marsupiales patagónicos (Didelphimorphia y Microbiotheria) en el noroeste de la provincia del Chubut, Argentina. Mastozoología Neotropical 10:148-153.

Massoia, E.

1970 Contribución al conocimiento de los mamíferos de Formosa con noticias de los que habitan zonas vinaleras. INTA (Instituto Nacional de Tecnología Agropecuaria), IDIA, 276:55-63.

1972 La presencia de *Marmosa cinerea paraguayana* en la República Argentina, Provincia de Misiones (Mammalia-Marsupialia-Didelphidae). Revista de Investigaciones Agropecuarias, Serie 1, Biología y Producción Animal 9:63-70.

1973 Observaciones sobre el género *Lutreolina* en la República Argentina (Mammalia-Marsupialia-Didelphidae). Revista de Investigaciones Agropecuarias, Serie 1, Biología y Producción Animal 10:13-20.

1976 Mammalia. In: Fauna de Agua Dulce de la República Argentina (Ringuelet, R., ed.), FECIC (Fundación para la Educación, la Ciencia y la Cultura), Buenos Aires 44:128 pp.

1980 Mammalia de Argentina. I. Los mamíferos silvestres de la Provincia de Misiones. Iguazú 1:15-43.

Massoia, E., A. Forasiepi, and P. Teta
2000 Los Marsupiales de Argentina. L.O.L.A. (Literature of Latin America), Buenos Aires, Argentina. 71 pp.

Massoia, E., and A. Fornes
1967 El estado sistemático, distribución geográfica y datos etoecológicos de algunos mamíferos neotropicales (Marsupialia y Rodentia) con la descripción de *Cabreramys* (género nuevo) (Cricetidae). Acta Zoológica Lilloana 23:407-430.

1972 Presencia y rasgos etoecológicos de *Marmosa agilis chacoensis* Tate en las provincias de Buenos Aires, Entre Ríos y Misiones (Mammalia-Marsupialia-Didelphidae). Revista de Investigaciones Agropecuarias, serie 1, Biología y Producción Animal 9:72-82.

Massoia, E., and J. A. Latorraca
1992 Contributión al conocimiento de la mastofauna reciente de la Provincia de Santiago del Estero-1. Boletín Científico, Asociación para la Protección de la Naturaleza (APRONA) 23:49-57.

Massoia, E., O. Vaccaro, C. Gallari, and S. Ambrossini
1987 La mastofauna del Río Uruguay - I, provincia de Misiones. Instituto Nacional de Investigaciones de Ciencias Naturales, Zoología 14:111-124.

McNab, B. K.
1982 The physiological ecology of South American mammals. Pp. 187-207 in Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, Special Publication Series, 6. University of Pittsburgh, Pennsylvania, USA.

Meserve, P. L., B. K. Lang, and B. D. Patterson
1988 Trophic relationships of small mammals in a Chilean temperate rainforest. Journal of Mammalogy 69:721-730.

Meserve, P. L., R. Murua, O. Lopetegui, and J. R. Rau
1982 Observations on the small mammals fauna in a primary temperate rain forest in southern Chile. Journal of Mammalogy 63:315-317.

Mondolfi, E., and G. Medina Padilla

1958 Contribución al conocimiento del "perrito de agua" (*Chironectes minimus* Zimermann). Memoria de la Sociedad de Ciencias Naturales La Salle 17:140-155.

Monjeau, J. A., E. C. Birney, N. Guthmann, and C. J. Philips

1997 Small mammal community composition within the major landcape divisions of Patagonia, Southern Argentina. Mastozoología Neotropical 1:113-127.

Monjeau, J. A., N. Bonino, and S. Saba

1994 Annotated checklist of the living land mammals in Patagonia, Argentina. Mastozoología Neotropical 1:143-156.

Noss, A., M. A. Mares, and M. M. Díaz

2002 El Chaco/The Chaco. Pp. 165-172 in Areas Silvestres: las Ultimas Regiones Vírgenes del Mundo/Wilderness: Earth's Last Wild Places (Mittermeier, R. A., C. G. Mittermeier, P. Robles Gil, J. Pilgrim, G. A. B. da Foseca, T. Brooks, and W. R. Konstant, eds.). CEMEX (Monterrey), Conservation International (Washington, D.C.) and Agrupación Sierra Madre (México City).

Nowak, R. M.

1991 Walker's mammals of the world. Fifth ed. Johns Hopkins University Press., Baltimore and London 1:1-642.

Ojeda, R. A., and M. A. Mares

1989 A biogeographic analysis of the mammals of the Salta Province, Argentina: patterns of species assemblage in the Neotropics. Special Publications, The Museum, Texas Tech University 27:1-66.

Oliver, W. L. R.

1976 The management of yapoks (*Chironectes minimus*) at Jersey Zoo, with observations on their behavior. Jersey Wildlife Preservation Trust Annual Report 13:32-36.

Olrog, C. C.

1959 Notas mastozoológicas. II. Sobre la Colección del Instituto Miguel Lillo. Acta Zoológica Lilloana 17:403-419.

1976 Sobre mamíferos del Noroeste Argentino. Acta Zoológica Lilloana 32:5-14.

1979 Los mamíferos de la Selva húmeda, Cerro Calilegua, Jujuy. Acta Zoológica Lilloana 33:9-14.

Olrog, C. C., and M. M. Lucero
1981 Guía de los Mamíferos Argentinos. Ministerio de Cultura y Educación, Fundación Miguel Lillo, Tucumán, Argentina. 151 pp.

Osgood, W. H.
1924 Review of living caenolestids with description of a new genus from Chile. Field Museum of Natural History, Zoology series 14:165-172.

Palma, R. E.
1995 Range expansion of two South American mouse opossum (*Thylamys*, Didelphidae) and their biogeographic implications. Revista Chilena de Historia Natural 68:515-522.

2003 Evolution of American marsupials and their phylogenetic relationships with Australian metatherians. Pp. 21-29 in Predators with Pouches: the Biology of Carnivorous Marsupials (Jones, M., C. Dickman, and M. Archer, eds.). CSIRO Publishing, Collingwood, Victoria, Australia.

Palma, R. E., E. Rivera-Milla, T. L. Yates, P. A. Marquet, and A. P. Meynard
2002 Phylogenetic and biogeographic relationships of the mouse opossum *Thylamys* (Didelphimorphia, Didelphidae) in southern South America. Molecular Phylogenetics and Evolution 25:245–253

Palma, R. E., and A. E. Spotorno
1999 Molecular systematics of marsupials based on the rRNA 12S mitochondrial gene: the phylogeny of Didelphimorphia and the living fossil Microbiotheriid *Dromiciops gliroides* Thomas. Molecular Phylogenetics and Evolution 13:525-535.

Palma, R. E., and T. Yates
1998 The chromosomes of Bolivian didelphid marsupials. Occasional Papers, The Museum, Texas Tech University 162:1-8.

Ulyses F. J. Pardiñas, Pablo Teta, Guillermo D'Elía, Sebastián Cirignoli, and Pablo E. Ortiz (This volume)
Resolution of Some Problematic Type Localities for Sigmodontine Rodents (Cricetidae, Sigmodontinae) / Resolución de Algunos Problemas Relativos a Localidades Típicas de Roedores Sigmodontinos (Cricetidae, Sigmodontinae). Pp. 391-416 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

Patterson, B., and M. Gallardo
1987 *Rhyncholestes raphanurus*. Mammalian Species 286:1-5.

Patton, J. L., and L. P. Costa

2003 Molecular phylogeography and species limits in rainforest didelphid marsupials of South America. Pp. 63-81 in Predators with Pouches: The Biology of Carnivorous Marsupials (Jones, M., C. Dickman, and M. Archer, eds). CSIRO Publishing, Collingwood, Victoria, Australia.

Patton, J. L., and M. N. F. da Silva.

1997 Definition of species of pouched four-eyed opossums (Didelphidae, *Philander*). Journal of Mammalogy 78:90-102.

Paynter, Jr., R. A.

1985 Ornithological Gazetteer of Argentina. Bird Department, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts., USA. 507 pp.

Pearson, O. P.

1995 Annotated keys for identifying small mammals living in or near Nahuel Huapi National Park or Lanin National Park, Southern Argentina. Mastozoología Neotropical 2:99-148.

Pearson, O. P., and A. K. Pearson

1982 Ecology and biogeography of the southern rainforest of Argentina. Pp. 129-142 in Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, Special Publication Series, 6. University of Pittsburgh, Pennsylvania, USA.

Pérez Hernández, R.

1985 Notas preliminares acerca de la taxonomía de la Familia Didelphidae (Mammalia, Marsupialia) en Venezuela. Memoria de la Sociedad de Ciencias Naturales La Salle 123: 47-46.

Pine, R. H.

1973 Anatomical and nomenclatural notes on opossums. Proceedings of the Biological Society of Washington 86:391-402.

1977 *Monodelphis iheringi*_(Thomas) is a recognizable species of Brazilian opossum (Mammalia: Marsupialia: Didelphidae). Mammalia 41:235-237.

Pine, R. H., and J. P. Abravaya

1978 Notes on the Brazilian opossum *Monodelphis scalops* (Thomas) (Mammalia: Didelphidae). Mammalia 42:379-382.

Pine, R. H., P. L. Dalby, and J. O. Matson

1985 Ecology, postnatal development, morphometrics, and taxonomic status of the short-tailed opossum, *Monodelphis dimidiata*, an apparently semelparous annual marsupial. Annals of Carnegie Museum 54:195-231.

Pine, R. H., S. D. Miller, and M. L. Schamberger
1979 Contributions to the mammalogy of Chile. Mammalia 43:339-376.

Rebin, J. A. G.
1901 The application of *Didelphis marsupialis* Linnaeus. American Naturalist 35:147-149.

Redford, K. H., and J. F. Eisenberg
1992 Mammals of the Neotropics. Vol. 2, The Southern Cone: Chile, Argentina, Uruguay, Paraguay. University of Chicago Press, Chicago, Illinois, USA. 430 pp.

Reid, F. A.
1997 A Field Guide to the Mammals of Central America and Southeast Mexico. Oxford University Press, New York, New York. 334 pp.

Reig, O. A.
1955 Noticia preliminar sobre la presencia de microbiotherinos vivientes en la fauna sudamericana. Investigaciones Zoológicas Chilenas 2:127-130.

1959 El segundo ejemplar conocido de *Lestodelphys halli* (Thomas) (Mammalia, Didelphydae). Neotropica 5:57-58.

1964 Roedores y marsupiales del Partido Gral. Pueyrredón y regiones adyacentes (Provincia de Buenos Aires, Argentina). Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata 1:203-224.

Reig, O. A., and N. O. Bianchi
1969 The occurrence of an intermediate didelphid karyotype in the short-tailed opossum (genus *Monodelphis*). Experientia 25:1210-1211.

Reig, O. A., A. Gardner, N. Bianchi, and J. L. Patton
1977 The chromosomes of the Didelphidae (Marsupialia) and their evolutionary significance. Biological Journal of Linnean Society 9:191-216.

Reig, O. A., J. A. W. Kirsch, and L. G. Marshall
1985 New conclusions on the relationships of the opossum-like marsupials, with an annotated classification of the Didelphimorphia. Ameghiniana 21:335-343.

1987 Systematic relationships of the living and Neocenozoic American opossum-like marsupials (suborder Didelphimorphia) with comments on the classification of these and of the Cretaceous and Paleocene New World and European metatherians. Pp. 1-92 in Possums and Opossums: Studies in Evolution (Archer, M., ed.). Surrey Beatty and Sons Pty. Ltd. and Royal Zoological Society of New South Wales, Sydney, Australia.

Retief, J. D., C. Krajewski, M. Westerman, R. J. Winkfein, and G. H. Dixon
1995 Molecular phylogeny and evolution of marsupial protamine P1 genes. Proceedings of the Royal Society of London 259:7-14.

Roig, V. G.
1965 Elenco sistemático de las aves y mamíferos de la Provincia de Mendoza y notas sobre su distribución geográfica. Boletín de Estudios Geográficos 12:175-222.

Rosenthal, M.
1975 Observations on the water opossum or yapok *Chironectes minimus*_in captivity. The International Zoo Yearbook 15:4-6.

Rougier, G. W., J. R. Wible, and M. J. Novacek
1998 Implications of *Deltatheridium* specimens for early marsupial history. Nature, 396:459-463.

Ruggiero, A.
1999 Spatial patterns in the diversity of mammal species: a test of the geographic area hypothesis in South America. Ecoscience 6: 338-354.

Shamel, H. H.
1930a A new murine opossum from Argentina. Journal of the Washington Academy of Sciences 20:83-84.

1930b A new name for *Marmosa muscula* Shamel. Journal of Mammalogy 11:311.

Simpson, G. G.
1972 Didelphidae from the Chapadmalal Formation in the Museo Municipal de Ciencias Naturales of Mar del Plata. Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata 2:1-40.

Solari, S.
2003 Diversity and distribution of *Thylamys* (Didelphidae) in South America, with emphasis on species from the western side of the Andes. Pp. 82-101 in Predators with Pouches: The Biology of Carnivorous Marsupials (Jones, M., C. Dickman, and M. Archer, eds.). CSIRO Publishing, Collingwood, Victoria, Australia.

2004 A new species of *Monodelphis* (Didelphimorphia: Didelphidae) from southeastern Peru. Zeitschrift für Säugetierkunde 69:145-152.

Streilein, K. E.
1982 Ecology of small mammals in the semiarid Brazilian Caatinga. I. Climate and faunal composition. Annals of Carnegie Museum 51:79-107.

Szalay, F. S.

1982 A new appraisal of marsupial phylogeny and classification. Pp. 621-640 in Carnivorous Marsupials, Vol. 2 (Archer, M., ed.). Royal Zoological Society of New South Wales, Mosman, Australia.

1994 Evolutionary History of the Marsupials and an Analysis of Osteological Characters. Cambridge University Press, Cambridge, England. 481 pp.

Tate, G. H. H.

1933 A systematic revision of the marsupial genus *Marmosa*, with discussion of the adaptive radiation of the murine opossum (*Marmosa*). Bulletin of the American Museum of Natural History 46:1-250.

Thomas, O.

1888 Catalogue of the Marsupialia and Monotremata in the Collection of the British Museum of Natural History. Trustees of the British Museum, London 401 pp.

1894 On *Micoureus griseus*, Desm., with the description of a new genus and species of Didelphydae. Annals and Magazine of Natural History, ser. 6, 14:184-188.

1901 The generic names *Myrmecophaga* and *Didelphis*. American Naturalist 35:143-145.

1902 On mammals collected at Cruz del Eje, central Cordova, by Mr. P. O. Simons. Annals and Magazine of Natural History, ser, 7, 9:237-245.

1904 On the mammals collected by Mr. A. Robert at Chapada, Mato Grosso, (Percy Sladen Expedition to Central Brazil). Proceedings of the Zoological Society of London, 2:232-244.

1905 New Neotropical *Chrotopterus, Sciurus, Neacomys, Coendu, Proechimys,* and *Marmosa*. Annals and Magazine of Natural History, ser. 7, 16:308-314.

1910 A collection of mammals from eastern Buenos Ayres, with descriptions of related new mammals from other localities. Annals and Magazine of Natural History, ser. 8, 5:239-247.

1912 Three small mammals from S. America. Annals and Magazine of Natural History, ser. 8, 9:408-410.

1917 On small mammals from the delta of the Parana. Annals and Magazine of Natural History, ser. 8, 20:95-100.

1918 On small mammals from Salta and Jujuy, collected by Mr. E. Budin. Annals and Magazine of Natural History, ser. 9, 1:186-193.

1919a On some small mammals from Catamarca. Annals and Magazine of Natural History, ser. 9, 3:115-118.

1919b List of mammals from the Highlands of Jujuy, North Argentina, collected by Sr. E. Budin. Annals and Magazine of Natural History, ser. 9, 4:128-135.

1920a A further collection of Mammals from Jujuy. Annals and Magazine of Natural History, ser. 9, 5:188-196.

1920b On small mammals from Famatina Chain, northwest Rioja. Annals and Magazine of Natural History, ser. 9, 6:417-422.

1921 A new genus of opossum from southern Patagonia. Annals and Magazine of Natutal History, ser. 9, 8:136-139.

1923 The geographical races of *Lutreolina crassicaudata*. Annals and Magazine of Natural History, ser. 9, 11:583-585.

1926 The Spedan Lewis South American Exploration. III. On mammals collected by Sr. Budin in the province of Tucuman. Annals and Magazine of Natural History, ser. 9, 17:602-609.

1929 The mammals of Señor Budin's Patagonian expedition, 1927-1928. Annals and Magazine of Natural History, ser. 10, 4:35-45.

Thomas, O., and J. St. Leger
1926 The Spedan Lewis South American Expedition. V. Mammals obtained by Señor Budin in Neuquen. Annals and Magazine of Natural History, ser. 18, 9:635-641.

Tognelli, M. F., and D. A. Kelt
2004 Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. Ecography 27:427-436.

Vargas J., T. Tarifa, and C. Cortez
2003 Nuevos registros de *Monodelphis adusta* y *Monodelphis kunsi* (Didelphimorphia: Didelphidae) para Bolivia. Mastozoología Neotropical 10:123-131.

Vieira, C. O. da C.
1951 Xenartros e marsupiais do estado de São Paulo. Arquivos de Zoologia do Estado de São Paulo 7:325-362.

Voss, R. S., and L. H. Emmons
1996 Mammalian diversity in Neotropical lowland rainforests: a preliminary assessment. Bulletin of the American Museum of Natural History 230:1-115.

Voss, R. S., A. L. Gardner, and S. Jansa
2004 On the relationships of "*Marmosa*" *formosa* Shamel, 1930 (Marsupialia: Didelphidae), a phylogenetic puzzle from the Chaco of Northern Argentina. American Museum Novitates 3442:1-18.

Voss, R. S., and S. Jansa
2003 Phylogenetic studies on Didelphid Marsupials II. Nonmolecular data and new IRBP sequences: separate and combined analyses of Didelphine relationships with denser taxon sampling. Bulletin of the American Museum of Natural History 276:1-82.

Voss, R. S., D. P. Lunde, and S. Jansa
2005 On the contents of *Gracilinanus* Gardner and Creighton, 1989, with the description of a previously unrecognized clade of small didelphid marsupials. American Museum Novitates 3482:1-34.

Voss, R. D., D. P. Lunde, and N. B. Simmons
2001 The Mammals of Paracou, French Guiana: a neotropical lowland rainforest fauna, Part 2: Nonvolant species. Bulletin of the American Museum of Natural History 263:1-236.

Wagner, J. A.
1843 Die Säugthiere in Abbildungen nach der Natur mit Beschreibungen von Dr. Johann Christian Daniel Schreber. Erlangen, Germany, Supplementband, 3(1):xvi+610 pp.

Wainberg, R. L.
1972 Cariología y cariometría de *Monodelphis dimidiata* Wagner (Marsupialia, Didelphidae). Physis 31:327-336.

Wainberg, R. L., and T. G. de Fronza
1969 Análisis métrico de los cromosomas somáticos de *Lutreolina crassicaudata paranalis* Thomas (Marsupialia, Didelphidae). Physis 29:261-267.

Wainberg, R. L., and G. E. Hurtado
1973 Cromosomas de Marsupiales sudamericanos del género *Didelphis* (Marsupialia, Didelphidae). Cariometría de *Didelphis marsupialis aurita* Wied 1826. Physis 32:373-381.

Waterhouse, G.R.
1846 A Natural History of the Mammalia 1, Marsupialia, or Pouched Animals. Hippolyte Bailliere, London, England. 553 pp.

Webb, S.D., and L.G. Marshall
1982 Historical biogeography of recent South American land mammals. Pp. 39-52 in Mammalian Biology in South America (Mares, M., and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, Special Publication Series, 6. University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

Wetmore, A.

1926 Observations on the birds of Argentina, Paraguay, Uruguay and Chile. Bulletin of the United States National Museum 133:1-448.

Williams, D. F., and M. A. Mares

1978 A new genus and species of Phyllotine rodent (Mammalia, Muridae) from northwestern Argentina. Annals of Carnegie Museum 47:193-221.

Ximénez, A.

1967 Contribución al conocimiento de *Lutreolina crassicaudata* (Desmarest, 1804) y sus formas geográficas (Mammalia-Didelphidae). Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo 9(112):1-7.

Yepes, J.

1936a Mamíferos colectados en la parte central y occidental de la Provincia de La Rioja. Physis 12:31-42.

1936b Los mamíferos de Mendoza y sus relaciones con las faunas limítrofes. Novena Reunión de la Sociedad Argentina de Patología Regional 31:689-725.

1944 Comentarios sobre cien localidades nuevas para mamíferos sudamericanos. Revista Argentina de Zoografía 4:59-71.

THE ECOLOGY AND EVOLUTIONARY HISTORY OF *OLIGORYZOMYS LONGICAUDATUS* IN SOUTHERN SOUTH AMERICA

ECOLOGÍA E HISTORIA EVOLUTIVA DE *OLIGORYZOMYS LONGICAUDATUS* EN EL SUR DE SUDÁMERICA

R. Eduardo Palma, Fernando Torres-Pérez, and Dusan Boric-Bargetto

DEDICATION

In the latter half of the past century, Dr. Oliver Pearson conducted several memorable studies mainly in southern South America, involving various topics in the biology of mammals including natural history, systematics, ecology, biogeography, and evolutionary biology. How could we forget his amazing contribution to the natural history and evolution of small mammals in central and southern Patagonia? One of the most abundant components of the Patagonian small mammal fauna is the "rice rat" Oligoryzomys longicaudatus (best known now as "colilargo", the long-tailed mouse); during the 1980's, Oliver Pearson synthesized several ecological traits of this species. We thus believe that the "colilargo" remained in his eye.

ABSTRACT

Oligoryzomys longicaudatus is a conspicuous species of sigmodontine rodent from the southern cone of South America, inhabiting Mediterranean environments and both Temperate and Patagonian forests of Chile and Argentina. Life history traits, as well as morphological, chromosomal, and molecular tools, have been useful to determine the ecology and evolutionary relationships among populations, whose results are synthesized in this chapter. Across its range, *O. longicaudatus* exhibits high genetic homogeneity, in spite of inhabiting very distinctive ecogeographic areas across a wide latitudinal gradient. The evolutionary history of this species has been mediated primarily by the biogeographic events of the Pleistocene, with a narrow association to the expansion and retraction of Temperate Forests during the Quaternary. Ecological traits show that this species differentiates from other sympatric sigmodontines in characters such as its large home range, high vagility, and an almost exclusively granivorous diet. These characteristics acquire additional importance since this

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species constitutes the sole reservoir and vector of the Andes strain of Hantavirus, which causes a dangerous human disease.

Key words: *Oligoryzomys longicaudatus*, ecology, systematics, Argentina, Chile

RESUMEN

Oligoryzomys longicaudatus es un ratón común de los ambientes mediterráneos y bosques templados y patagónicos de Chile y Argentina. En este trabajo resumimos varios aspectos sobre la ecología, la historia natural y evolución de la especie. Aún cuando *O. longicaudatus* está ampliamente distribuido y habita diferentes regiones ecogeográficas, la especie mantiene una alta homogeneidad genética, lo que sugiere que su historia evolutiva ha estado influenciada principalmente por eventos biogeográficos del Pleistoceno, incluyendo una asociación estrecha con los eventos de expansión y retracción de los bosques templados durante el Cuaternario. Los estudios ecológicos sugieren que esta especie se diferencia de otros sigmodontinos simpátricos por poseer un ámbito de hogar amplio, alta vagilidad, y una dieta casi exclusivamente granívora. Estas características adquieren importancia adicional, dado que esta especie de roedor constituye el único reservorio de la cepa Andes del Hantavirus, el agente etiológico de un síndrome cardiopulmonar muy peligroso.

Palabras claves: *Oligoryzomys longicaudatus*, ecología, sistemática, Argentina, Chile

INTRODUCTION

Oligoryzomys longicaudatus (Bennet 1832) belongs to a genus of small-sized mice classified in the New World Tribe Oryzomyini (Muridae: Sigmodontinae). Musser and Carleton (1993) recognized 15 species distributed throughout the Neotropics from Mexico southward to Argentina and Chile. However, earlier taxonomic revisions recognized about 30 species (Tate, 1932), while Hershkovitz (1966) suggested that all then-named *Oligoryzomys* probably constituted a single species. Recent studies have documented new species in the genus *Oligoryzomys*: *O. stramineus,* an endemic species of the Brazilian Cerrado and the Caatinga (Bonvicino and Weksler, 1998), and *O. fornesi* Massoia, 1973 that was recognized as a valid species (Myers et al., 1995; Bonvicino and Weksler, 1998). Previous studies based on morphologic characters and G-band patterns suggested that *O. nigripes* was a senior synonym of *O. delticola* and *O. eliurus*. Silva and Yonenaga-Yassuda (1997) recognized *Oligoryzomys* sp1 (from Bahia), and *Oligoryzomys* sp2 (from Minas Gerais), both in Brazil. The most recently described species are *O.* cf. *mesorrius* from the Amazon (Andrades-Miranda et al., 2001) and *Oligoryzomys* sp. from the Tocantins State in the Brazilian Cerrado (de S. Lima, 2003). Externally, *O. longicaudatus* is characterized by its long tail (almost twice the body length), large hind limbs, reduced ears, a general yellowish dorsal color pattern without a particular design, and a whitish ventral coloration (Osgood, 1943; Mann, 1978).

Two species are currently recognized in Chile, *O. magellanicus* and *O. longicaudatus*, the latter of which is characterized by a broad geographic range (Gallardo and Palma, 1990). The distribution of *O. longicaudatus* (“lauchita de los espinos” or ”colilargo” as it is best known in Chile; Fig. 1) encompasses 3 of the major ecogeographic zones in

Figure 1. Adult "colilargo" *O. longicaudatus* from central Chile (photo by Mariana Acuña R.).

Chile, from the Mediterranean region in the north, to the Temperate and Patagonian forests in the south, spanning a range that runs from approximately 28° to 51°S (Fig. 2). Altitudinally, it occurs from sea level to about 1000 m (Mann, 1978). Additionally, this taxon is relatively common along its range, particularly in the temperate forests of southern Chile and adjacent Argentina, occurring in sympatry in most of its distributional range with other sigmodontine mice such as species of the genus *Abrothrix*. *O. longicaudatus* is found preferentially in forest habitats associated with mesic environments, while in central Chile it occurs in shrubby areas, but always associated with humid conditions (Mann, 1978).

Genetic and molecular studies have shown that this species is highly homogeneous along its extended range, agreeing with earlier analyses of morphological traits (Gallardo and Palma, 1990). Since this taxon is primarily restricted to forest environments, its biogeographic history seems to be closely related to the expansion and retractions of forests associated with the last glacial cycles of the Pleistocene (Moreno et al., 1999). Molecular phylogeographic data are consistent with this hypothesis (Palma et al., 2005).

The ecology of *O. longicaudatus* is characterized by its high vagility and large home range, in contrast to coexisting species, particularly in the southern part of its distributional range (Murúa et al., 1986). A remarkable feature in the ecology of this species is its strong response to a mast seeding phenomenon due to periodic flowering of "bamboo" (e.g., *Chusquea* spp.) in southern Chile and Argentina (Gallardo and Mercado, 1999; Jaksic and Lima, 2003; Sage et al. This volume). Since the species is primarily granivorous, such mast-seeding events allow for demographic eruptions

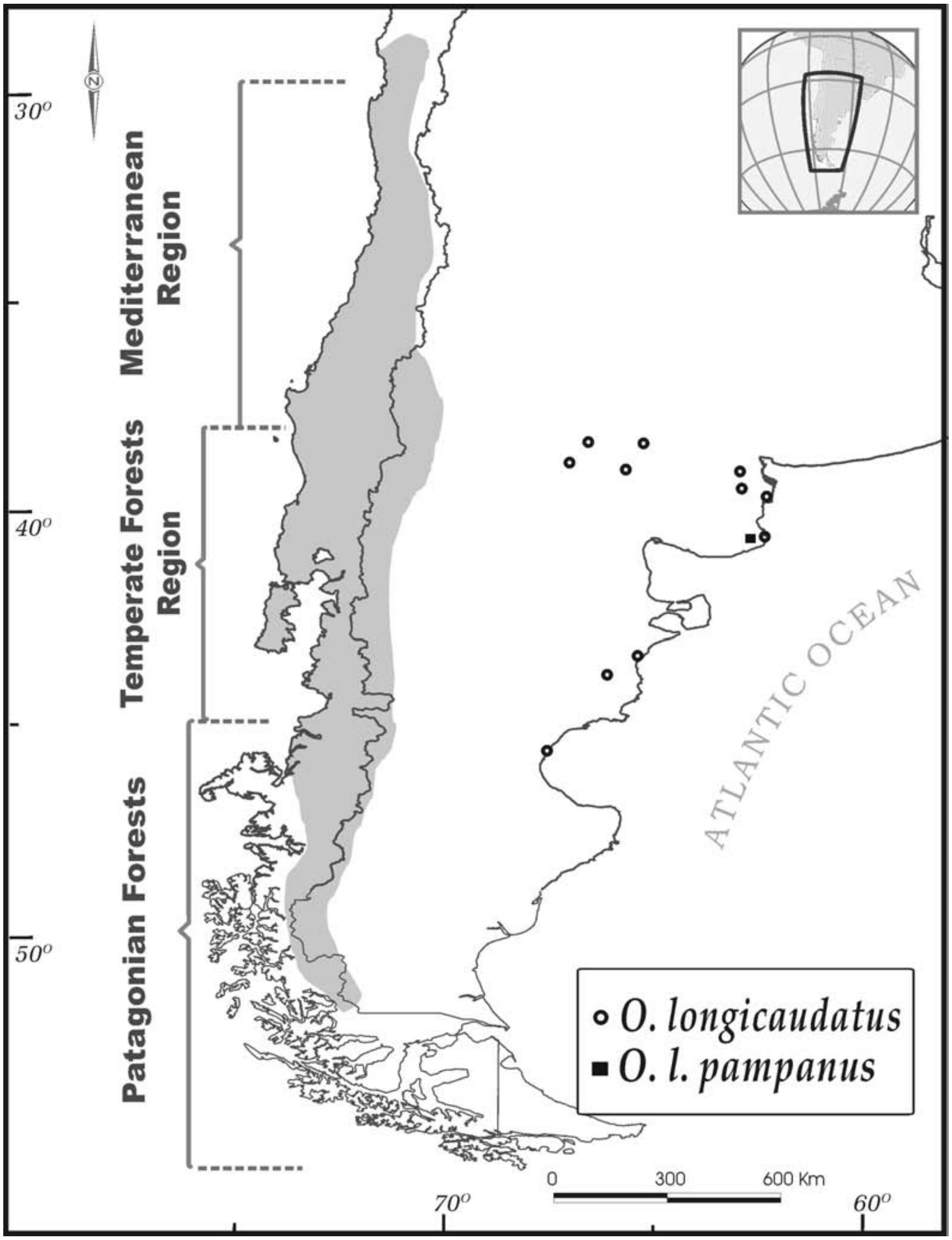

Figure 2. Map of the distribution of *Oligoryzomys longicaudatus* in Chile and Argentina (shaded area) showing 3 of the Chilean ecogeographic zones; circles represent other localities where the species has been reported in Argentina.

commonly known as "ratadas," and *O. longicaudatus* exhibits the greatest numerical increases during these events. Interestingly, similar outbreaks of *O. longicaudatus* occur in central Chile in response to high precipitation triggered by "El Niño" Southern Oscillation (ENSO; Meserve et al., 1993, 1995, 1999a, 2003).

Oligoryzomys longicaudatus has attracted the attention of epidemiologists, particularly in the last decade, since it was confirmed as the primary reservoir of the Andes virus, both in southern Argentina and south-central Chile (Levis et al., 1998; Toro et al., 1998). This is one of the Hantavirus strains responsible for the Hantavirus Pulmonary Syndrome (HPS) in humans, an emerging disease that produces acute respiratory distress (Duchin et al., 1994). In connection with this, several studies have been directed at better understanding the population dynamics and genetics of the species that could prevent risky contacts to human population.

Given this background it is clear that this species plays a pivotal role in the ecology of the small mammal fauna of the southern cone of South America. Our objective with this manuscript is to review what is known about this important component of this fauna, as well as give new antecedents regarding the ecology and evolution of *O. longicaudatus*.

Systematics and Evolutionary History

Recent molecular calibrations have placed the differentiation of South American sigmodontines between 4.5 and 9.5 mya with the origin of *Oligoryzomys* occurring around 8 mya (Smith and Patton, 1999). Carleton and Musser (1989) suggested that the evolution of the genus *Oligoryzomys* proceeded in stages and probably involved repeated invasions of this genus from the Andean uplands (e.g., *O. andinus*) to other Neotropical habitats such as lowlands, forests, savannah, and shrublands. Until recently, *Oligoryzomys* was recognized as a subgenus of *Oryzomys*, but morphological revisions based on external, cranial, dental, and stomach morphology led to generic recognition (Carleton and Musser, 1989). This study concluded that *Oligoryzomys* is a monophyletic lineage, later corroborated by protein electrophoresis and partial sequences of the cytochrome *b* gene (Dickerman and Yates, 1995; Myers et al., 1995). In summary, at least 20 species are currently recognized in the genus (Musser and Carleton, 1993; Silva and Yonenaga-Yassuda, 1997; Bonvicino and Weksler, 1998; Andrades-Miranda et al., 2001; de S. Lima et al. 2003) distributed throughout the Neotropics from Mexico (e.g., *O. fulvescens*) southward to Argentina and Chile (e.g., *O. longicaudatus*).

Two species are currently recognized in Chile: *O. longicaudatus* and *O. magellanicus* (Gallardo and Palma, 1990). Previously, a single species of *Oligoryzomys* was recognized along an extensive geographical range in Chile, differentiated into 3 subspecies based on morphological features such as dorsal coloration patterns and tail length (Osgood, 1943; Mann, 1978). These were *O. l. longicaudatus*, from the Copiapó Valley south to the Bio-Bio River (Concepción Province), *O. l. philippii* from the latter region southward to 50°S, and *O. l. magellanicus* in the southernmost parts of Chile south of 50° (Magallanes and Tierra del Fuego). A fourth subspecies, *O. l. pampanus*, was described from Buenos Aires province in Argentina and later assigned to *O. longicaudatus* (Massoia, 1973). Studies of cranial and bacular morphology from representative specimens of several populations throughout the range of *O. longicaudatus* in Chile failed to demonstrate evidence of differentiation among subspecies (Gallardo and Palma, 1990). However, populations ascribed to *magellanicus* were strongly differentiated from northern populations for almost all morphological features analyzed. For example, Gallardo and Palma (1990) reported differences in bacular morphology between *longicaudatus-philippii* and *magellanicus*, with the baculum of the latter species being significantly larger than that of the northern forms. The same study showed that the karyotypes of *O. l. longicaudatus* and *O. l. philippii* were identical, with 2n = 56, NF = 70, whereas that of *O. l. magellanicus* exhibited 2n = 54, NF = 70 (Fig. 3; Gallardo and Patterson, 1985; Palma, 1987). Finally, analyses of allozyme data comparing 15 loci in 60 specimens among 10 populations of *O. l. longicaudatus* and *O. l. philippii* in Chile (between Coquimbo in Region IV and Aysén in Region XI; data not available for *O. l. magellanicus*) showed high levels of genetic similarity (Palma, 1987). Thus, based on the strong morphologic and genetic uniformity detected among populations along the range of the two northern subspecies, Gallardo and Palma (1990) recognized a single species between 28-50° S, *O. longicaudatus*, with *philippii* as a full synonym of *longicaudatus*. They also concluded that Patagonian populations of the southernmost part of the distribution constituted a valid species (*magellanicus*), ranging from 50° S south to the Patagonian forests and adjacent islands in Magallanes, Chile.

Recent molecular analyses evaluated the phylogeographic relationships across most of the range of *O. longicaudatus* by sequencing the cytochrome *b* mitochondrial gene (Palma et al., 2005). This study also included some additional localities south of 50° S, recognized as *O. magellanicus* by Gallardo and Palma (1990). Palma et al. (2005) documented a high degree of molecular homogeneity, suggesting high gene flow along the species range, congruent with previous data based on morphology, chromosomes, and isozymes (Palma, 1987; Gallardo and Palma, 1990). However, this homogeneity also encompassed localities as far south as Torres del Paine National Park, in the southern Chilean Patagonia (52° S). No significant relationship was found between geographic distance and the degree of genetic variation among populations, evaluated by different statistical tests (e.g., Mantel test, Nested Clade Analysis; Palma et al., 2005). All these results confirm the occurrence of a single species, from the southern portion of the Atacama Desert to as far south as 52° S in Chile. *Oligoryzomys magellanicus* should be restricted to specimens south of 52° S. In fact, the specimens ascribed to this taxon with 2n = 54 were captured in Harrison Island (54° S), across from Cape Froward in the islands of Chilean Patagonian (Gallardo and Patterson, 1985). Interestingly, recent karyotypes obtained from Torres del Paine National Park (Río Pingo; 51° S) and that theoretically lie within the range of *O. magellanicus* (Gallardo and Palma, 1990) showed a karyotype identical to that of *O. longicaudatus* both in the 2n and FN (Palma et al., 2005). Furthermore, cytochrome *b* sequences of specimens from Torres del Paine did not show any significant difference with respect to northern populations, thus expanding the known range of *O. longicaudatus* to the south (Fig. 4). A similar latitudinal distribution is recognized for *O. longicaudatus* on the Argentinean side (Pardiñas et al., 2002). Therefore, *O. magellanicus* is restricted to higher southern latitudes in the continent and nearby islands in the Patagonia (e.g., Harrison Island), but further sampling efforts are needed for delimiting the geographic distribution of this species.

The phylogeny of the species recovered *O. l. pampanus* in a basal position together with other southern localities of Chile (e.g., Mininco, Río Simpson, Torres del Paine) that according to Palma et al. (2005) should be recognized as *O. longicaudatus*. However, the locality of *O. l. pampanus* (Bahía San Blas, Buenos Aires Province) is separated by

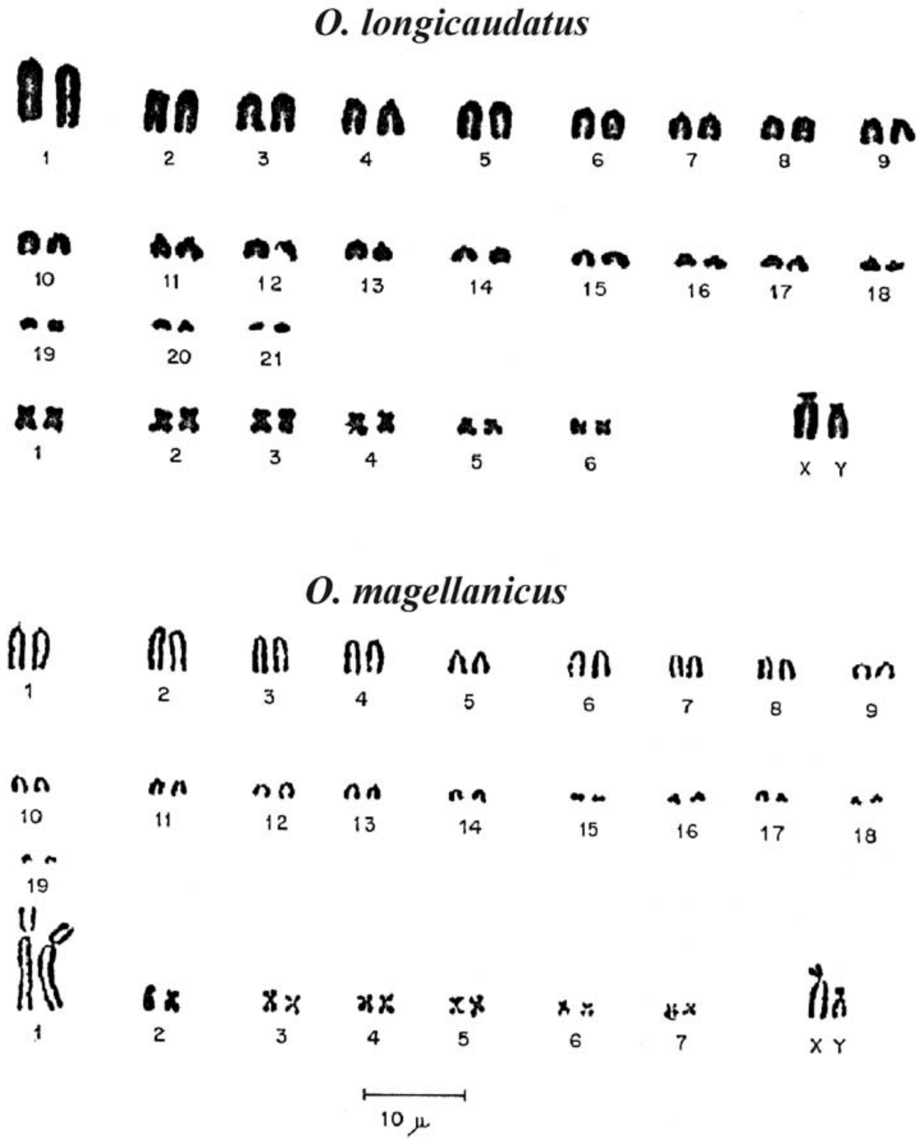

Figure 3. Karyotype of *Oligoryzomys longicaudatus* (2n = 56 chromosomes), and *O. magellanicus* (2n = 54).

about 898 km from the temperate forests (e.g., Temuco, Araucanía Region) in Chile, and by 757 km from Las Breñas (Neuquén province) in western Argentina. Thus, further sampling from additional, intermediate localities between Buenos Aires province and central-west Argentina will be necessary to adequately assess the taxonomic status of this form. At this point it is unclear whether *O. l. pampanus* constitutes a valid subspecies. Chromosomal analyses have proven useful for identifying new species within *Oligoryzomys* (Andrades-Miranda et al., 2001) and should be applied to this case as well.

The origin of *Oligoryzomys longicaudatus* is unresolved, although ongoing studies

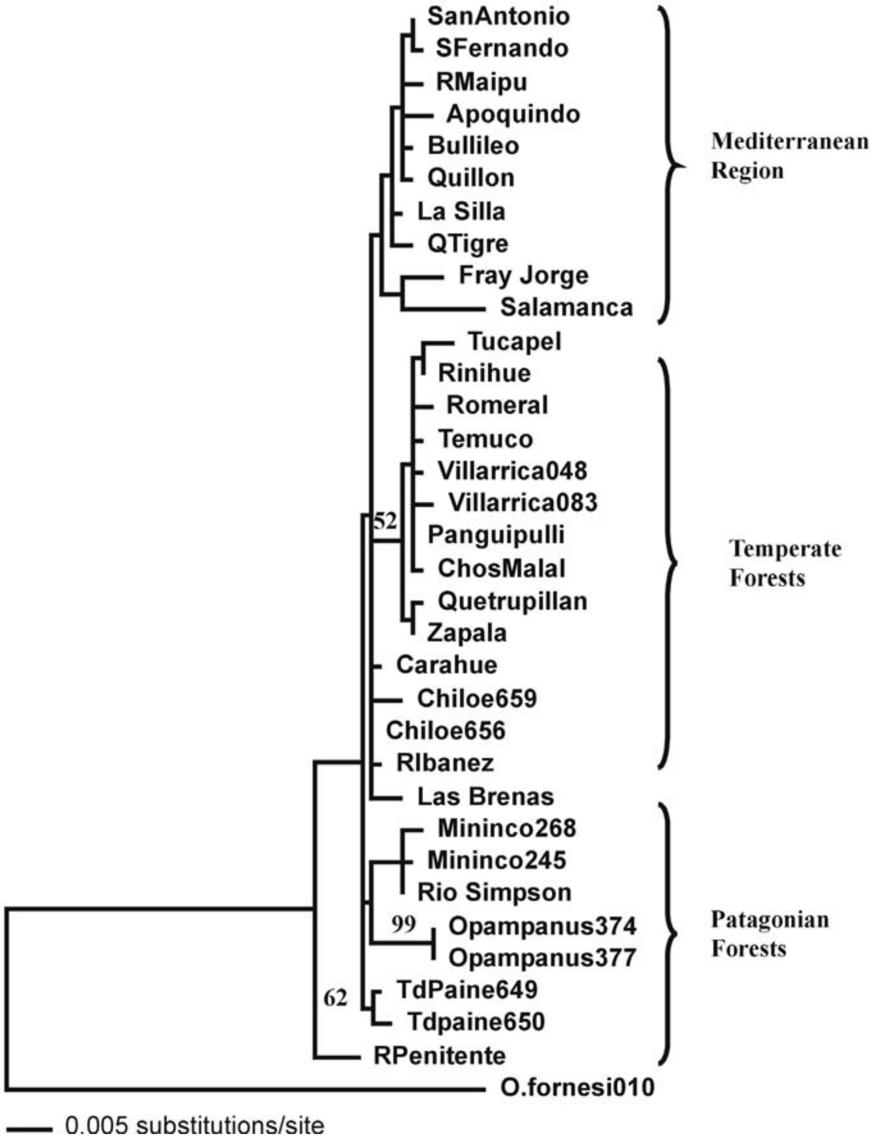

Figure 4. Maximum-likelihood tree obtained from the cytochrome b gene sequences of *Oligoryzomys longicaudatus*. Numbers on the nodes represent 100 bootstrap replicates, keys represent ecogeographic regions.

suggest that it is part of an Andean-Chacoan clade (Palma et al., in prep.). *O. longicaudatus* has been reported as far north as the Yungas of Argentina (Mares et al., 1989; Redford and Eisenberg, 1992), although recent molecular studies suggest that populations from northwestern Argentina do not belong to this species (González-Ittig et al., 2002). On the basis of the phylogenetic tree and the basal position of samples from southern localities, we postulated that *O. longicaudatus* entered Chile from Argentina across the continuous *Nothofagus* forest vegetation that crosses the southern Andes (approximate latitude 40°S; Palma et al. 2005). Further dispersal of *Oligoryzomys* to central and northern Chile may have been facilitated during Pleistocene times, since southern Chile (and Argentina) was severely affected by glaciations (Holling and Schilling, 1981; Mercer, 1983). *Oligoryzomys* may have migrated north along non-glaciated routes such as the Coastal Cordillera and the central valleys in Chile, since glaciations to the north advanced mainly throughout the Andes (Holling and Schilling 1981; Moreno et al., 1999). This biogeographic scenario is consistent with the observation that more derived populations of *O. longicaudatus* in the phylogenetic tree are found in north-central Mediterranean region of Chile (Fig. 4).

ECOLOGY

Oligoryzomys longicaudatus are most abundant in mesic areas of the Temperate and Patagonian Forests of southern Chile and Argentina. In Chile, however, this species has expanded northward as far as 28° S in the Mediterranean region where more open and almost xeric areas prevail (Osgood, 1943; Mann, 1978). Within its extended geographical range, the species has adapted to very distinct vegetative types and climatic conditions. Habitats used are mainly terrestrial (Murúa and González 1982; Pearson, 1983; Murúa, 1996) although occasionally scansorial, even occupying abandoned nests of some birds or generating its own arboreal nests for offspring (Mann, 1978). However, in the Mediterranean region, this species has colonized and adapted to other vegetation types such as scrubland environments, but always associated with humid areas (Mann, 1978). For example, in Fray Jorge National Park *O. longicaudatus* is a permanent inhabitant of the "aguadas" (= mesic vegetation with standing water; Meserve et al. 2003), but it also occurs in the scrublands. However, the species disappears from the latter environments in dry years (e.g. La Niña events). In fact, the "colilargo" is so water-dependant, in contrast to other Chilean sigmodontines, that it has one of the lowest survival rates when water-deprived (Cortés et al., 1988). The increase in abundance of populations during and after ENSO events may reflect an increase in the availability of food and/or a reduction in water stress, allowing populations to move out of the "aguadas" (Meserve et al. 2003). In southern Chile, the species is a common inhabitant of temperate forests (Meserve et al., 1991a, 1991b) and one of the most abundant taxa in forest remnants (Kelt, 2000). In these environments, *O. longicaudatus* uses sites with greater shrub and tree overstory vegetation, and during the summer season the species is absent from the forests. Therefore, in spite of its high vagility, *O. longicaudatus* maintains strong habitat selection (Kelt et al., 1994).

The diet of *O. longicaudatus* changes latitudinally. In Mediterranean Chile it has been reported as granivorous-frugivorous (e.g., Meserve, 1981a), changing to herbivorous in the region between the Mediterranean and Temperate Forests ecoregions (e.g, Burca, VIII region; Muñoz-Pedreros et al., 1990). In the temperate forest of Chile's Coastal Range the diet has been reported as granivorous-frugivorous (e.g., Fundo San Martín, X Region; Murúa and González, 1981), whereas slightly further south and in the Andean precordillera it is herviborous/granivorous-frugivorous (e.g., Vicente Pérez Rosales National Park, X Region; Meserve et al., 1988). During summer seasons *O. longicaudatus* prefers fruits and seeds, changing almost exclusively to seeds as winter season approaches (Meserve et al., 1988), although it occasionally can adopt an omnivorous diet, consuming some arthropods and/or annelids (Mann 1978; Meserve et al., 1988; Kelt et al., 1994). Interestingly, the granivory of this species is one of the most remarkable aspects in the diet of *O. longicaudatus*, since it is the sole member of the small mammal Chilean fauna that is strongly granivorous (Glanz, 1977; Meserve and Glanz, 1978; Murúa et al., 1980; Murúa and González, 1981; Murúa et al., 1986; Meserve et al., 1988; Silva, 2005).

Oligoryzomys longicaudatus can produce up to 3 litters of 3-5 offspring per year, and females reach sexual maturity in a few months (Greer, 1966; Mann, 1978; Pearson, 1983). Individuals of this species rarely live more than 12 months (R. E. Palma, personal observation). In temperate forests animals born in more favorable seasons (e.g., towards the middle or the end of the summer; Murúa et al., 1986) live an average of 10 months, whereas in more xeric regions (Fray Jorge National Park, 30˚S; Meserve et al., 1995) they average only 9 months. Of course, the upper age limit remains unknown. Pearson (1967) stated that the best way to determine the age in brachiodont rodents was through a correlation between morphometric measures and tooth wear; for *O. longicaudatus*, this was empirically evaluated with known-aged animals, and tail length was the best morphometric variable significantly correlated with tooth wear (males, $r = 0.9742$, $p < 0.001$; females, $r = 0.9312$, $p < 0.001$; Santana, 1981).

Murúa and González (1986) and Murúa et al. (1986) estimated a large home range (HR) and high vagility of *O. longicaudatus* when compared to other sigmodontine mice. In temperate forests Murúa et al. (1986) reported a home range between 320 to 4800 m^2, which is more than twice the value estimated for *Abrothrix olivaceus* (730 to 2530 m^2; González et al.1982), one of the other most abundant rodents in Chile (González et al., 2000). However, when evaluating home range data for *O. longicaudatus* based on Kelt and Van Vuren's (2001) allometric equation that considers the weight and diet of species, the home range of the latter is about 1/4 that of *A. olivaceus* (at 30 g, about 0.414 ha for the omnivorous *A. olivaceus* vs, about 0.090 ha for the herbivorous *O. longicaudatus*).

Further north the *Nothofagus* forests are restricted and become replaced by evergreen sclerophyllous vegetation (Kalin-Arroyo et al.1994). This different habitat is associated with a reduction in home range of *O. longicaudatus*, particularly in the Mediterranean region, where species better adapted to xeric conditions occur (e.g., *Phyllotis darwini*, *Octodon degus*; Simonetti and Agüero, 1990; Jimenez et al., 1992). Not surprisingly, the heterogeneity of the environment across the geographic range of *O. longicaudatus* (encompassing 3 ecogeographic regions) results in substantial variation in population density. Low population abundance has been reported in more xeric regions in northern Chile (Fulk, 1975; Glanz 1977; Meserve and Glanz, 1978; Meserve, 1981b), whereas greater densities are achieved southward (Greer, 1968; Lopetegui, 1980; Murúa et al. 1986). This suggests a latitudinal gradient of abundance, which probably is related to an increase in the precipitation regime from north to south, and/or that in northern regions it is foraging in a heterogeneous habitat but utilizing a highly localized and temporally variable resource of seeds. This pattern of abundance would be more influenced by availability of seeds throughout the year, which in turn is water limited (Murúa et al., 1986; Meserve et al. 1991b). Thus, during 1976 in the central Mediterranean locality of San Carlos de Apoquindo (Santiago, Chile), "colilargos" were recorded only during September, while 2 years later, in 1978, they appeared in higher numbers between June and December (Jaksic et al., 1981). In Fray Jorge the species showed strong oscillation in 1992 increasing from zero to > 45 ind/

ha, and it had a high coefficient of variation (1.237; Meserve et al.1995). Densities are greatest in temperate forest, which consequently are presumed to be a preferred habitat for this species (Greer, 1968; Lopetegui, 1980; Murúa et al. 1986). In regular years (without population outbreaks), among 20 and 59 ind/ha have been reported (Murúa and González, 1986; Murúa, 1996), whereas in winter these values have varied between 0 to 10-20 ind/ha (Meserve et al. 1999b).

The population dynamics of small mammals and animals have been hypothesized to respond to both endogenous (e.g., intraspecific competition) and exogenous forces (e.g., abiotic events; Flowerdew, 1987; Berryman, 1999; Lima et al., 1999; Vaughan et al., 2000; Lima et al., 2001a, 2001b; Lima et al., 2002; Murúa et al., 2003a). Numerous studies have documented massive demographic variation in *O. longicaudatus* (Pearson, 1975; Meserve and Le Boulenge, 1987; Lima and Jaksic, 1998, 1999; Meserve et al., 1999b; Meserve et al., 2003; Murúa et al., 2003a; Murúa and Briones, 2005). In fact, *O. longicaudatus* is one of the sigmodontine rodents more strongly affected by climatic and mast seeding events, yielding populational outbreaks in anomalous densities known as "ratadas" (Fuentes et al., 1985; Murúa et al., 1986; Jimenez et al., 1992; Gallardo and Mercado, 1999; Lima et al., 1999; Meserve et al., 1999a, 1999b; González et al., 2000; Jaksic and Lima 2003).

Other Chilean small mammals affected by these events include the rodents *Abrothrix olivaceus*, *A. longipilis*, *Phyllotis darwini*, *Octodon degus*, and the didelphid marsupial *Thylamys elegans* (Meserve et al., 1999a; Jaksic and Lima, 2003). During outbreaks, small mammal populations increase dramatically in density (up to 100 ind/ha; Jaksic and Lima, 2003), generating several ecological impacts on the terrestrial ecosystems (Holmgren et al., 2001; Jaksic, 2001). ENSO events, which are the result of atmospheric and oceanographic interactions throughout the tropical Pacific (Stenseth et al., 2003), result in anomalous high rainfall, with 4- to 10-fold increases on average (Holmgren et al., 2001), affecting primary productivity and small mammal population dynamics (Meserve et al., 1993, 1995, 1999a, 2003; Jaksic et al., 1997; Lima et al., 1999, 2002). Outbreaks mediated by high rainfalls have been recorded in southern South America since the first half the 19th century (Jaksic and Lima, 2003). These abnormal mouse abundances have been studied in the semi-arid region of Chile as result of ENSO events in 1986-1987 (Jimenez et al., 1992), 1991-1992 (Meserve et al., 1995), and 1997-1998 (Lima et al., 2001a, 2001b), as well as in Argentina in 2000 (Sage et al., This volume). Historically, "ratadas" have been more frequently due to mast seeding than to climatic events (Jaksic and Lima, 2003). "Bamboo" blooms, flowering and production of seeds as a supra-annual phenomenon in long-lived plants (Kelly, 1994), have been reported several times in southern Chile (Jaksic and Lima, 2003), but appear to be weaker events to the east of the Andes (Pearson, 1994; but see Sage et al., This volume). The latest such bloom involved "quila" (*Chusquea valdiviensis*) and took place in Rio Negro Province in Argentina during the spring of 2000, resulting in the increase of local populations of *O. longicaudatus* in the Chilean localities of Riñihue, Panguipulli and Villarrica National Park (39-40° S).

O. longicaudatus as a Reservoir of Hantavirus.

The characteristic that has most strongly established this species as a focus of epidemiological research in the last decade is that it is the reservoir of the Andes strain of Hantavirus (Levis et al., 1998; Toro et al., 1998; Bohlman et al., 2002). The virus is the etiologic agent of the Hantavirus Pulmonary Syndrome (HPS), which is an emerging infectious disease first recorded in North America in 1993 (Nichol et al., 1993; Schmaljohn and Hjelle, 1997), and later reported in Argentina and Chile (Levis et al., 1998; Toro et al., 1998). The virus is transmitted to humans by inhalation of aerosols of urine and feces, and/or mucose secretions (Tsai, 1987; Lee and van der Groen, 1989; Botten et al., 2002).

In Chile *O. longicaudatus* has the highest rate of positive serological test among rodents in the area (Pavletic, 2000). In addition, *O. longicaudatus* has been found to be the only seropositive species associated with confirmed human cases of HPS (Torres-Pérez et al., 2004). However, 4 other sigmodontine rodent species (*Abrothrix longipilis*, *A. olivaceus*, *Phyllotis darwini*, and *Loxodontomys micropus*) have also been identified to be serologically positive to hantavirus in Chile, although at considerably lower rates (Pavletic, 2000; Spotorno et al., 2000). These species all are sympatric with *O. longicaudatus* over all or part of their distribution (Mann, 1978). The presence of Hantavirus antibodies in these species has been explained as the result of "spill-over," a mechanism of horizontal transmission when individuals become into contact (Hjelle and Yates, 2001).

In southern Argentina, *O. longicaudatus* has been the focus of several studies on Hantavirus (Levis et al., 1998; Calderon et al., 1999; Cantoni et al., 2001). There, 3 other *Oligoryzomys* species have been reported as hosts for different Hantavirus strains (López et al., 1996; Levis et al., 1997, 1998), supportive of the narrow co-evolutionary relationship between the virus and its reservoir (Yates et al., 2002). Each of 3 *Oligoryzomys* species carries a specific Hantavirus strain in northwestern Argentina: (*O. chacoensis*, Bermejo strain), central Argentina (*O. flavescens*, Lechiguanas strain), and southern Chile and Argentina (*O. longicaudatus*, Andes strain). A fourth strain has recently been reported for *O. longicaudatus* in northwestern Argentina (Oran strain; Pini et al., 2003), although, as explained above, genetic studies do not recognize this northern taxon as *O. longicaudatus* (González-Ittig et al., 2002).

Besides the restricted home range and lower population density of *O. longicaudatus* in central Chile, its high vagility and home range, as well as its high molecular homogeneity across the range, suggest that the risk of acquiring the disease is roughly similar throughout across the species distribution. In addition to molecular analyses, studies on the population dynamics of *O. longicaudatus* in the Lakes Region of Chile are particularly important since local abundance appears to be positively correlated with the number of seropositive individuals with IgG antibodies of Andes strain Hantavirus (with $N = 18$, $r = 0.95$, $p = 0.045$) (Murúa et al., 2003b). However, this is not the pattern found in other species of sigmodontines (Mills et al., 1997; Abbott et al., 1999). Long-term studies are needed to model the prevalence of the virus in natural populations (Galvani, 2003), to establish areas of relatively high risk, and to predict future human Hantavirus outbreaks. Knowledge of the ecology and genetic structure of reservoir populations will provide insights into the factors responsible for the maintenance and spread of the virus in natural populations. In this sense, *O. longicaudatus* represents one of the most important species in the southern cone of South America.

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LITERATURE CITED

Abbot K. D., T. G. Ksiazek, and J. N. Mills
1999 Long-term hantavirus persistence in rodents populations in central Arizona. Emerging Infectious Diseases 5:102-112.

Andrades-Miranda, J., L. F. B. Oliveira, C. A. V. Lima-Rosa, A. P. Nunes, N. I. T. Zanchin, and M. S. Mattevi
2001 Chromosome studies of seven species of *Oligoryzomys* (Rodentia: Sigmodontinae) from Brazil. Journal of Mammalogy 82:1080-1091.

Berryman, A. A.
1999 Principles of population dynamics their application. Stanley Thornes Publishers Ltd., Cheltenham, UK.

Bohlman M. C., S. P. Morzunov, J. Meissner, M. Beth-Taylor, K. Ishibashi, J. Rowe, S. Levis, D. Enria, S. C. St. Jeor
2002 Analysis of hantavirus genetic diversity in Argentina: S segment- derived phylogeny. Journal of Virology 76:3765-3773.

Bonvicino, C. R., and M. A. Weksler
1998 A new species of *Oligoryzomys* (Rodentia, Sigmodontinae) from northeastern and central Brazil. Mammalian Biology 63: 90-103.

Botten, J., K. Mirowsky, C. Ye, K. Gottlieb, M. Saavedra, L. Ponce, B. Hjelle
2002 Shedding and intracage transmission of Sin Nombre Hantavirus in the deer mouse (*Peromyscus maniculatus*) model. Journal of Virology 76:7587-7594.

Calderón G., N. Pini, J. Bolpe, S. Levis, J. Mills, E. Segura, N. Guthmann, G. Cantoni, J. Becker, A. Fonollat, C. Ripio, M. Bortman, R. Benedetti, M. Sabattini, D. Enria
1999 Hantavirus reservoir host associated with peridomestic habitats in Argentina. Emerging Infectious Diseases 5:792-797.

Cantoni G., P. Padula, G. Calderón, J. Mills, E. Herrero, P. Sandoval, V. Martínez, N. Pini, E. Larrieu
2001 Seasonal variation in prevalence of antibody to hantaviruses in rodents from southern Argentina. Tropical Medicine and International Health 6:811-816.

Carleton, M. D., and G. G. Musser
1989 Systematic studies of oryzomyine rodents: (Muridae, Sigmodontinae): a synopsis of *Microryzomys*. Bulletin of the American Museum of Natural History 191:1-83.

Cortés, A., C. Zuleta, and M. Rosenmann
1988 Comparative water economy of sympatric rodents in a Chilean semi-arid habitat. Comparative Biochemistry and Physiology A 97:711-714.

Dickerman, A. W., and T. L. Yates
1995 Systematics of *Oligoryzomys*: Protein electrophoretic analyses. Journal of Mammalogy 76:172-188.

Duchin J. S., Koster F. T., Peters C. J., Simpson G. L., Tempest B., Zaki S. R., Ksiazek T. G, Rollin P. E., Nichol S., Umland E. T., Moolenaar R. L., Reef S. E., Nolte K. B., Gallaher M. M., Butler J. C., and R. F. Breiman
1994 Hantavirus pulmonary syndrome: A clinical description of 17 patients with a newly recognized disease. New England Journal of Medicine 330:949-955.

Flowerdew, J. R.
1987 Mammals: Their Reproductive Biology and Population Ecology. Cambridge University Press, New York, New York, USA. 248 pp.

Fuentes, E. R., and C. Campusano
1985 Pest outbreaks and rainfall in the semi-arid region of Chile. Journal of Arid Environments 8:67-72

Fulk, G.
1975 Population ecology of rodents in semiarid shrublands of Chile. Occasional Papers, The Museum, Texas Tech University 33:1-40.

Gallardo, M. H., and C. Mercado
1999 Mast seeding of bamboo shrubs and mouse outbreaks in southern Chile. Mastozoología Neotropical 6:103-111.

Gallardo, M. H., and R .E. Palma
1990 Systematics of *Oryzomys longicaudatus* (Rodentia: Muridae) in Chile. Journal of Mammalogy 71:333-343.

Gallardo, M. H., and B. D. Patterson
1985 Chromosomal differences between two nominal subspecies of *Oryzomys longicaudatus* Bennet. Mammalian Chromosomes Newsletter 25:49-53.

Galvani, A. P.
2003 Epidemiology meets evolutionary ecology. Trends in Ecology and Evolution 18:132-139.

Glanz, W. E.
1977 Comparative Ecology of Small Mammals Communities in California and Chile. Unpublished Ph.D. thesis, University of California, Berkeley, USA.

González, L. A., R. Murúa, and R. Feito
1982 Densidad poblacional y padrones de actividad espacial en *Akodon olivaceus* (Rodentia: Cricetidae) en habitats diferentes. Pp. 635-647 in Zoología Neotropical (Salinas, P., ed.). Actas VIII Congreso Latinoamrericano de Zoología, Mérida, Venezuela.

González, L. A., R. Murúa, and C. Jofré
2000 Habitat utilization of two muroid species in relation to population outbreaks in southern temperate forests of Chile. Revista Chilena de Historia Natural 73:489-495.

González-Ittig, R. E., G. R. Theiler, and C. N. Gardenal
2002 A contribution to the subgeneric systematics of *Oligoryzomys* (Rodentia: Muridae) from Argentina by means of PCR-RFLP patterns of mitochondrial DNA. Biochemical Systematics and Ecology 30:23-33.

Greer, J. K.
1966 Mammals of Malleco Province, Chile. Publications of the Museum, Michigan State University, Biological Series 3:49-152.

1968 Mamíferos de la Provincia de Malleco. Publicación Museo "Dillman S. Bulluck", El Vergel (Angol, Chile)

Hershkovitz, P.
1966 South American swamp and fossorial rats of the scapteromyine group (Cricetinae, Murinae), with comments on the glans penis in murid taxonomy. Zeitschrift für Saugetierkunde 31:81-149.

Hjelle, B., and T. L. Yates
2001 Modeling hantavirus maintenance and transmission in rodent communities. Current Topics in Microbiology and Immunology 256:77-90.

Holling, J. T., and D. H. Schilling
1981 Late Wisconsin-Weichselian mountains glaciers and small ice caps. Pp.179-206 in The Last Great Ice Sheets (Denton, G. H., and T. J. Hughes, eds.). John Wiley and Sons. New York, New York, USA.

Holmgren, M., M. Scheffer, E. Ezcurra, J. R. Gutiérrez, and G. M. J. Mohren
2001 El NIÑO effects on the dynamics of terrestrial ecosystems. Trends in Ecology and Evolution 16:89-94.

Jaksic, F. M.
2001 Ecological effects of El Niño in terrestrial ecosystems of western South America. Ecography 24:241-250.

Jaksic, F. M., and M. Lima
2003 Myths and facts on "ratadas": Bamboo blooms, rainfall peaks and mouse outbreaks. Austral Ecology 28:237-251.

Jaksic, F. M., S. I. Silva, P. L. Meserve, and J. R. Gutierrez
1997 A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South America. Oikos 78:341-354.

Jaksic, F. M., J. L. Yañez, and E. R. Fuentes
1981 Assessing a small mammal community in central Chile. Journal of Mammalogy 62:391-396.

Jiménez. J. E., P. Feinsinger, and F. M. Jaksic
1992 Spatiotemporal patterns of an irruption and decline of small mammals in northcentral Chile. Journal of Mammalogy 73:356-364.

Kalin-Arroyo, M. T., L. Cavieres, C. Marticorena & M. Muñoz-Schick
1994 Covergence in the mediterranean floras in Central Chile and California: insights from comparative biogegraphy. Pp. 43-88 in Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia (Kalin-Arroyo, M. T, P. H. Zedler, M. D. Fox., eds.). Springer Verlag, New York, New York, USA.

Kelly, D.
1994 The evolutionary ecology of mast seeding. Trends in Ecology and Evolution 9:465-470.

Kelt, D. A.
2000 Small mammal communities in rainforest fragments in central southern Chile. Biological Conservation 92: 345-358.

Kelt, D. A., P. L. Meserve, and B. K. Lang
1994 Quantitative habitat associations of small mammals in a temperate rainforest in southern Chile: empirical patterns and the importance of ecological scale. Journal of Mammalogy 75:890-904.

Kelt, D. A., and D. H. Van Vuren
2001 The ecology and macroecology of mammalian home range area. American Naturalist 157: 637-645.

Lee H. W., and G. van der Groen
1989 Hemorrhagic fever with renal syndrome. Progress in Medical Virology 36:62-102.

Levis, S., S. P. Morzunov, J. E. Rowe, D. Enria, N. Pini, G. Calderon, M. Sabattini, and S. C. St Jeor
1998 Genetic diversity and epidemiology of hantavirus in Argentina. Journal of Infectious Diseases 177:529-538.

Levis, S., J. E. Rowe, S. P. Morzunov, D. A. Enria, and S. C. St. Jeor
1997 New hantaviruses causing hantavirus pulmonary syndrome in central Argentina. Lancet 349:998-999.

Lima, M., and F. M. Jaksic
1998 Population variability among three small mammal species in the semiarid Neotropics: the role of density-dependent and density-independent factors. Ecography 21:175-180.

1999 Population dynamics of three Neotropical small mammals: time series models and the role of delayed density-dependence in population irruptions. Australian Journal of Ecology 24:25-34.

de S. Lima.,J. F., C. R. Bonvicino, and S. Kasahara
2003 A new karyotype of *Oligoryzomys* (Sigmodontinae, Rodentia) from central Brazil. Hereditas 139:1-6.

Lima, M., R. Julliar, N. C. Stenseth, and F. M. Jaksic
2001a Demographic dynamics of a neotropical small rodent (*Phyllotis darwini*): feedback structure, predation and climate. Journal of Animal Ecology 70:761-775.

Lima, M., P. A. Marquet, and F. M. Jaksic
1999 El NIÑO events, precipitation and rodent outbreak are statistically associated in semiarid Chile. Ecography 22:213-8.

Lima, M., N. C. Stenseth, and F. M. Jaksic
2002 Populations dynamics of South American rodent: seasonal structure interacting with climate, density dependence and predator effects. Proceedings of the Royal Society of London Ser. B 269:2579-2586.

Lima, M., N. C. Stenseth, N. G. Yoccoz, and F. M. Jaksic
2001b Demography and populations dynamics of the mouse-opposum (*Thylamys elegans*) in semiarid Chile: feedback structure signatures and climate. Proceeding of Royal Society of London Ser. B 268:2053-2064.

Lopetegui, O.
1980 Dinámica poblacional y utilización del hábitat de *Akodon olivacues brachiotis*, *Oryzomys longicaudatus philipii* y *Akodon longipilis apta* (Cricetidae) en la pluviselva valdiviana. Licenciatura thesis, Faculty of Sciences, Universidad Austral de Chile (Valdivia, Chile).

López, N., P. Padula, C. Rossi, M. E. Lázaro, and M. T. Franze-Fernández
1996 Genetic identification of a new hantavirus causing severe pulmonary syndrome in central Argentina. Virology 220:223-226.

Mann, G.
1978 Los Pequeños Mamíferos de Chile. Gayana:zoología 40:1-342.

Mares, M. A., R. A. Ojeda, and R. M. Barquez
1989 Guide to the Mammals of Salta Province, Argentina. University of Oklahoma Press, Norman, Oklahoma, USA. 303 pp.

Massoia, E.
1973 Presencia y rasgos bioecológicos de *Oryzomys longicaudatus pampanus*, nueva subespecie en la provincia de Buenos Aires (Mammalia, Rodentia, Cricetidae). Revista de Investigaciones Agropecuarias, ser. 1, Biología y Producción Animal 10:43-49.

Mercer, J. H.
1983 Cenozoic glaciation in the Southern Hemisphere. Annual Review of Earth and Planetary Science 11:99-132.

Meserve, P. L.
1981a Trophic relationships among small mammals in a Chilean semiarid thorn scrub community. Journal of Mammalogy 62:304-314

1981b Resource partitioning in a Chilean semi-arid small mammal community. Journal of Animal Ecology 50:745-757.

Meserve, P. L., and W. E. Glanz
1978 Geographical ecology of small in the northern Chilean arid zone. Journal of Biogeography 5:125-148.

Meserve, P. L, J. R. Gutiérrez, L. C. Contreras, and F. M. Jaksic
1993 Role of biotic interactions in a semiarid scrub community in north-central Chile: A long term ecological experiment. Revista Chilena de Historia Natural 66:225-241.

Meserve, P. L., D. A. Kelt, and D. R. Martínez
1991a Geographical ecology of small mammals in continental Chile Chico, South America. Journal of Biogeography 18:179-187.

Meserve, P. L, D. A. Kelt, B. Milstead, and J. R. Gutiérrez
2003 Thirteen years of shifting top-down and bottom-up control. BioScience 53:633-646.

Meserve, P. L., B. K. Lang, R. Murúa, A. Muñoz-Pedreros, and L. A. González
1991b Characteristics of a terrestrial small mammal assemblage in a temperate rain-forest in Chile. Revista Chilena de Historia Natural 64:157-169.

Meserve, P. L., B. K. Lang, and B. D. Patterson
1988 Trophic relationship of small mammals in a Chilean Temperate rain forest. Journal of Mammalogy 69:721-730.

Meserve, P. L., and E. R. Le Boulengé

1987 Population dynamics and ecology of small mammals in the northern Chilean semiarid region. Pp. 413-431 in Studies in Neotropical Mammalogy: essay in honor of Philip Hershkovitz (Patterson, B. D., and R. M, Timm, eds). Fieldiana: Zoology, new series 39.

Meserve, P. L, D. R. Martínez, J. R. Rau, R. Murúa, B. K. Lang, and A. Muñoz-Pedreros

1999b Comparative demography and diversity of small mammals in precordilleran temperate rainforest of southern Chile. Journal of Mammalogy 80:880-890.

Meserve, P. L., W. B. Milstead, J. R. Gutiérrez, and F. M. Jaksic

1999a The interplay of biotic and abiotic factors in a semiarid Chilean mammal assemblage: results of a long-term experiment. Oikos 85:364-372.

Meserve, P. L, J. A. Yunger, J. R. Gutiérrez, L. C. Contreras, W. B. Milstead, B. K. Lang, K. L. Cramer, S. Herrera, V. O. Lagos, S. I. Silva, E. L. Tabilo, M. A. Torrealba, and F. M. Jaksic

1995 Heterogeneous responses of small mammals to an El Niño southern oscillation event in north central semiarid Chile and the importance of ecological scale. Journal of Mammalogy 76:580-595.

Mills, J. N, T. G. Ksiazek, B. Ellis, P. E. Rollin, S. T. Nichol, T. L. Yates, W. L. Gannon, C. E. Levy, D. M. Engelthaler, T. Davis, D. T. Tanda, J. W. Frampton, C. R. Nichols, C. J. Peters, and J. E. Childs

1997 Patterns of association with lost and habitat: antibody reactive with sin nombre virus in small mammals in the major biotic communities of southern United States. American Journal of Tropical Medicine & Hygiene 56:273-284.

Moreno, P. I., T. V. Lowell, J. R. Jacobson Jr., and G. H. Denton

1999 Abrupt vegetation and climate changes during the Last Glacial Maximum and last termination in the Chilean Lake District: A case study from Canal de la Puntilla (41°S). Geografiska Annaler, Ser. A 81A:285-311

Muñoz-Pedreros, A., R. Murúa, and L. González

1990 Nicho ecológico de micromamíferos en un agroecosistema forestal de Chile Central. Revista Chilena de Historia Natural. 63:267-277.

Murúa, R.

1996 Comunidades de mamíferos del bosque templado de Chile. Pp. 113-133 in Ecología de los Bosques Nativos de Chile (Armesto, J. J., C. Villagrán, M. T. K. Arroyo, eds.). Editorial Universitaria S.A., Santiago, Chile.

Murúa, R., and M. Briones
2005 Abundance of the sigmodont mouse *Oligoryzomys longicaudatus* and patterns of tree seeding in Chilean temperate forest. Mammalian Biology 70: 321-326.

Murúa, R., and L. A. González
1981 Estudio de preferencias y hábitos alimentarios en dos especies de roedores cricétidos. Medio Ambiente (Valdivia, Chile) 5:115-124.

1982 Microhabitat selection in two Chilean cricetid rodents. Oecologia 52:12-15.

1986 Regulation of numbers of two rodent species. Revista Chilena de Historia Natural 59:193-200.

Murúa, R., L. A. González, and C. Jofré
1980 Experimental food preferences of two southern Chilean rodents. Journal of Mammalogy 61:138-140.

Murúa, R., L. A. González, and M. Lima
2003a Populations dynamics of rice rats (a Hantavirus reservoir) in southern Chile: feedback structure and non-linear effects of climatic oscillations. Oikos 102:137-145.

Murúa, R., L. A. González, and P. L. Meserve
1986 Population ecology of *Oryzomys longicaudatus philippii* (Rodentia: Cricetidae) in southern Chile. Journal of Animal Ecology 55:281-293.

Murúa, R., M. Navarrete, R. Cádiz, R. Figueroa, P. Padula, L. Zaror, R. Masilla, L. A. González, A. Muñoz-Pedreros
2003b Síndrome pulmonar por hantavirus: situación de los roedores reservorios y la población humana en la Décima Región. Revista Medica de Chile 131:169-176.

Musser, G. G., and M. D. Carleton
1993 Order Rodentia. Pp. 501-756 in Mammal Species of the World: A Taxonomic and Geographic Reference. Second ed. (Wilson, D. E., and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C., USA.

Myers, P., B. Lundrigan, and P. K. Tucker
1995 Molecular phylogenetics of Oryzomyine rodents: the genus *Oligoryzomys.* Molecular Phylogenetics and Evolution 4:372-382.

Nichol, S. T, C. F. Spiropoulou, S. Morzunov, P. E. Rollin, T. G. Ksiakek, H. Feldman, A. Sanchez, J. Childs, S. Zaki, and C. J. Peters
1993 Genetic identification of hantavirus associated with an outbreak of acute respiratory illness. Science 262:914-917.

Osgood, W. H.
1943 The mammals of Chile. Field Museum of Natural History, Zoology Series 30:1-268.

Palma, R. E.
1987 Sistemática Evolutiva del Genero *Oryzomys* Baird en Chile (Rodentia: Cricetidae). M. Sc. Thesis, Universidad Austral Chile, Valdivia, Chile.

Palma, R. E., E. Rivera-Milla, J. Salazar-Bravo, F. Torres-Pérez, U. F. J. Pardiñas, P. A. Marquet, A. E. Spotorno, A. P. Meynard, and T. L. Yates
2005 Phylogeography of *Oligoryzomys longicaudatus* (Rodentia: Sigmodontinae) in temperate South America. Journal of Mammalogy 86:191-200

Pardiñas, U. F. J., G. D'Elía, P. E. Ortiz
2002 Sigmodontinos fósiles (Rodentia, Muroidea, Sigmodontinae) de América del Sur: estado actual de su conocimiento y prospectiva. Mastozoología Neotropical 9:209-252.

Pavletic, C.
2000 Hantavirus: Su distribución geográfica entre los roedores silvestres de Chile. Revista Chilena de Infectología 17:186-196.

Pearson, A. K., O. P. Pearson, and I. A. Gómez
1994 Biology of the bamboo *Chusquea coleou* (Poaceae: Bambusoideae) in southern Argentina. Vegetatio 111:93-126.

Pearson, O. P.
1967 La estructura por edades y la dinámica reproductiva en una población de ratones del campo *Akodon azarae*. Physis (Buenos Aires) 27:53-58.

1975 An outbreak of mice in coastal desert of Perú. Mammalia 39:375-386.

1983 Characteristic of mammalian faunas from forests in Patagonia, southern Argentina. Journal of Mammalogy 64:476-492.

Pini N., S. Levis, G. Calderón, J. Ramírez, D. Bravo, E. Lozano, C. Ripoll, S. St. Jeor, T. G. Ksiazek, R. M. Barquez, and D. Enria
2003 Hantavirus infection in humans and rodents, northwestern Argentina. Emerging Infectious Diseases 9:1070-1076.

Redford, K. H., and J. F. Eisenberg
1992 Mammals of the Neotropics. Vol. 2. The Southern Cone. The University of Chicago Press, Chicago, Illinois, USA. 430 pp.

Sage, R. D., O. P. Pearson, J. Sanguinetti,, and A. K. Pearson (This volume)
Ratada 2001: A rodent outbreak following the flowering of bamboo (*Chusquea culeou*) in southern Argentina. Pp. 177-224 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

Santana, A. M.
1981 Determinación de Edad y Clases de Edad en *Oryzomys longicaudatus philipii*, Roedor Silvestre del Bosque Hidrófilo Templado en el Sur de Chile. Licenciatura thesis, Faculty of Science, Universidad Austral de Chile, Valdivia, Chile.

Schmaljohn, C., and B. Hjelle
1997 Hantaviruses – a global disease problem. Emerging Infectious Diseases 3:95-104.

Simonetti, J. A., and T. Agüero
1990 Assessing independence of animal movements: spatio-temporal variability in *Oryzomys longicaudatus*. Mammalia 54:316-320.

Silva, S. I.
2005 Posiciones tróficas de pequeños mamíferos en Chile: una revisión. Revista Chilena de Historia Natural 78:589-599.

Silva, M. J. J., and Y. Yonenaga-Yassuda
1997 New karyotypes of two related species of *Oligoryzomys* genus (Cricetidae, Rodentia) involving centric fusion with loss of NORs and distribution of telomeric $(TTAGGG)_n$ sequences. Hereditas 127: 217-229.

Smith, M. F., and J. L. Patton
1999 Phylogenetic relationships and the radiation of Sigmodontine rodents in South America: evidence from cytochrome *b*. Journal of Mammalian Evolution 6:89-128

Spotorno, A. E, R. E. Palma, and J. P. Valladares
2000 Biología de los roedores reservorios de hantavirus en Chile. Revista Chilena de Infectología 17:197-210.

Stenseth, N. C., G. Ottersen, J. W. Hurrell, A. Mysterud, M. Lima, C. Kung-Sik, N. G. Yoccoz, and B. Adlandsvik
2003 Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. Proceedings of the Royal Society of London Ser. B 270:2087-2096.

Tate, G. H. H.
1932 The taxonomic history of the South and Central American cricetid rodents of the genus *Oryzomys*-Part 2. Subgenera *Oligoryzomys, Thallomyscus*, and *Melanomys*. American Museum Novitates 580:1-17.

Toro, J., J. D. Vega, A. S. Khan, J. N. Mills, P. Padula, W. Terry, Z .Yadón, R. Valderrama, B. A. Ellis, C. Pavletic, R. Cerda, S. Zaki, S. Wun-Ju, R .Meyer, M. Tapia, C. Mansilla, M. Baró, J.A. Vergara, M. Concha, G. Calderon, D. Enria, C. J. Peters, and T. G. Ksiazek
1998 An outbreak of hantavirus pulmonary syndrome, Chile, 1997. Emerging Infectious Diseases 4:687-694.

Torres-Pérez F., J. Navarrete-Droguett, R. Aldunate, T. L. Yates, G. J. Mertz, P. A. Vial, M. Ferrés, P. A. Marquet, and R. E. Palma
2004 Peridomestic small mammals associated with confirmed cases of human Hantavirus disease in southcentral Chile. American Journal of Tropical Medicine & Hygiene 70:305-309.

Tsai, T.
1987 Hemorrhagic fever with renal syndrome: mode of transmission to humans. Laboratory Animal Science 37:428- 430.

Vaughan, T. A., J. M. Ryan, and J. J. Czaplewski
2000 Mammalogy. 4th Edition. Saunders College Publishing, Orland, Florida, USA. 565 pp.

Yates T. L., J. N. Mills, C. A. Parmenter, T. G. Ksiazek, R. R. Parmenter, J. R. Vande Castle, C. H. Calisher, S. T. Nichol, K. D. Abbot, J. C. Young, M. L. Morrison, B. J. Baety, J. L. Dunnum, R. J. Baker, J. Salazar-Bravo, and C. J. Peters
2002 The ecology and evolutionary history of an emergent disease: Hantavirus pulmonary syndrome. BioScience 52:989-998.

THE OCTODONTIDAE REVISITED

UNA REVISION DE OCTODONTIDAE

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ABSTRACT

The monophyletic and depauperate assemblage of South American octodontid rodents has experienced an extensive adaptive radiation from above-ground dwellers to subterranean, saxicolous, and gerbil-like deserticolous life forms. Complex and saltational chromosomal repatterning is a hallmark of octodontid evolution. Recent molecular evidence links these chromosome dynamics with quantum genome size shifts, and probably with reticulate evolution via introgressive hybridization in the desert dwellers *Tympanoctomys barrerae* and *Pipanacoctomys aureus*. Genome duplication represents a novel mechanism of evolution in mammals and its adaptive role is reflected in the ability of deserticolous species to colonize the extreme environment of salt flats. Unique to *Tympanoctomys* is a the rigid bundle of hairs behind the upper incisors which is crucial to efficiently peel saltbush leaves and probably explains its broader distribution relative to *P. aureus*. This feature, in association with other attributes (e. g., specialized kidneys, large bullae, feeding behavior) has enabled *Tympanoctomys* to cope with extreme environmental conditions.

Key words: Octodontidae, Octodontids, South American mammals, tetraploidy, *Tympanoctomys barrerae*.

RESUMEN

Los octodóntidos son un grupo de roedores monofiléticos que han experimentado una extensa radiación adaptativa desde especies que viven en la superficie a formas de vida subterráneas o de tipo gerbos, especializados a la vida desertícola. La evolución de los octodóntidos está marcada por reordenamientos cromsómicos complejos y de tipo saltatorio. Las evidencias moleculares recientes indican una estrecha asociación entre esta dinámica cromosómica, los cambios genómicos cuánticos y la evolución

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Pp. 695-720 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

reticulada mediante hibridización introgresiva de los desertícolas *Tympanoctomys barrerae* y *Pipanacoctomys aureus.* La duplicación genómica representa un nuevo mecanismo de evolución en los mamíferos y su rol adaptativo se refleja en la habilidad de estas formas desertícolas para colonizar los ambientes extremos de los salares. Un rasgo único de *Tympanoctomys* son sus cerdas bucales, ubicadas detrás de los incisivos. Esta adaptación es crucial para pelar las hojas de las plantas halofíticas y seguramente constituye la ventaja que explica su mayor distribución en relación a *Pipanacoctomys aureus.* Este rasgo, asociado a otros atributos (e.g. riñones especializados, grandes bullas y comportamiento de alimentación) ha permitido la adaptación de *Tympanoctomys* a estos ambientes de condiciones extremas.

Palabras claves: Octodontidae, Octodontids, mamíferos Sudamericanos, tetraploidía, *Tympanoctomys barrerae*.

INTRODUCTION

Endemic of South America, octodontid rodents represent a monophyletic, species-poor but ecologically diverse assemblage of genera including above-surface dwellers, deserticolous, fossorial, and strictly subterranean forms (Table 1). Electrophoretic patterns (Köhler et al., 2000), DNA-DNA hybridization data (Gallardo and Kirsch, 2001), and sequencing of nuclear and mitochondrial markers support a basal clade containing the desert specialists, distributed along the eastern slope of the Andes. This clade is genetically distinct from the species distributed along the western slope (Honeycutt et al., 2003). Extensive chromosomal repatterning, absence of intra- or interpopulational chromosome polymorphism and a bidirectional trend of karyotypic evolution are characteristic of the Octodontidae (Gallardo, 1992, 1997). Indeed, a decrease from the modal 2n = 56-58 characterizes *Octodontomys gliroides* (2n = 38) whereas a saltational increase in diploid number (2n = 102) associated to genome size duplication has been reported for the red vizcacha rat, *Tympanoctomys barrerae* (Gallardo et al., 2003, 2004a).

The recent description of the salt flat dwellers, *Pipanacoctomys aureus and Salinoctomys loschalchalerosorum* has increased the recognized diversity of the deserticolous octodontids (Mares et al., 2000). The phylogenetic relationships of *P. aureus* to *T. barrerae*, its fully biarmed, 92-chromosome karyotype, and its unexpected double genome size provides evidence to advance a hybrid origin for *T. barrerae* (Gallardo et al., 2004a). Quantum increases of DNA content in the Octodontidae represent a unique trajectory in the group´s diversification and a novel mechanism of genome evolution in mammals. The buccal structures that allowed *T. barrerae* to feed on halophytic plants, and hence to colonize the arid salt flat formations, reflect the adaptive nature of this novelty. Data at hand have helped our understanding of the groups reticulate history and a shift from the idea that extant octodontids are remnants of a past and wider adaptive radiation (Reig, 1981). All these features make the octodontids a very distinctive group for studying its genome dynamics, and for contrasting macroecological and phylogenetic hypotheses. Here, updated data on the distribution, systematics, and natural history of the Octodontidae are provided, and a model to account for the genome duplication involving *T. barrerae* and *P. aureus* is advanced.

Table 1.- Ecological diversification of living octodontids and their latitudinal distribution ranges. Sources: Contreras et al., 1987; Mares and Ojeda, 1982; Mares et al., 2000; Nowak, 1991, 1999; Ojeda et al., 1996; Muñoz-Pedreros, 2000; Oyarce et al., 2003; Redford and Eisenberg, 1992.

SPECIES	Body Mass (g)	Ecoregion	Habits	Habitat	Diet	Distribution (Latitudinal Range)
Aconaemys fuscus	123 - 134	Andean –Patagonian forest	Semifossorial, colonial burrows	*Nothofagus* and *Araucaria* forests; sandy and xerophytic shrubs	Seeds and bulbs	35° - 36° S
Aconaemys sagei	83 - 110	Mediterranean, Matorral	Semifossorial	Bunchgrass and *Nothofagus* forests	?	37° - 39° S
Aconaemys porteri	80-110	Andean forest	Semifossorial	*Nothofagus* and *Araucaria* forests	Araucaria seeds, bamboo shots	39° - 40º S
Spalacopus cyanus	60 - 110	Andean and coastal areas	Fossorial, colonial burrows	Semidesert sandy loam, pasture lands,	Geophytes, Hemicryptophytes	27°- 36° S
Octodon degus	170-260	Mediterranean, Matorral	Terrestrial, colonial	Coastal and central scrublands	Chenopods, grasses, forbs, roots, seeds, leaves	28°- 33° S
Octodon bridgesi	155-240	Mediterranean, Matorral	Scansorial	Rocky and dense scrubland	Leaves, seeds, grasses	34° - 38° S
Octodon lunatus	130-235	Mediterranean, Matorral	Scansorial	Rocky and dense coastal scrublands	Shrubs, forbs, grasses	30º - 36° S
Octodon pacificus	290	Insular habitats	Scansorial	Mocha Island	?	38° S

Table 1 (continued).

Octodontomys gliroides	115 - 176	Highland; Puna and Prepuna	Scansorial, superficial burrows, solitary?	Rocky slopes; near rocky walls (pircas)	Cacti, acacia pods, seeds	15° - 28° S
Octomys mimax	80-110	Lowland ; Monte desert,	Saxicollous, solitary?	Rock outcrops	mesquite, shrubs, cacti	28° - 32° S
Tympanoctomys barrerae	81 - 104	Lowland; Monte desert; Monte-Chaco ecotone; Monte –Patagonia ecotone	Ground dwellers, burrow system, solitary	Salt basins; sand dunes	chenopodes, mesquite leaves	29°- 39ª S
Pipanacoctomys aureus	107	Monte desert	Ground dwellers, burrow system, solitary	Salt basin	chenopodes, mesquite	27° S
Salinoctomys loschalchalerosorum	?	Monte-Chaco ecotone	Ground dwellers, burrow system, solitary	Salt basin	Chenopodes?	30° S

BIOGEOGRAPHY, DISTRIBUTION, AND NATURAL HISTORY

The history and evolution of the South American caviomorph rodents has been thoroughly discussed by different authors (Patterson and Pascual, 1972; Reig, 1981; Woods, 1982; and references therein). The most ancestral caviomorph fossil, *Platypittamys*, known from the Oligocene of Bolivia and Patagonia (Wood and Patterson, 1959; Patterson and Pascual, 1972; Patterson and Wood, 1982) was a generalized ground-dweller lacking the hypsodont teeth that evolved concomitantly as aridity increased (Webb, 1978).

The radiation of the octodontids is connected with the Andean orogenesis as exemplified by the major Miocene-Pliocene faunistic diversification and subsequent climatic and vegetational changes (Contreras et al., 1987 and references therein). As the Andes rose up, new wind patterns resulted in different precipitation regimes across the mountain range (Solbrig, 1976; Mares, 1985). While humid forests and scrublands flourished along the western slope of the Andes, a gradual increase in arid conditions took place on its eastern side (Contreras et al., 1987). Central Argentina was already semiarid during the Eocene whereas Patagonia had a humid climate that supported woodlands during early Miocene (Wolkheimer, 1971). The shift to aridity occurred at the Miocene-Pliocene boundary whereas the northern Puna Desert developed as the Andes uplift took place during the Pleistocene (Simpson, 1975). Several families of caviomorph rodents (abrocomids, caviids, chinchillids, and octodontids) evolved to exploit diverse niches in response to the increasing aridity derived from these orogenic events (Mares and Ojeda, 1982; Mares, 1985).

The narrow, longitudinal distribution of the Octodontidae ranges from coastal central Chile to pre-Andean or Andean regions of Chile and Argentina. Latitudinally, it ranges from semiarid and desert shrublands to Mediterranean scrublands and humid forests between 15° to 40° S (Fig. 1). The diversification of this family in ecological (Mares and Ojeda, 1982), morphological (Mares et al., 1997), physiological (Díaz and Ojeda, 1999), and behavioral terms (Giannoni et al., 2000; Torres et al., 2003) shows some remarkable examples of convergence with rodents from other deserts (Ojeda et al., 1999).

Three major divisions can be recognized in the Octodontidae; an Andean-pre Andean group is represented by the scansorial *Octodontomys gliroides* (Fig. 1I) and there are 2 mainly lowland groups, the "Chilean" and the "Argentinean." The "Chilean" forms radiated into fossorial (*Aconaemys*; Fig 1B-D) and strictly subterranean forms (*Spalacopus cyanus*; Fig 1K) while another genus diversified into above-surface generalists (*Octodon*; Fig 1E-G) within Mediterranean scrubland and forests. The "Argentinean" group radiated into saxicolous (*Octomys* Fig 1J) and burrowing (*Pipanacoctomys, Tympanoctomys* and *Salinoctomys*; Figs. 1L-N) species, highly adapted to the desert patchy habitats of salt basins, sand dunes, and rock outcroppings.

SYSTEMATICS

The monophyly of the Octodontidae is well supported and the initial diversification of extant genera is estimated to have occurred at 9 myr bp (Gallardo and Kirsch, 2001). Although the sister taxon and the taxonomic rank of the Octodontidae was debated, the group´s close affinity to *Ctenomys* has been corroborated by molecular

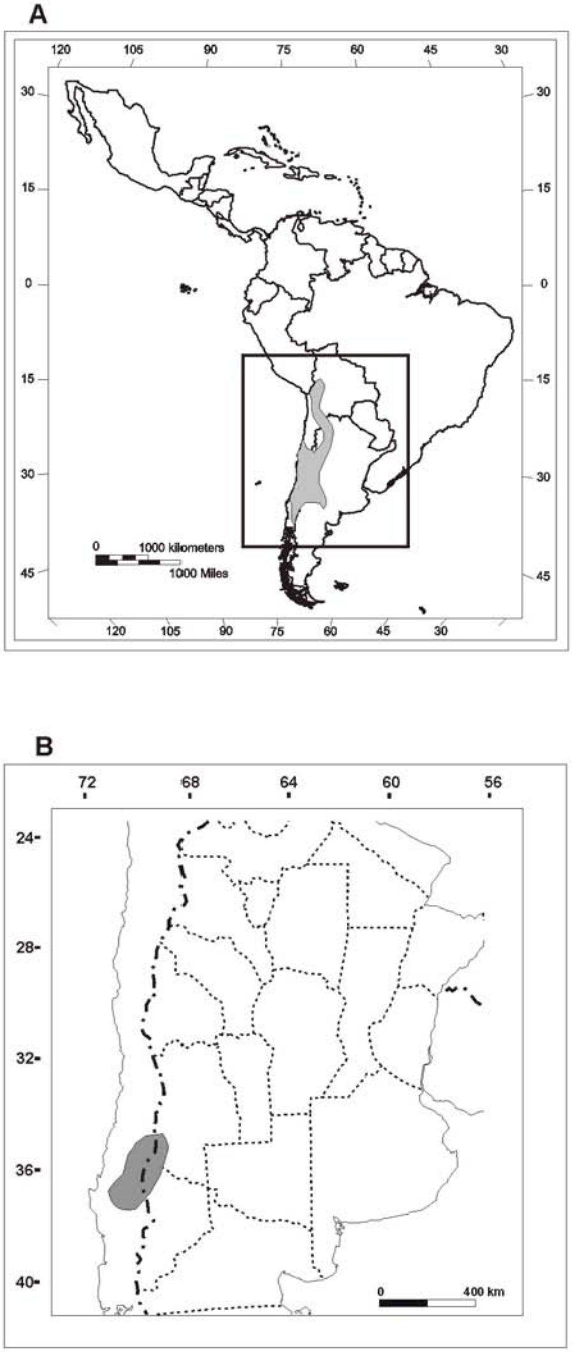
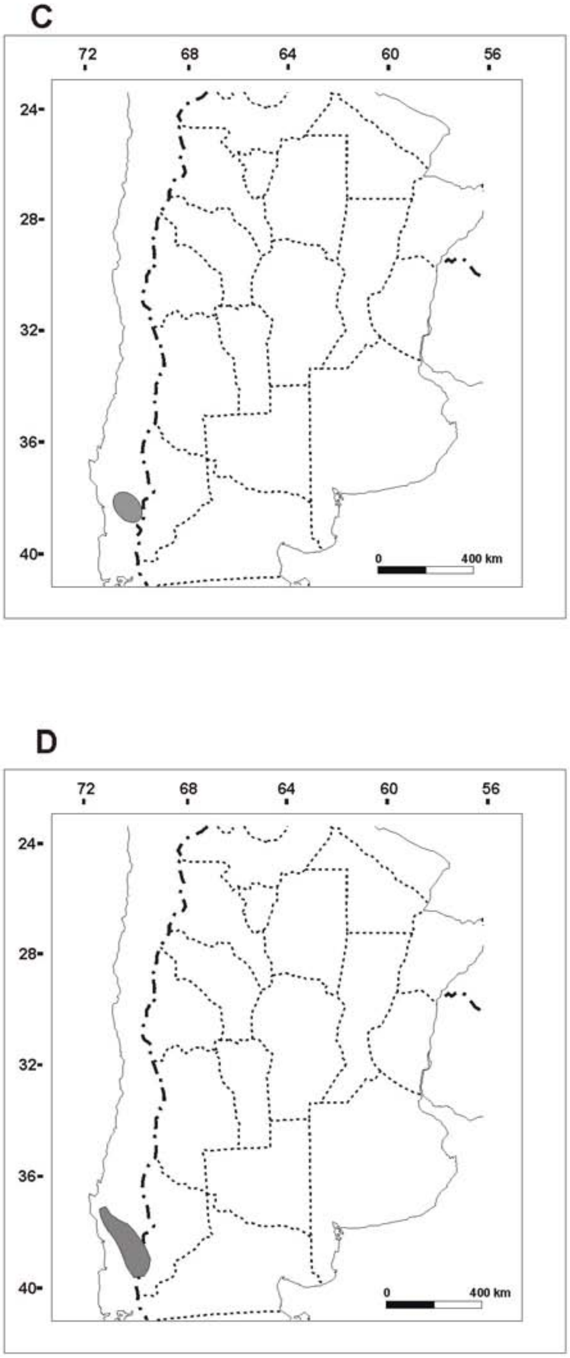
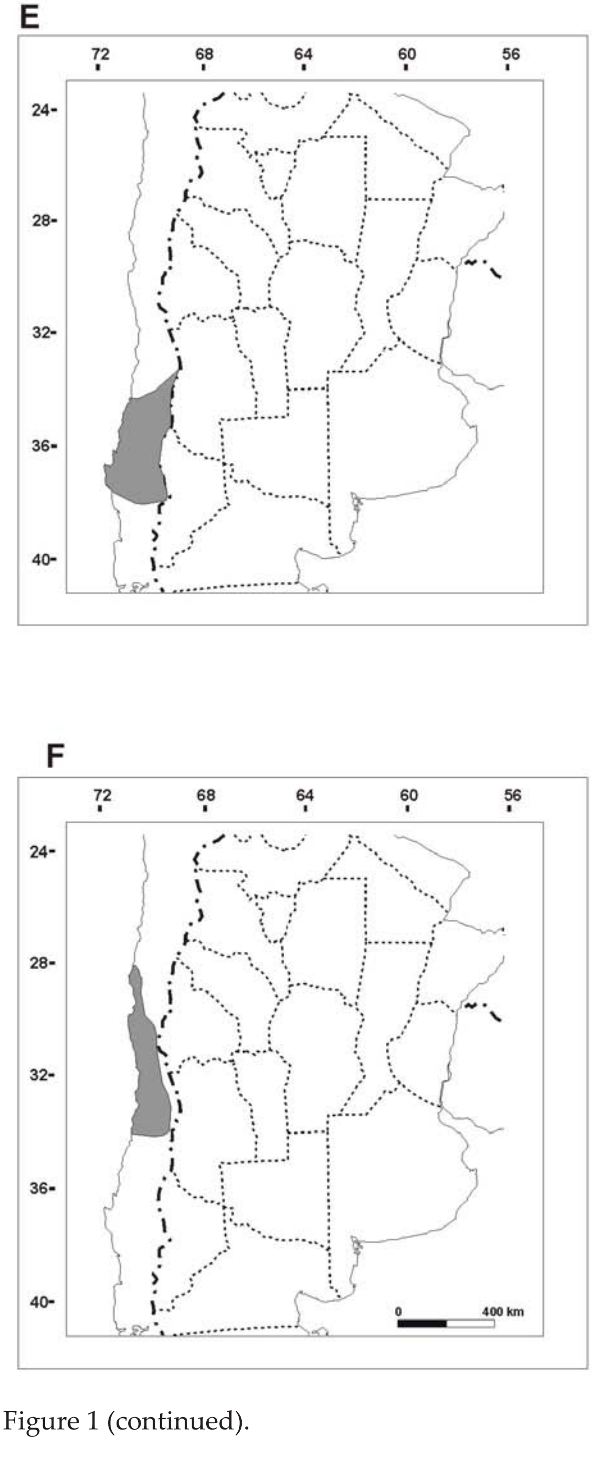


Figure 1. Geographic distribution of the Family Octodontidae (A) and their species: B) *Aconaemys fuscus*; C) *Aconaemys porteri*; D) *Aconaemys sagei*; E) *Octodon bridgesi*; F) *Octodon degus*; G) *Octodon lunatus*; H) *Octodon pacificus*; I) *Octodontomys gliroides*;



J) *Octomys mimax*; K) *Spalacopus cyanus*; L) *Pipanacoctomys aureus*; M) *Salinoctomys loschalchalerosorum*, and N) *Tympanoctomys barrerae*. The box in panel A shows the area that is enlarged in subsequent panels.



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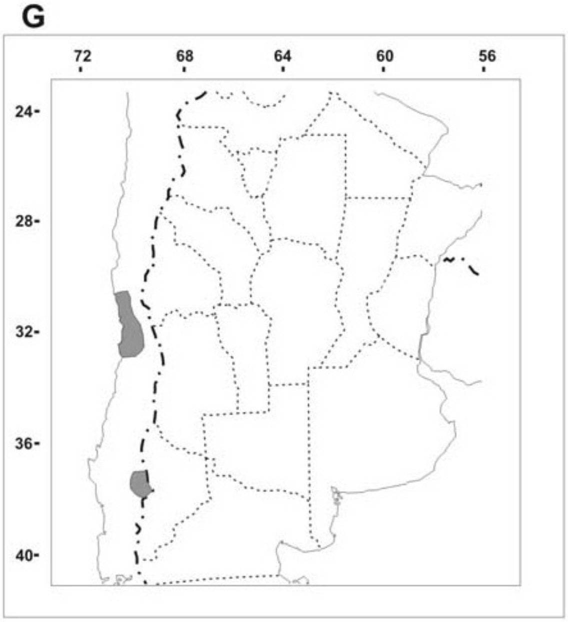

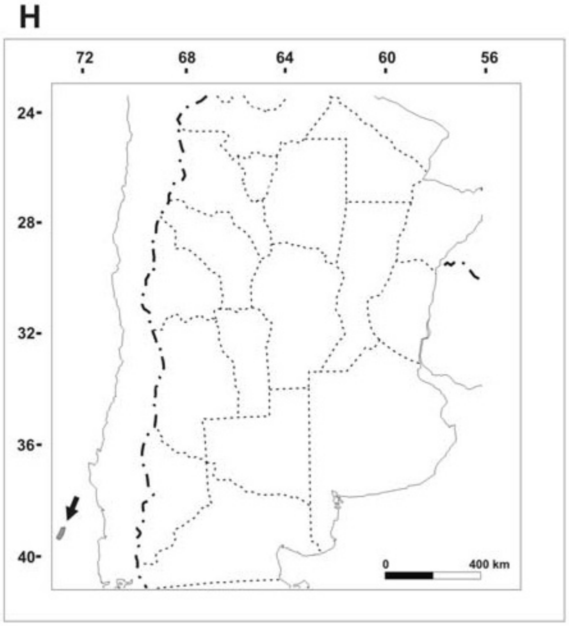

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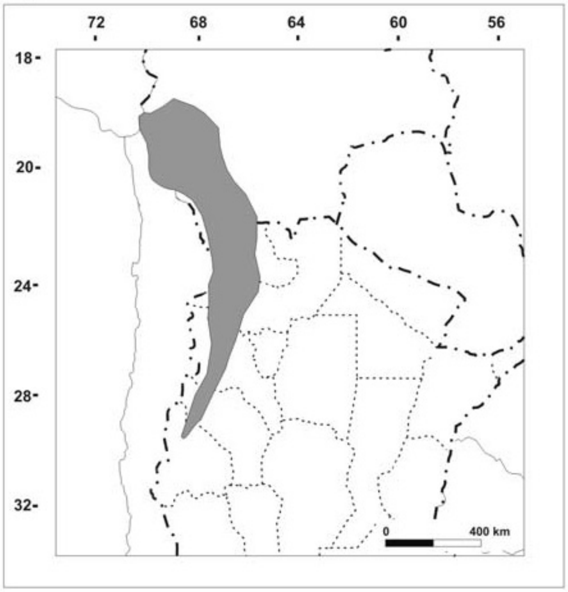

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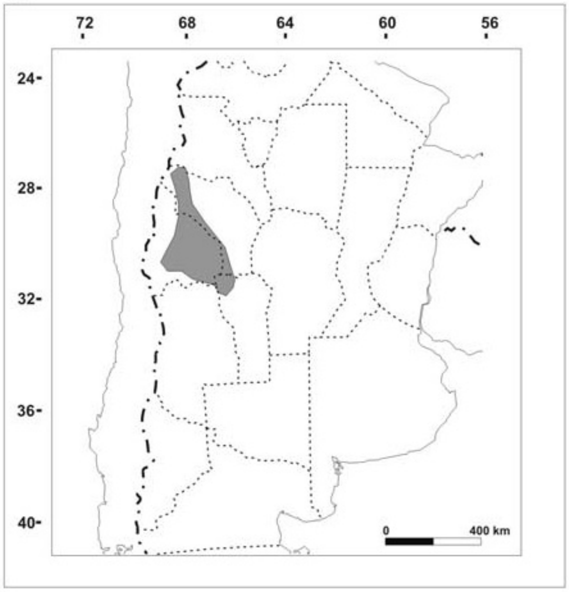

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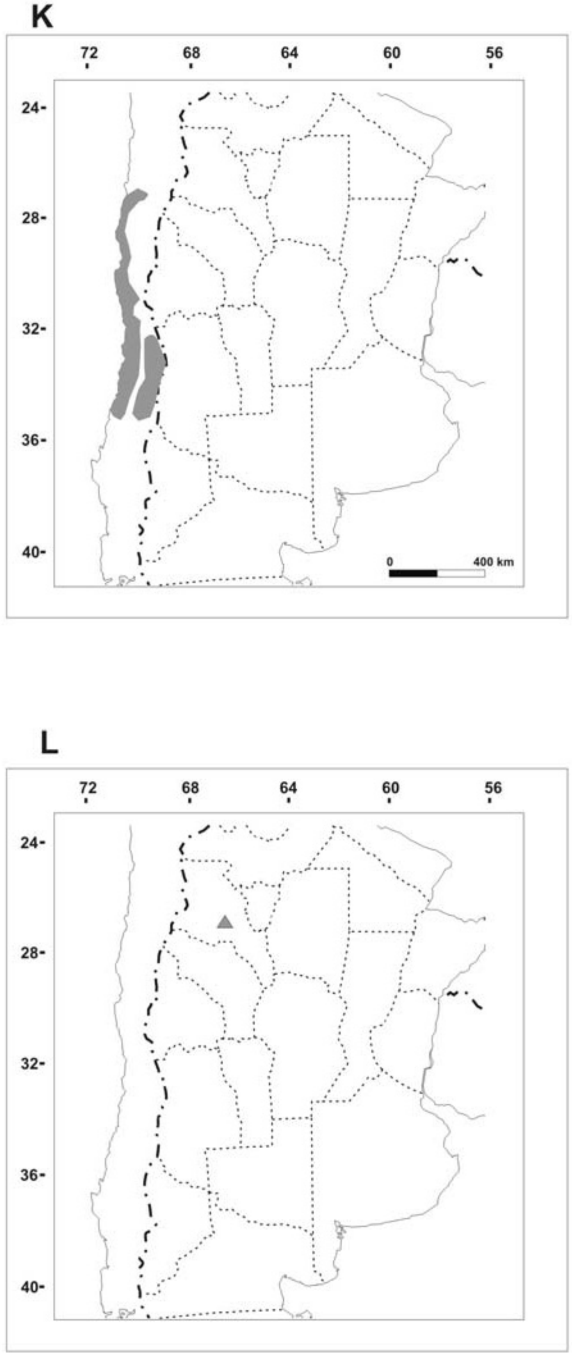

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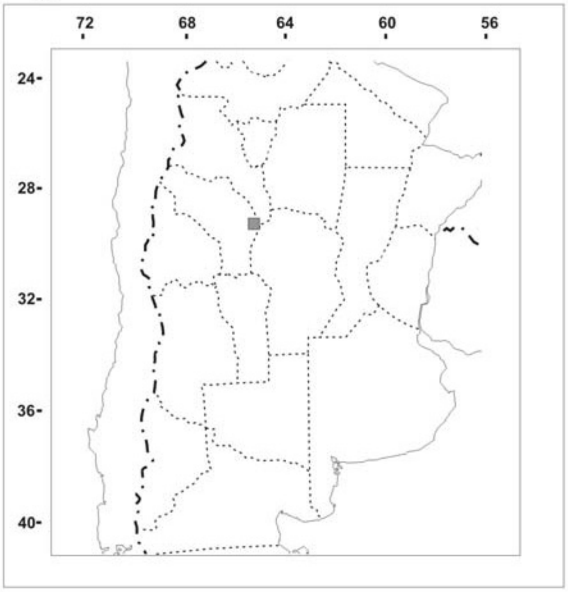

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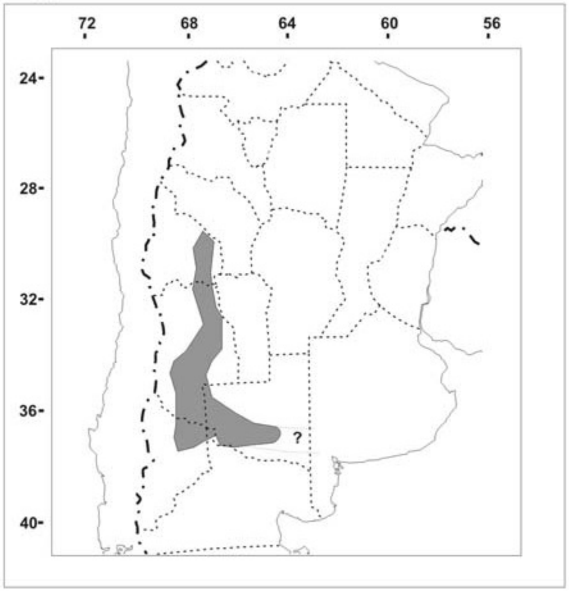

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data sets (Gallardo and Kirsch, 2001; Honeycutt et al., 2003). Indeed, molecular differentiation supports the family ranks of Ctenomyidae and Abrocomidae and place the latter at the base of the octodontid clade. The clade containing the Echimyidae and the Myocastoridae branches off between the Ctenomyidae and the Abrocomidae (Honeycutt et al., 2003). The robustness and consistency of molecular data provides no evidence for excluding *Octodontomys* from the Octodontidae *sensu stricto*, as had been suggested by Verzi (1994). It also suggests that the cranio-mandibular and dental morphology analyses of Verzi (2001) as well as the analysis of penial morphology of Contreras et al. (1993) may bear high levels of homoplasy.

Several accounts have stressed the wide range in chromosome number (2n = 38 -102) of the octodontids and its coincidence with the specific status of each form (Contreras et al., 1990; Gallardo, 1992; Spotorno et al., 1995). These extreme differences were interpreted as resulting from chromosome fusions with lower numbers derived from a high-numbered ancestral karyotype (Spotorno et al., 1988). Alternatively, Gallardo (1992, 1997) proposed a birectional trend, with a decrease from the modal 2n = 56-58 as observed in *O. gliroides* (2n = 38), and a saltational increase in chromosome number in *T. barrerae* (2n = 102). Combined analysis of mitochondrial and nuclear genes as an interpretative framework to test this hypothesis implied an ancestral 2n between 46 and 56 for the Octodontidae, thus supporting the bidirectional evolution of diploid numbers (Honeycutt et al., 2003)

Based on the close allozymic association between 102-chromosome *Tympanoctomys and-56-chromosome Octomys,*, the saltational model of karyotypic evolution predicted double genome size in *T. barrerae* (Gallardo, 1997). This was confirmed by genome size estimates although the suggestion advanced for *O. lunatus* was not supported by the data (Gallardo et al., 2003). The origin of *T. barrerae* has remained enigmatic since no karyotypic combination of any known octodontid species could originate its 102-chromosome karyotype (Gallardo et al., 1999). The subsequent description of *P. aureus* (Mares at al., 2000) has helped to resolve the reticulate history of the desert dwellers, and to document that speciation by polyploidy is possible in mammals (Gallardo et al., 2004a). *P. aureus* has a totally biarmed, 92-chromosome karyotype having several heteromorphic pairs. The Y chromosome is the only acrocentric of the male karyotype. The pair having a secondary constriction is present also in 2 biarmed chromosomes, as reported for *T. barrerae* (Gallardo et al., 2004a). The genome size of *P. aureus* is 2C = 15.34 ± 0.67 pg DNA whereas gametic DNA content is 1C = 7.18 ± 0.56 pg in the sperm cells. These estimates, although less than in *T. barrerae*, also are indicatative of genome doubling since the average 2C value of hystricognath rodents is 7.9 pg DNA (Gallardo et al., 2003).

Increased nuclear size and cell dimensions result from quantum increases in genome size (Gregory and Hebert, 1999; Gregory, 2001). These nucleotypic effects are observed in the spermatozoa as well as in liver cells and lymphocytes of *T. barrerae* (Gallardo et al., 2002). They are also observed in the kidney mass of *T. barrerae* (1.27 ± 0.11g) which is double that of *O. mimax* (0.52 ± 0.11g; Díaz, 2001). The nucleus diameter of primordial and growing follicles as well as those of the Graafian follicles, of the granulose, and of luteal cells are significantly larger and heavily heterochromatic compared to *S. cyanus* (Gallardo et al., 2004b). This high heterochromatin content probably is associated with the doubling of the species genome so that redundant genetic information may be silenced through permanent chromatin modifications.

The inclusion of nuclear and mitochondrial gene sequences for *P. aureus* did not alter the tree topology for the Octodontidae (Honeycutt et al., 2003) Fig. 2). *Tympanoctomys* and *Pipanacoctomys* are sister taxa, casting some doubts about the generic status of the latter. *Octomys* is sister to the *Tympanoctomys-Pipanacoctomys* clade, and forms a distinctive clade close to the root. The scansorial *Octodontomys gliroides* is basal to the second major clade which contains the Chilean genera *Aconaemys, Octodon*, and *Spalacopus*. The monophyletic derivation of *Aconaemys* and the genetic distinctiveness of its 3 species also is supported by chromosomal data (Gallardo and Mondaca, 2002). Likewise, the 3 *Octodon* species, recognized by DNA annealing data (Gallardo and Kirsch 2001), are corroborated by sequencing data (Honeycutt et al., 2003). Subterranean *Spalacopus* is related to fossorial *Aconaemys*, suggesting a common origin for adaptations to the underground niche (Fig. 2). No comparative genetic information exists for either the insular *Octodon pacificus* (Hutterer, 1994) or the deserticolous *Salinoctomy*s *loschalchalerosorum* to test their taxonomic status and phylogenetic affinities.

The extensive morphological, physiological, and ecological radiation of the depauperate octodontids contrasts with that of its highly speciose sister taxon, *Ctenomys*. This latter has radiated into approximately 60 species of similar bauplan, specialized in the exploitation of the subterranean niche only. These contrasting patterns of differentiation have been used to claim that extant Octodontidae are the remnants of an extensive past radiation (Reig, 1981). Nevertheless, standing diversities of *Ctenomys* and Octodontidae are not statistically different (Cook and Lessa, 1998). Molecular data and variation in DNA content implies that octodontid evolution was accompanied by a complex and saltational mode of chromosomal repatterning, probably through reticulate evolution. In contrast, genome size variation and the explosive chromosomal evolution in *Ctenomys* ($2n = 10\text{-}70$) may have followed a gradual pattern (Gallardo et al., 2003). The trajectories of genome evolution in these taxa are thus totally different and mark intrinsic differences, not considered by statistical tests. Genome duplication constitutes a novel mechanism of evolution in mammals and, as in plants, may be associated with quantum leaps to new adaptive zones without gradual interpopulational differentiation (Simpson, 1944).

ORIGIN OF GENOME DUPLICATIONS: A MODEL

Polyploidy in mammals is considered unlikely because the dosage compensation mechanism (X:A ratio) is disrupted after chromosome doubling (Orr, 1990). Subsequent imbalances derived from the constrained sex determination system further affect the normal developmental processes, and thus constitute an evolutionary dead end, as reported in humans (Goto and Monk, 1998). More recently, the lack of hybridization in animals has been argued to be the main factor preventing polyploidy in mammals (Otto and Whiton, 2000). However, since failure to hybridize is a consequence rather than a cause of genetic incompatibility, we consider the hybridization issue not to be a valid argument for the rarity of polyploid mammals.

Phylogenetic proximity, strict bivalent formation at meiosis, matching combinations of chromosome numbers, and similar patterns of intergenomic southern hybridization among *O. mimax*, *T. barrerae*, and *P. aureus* support the notion of introgressive hybridization (Gallardo et al., 2004a). A hypothetical scenario to account for the origin of the duplicated genome of *P. aureus* (Fig. 3) assumes the production of non-reduced

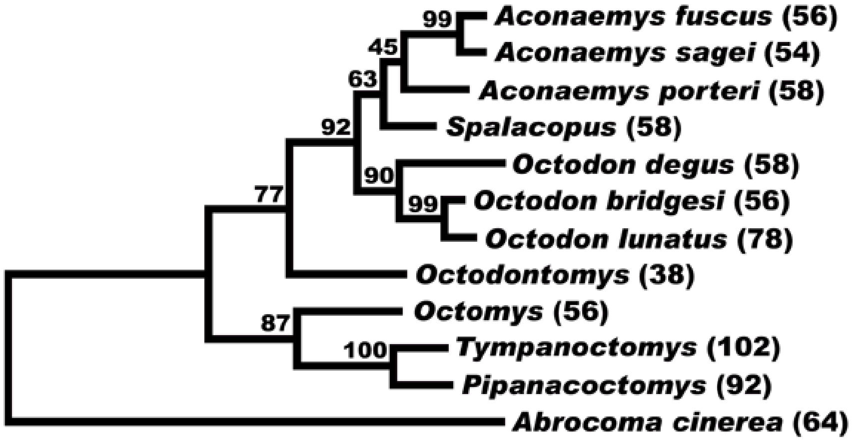

Figure 2. Phylogenetic tree of the Octodontidae based on sequencing data of the mitochondrial 12S rDNA gene and the nuclear growth hormone receptor (GHR) gene. *Abrocoma cinerea* is used to root the tree. Diploid number for each species is given in parentheses. This total evidence tree is based on 1000 bootstrap iterations.

gametes in 2 putative *Octomys* lineages that likely differed in chromosome number. Alternatively, tetraploidy in *Pipanacoctomys* could have originated by an additional set of maternal chromosomes (due to the incorporation of the polar body of meiosis I and double fertilization (dispermy) as reported in humans (Guc-Scekic et al., 2002; Baumer et al., 2003). Under this mechanism, tetraploid *Pipanacoctomys* males would inherit only one Y chromosome thereby avoiding the developmental failure experienced by double-Y tetraploid humans derived by endorreduplication (Goto and Monk, 1998). By the same token, the origin of *T. barrerae* may be hypothesized by assuming backcross of the tetraploid *Pipanacoctomys* lineage to the *Octomys* lineage. Again, either the production of unreduced gametes or double fertilization of a diploid oocyte is needed to account for the data and to explain the intriguing 102-chromosome complement of *T. barrerae* (Fig. 3).

The recurrent production of unreduced gametes is a common feature in polyploid fish and plants (Pagliarini et al., 1999; Alves et al., 2001). On the other hand, if both parental species differed in chromosome number (dibasic origin) as inferred from the heteromorphic chromosome pairing observed in *P. aureus,* some chromosome combinations must have been selected against. These incompatibilities must have reduced the effective population size and the chances of successful matings. Thus, the frequency of of polyploid mammals seem to be constrained by the uncommon events of their genesis and subsequent lineage sorting for the karyotypic uniformity reported in *T. barrerae* and *P. aureus*. Nevertheless, further research will be needed to substantiate these ideas.

Although the mechanisms to promote or initiate whole-genome duplications are unknown, the coincidental appearance of polyploids in extreme environments suggest the effect of external triggering factors. The Milankovitch climatic oscillation events in the Quaternary (e.g., dramatic environmental change in the past 1.8 Myr) have been advanced as factors promoting marked demographic and geographic

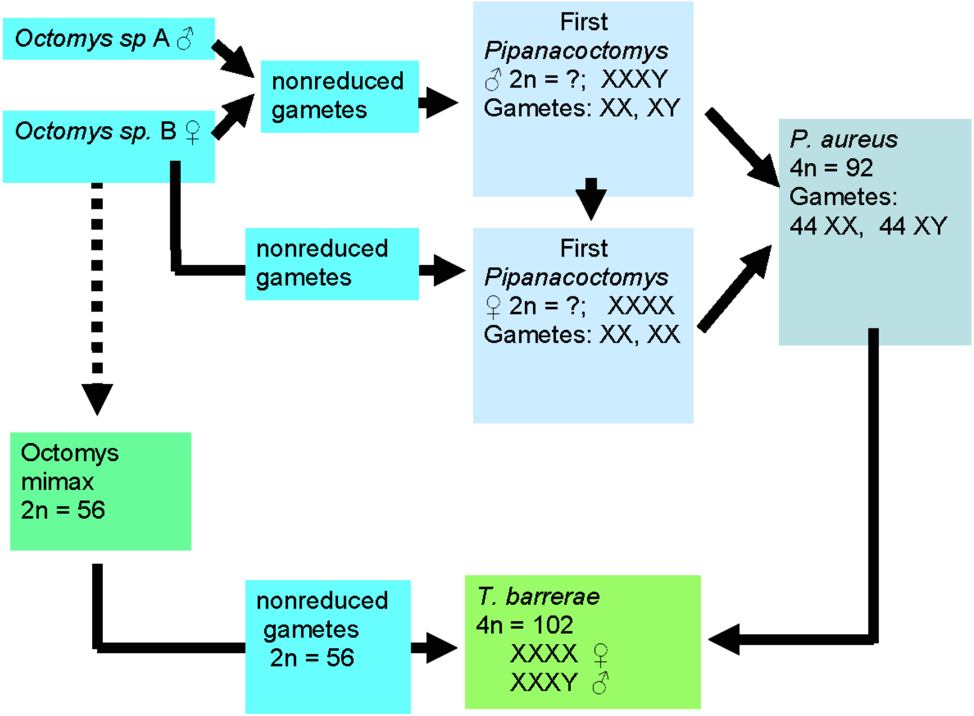

Figure 3. Proposed reticulated speciation events in the genesis of *Pipanoctomys aureus* and *Tympanoctomys barrerae*. *Octomys* "A" and "B" refer to putative species that probably no longer exist. The evolution of one of these lineages to originate extant *O. mimax* is suggested by dashed lines. The putative origin of *Pipanacoctomys* sp., is referred here as the "first" tetraploid taxon which subsequently evolved into extant *P. aureus*.

changes. Although a single Milankovitch cycle (on a temporal scale of 10^4-10^5 yrs) is not necessarily implicated to cause such evolutionary changes, repeated cycles may have additive effects that do lead to such changes (Bennett 1990; Dynesius and Jansson, 2000; Lister, 2004). Moreover, the high percentage of polyploids among the halophytic flora on islands in the North Sea (65%) is thought to be causally associated to extreme saline habitats (Stebbins, 1971), although such a proposition is derived from the present distribution of these species, and not from original causes. It is also well known that the frequency of polyploid plants increases at higher latitude and altitude, and that the highest number of polyploids is found in areas covered with ice sheets during Pleistocene glacial maxima (Stebbins, 1971). For the octodontid rodents, the close timing between the formation of South American deserts and the origin of genome size duplication (6.5-7.0 mybp; Gallardo and Kirsch, 2001) may suggest a causal connection yet to be studied; divergence time between *P. aureus* and *T. barrerae* assuming a molecular clock indicates 2.8-3.1 myr whereas new data analysis indicates 1.8 myr, at the Pliocene-Pleistocene boundary (Opazo, 2005).

The non-overlapping geographical ranges of *P. aureus* and *T. barrerae* have been interpreted as a result of vicariant events that broke the species geographic range and allowed allopatric differentiation (Mares at al., 2000). Although the distributional range of these populations may have been broken during the Quaternary events of dry and humid cycles, the genetic barrier between them was achieved while in contact, as in plants with duplicated genomes (Stebbins, 1971). The co-occurrence of *T. barrerae* and *O. mimax* in Ischigualasto National Park (La Rioja, Argentina), and the proximity of *P. aureus* type locality to that area provides a plausible biogeographic setting for understanding the reticulate history proposed here for these species.

A recent claim, using chromosome paints from *Octodon degus* hybridized to the mitotic plates of *T. barrerae*, concluded that the latter species is not in fact a tetraploid (Svartmann et al., 2005). The authors resort to discrediting arguments over tetraploidy by avoiding citation and discussion of recent molecular evidence (Gallardo et al., 2004a, 2004b). Moreover, their identification of the sex chromosomes of *Octodon degus* contradicts previous reports (Fernández, 1968; Gallardo 1992; Spotorno et al., 1995) but this discrepancy is not explained. In addition, the Y chromosome of *T. barrerae* and *P. aureus* (easily recognized as the only acrocentric chromosome in the male karyotype; Gallardo et al., 1999; Gallardo et al., 2004a) is misidentified as an autosome. This confusion stems from the assumption that gender could unequivocally be identified from a primary culture of a non-sexed *T. barrerae* embryo. We found their arguments against our work somewhat vague, especially because incorrect sex determination on their part resulted in a mis-paired karyotype (their Fig. 3B), which in turn was used as evidence to claim that large-scale heterochromatin accumulation explained the double genome size of the red vizcacha rat. Contrary to their conclusions, the chromosome mis-pairing of *T. barrerae* is not a consequence of its diploid condition, but a reflection of the species´ hybrid origin. Indeed, the banding heteromorphisms of *T. barrerae* strongly resemble the G- and C-banding differences in interspecific hybrids of the rodent genera *Uromys* (Baverstock et al., 1982) and *Melomys* (Baverstock et al., 1980). Methodologically, the use of chromosome painting has been criticized on several grounds when dealing with organisms having complex genomes intra- or interspecifically (Fuchs et al., 1996). The technique is highly inefficient at blocking disperse repetitive sequences (like in *T. barrerae*) and fails to detect the signal intensity of unique sequences. This may explain the paradox of obtaining stronger hybridization signals in heterologous assays relative to signal intensity in homologous hybridizations (Figs. 4B, 4C, 5B, 5C in Svartman et al., 2005). It seems likely that the stringency used to remove excessive background noise from the mitotic plates resulted in washing off weaker signals due to the limited affinity of heterologous probes to target chromosomes (Fuchs et al., 1996). Finally, we regret the authors´ confusion between quantum genome size shifts (Gallardo et al., 2003) and chromosome evolution in the octodontids. In fact, the 78-chromosome *Octodon lunatus* is half-way in a progression between 56 to102 chromosomes. Nevertheless, the 8.8 pg DNA of *O. lunatus* is not intermediate between diploid average in hystricognaths (7.9 pg DNA) and the record value of 16.8 pg DNA in *T. barrerae*, as argued by Svartmann et al. (2005).

THE SPECIAL CASE OF THE RED VIZCACHA RAT

The inflated bullae, specialized kidneys, and the rigid bundle of buccal hairs are part of the ecomorphological and physiological attributes that enabled the red vizcacha rat to cope with open, extreme habitats and their specialized food resources (Ojeda et al., 1996, 1999; Díaz and Ojeda, 1999; Díaz et al., 2000). Indeed, the restricted distributions of *P. aureus* and *S. loschalchalerosorum* (known from their type localities only; Mares et al., 2000) are in sharp contrast with that of *T. barrerae* (Fig**.** 1L-N). Fossil remains from the Atlantic coast of Argentina (Verzi et al., 2002) indicate a wider past distribution of the red vizcacha rat and imply that its present distributional record is a relict of a larger geographic range. The stratigraphic setting of this fossil of about 1myr, corresponding with the expansion of arid landscapes during the dry phases of the Quaternary events.

The different distributional ranges between *S. loschalchalerosorum, P. aureus*, and *T. barrerae* argue against interspecific competition for ephemeral food items. Indeed, saltbush plants (*Atriplex* sp.) and other chenopodes constitute a stable food and water resource in most salt basins and sand dunes (Torres-Mura et al., 1989; Ojeda et al., 1996) such that the colonization success of *T. barrerae* has been advanced to result from its buccal modifications. This feature, the buccal comb unique to the red vizcacha rat, allows efficient peeling of *Atriplex sp.* leaves (Mares et al., 1997; Giannoni et al., 2000), which in association with other ecological, physiological, and behavioral attributes, enabled the species to occupy a new adaptive zone (Simpson, 1944).

Note added in proof

Recently, duplication of loci in multiple-copy (major rDNAs) and single-copy (Hoxc8) genes has been corroborated by fluorescence *in situ* hybridization in *T. barrerae* (Gallardo et al., 2006). Moreover, nucleolar dominance, a large-scale epigenetic silencing phenomenon characteristic of allopolyploids, has been demonstrated to explain the presence of one AG-NOR chromosome pair in the red vizcacha rat. Nucleolar dominance, together with the chromosomal heteromorphism detected in the G-banding pattern and synaptonemal complexes of the species´ diploid-like meiosis, consistently indicates allotetraploidy. Allotetraploidization can coherently explain the peculiarities of gene silencing, increased cell dimensions, and karyotypic evolution of *T. barrerae* that remain unexplained by assuming diploidy and a large genome size attained by the dispersion of repetitive sequences (Gallardo et al., 2006).

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LITERATURE CITED

Alves, M. J., M. M. Coehlo, and M. J. Collares- Pereira
2001 Evolution in action through hybridization and polyploidy in an Iberian freshwater fish: a genetic review. Genetica 111:375-385.

Baumer A., D. Dres, S. Basaran, H. Isci, T. Dehgan, and A. Schinzel
2003 Parental origin of the two additional haploid sets of chromosomes in an embryo with tetraploidy. Cytogenetics and Genome Research 101:5-7.

Baverstock, P. R., M. Gelder, and A. Jahnke
1982 Cytogenetic studies of the Australian rodent *Uromys caudimaculatus*, a species showing extensive heterochromatin variation. Chromosoma 84:517-533.

Baverstock, P. R., C. H. S. Watts, M. Adams, and M. Gelder
1980 Chromosomal and electrophoretic studies of Australian *Melomys* (Rodentia: Muridae). Australian Journal of Zoology 28:553-574.

Bennett, K. D.
1990 Milankovitch cycles and their effects on species in ecological and evolutionary time. Paleobiology 16:11-21.

Contreras, L. C., J. C. Torres-Mura, and A. E. Spotorno
1990 The largest known chromosome number for a mammal in a South American desert rodent. Experientia 46:506-509.

Contreras, L. C., J. C. Torres-Mura, A. E. Spotorno, and F. M. Catzeflis
1993 Morphological variation of the glans penis of South American octodontid and abrocomid rodents. Journal of Mammalogy 74:926- 935.

Contreras, L. C., J. C. Torres-Mura, and J. L. Yáñez
1987 Biogeography of octodontid rodents: an eco-evolutionary hypothesis. Pp. 401-411 in Studies in Neotropical Mammalogy. Essays in Honor of P. Hershkovitz (Patterson, B. D., and R. E. Timm, eds.). Fieldiana: Zoology, new series 39.

Cook J. A., and E. Lessa
1998 Are rates of diversification in subterranean South American tuco-tucos (Genus *Ctenomys*, Rodentia, Octodontidae) unusually high? Evolution 52:1521-1527.

Díaz, G. B.
2001 Ecofisiología de Pequeños Mamíferos de las Tierras Áridas de Argentina: Adaptaciones Renales. Ph.D. Dissertation, Universidad Nacional de Cuyo, Mendoza, Argentina. 123 pp.

Díaz, G.B., and R. A. Ojeda
1999 Kidney structure of Argentine desert rodents. Journal of Arid Environments 41:453-461.

Díaz, G. B., R. A. Ojeda, M. H. Gallardo, and S. M. Giannoni
2000 *Tympanoctomys barrerae*. Mammalian Species 646:1-4.

Dynesius M., and R. Jansson
2000 Evolutionary consequences of changes in species´ geographic distributions driven by Milankovitch climate oscillations. Proceedings of the National Academy of Science (USA) 97:9115-9120.

Fernández, R.
1968 El cariotipo del *Octodon degus* (Rodentia-Octodontidae). Archivos de Biologia y Medicina Experimentales 5:33-37.

Fuchs, J., A. Houben, A., Brandes, and I. Schubert
1996 Chromosome "painting" in plants - a feasible technique? Chromosoma 104:315-320.

Gallardo, M. H.
1992 Karyotypic evolution in octodontid rodents based on C-band analysis. Journal of Mammalogy 73:89-98.

1997 A saltation model of karyotypic evolution in the Octodontoidea (Mammalia, Rodentia). Pp. 347-365 in Chromosomes Today, vol. 12 (Henríquez-Gil, N., J. S. Parker, and M. J. Puertas, eds.). Chapman and Hall, London, UK.

Gallardo, M. H. J. W. Bickham, G. Kausel, N. Köhler, and R. L. Honeycutt
1999 Discovery of tetraploidy in a mammal. Nature 401:341.

2003 Gradual and quantum genome size shifts in the hystricognath rodents. Journal of Evolutionary Biology 16:163-169.

Gallardo, M. H, O. Garrido, R. Bahamonde, and M. González
2004b Gametogenesis and nucleotypic effects in the tetraploid red vizcacha rat, *Tympanoctomys barrerae* (Rodentia, Octodontidae). Biological Research 37:767-775.

Gallardo, M. H., C. A. González, I. Cebrián.
2006 Molecular cytogenetics and allotetraploidy in the red vizcacha rat, Tympanoctomys barrerae (Rodentia, Octodontidae). Genomics, 88: 214-221

Gallardo, M. H., G. Kausel, A. Jiménez, C. Bacquet, C. A. González, J. Figueroa, N. Köhler, and R. A. Ojeda
2004a Whole-genome duplications in South American desert rodents (Octodontidae). Biological Journal of the Linnean Society 82:443-451.

Gallardo, M. H., and J. A. W. Kirsch
2001 Molecular relationships among Octodontidae (Mammalia: Rodentia: Caviomorpha). Journal of Mammalian Evolution 8:73-89.

Gallardo, M. H., and F. Mondaca
2002 The systematics of *Aconaemys* (Rodentia, Octodontidae) and the distribution of *A. sagei* in Chile. Mammalian Biology 67:105-112.

Gallardo, M. H., F. Mondaca, R. A. Ojeda, N. Köhler, and O. Garrido
2002 Morphological diversity in the sperms of caviomorph rodents. Mastozoología Neotropical 9:159-170.

Giannoni, S. M., C. E. Borghi, and R. A. Ojeda.
2000 Foraging ecology of *Tympanoctomys barrerae*. Journal of Arid Environments 46:117-121.

Goto T, and M. Monk
1998 Regulation of X-chromosome inactivation in development in mice and humans. Microbiology and Molecular Biology Reviews 62:362-378.

Gregory, T. R.
2001 Coincidence, coevolution, or causation? DNA content, cell size, and the C-value enigma. Biological Review 76:65-101.

Gregory, T. R., and P. D. N. Hebert
1999 The modulation of DNA content: proximate causes and ultimate consequences. Genome Research 9:317-324.

Guc-Scekic, M., J. Milasin, M. Stevanovic, J. L. Stojanov, and M. Djorjevic
2002 Tetraploidy in a 26-month old girl (cytogenetic and molecular studies). Clinical Genetics 61:62-65

Honeycutt, R. L., D. L. Rowe, and M. H. Gallardo
2003 Molecular systematics of the South American caviomorph rodents: relationships among species and genera in the family Octodontidae. Molecular Phylogenetics and Evolution 26:476-489.

Hutterer, R.
1994 Island rodents: a new species of *Octodon* from Isla Mocha, Chile. Zeitschrift für Säugetierkunde 59:27-41.

Köhler, N., M. Gallardo, L. C. Contreras, and J. C. Torres-Mura
2000 Allozymic variation and systematic relationships of the Octodontidae and allied taxa (Mammalia, Rodentia). Journal of Zoology (London) 252:243-250.

Lister, A. M.
2004 The impact of Quaternary Ice Ages on mammalian evolution. Philosophical Transactions of the Royal Society of London B 359:221–241.

Mares, M. A.
1985 Mammal faunas of xeric habitats and the Great American Interchange. Pp. 489-520 in The Great American Biotic Interchange (Stehli, F. G., and S. D. Webb, eds.). Plenum Publishing Corporation, New York, New York, USA.

Mares, M. A., J. K. Braun, R. M. Barquez, and M. M. Díaz
2000 Two new genera and species of halophytic desert mammal from isolated salt flats in Argentina. Occasional Papers, The Museum, Texas Tech University 203:1-27.

Mares, M. A., and R. A. Ojeda
1982 Patterns of diversity and adaptation in South American Histricognath Rodents. Pp. 393-432 in Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, Special Publication Series, 6. University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

Mares, M. A., R. A. Ojeda, C. E. Borghi, S. M. Giannoni, G. B. Diaz, and J. K. Braun
1997 A desert rodent uses hair as a tool to overcome halophytic plant defenses. BioScience 47:699-704.

Muñoz-Pedreros, A.
2000 Orden Rodentia. Pp. 73-126 in Mamíferos de Chile (Muñoz Pedreros, A., and J. Yáñez-Valenzuela, eds). CEA Ediciones, Valdivia, Chile.

Nowak, R. M.
2001 Walker´s Mammals of the World, vol. II. Sixth edition. The Johns Hopkins University Press, Baltimore and London. 1936 pp.

Ojeda, R. A., C. E. Borghi, G. B. Diaz, S. M. Giannoni, M. A. Mares, and J. K. Braun
1999 Evolutionary convergence of the highly adapted desert rodent *Tympanoctomys barrerae* (Octodontidae). Journal of Arid Environments 41:443-452.

Ojeda, R. A., J. Gonnet, C. Borghi, S. Gianonni, C. Campos, and G. Diaz.
1996 Ecological observations of the red vizcacha rat *Tympanoctomys barrerae* in two desert habitats of Argentina. Mastozoología Neotropical 3:183-191.

Opazo, J. C.
2005 A molecular timescale for caviomorph rodents (Mammalia, Hystricognathi). Molecular Phylogenetics and Evolution 37:932-937.

Orr, H. A.
1990 “Why polyploidy is rarer in animals than in plants” revisited. American Naturalist 136:759-770.

Otto, S. P., and J. Whitton
2000 Polyploid incidence and evolution. Annual Reviews of Genetics 34:401-437.

Oyarce, C. E, C. M. Campos, G. B. Díaz, and M. A. Dacar
2003 Hábitos alimentarios de *Octomys mimax* (Rodentia: Octodontidae), en el parque provincial Ischigualasto (San Juan, Argentina). Pp. 59, XVIII Jornadas SAREM, La Rioja, Argentina.

Pagliarini, M. S., S. Y. Takayama, P. M. de Freitas, L. R. Carraro, E. V. Adamowski, N. Silva, and L. A. R. Batista
1999 Failure of cytokinesis and 2n gamete formation in Brazilian accessions of *Paspalum*. Euphytica 108:129-135.

Patterson, B., and R. Pascual
1972 The fossil mammal fauna of South America. Pp. 247-309 in Evolution, Mammals and Southern Continents (Keast, A., F. C. Erk, and B. Glass, eds.). State University of New York Press, Albany, New York, USA.

Patterson, B., and A. E. Wood
1982 Rodents from the Deseadan Oligocene from Bolivia and the relationships of the Caviomorpha. Bulletin of the Museum of Comparative Zoology 149:371-543.

Redford, K. H., and J. F. Eisenberg
1992 Mammals of the Neotropics. Vol. 2, The Southern Cone: Chile, Argentina, Uruguay, Paraguay. The University of Chicago Press, Chicago, Illinois, USA. 430 pp.

Reig, O.
1981 Teoría del Origen y Desarrollo de la Fauna de Mamíferos de América del Sur. Monographie Naturae, Museo Municipal de Ciencias Naturales "Lorenzo Scaglia," Mar del Plata, Argentina.

Simpson, B. B.
1975 Pleistocene changes in the flora of the high tropical Andes. Paleobiology 1:273-294.

Simpson, G. G.
1944 Tempo and Mode in Evolution. Columbia University Press, New York, New York, USA. 237 pp

Solbrig, O.
1976 The origin and floristic affinities of the South American temperate desert and semidesert regions. Pp. 7-49 in Evolution of Desert Biota (Goodall, D.W., ed.). University of Texas Press, Austin, Texas, USA.

Spotorno, A., L. Walker, L. C. Contreras, J. Pincheira, and R. Fernández Donoso
1988 Cromosomas ancestrales en Octodontidae y Abrocomidae. Archivos de Biologia y Medicina Experimentales 21:527.

Spotorno, A. E., L. Walter, L. C. Contreras, J. C. Torres-Mura, R. Fernández-Donoso, M. S. Berríos, and J. Pincheira
1995 Chromosome divergence of *Octodon lunatus* and the origins of Octodontoidea (Rodentia, Hystricognathi). Revista Chilena de Historia Natural 68:227-239.

Stebbins G. L.
1971 Chromosomal Evolution in Higher Plants. Edward Arnold Publishers, London, UK. 216 pp.

Svartman, M, G. Stone, and R. Stanyon
2005 Molecular cytogenetics discards polyploidy in mammals. Genomics 5:425.430.

Torres, M. R., C. A. Borghi, S. M. Giannoni, and A. Pattini
2003 Portal orientation and architecture of burrows in *Tympanoctomys barrerae* (Rodentia, Octodontidae). Journal of Mammalogy 84:541-546.

Torres-Mura, J. C., M. I. Lemus, and L. C. Contreras
1989 Herbivorous specialization of the South American desert rodent *Tympanoctomys barrerae*. Journal of Mammalogy 70:646-648.

Verzi, D. H.
1994 Origen y Evolución de los Ctenomyinae (Rodentia, Octodontidae): un análisis de anatomía cráneo-dentaria. Ph.D. Dissertation, Universidad Nacional de La Plata, Argentina. 226 pp.

2001 Phylogenetic position of *Abalosia* and the evolution of extant Octodontinae (Rodentia, Caviomorpha, Octodontidae. Acta Theriologica 46:243-268.

Verzi, D. H., E. P. Tonny, O. A. Scaglia, and J. O. San Cristobal
2002 The fossil record of the desert-adapted South American rodent *Tympanoctomys* (Rodentia, Octodontidae). Paleoenvironmental and biogeographic significance. Palaeogeography, Palaeoclimatology, Palaeoecology 179:149-158.

Webb, D.
1978 A history of savanna vertebrates in the New World, Part II. South America and the Great Interchange. Annual Reviews of Ecology and Systematics 9:393-426.

Wolkheimer, W.
1971 Aspectos paleoclimatológicos del Terciario Argentino. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigación de las Ciencias Naturales. Paleontología 1:243-262.

Wood A. E., and B. Patterson
1959 The rodents of the Deseadan Oligocene of Patagonia and the beginning of South American rodent evolution. Bulletin of the Museum of Comparative Zoology, Harvard University 120:279-428.

Woods, C. A.
1982 The history and classification of South American hystricognath rodents: Reflections on the far away and long ago. Pp. 377-392 in Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, Special Publication Series, 6. University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

MORPHOLOGICAL AND MOLECULAR VARIATION WITHIN LITTLE BIG-EARED BATS OF THE GENUS *MICRONYCTERIS* (PHYLLOSTOMIDAE: MICRONYCTERINAE) FROM SAN LORENZO, ECUADOR

VARIACIÓN MORFOLÓGICA Y MOLECULAR EN EL GÉNERO *MICRONYCTERIS* (PHYLLOSTOMIDAE: MICRONYCTERINAE) DE SAN LORENZO, ECUADOR

René M. Fonseca[1], Steven R. Hoofer, Calvin A. Porter, Chrissy A. Cline,
Deidre A. Parish, Federico G. Hoffmann, and Robert J. Baker[2]

DEDICATION AND ENCOMIUM: The following statement is by Robert Baker.

I first became aware of the significance of Oliver Pearson's work through the classic paper "Reproduction of the Lump-Nosed Bat (Corynorhinus rafinesquei) in California" (Pearson, O.P, M. R. Koford, and A. K. Pearson. 1952 J. Mammal. 33: 273-320), which impressed me as a standard for scientific research. At the mammal meetings, I had the pleasure of interacting with Professor Pearson and his wife Anita and they always were happy discussing mammalogy, South American research, or a wide array of other topics of interest such as how to keep the birds from eating the fruit from the trees in your yard. It was in Pittsburgh at the Pymatuning Symposium on Mammalian Biology in South America that I became fascinated with his class and style in presentations of papers. I would ask my students that attended the mammal meetings to sit with me and listen to Dr. Pearson present his work because he had such control over the English language and word order that many of his sentences were poetic. My response to such papers was usually something like "Wow! I wish I could present a paper like that." In that way, he was a mentor to many of my graduate students. I always admired both his science and his dedication to field work. Paynie brought class to our beloved science. The world is a lesser place in his absence.

There are seven authors on this paper, including two South American students of mammalogy (René Fonseca and Federico Hoffmann). Whereas Robert Baker is the only author who had the privilege of personally meeting Dr. Pearson, all authors are aware of Dr. Pearson's incredible contribution to understanding the mammalian fauna of South America and enthusiastically dedicate our work to Dr. Pearson.

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[2] Author for correspondence.

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ABSTRACT

The genus *Micronycteris* has undergone several taxonomic changes in recent years. The most recent morphological review of *Micronycteris* recognizes 9 species, including 4 dark-bellied species (*hirsuta*, *matses*, *megalotis*, *microtis*), and 5 pale-bellied species (*brosseti*, *homezi*, *minuta*, *sanborni*, *schmidtorum*). Specimens of *Micronycteris* from Ecuador are poorly represented in museum collections, and some important areas within the country have few voucher specimens. Only 3 species (*hirsuta*, *megalotis*, and *minuta*) have been recorded in Ecuador. We collected a small series (*N* = 10) of dark-bellied specimens of *Micronycteris* during the Sowell Expedition 2001 to northwest Ecuador. In this paper we assess the morphological and molecular interspecific variation within the genus, comparing our series to other *Micronycteris* found in Ecuador and other Latin American countries. In Ecuador we distinguish 3 morphotypes among dark-bellied forms. With one exception, our specimens except are referable either to *M. megalotis* or *M. hirsuta*. The one exception is unlike any other recognized species of *Micronycteris*. We provide a set of characters useful to distinguish dark-bellied species of *Micronycteris* in Ecuador and describe a new species.

Key words: Phyllostomidae, genetic species concept, *Micronycteris*, *M. giovanniae*, *M. megalotis*, *M. matses*, *M. hirsuta*, cytochrome-*b*, karyotypes, morphometrics

RESUMEN

El género *Micronycteris* ha sufrido varios cambios taxonómicos en los últimos años. La revisión morfológica más reciente reconoce 9 especies, incluyendo 4 con vientre oscuro (*hirsuta*, *matses*, *megalotis*, *microtis*), y 5 con vientre pálido (*brosseti*, *homezi*, *minuta*, *sanborni*, *schmidtorum*). Los ejemplares de Ecuador están pobremente representados en colecciones de museo, y algunas áreas importantes de ese país están representadas por pocos ejemplares. Sólo 3 especies (*hirsuta*, *megalotis*, y *minuta)* han sido registradas en Ecuador. Colectamos una pequeña serie (*N*=10) de especímenes de vientre oscuro de *Micronycteris* durante la Expedición Sowell del 2001 al noroeste de Ecuador. En este trabajo evaluamos la variación morfológica y molecular interespecífica dentro del género, comparando nuestra serie con otros *Micronycteris* encontrados en Ecuador y otros países latinoamericanos. En Ecuador, distinguimos 3 morfotipos entre las formas de vientre oscuro. Con una única excepción, nuestros ejemplares son asignables a *M. megalotis* o a *M. hirsuta*. El ejemplar excepcional no se parece a ninguna especie reconocida de *Micronycteris*. Proveemos un conjunto de caracteres útiles para distinguir a las especies de vientre oscuro de *Micronycteris* en Ecuador y describimos una nueva especie.

Palabras claves: Phyllostomidae, concepto genético de especie, *Micronycteris*, *M. giovanniae*, *M. megalotis*, *M. matses*, *M. hirsuta*, citocromo *b*, cariotipos, morfometría

INTRODUCTION

The genus *Micronycteris* Gray comprises a group of morphologically diverse phyllostomid bats that has undergone several taxonomic changes in recent years. Based on morphological analyses several authors have suggested that *Micronycteris* (sensu Sanborn, 1949) is not monophyletic (Simmons, 1996; Simmons and Voss, 1998; Wetterer et al., 2000). The subgenera *Glyphonycteris*, *Lampronycteris*, *Micronycteris*, *Neonycteris*, and *Trinycteris* were then elevated to generic level (Wetterer et al., 2000), and these conclusions have been supported by molecular data (Baker et al., 2000, 2003a). Additionally, *Micronycteris* traditionally is placed in the subfamily Phyllostominae (Koopman, 1993) according to morphological similarities with other members of this taxon. However, Baker et al. (2003a) provided strong evidence for placing *Micronycteris* and *Lampronycteris* in the subfamily Micronycterinae, and *Glyphonycteris* and *Trinycteris* in a distantly related subfamily Glyphonycterinae. They were unable to sample *Neonycteris*, and its status is defined based on morphological differences with related taxa (Wetterer et al., 2000).

Micronycteris is more narrowly defined today than it has been traditionally based on Sanborn's (1949) review of the genus. Simmons and Voss (1998) provided an emended diagnosis for the genus. The most recent morphological review of *Micronycteris* (Simmons et al., 2002) recognized 9 species, including 4 dark-bellied species (*hirsuta*, *matses*, *megalotis*, *microtis*), and 5 pale-bellied species (*brosseti*, *homezi*, *minuta*, *sanborni*, *schmidtorum*). Only 3 of these (*hirsuta*, *megalotis*, *minuta*) have been recorded in Ecuador (Albuja, 1999; Tirira, 1999). Specimens of *Micronycteris* from Ecuador are poorly represented in museum collections, and some important areas within the country considered as centers of endemism have few voucher specimens.

During July and August 2001, researchers from Texas Tech University (TTU) and the Museo de Zoología (QCAZ) of the Pontificia Universidad Católica del Ecuador were involved in the Sowell Expedition to northwest Ecuador with the main purpose of documenting the mammalian diversity of several localities surrounding San Lorenzo. During this fieldtrip, we collected a small series of dark-bellied specimens of *Micronycteris*, giving us the opportunity to study interspecific variation within the genus in this poorly sampled geographic region. The purpose of this paper is to document variation present in dark-bellied species from San Lorenzo, to place this variation in the context of the genus, and to describe a new taxon from the *M. megalotis* complex.

MATERIALS & METHODS

Study Area. The study area constitutes the surroundings of San Lorenzo (01° 16′ N, 78° 49′ W), a small town located in Esmeraldas Province of Ecuador (Fig. 1). The area is part of the southernmost limit of the Chocó region, characterized by high endemism of plants and animal species (Dodson and Gentry, 1991; Myers et al., 2000). The plant community is dominated by palms and species of the family Moraceae (Gentry, 1986). Common species are *Brosimun utile*, *Castilla elastica* (Moraceae); *Wettinia quinaria*, *Phytelephas aequatorialis* (Arecaceae); *Guarea polymera* (Meliaceae); *Otoba gordonifolia* (Myristicaeae); *Inga sichalensis* (Mimosaceae); *Theobroma gileri* (Sterculeaceae); and

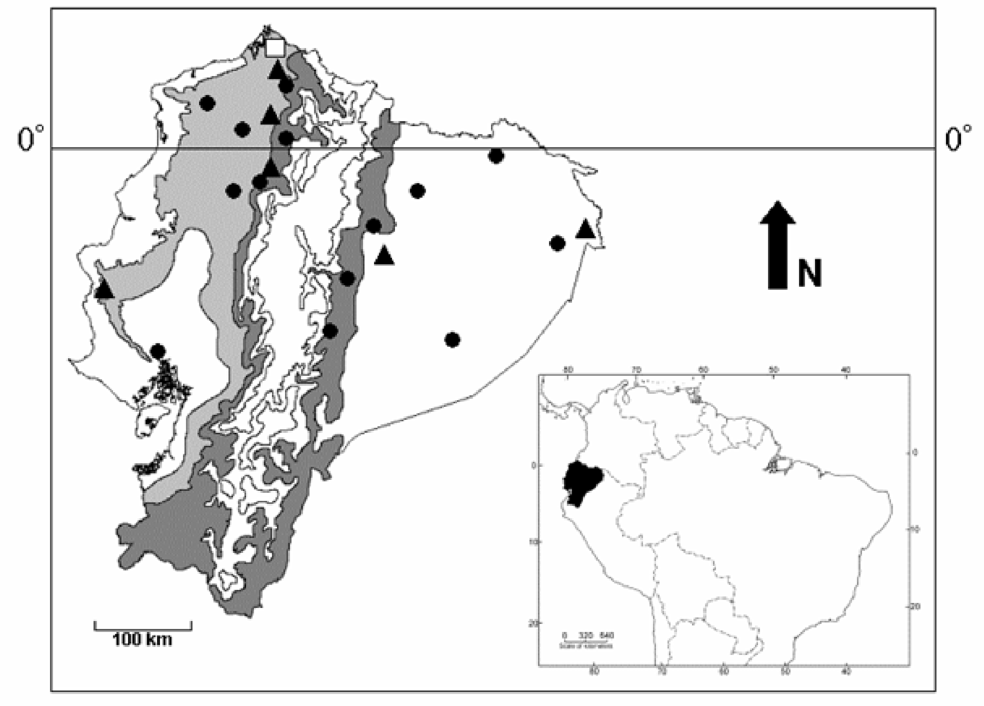

Figure 1. Geographic distribution of dark-bellied species of *Micronycteris* in Ecuador. Records are based on museum specimens and Albuja (1999). Circles represent records of *M.megalotis*; solid triangles represent records of *M. hirsuta*. The area in this study is represented by a white square. Inset: Map of South America with Ecuador shaded.

Xanthosoma daguense (Araceae). A detailed description of soils and vegetation is presented by Gentry (1986) and Cerón et al. (1999).

Morphological Comparisons. To identify specimens of *Micronycteris* from San Lorenzo, we compared the morphological features of this series with other dark-bellied specimens of the genus from several localities in South America. We examined external and cranial differences and measured available specimens with a digital caliper to the nearest 0.01 mm. Measurements (following Simmons, 1996) included for comparisons are: total length, tail length, hind foot length, ear length, forearm length, metacarpal III length, length of the first phalanx of the third digit, second phalanx of the third digit, first phalanx of the fourth digit, thumb length, tibia length, calcar length, greatest length of the skull, condylobasal length, zygomatic width, mastoid width, braincase width, braincase height, palatal length, post-palatal length, post-orbital constriction width, interorbital width, greatest width across the molars, greatest width across the canines, maxillary toothrow length, mandibular toothrow length, coronoid process length, and mandibular length.

Genetic Comparisons. We extracted genomic DNA from liver tissue of 15 bats by standard methods (Longmire et al., 1997) representing most of the recognized species within the genus (*M. brosseti*, *M. hirsuta*, *M. homezi*, *M. matses*, *M. megalotis*, *M. microtis*, *M. minuta*, *M. schmidtorum*). We amplified and sequenced the mitochondrial cytochrome-*b* gene (Cyt *b*; 1,140 base pairs) using primers and conditions reported in Hoffmann and Baker (2001). We amplified and sequenced intron 7 (Fgb-I7; approximately 530 base pairs) of the fibrinogen, B beta polypeptide (Fgb) using primers and conditions modified from those in Wickliffe et al. (2003); those modifications will be described elsewhere (Porter et al, unpubl. ms).

We purified double-stranded amplicons with the QIAquick® PCR Purification Kit (QIAGEN, Inc., Valencia, California) and sequenced both strands with Big-Dye™ chain terminators followed by electrophoresis on a 3100-Avant automated sequencer (Applied Biosystems, Inc., Foster City, California). We used AssemblyLIGN™ 1.0.9 software (Oxford Molecular Group PLC, 1998) to assemble overlapping fragments. We performed multiple sequence alignment for the mitochondrial and nuclear data separately in CLUSTAL X software (Thompson et al., 1997), with default parameters for costs of opening and extending gaps. We viewed resulting alignments in MacClade (version 4; Maddison and Maddison, 2002) to assure there were no gaps or stop codons in mitochondrial coding alignment and to inspect gapped regions in nuclear intron alignment.

We coded nucleotides as unordered, discrete characters (G, A, T, C), multiple states as polymorphisms, and gaps as missing. In PAUP* software (test version 4.0b10; Swofford, 2002), we examined levels of phylogenetic signal via g1-statistics (relative to 100,000 randomly drawn trees) for each data set separately; we compared g1-values with critical values of Hillis and Huelsenbeck (1992). We inferred phylogenetic relationships by using two optimality criteria: Minimum Evolution, with Tamura-Nei (1993) distances and with starting trees obtained via neighbor-joining; and Parsimony, with equal weights applied to all characters and substitution types. For both criteria and data sets, we designated two outgroups (*Trachops* and *Lampronycteris*) and assessed clade reliability via bootstrap analysis (Felsenstein, 1985) of 500 heuristic iterations, each with 10 random additions of input taxa, random starting trees, and tree-bisection-reconnection.

Karyological Comparisons. Karyotypes were prepared from nine individuals of *Micronycteris*. Karyotypic preparations were made within 24 hours of capture using the methods described in Baker et al. (2003b). Images were recorded and karyotypes were prepared using the GENUS System by Applied Imaging.

RESULTS

Morphological Comparisons. A combination of external and cranial characters, as well as size differences, allows distinguishing 3 morphotypes among dark-bellied forms of *Micronycteris* from northwestern Ecuador. These 3 morphotypes correspond to *M. hirsuta*, *M. megalotis*, and one specimen (QCAZ 7200) externally similar to *M. matses*. Differences among these types with other dark-bellied species are explained below.

External size differences distinguish *M. megalotis* as the smallest species of the genus inhabiting the San Lorenzo area. The specimen QCAZ 7200 represents an intermediate form in size, whereas specimens assignable to *M. hirsuta* constitute the largest species from the area.

Figure 2. Dorsal and ventral views of *Micronycteris giovanniae* [Holotype: QCAZ 7200 (= TTU 85445); left] and *M. matses* (ANMH 15231; right) showing size and cranial differences. Notice the differences in the width of rostrum, length of palatal extension, and width of basioccipital. Scale bar equals 5 mm.

Length and coloration of the fur are similar among specimens of *Micronycteris* from San Lorenzo. In all of them, a basal whitish band is present, but is less conspicuous in QCAZ 7200. Differences in the length of the hair covering the inner border of ears are also evident. Specimens assignable to *M. megalotis* from San Lorenzo possess hair on the inner border of the ears exceeding 5 mm in length, similar to values reported for other populations of *M. megalotis* and *M. matses* (according to Simmons et al., 2002). The specimen QCAZ 7200 and specimens referable to *M. hirsuta* possess shorter hair on the inner border of the ears. Wings and other membranes are naked in all *Micronycteris* specimens except those of *M. hirsuta*, which are hairy at the base of the thumb.

Skull structure differs substantially among *Micronycteris* forms from San Lorenzo. The specimen QCAZ 7200 is intermediate in size compared to *M. megalotis* and *M. hirsuta,* but similar to *M. matses*. The rostrum in QCAZ 7200 is longer than in *M. megalotis* and *M. matses*, proportional to the skull length, but is less elongated than in *M. hirsuta*. Maxillae in QCAZ 7200 are more inflated than the other dark-bellied species; in *M. matses* and *M. megalotis* the rostrum is slender and generally the cingulum of the upper molars is visible from a superior view (Fig. 2). The zygomatic arch in QCAZ 7200 is robust and well developed as in *M. hirsuta*, not weak as in *M. matses*; the fusion between the jugal and the squamosal bones is poorly developed in *M. matses*, distinguishing it from *M. megalotis*, *M. hirsuta*, and QCAZ 7200 in this feature. In QCAZ 7200, *M. matses*, and *M. megalotis* the sagittal crest is elevated in similar proportions from the skull, whereas in *M. hirsuta* this structure is more elevated than in the former species, especially in specimens from San Lorenzo. Furthermore, the lambdoidal crest and the mastoid process in *M. hirsuta* are developed more than in the rest of the species included in our comparisons. Backward projection of interparietals also differs among these species: in QCAZ 7200 and *M. matses* the projection of the interparietals gives the skull a rounded ending from a superior view; the skull of *M. megalotis* possesses a more globular ending whereas in *M. hirsuta* this projection results in a sharp ending of the skull. Paraoccipital processes, occipital condyles, and auditory bullae have similar

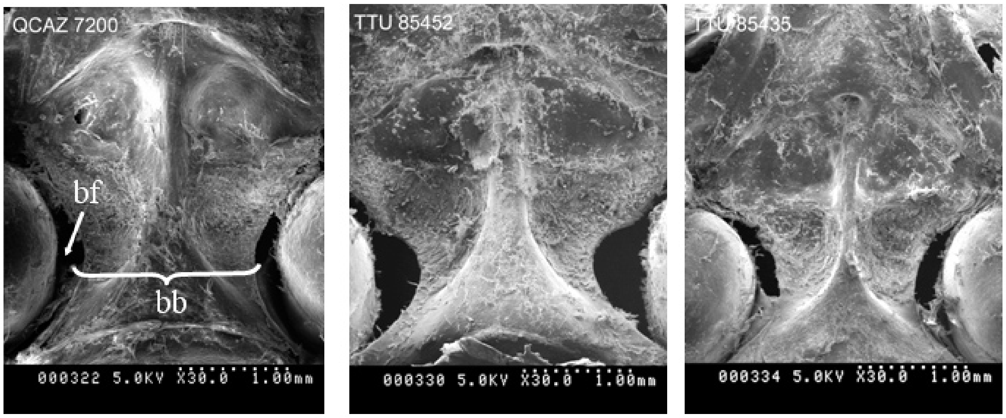

Figure 3. Electron micrographs showing differences in the shape of the basioccipital bone (bb), and in the basicochlear fissure (bf) among *Micronycteris giovanniae* (QCAZ 7200), *M. hirsuta* (TTU 85452), and *M. megalotis* (TTU 85435) from San Lorenzo, Ecuador. Notice that *M. giovannieae* possesses a wider basioccipital bone and a narrower basicochlear fissure than other species.

proportions in all these dark-bellied species. There are noticeable differences in several basicranium structures between QCAZ 7200 and other species, especially compared to *M. matses*. The basioccipital bone is wide in QCAZ 7200, forming a narrow and elongated basicochlear fissure; shape of basioccipital is similar to that found in some populations of *M. megalotis*, especially from San Lorenzo, but is always narrower in *M. hirsuta* in which it forms a wide basicochlear fissure (Fig. 3). Shape of basioccipital in *M. matses* is the narrowest among dark-bellied species, forming an extremely wide and long fissure that distinguishes it from QCAZ 7200.

Simmons (1996) indicated that basisphenoid pits are present in species of *Micronycteris*. According to Debaeremaeker and Fenton (2003), basisphenoid pits are absent and basioccipital pits are present in *M. megalotis* and *M. minuta*, but in *M. hirsuta* both types of pits are absent. From our examinations we conclude that the structures present in *Micronycteris* are basisphenoid pits. The shallow basisphenoid pits present in QCAZ 7200 contrast with the extremely deep pits typical in *M. megalotis*; in *M. matses* and *M. hirsuta*, the pits are shallower than in QCAZ 7200, almost indistinguishable in some specimens examined of *M. hirsuta*. A septum dividing the basisphenoid pits is present in all forms, but it is highly developed in *M. megalotis*. The anterior opening of the alisphenoid canal is small, ovoid, and with similar dimensions to the posterior opening in QCAZ 7200 and *M. megalotis*; but in *M. hirsuta* and *M. matses* the anterior opening is large, elongated and differing in size from the posterior and anterior openings in QCAZ 7200 and *M. megalotis* (Fig. 4). The extension of the palate over the mesopterygoid fossa in QCAZ 7200 is noticeably shorter than in *M. matses*. The palate is wider in QCAZ 7200 than in *M. matses*.

Dentition of QCAZ 7200 is robust in relation to the size of the skull compared to other dark-bellied species. Inner upper incisors are wider and more robust than those present in *M. matses* and *M. megalotis*, and wider and stronger than the outer incisors and canines. As in other species of the genus, P3 and P4 in QCAZ 7200 have similar dimensions but unlike some specimens of *hirsuta* and *megalotis* they are not separated by

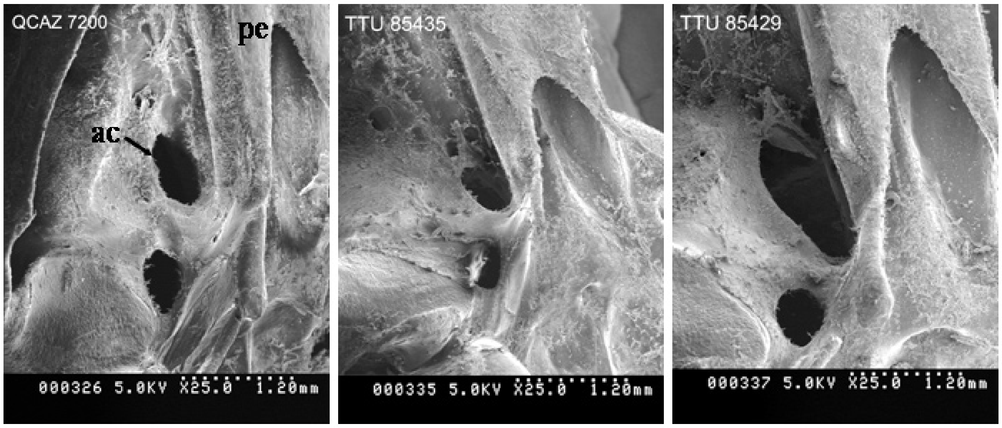

Figure 4. Electron micrographs of the basicranium, showing the palate extension (pe) and differences in the shape and size of the anterior opening of the alisphenoid canal (ac) among *Micronycteris giovanniae* (QCAZ 7200), *M. hirsuta* (TTU 85429), and *M. megalotis* (TTU 85435) from San Lorenzo, Ecuador. Notice that *M. giovanniae* and *M. megalotis* have smaller openings compared to *M. hirsuta* (condition in *matses* is similar to *hirsuta*).

Table 1. Frequencies of the two types of postero-internal projection of P4 in the dark-bellied species of *Micronycteris* included in our comparisons. Type I: reduced; Type II: well developed.

Populations	*N*	Type I	Type II
M. giovanniae: Western Ecuador	1	1	0
M. matses: Peru	8	0.25	0.75
M. megalotis: Brazil	20	0.05	0.95
M. megalotis: Colombia	3	0	1
M. megalotis: Ecuador	10	0	1
M. megalotis: Honduras	7	0	1
M. megalotis: Panama	2	0	1
M. megalotis: Peru	5	0	1
M. megalotis: Trinidad	7	0.14	0.86
M. megalotis: Venezuela	13	0.08	0.92
M. hirsuta: Western Ecuador	8	1	0

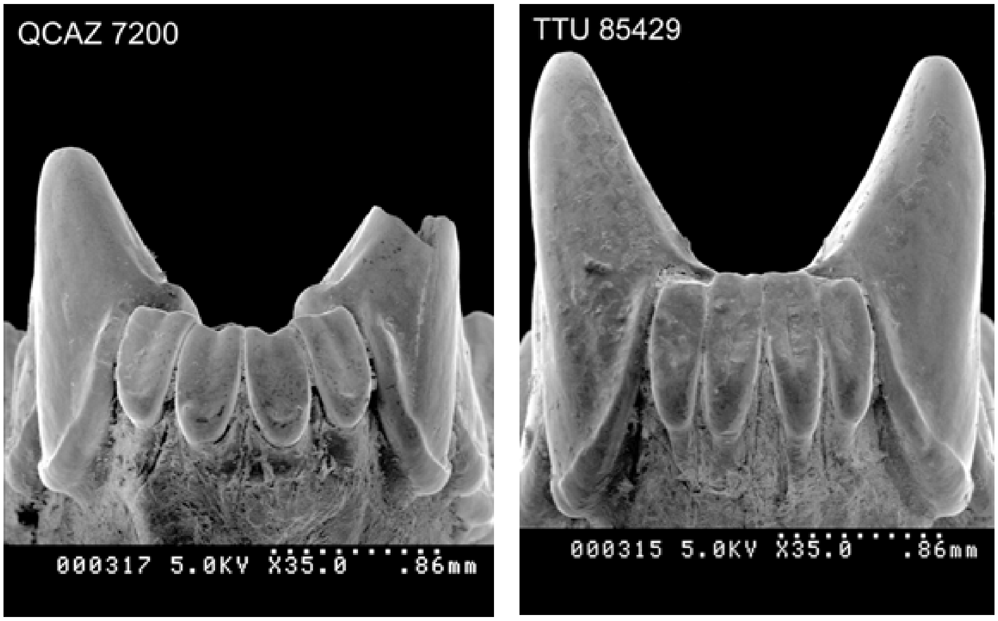

Figure 5. Electron micrographs showing differences in morphology of the lower incisors between *Micronycteris giovanniae* (QCAZ 7200) and *M. hirsuta* (TTU 85429). Notice that *M. hirsuta* has hypsodont lower incisors, a condition unique within the genus.

a short diastema. The posterior projection of P4 (“lingual heel” according to Simmons et al., 2002) stands out from the lingual side of the upper toothrow in *M. matses* and *M. megalotis*, whereas it is highly reduced in QCAZ 7200 and *hirsuta* (Table 1). Lower dentition in QCAZ 7200 is as robust as that of *hirsuta*. Lower incisors of QCAZ 7200 are not hypsodont as in *hirsuta* (Fig. 5), but are wider and longer than those present in *matses* and *megalotis*; lower incisors of *matses* are about 2/3 the size of those in QCAZ 7200. The gap separating the canines posterior-medially in QCAZ 7200 is also present in *M. matses* and *M. megalotis* but reduced in *M. hirsuta*. Compared to *M. hirsuta* and *M. megalotis*, the angular process is less developed, in lateral view, in QCAZ 7200.

Descriptive statistics indicate features with no overlap in measurements among dark-bellied forms of *Micronycteris* from San Lorenzo (Table 2). Specimens of *M. megalotis* are distinguished by having shorter forearm length, metacarpal III length, greatest length of the skull, condylobasal length, zygomatic width, mastoid width, interorbital width, maxillary toothrow length, and mandibular length. Specimens assignable to *M. hirsuta* are distinguished mainly by greater forearm length, metacarpal III length, greatest length of the skull, palatal length, post-palatal length, mandibular toothrow length, and coronoid process length. The specimen QCAZ 7200 differs in all measurements from *M. megalotis* and *M. hirsuta*, but falls in the size range of *M. matses* (see Table 2 and Simmons et al., 2002).

Genetic Comparisons. We deposited in GenBank complete sequences of the cytochrome *b* gene (1,140 base pairs) and intron 7 of the fibrinogen, B beta polypeptide (510—529

Table 2. Mean (± 1 standard deviation) values for 18 characters measured in four species of *Micronycteris*. Abbreviations: Forearm length (FA), metacarpal III length (Mc3), greatest length of the skull (GLS), condylobasal length (CBL), zygomatic width (ZW), mastoid width (MW), braincase width (BCW), braincase hight (BCH), palatal length (PL), post-palatal length (PPL), post-orbital constriction width (PC), interobital width (IOW), greatest width across molars (GMW), greatest width across canines (GCW), maxillary toothrow length (MxL), mandibular toothrow length (MnL), coronoid process length (CPL), and mandibular length (MDL).

SPECIES	FA	Mc3	GLS	CBL	ZW	MW	BCW	BCH	PL
M. hirsuta	42.19	37.00	23.57	20.96	11.55	10.51	8.69	9.42	10.79
	(1.48)	(1.34)	(0.91)	(1.12)	(0.38)	(0.32)	(0.22)	(0.29)	(0.36)
M. megalotis	33.58	29.55	18.01	16.11	8.83	8.24	7.41	7.43	8.02
	(1.60)	(1.34)	(0.56)	(0.56)	(0.38)	(0.32)	(0.24)	(0.24)	(0.36)
M. matses	–	–	20.28	18.01	9.98	9.25	8.08	8.10	9.46
	–	–	(0.30)	(0.35)	(0.13)	(0.16)	(0.13)	(0.10)	(0.36)
M. giovanniae	37.03	32.79	20.86	19.02	10.25	9.35	8.18	8.30	9.45

SPECIES	PPL	PC	IOW	GMW	GCW	MxL	MnL	CPL	MDL
M. hirsuta	7.12	4.81	5.32	7.43	4.24	9.21	10.04	5.92	15.87
	(0.42)	(0.12)	(0.19)	(0.28)	(0.19)	(0.42)	(0.39)	(0.26)	(0.66)
M. megalotis	5.59	3.93	4.47	5.90	3.18	6.87	7.43	3.91	11.83
	(0.23)	(0.16)	(0.27)	(0.24)	(0.15)	(0.25)	(0.30)	(0.22)	(0.45)
M. matses	6.01	4.45	4.97	6.68	3.62	7.90	8.38	4.65	13.52
	(0.12)	(0.12)	(0.19)	(0.20)	(0.10)	(0.13)	(0.20)	(0.14)	(0.14)
M. giovanniae	6.76	4.72	5.19	6.77	4.00	8.28	8.86	4.89	14.29

base pairs; see Tissues Examined for accession numbers). Due to the morphological differences between the specimen QCAZ 7200 and other dark-bellied forms from San Lorenzo, we focused on determining the genetic identity of QCAZ 7200. Phylogenetic analysis of both nuclear and mitochondrial DNA sequences places QCAZ 7200 in a clade (bootstrap value >75%) along with 3 other dark-bellied forms (*M. matses*, *M. microtis*, *M. megalotis*; Fig. 6). The exact position of QCAZ 7200 within this clade differs between nuclear and mitochondrial data sets. Whereas nuclear data support QCAZ 7200 as sister to *matses*, mitochondrial data support a basal position for QCAZ 7200, sister to a (*M. matses* (*M. microtis*, *M. megalotis*)) clade. The relationship of QCAZ 7200 to the other dark-bellied forms indicates that *M. hirsuta* clearly is more distant based on phylogenetic analysis and percent sequence distance (Table 3).

Uncorrected genetic distances between QCAZ 7200 and other dark-bellied species in the genus range from 5.3% to 9.8% in the complete cytochrome-*b* gene, and from 1.0% to 5.8% in intron 7 of the fibrinogen, B beta polypeptide. In each case, the genetic distances are similar to those for comparisons between other currently recognized species within the genus *Micronycteris* (Porter et al., unpubl. ms).

Karyological Comparisons: Individuals identified as *M. hirsuta* have a diploid number (2N) of 26 and a fundamental number (FN) of 30 (Fig. 7). This karyotype is similar but not identical to those described for this species by Baker et al. (1973). Two karyotypes have been described for *M. hirsuta* (Baker et al., 1973). For specimens from Trinidad, 2N is 30 and FN is 32, and for specimens from Honduras and Nicaragua, 2N is 28 and FN is 32. The remainder of the specimens from northwestern Ecuador have a karyotype with a 2N=40 and a FN=68 (Fig. 8). This karyotype is like that described by Baker (1967) for *M. megalotis*. The specimen QCAZ 7200 also has this *M. megalotis*-type karyotype (Fig. 9).

DISCUSSION

Morphological, karyotypical, and molecular comparisons permit the distinction of 3 taxa among specimens of *Micronycteris* from San Lorenzo, northwestern Ecuador. The specimens smallest in size represent the species *megalotis*, which is widely distributed throughout South America and present on both sides of the Andes in Ecuador (Albuja, 1999; Tirira, 1999). They are distinguishable from other dark-bellied species included in our comparisons mainly by their small size, the presence of fur on the inner border of the ears longer than 5 mm (character that distinguishes these specimens from *M. microtis* according to Simmons, 1996), and the shape of the basioccipital. Specimens of *M. hirsuta* are also distinguishable from other forms of *Micronycteris* from San Lorenzo mainly by their larger size and by the hypsodont dentition. In the case of both taxa, further analyses concerning intraspecific variation at both morphological and molecular levels are warranted. Karyotypic data distinguish *M. megalotis* (2N=40; FN=68) from *M. hirsuta* (2N=26; FN=30). Each of these karyotypes is unique among bats. The karyotype of QCAZ 7200 is indistinguishable from that described for *M. megalotis* (Baker, 1967), and unfortunately *M. matses* and *M. microtis* have not been karyotyped.

We found one dark-bellied specimen of *Micronycteris* (QCAZ 7200) to be unique, differing morphologically from all other dark-bellied members of the genus. Data from mitochondrial cytochrome-*b* gene and nuclear intron sequences indicate that this specimen is related closely to *M. matses*, *M. megalotis*, and *M. microtis*, and most similar to *M. matses*; however, several cranio-dental characters distinguish this specimen from any dark-bellied species currently recognized. Based on morphological data, this specimen is unique within *Micronycteris* and should be recognized as a distinct species; molecular data are compatible with this interpretation of the morphological evidence.

There are 3 synonyms available within the species *M. megalotis* (Alonso-Mejía and Medellín, 1991; Simmons, 1996): *M. elongata* (Gray, 1842), *M. pygmaeus* (Rehn, 1904), and *M. scrobiculatum* (Wagner, 1855). Based on original descriptions, the distribution of the type localities, taxonomic comments of Simmons (1996:4), and measurements of the holotypes of *M. elongata* and *M. scrobiculatum* provided by Carter and Dolan (1978), we conclude that none of these names are applicable to QCAZ 7200 from northwestern Ecuador. No synonym is available for *M. matses* (sensu Simmons et al., 2002). The section below introduces a new species name and provides a description of this taxon.

Table 3. Uncorrected ("p") distances for all pairwise comparisons of DNA sequences of intron 7 of the beta-fibrinogen gene (below diagonal) and the complete mitochondrial cytochrome-b gene (above diagonal).

	giovanniae (TK104673)	*brosseti* (KU155163)	*hirsuta* (TK104680)	*hirsuta* (TK104677)	*hirsuta* (NK101615)	*homezi* (TK86643)	*matses* (TK82756)	*megalotis* (TK104663)	*megalotis* (TK20558)	*megalotis* (TK16372)	*microtis* (TK16377)	*minuta* (TK16371)	*schmidtorum* (TK40447)	*Lampronycteris* (TK25239)	*Trachops* (TK18829)
giovanniae (TK104673)		9.56	10.09	10.09	9.30	14.30	5.26	5.53	5.96	5.53	6.67	13.51	13.07	17.54	19.21
brosseti (KU155163)	4.01		11.32	11.32	11.40	15.00	9.39	9.39	9.56	8.95	10.18	13.33	13.77	16.75	19.21
hirsuta (TK104680)	5.61	5.23		0.35	2.02	15.53	10.00	9.91	10.26	10.53	11.14	13.86	14.12	17.54	18.60
hirsuta (TK104677)	5.93	5.56	0.97		2.02	15.35	9.82	9.74	10.09	10.53	11.14	13.86	14.12	17.54	18.68
hirsuta (NK101615)	5.96	5.58	0.38	1.35		15.53	10.09	10.18	10.70	10.44	11.40	14.04	14.30	16.75	18.77
homezi (TK86643)	4.20	4.40	4.45	4.78	4.81		13.77	14.30	14.82	14.56	14.56	6.05	4.65	19.30	19.04
matses (TK82756)	0.95	4.20	5.79	6.11	6.14	4.38		4.47	4.04	4.39	5.18	13.77	12.89	16.49	18.86
megalotis (TK104663)	1.71	3.44	5.22	5.54	5.57	3.81	1.90		2.19	4.21	5.26	13.42	13.36	17.28	18.16

Table 3 (continued).

megalotis (TK20558)	1.71	3.25	5.03	5.35	5.38	3.62	1.90	0.38		3.60	5.00	14.04	13.42	17.54	19.04
megalotis (TK16372)	1.91	3.44	4.85	5.17	5.20	3.43	2.09	0.57	0.19		5.09	13.95	12.89	17.11	18.42
microtis (TK16377)	2.48	4.20	5.99	6.30	6.34	4.57	2.66	1.90	1.90	2.10		14.65	13.16	17.72	18.07
minuta (TK16371)	4.40	4.61	4.66	4.98	5.01	0.19	4.58	4.01	3.82	3.63	4.58		5.79	18.68	19.39
schmidtorum (TK40447)	--	--	--	--	--	--	--	--	--	--	--	--		18.51	19.30
Lampronycteris (TK25239)	8.57	9.81	10.11	10.57	10.44	9.33	8.96	8.94	8.74	8.74	9.73	9.56	--		20.96
Trachops (TK18829)	10.18	11.17	10.72	11.95	11.06	10.55	10.36	10.54	10.35	10.36	11.31	10.77	--	9.15	

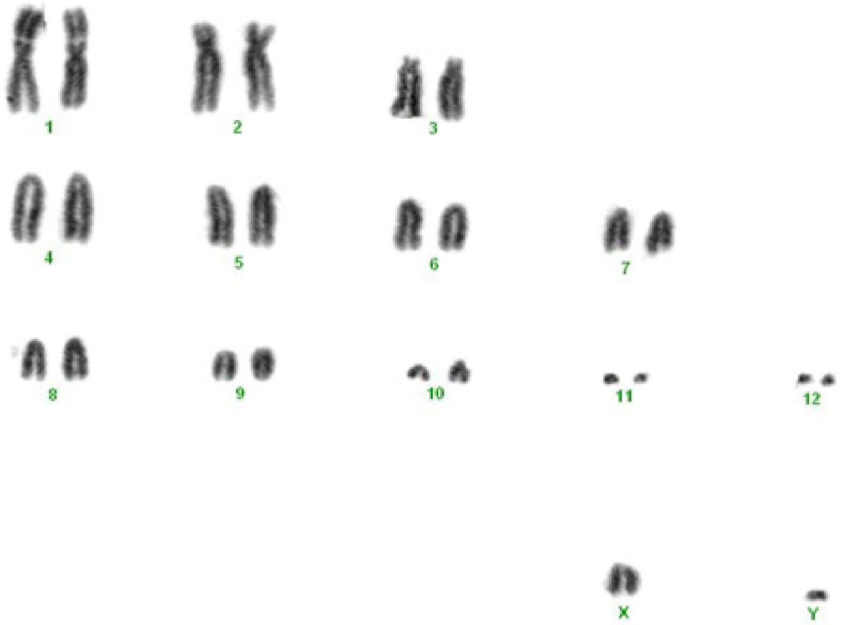

Figure 7. Karyotype prepared from a male *Micronycteris hirsuta* (TK 104677) collected from ECUADOR: Esmeraldas: E. San Lorenzo (toward Lita), Finca San José.

Figure 8. Karyotype prepared from a male *Micronycteris megalotis* (TK 104663) collected from ECUADOR: Esmeraldas: San Lorenzo, Estación Científica la Chiquita.

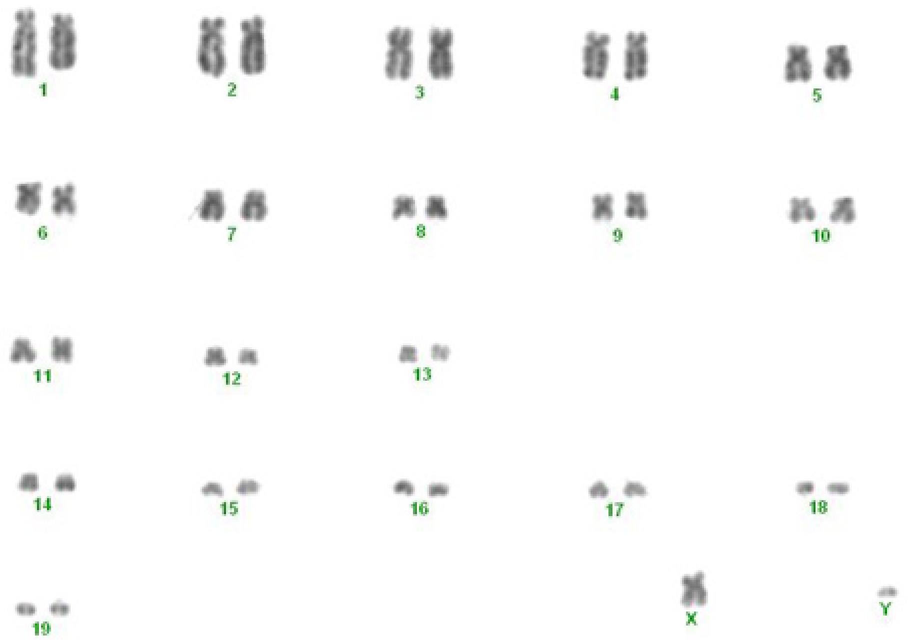

Figure 9. Karyotype prepared from the holotype of *Micronycteris giovanniae* (TK 104673), a male collected from ECUADOR: Esmeraldas: E. San Lorenzo (toward Lita), Finca San José.

SYSTEMATICS

Micronycteris giovanniae Baker and Fonseca, new species

Holotype. QCAZ 7200, adult male, skin, skull, and skeleton deposited in the Museo de Zoología (QCAZ) of the Pontificia Universidad Católica del Ecuador. Originally catalogued with the number TTU 85445 for the processing of the Sowell Expedition 2001. Collected on 6 August 2001 from ECUADOR — Esmeraldas: E. San Lorenzo (toward Lita), Finca San José (01° 3′ 32.1″ N, 78° 37′ 20.7″ W) by a TTU and QCAZ field party on the Sowell Expedition, 2001. The number TK 104673 identifies tissue samples housed in the Natural Science Research Laboratory (NSRL) at Texas Tech University and in the Museo de Zoología (QCAZ), as well as karyotype preparations housed in the Department of Biological Sciences, Texas Tech University.

The holotype was prepared as skin, skull, and postcranial skeleton by Jana L. Higginbotham (original number JLH-279). Standard measurements (in millimeters) of the holotype are: total length – 71; tail length – 16; hind foot – 11; ear – 21; weight – 8.6 grams. Wing and hand limb measurements of the dried specimen are: forearm length – 37; metacarpal III length – 46.7; first phalanx of third digit – 15.3; second phalanx of third digit – 16.1; first phalanx of fourth digit –12.7; thumb length – 5.9; tibia length – 16.4; calcar length – 13.1. Cranial measurements (in mm) of the holotype are as follows: greatest length of the skull – 20.9; condylobasal length – 19.0; zygomatic width

– 10.3; mastoid width – 9.4; braincase width – 8.2; braincase depth – 8.3; palatal length – 9.5; post-palatal length – 6.8; width of post-orbital constriction – 4.7; interorbital width – 5.2; greatest width across molars – 6.8; greatest width across canines – 4.0; maxillary toothrow length – 8.3; mandibular toothrow length – 8.9; coronoid process length – 5.0; mandibular length – 14.3. The holotype had testes 6 x 5 mm.

Etymology. This species is named to honor Nikki Giovanni in recognition of her poetry and writings.

Distribution. Known only by the type specimen from the type locality (Fig.1). ECUADOR: Esmeraldas: E. San Lorenzo (toward Lita), Finca San José (01° 3′ 32.1″ N, 78° 37′ 20.7″ W).

Diagnosis. Morphologically, *M. giovanniae* warrants taxonomic comparisons only with other dark-bellied species within the genus. Genetic distances indicating that *M. matses* may be the sister taxon to *M. giovanniae* and therefore special attention is paid to comparisons of these 2 species. The distribution of *M. giovanniae* (restricted to the type locality) and *M. matses* (known only from the type locality; Simmons, 2005) are geographically distant from each other and separated by the Andes; nonetheless both species are externally similar, further justifying close comparison of these 2 taxa.

M. megalotis and *M. microtis* differ from *M. giovanniae* by having thinner, longer fur on the inner border of ears (only in *M. megalotis*), deeper basisphenoid pits, a globular ending of the skull in the interparietal region, and a well developed posterior projection of the P4 on the lingual side. *M. hirsuta* differs from *M. giovanniae* by having a hairy base of the thumb, a stronger and well developed zygomatic arch, more developed sagittal and lambdoidal crests and mastoid processes, a sharp ending of the skull in the interparietal region, a narrower basioccipital bone, a larger and elongated anterior opening of the alisphenoid canal, hypsodont lower incisors, and a reduced posterior-medial gap separating the lower canines. *M. matses* differs from *M. giovanniae* by having a shorter rostrum, a weaker and poorly developed zygomatic arch, a narrower basioccipital bone, a larger and elongated anterior opening of the alisphenoid canal, a longer palate extension, a narrower palate, weaker canines, a well developed posterior projection of P4 on the lingual side, and shorter lower incisors. Also, *M. giovanniae* can be distinguished from other dark-bellied species by a combination of external and cranial variables (Table 2).

Genetically, *M. giovanniae* can be distinguished from other species in the genus by variation in the cytochrome-*b* gene and in the Fgb-I7 (Fig. 6). Application of the Genetic Species Concept (Dobzhansky, 1950) requires identification of the species related most closely to the taxon being described (= sister taxon; Bradley and Baker, 2001). *M. giovanniae* is sister to a complex of 3 dark-bellied species (*M. matses*, *M. megalotis*, and *M. microtis*) in the cytochrome-*b* tree, whereas it is sister to *M. matses* in the Fgb-I7 tree. Therefore, to apply the Genetic Species Concept, comparisons among *M. giovanniae* to *M. megalotis*, *M. microtis*, and *M. matses* are warranted. Uncorrected distances in the cytochrome-*b* gene distinguishing *M. giovanniae* from these species are > 9% for *M. hirsuta*, > 5% for *M. megalotis*, > 6% for *M. microtis*, and > 5% for *M. matses*. In all comparisons, genetic distance values are more typical of interspecific rather than intraspecific variation (Bradley and Baker, 2001). These 4 taxa are also distinguished by the sequence variation in the Fgb-I7 (Fig. 6; Table 3). Whereas there are few sequences available for Fgb-I7 to facilitate meaningful comparisons (as with cytochrome- *b* data), the distances between *M. giovanniae* and other taxa in the *M. megalotis* complex are similar to those values distinguishing other *Micronycteris* species (recognized on a morphological basis; Table 3). We interpret these data as support for recognizing *M. giovanniae* as a specific level taxon rather than a sub-specific level taxon. According to percent sequence distance (but not necessarily phylogenetic analysis), *M. giovianniae* and *M. matses* are most similar in both mitochondrial and nuclear datasets.

Karyotypic data for the genus *Micronycteris* (sensu lato) were reviewed by Baker (1979). Most species of *Micronycteris* have a unique karyotype. However, karyotypic data are missing for *Glyphonycteris sylvestris*, *M. matses*, *M. microtis*, *M. sanborni*, and *Neonycteris pusilla*. The karyotype of *M. giovanniae* (2N=40, FN=68; Fig. 9) is easily distinguished from *M. hirsuta* (2N=26, FN=30, Fig. 6). The karyotype for *M. giovanniae* (Fig. 9) appears to be indistinguishable from *M. megalotis* (Fig. 8) and this unique derived karyotype [assuming *Macrotis waterhousii* has the primitive karyotype for the Phyllostomidae (Baker, 1979; Baker et al., 2003a)] places *M. giovanniae* in the *M. megalotis* complex. This conclusion is compatible with the relationships implied in the two trees generated from DNA sequence data (Fig. 6).

Description. *Micronycteris giovanniae* is a medium-sized dark-bellied species, Mummy Brown dorsally, Buffy Brown ventrally, and Blackish Brown on wings and membranes except on ears, which also are Mummy Brown (capitalized color names from Ridgway, 1912). Fur is uniformly colored throughout dorsum, including areas between the ears and the forehead. Dorsal fur is pale basally, but not forming a distinguishable white band. This pale region is reduced on the upper back and behind the ears, covering 1/5 of the fur length, whereas it is lighter on the shoulders and extends over 2/5 of the fur length. Fur coloration tends to be uniform in the lower dorsal region; no basal pale band is present. Dorsal fur is long, exceeding 7 mm. Fur on rostrum and areas between ears tends to be shorter, but also exceeding 5 mm. Hair behind the ears and on the inner border of ears is extremely short (< 5 mm), extending no more than the half of ear length. A band with an evident notch connects the ears, but the skin preparation of the holotype does not allow determining if this is deep or shallow. Hair on rostrum is variable in length, with short fur (< 5 mm) covering the forehead, areas between and below the eyes, and areas below the ears. Ventral fur is also short (< 6 mm). Dorsal and ventral pelage does not extend over the uropatagium; wings and other membranes are also naked, as well as the forearm and the thumb. Wing formula is the same as that described for the genus (Simmons, 1996; Simmons et al., 2000).

Skull is medium-sized and robust (Fig. 10). Rostrum is elongated; premaxillae are short and wide; maxillae are large and highly inflated, especially over the region between the premolars and the first molar in the upper toothrow, giving a slight appearance of a globular rostrum. Incisive foramina are wide and considerably elongated. A small foramen anterior to the incisive foramina is also present. Infraorbital foramen is wide and deep. Maxillae join the frontal in the middle of the orbital. A moderately elevated sagittal crest arises from this point and has a constant height along the skull. Lambdoidal crest is present, and is obvious from lateral and posterior views. Interparietals are not projected backward. Mastoid process is slender and elongated, and slightly protrudes from the skull in superior view. Mastoid width is less than zygomatic width. Zygomatic arch is robust, with the fusion between the jugal and the squamosal highly developed upward. Paraoccipital processes are poorly developed and do not exceed the occipital

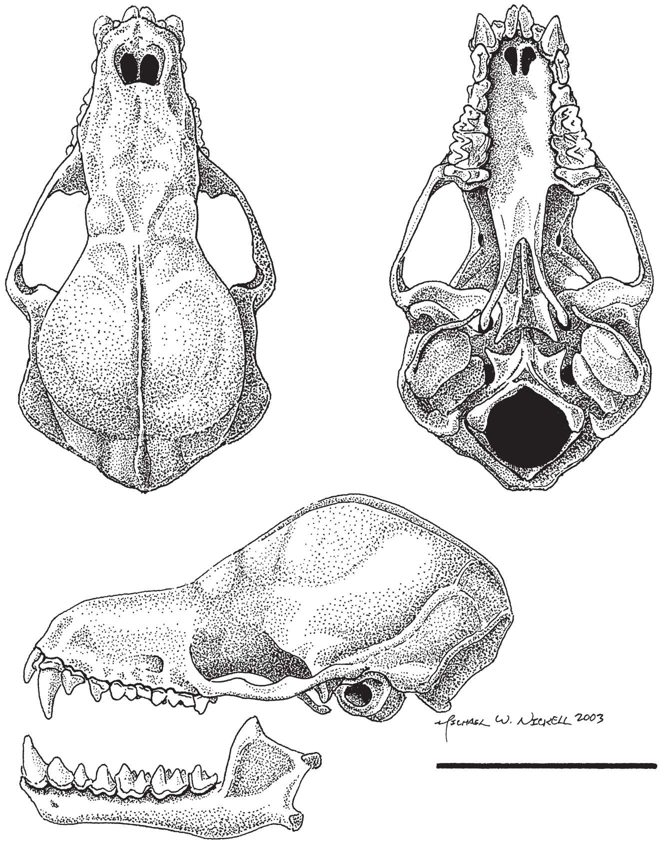

Figure 10. Dorsal, ventral, and lateral views of the skull and lower jaw of the holotype (QCAZ 7200) of *Micronycteris giovanniae*. Bar represents 10 mm. Drawing by Michael W. Nickell.

condyles. Foramen magnum is wide and ovoid. Shallow basisphenoid pits are present, separated medially by a poorly developed septum. Basioccipital bone is fairly wide. Basicochlear fissure is narrow and elongate. Anterior and posterior openings of the alisphenoid canal are small and ovoid. Palate is wide and convex. Postpalatal extension is short and narrow over the mesopterygoid fossa. Dental formula (i 2/2, c 1/1, p 2/3, m 3/3) is typical of the genus (see Simmons et al., 2002). Inner upper incisors are large, robust, and protruding from the skull in superior view. Outer upper incisors are smaller and convergent, not completely filling the space between the inner incisor and the canines. Canines are large, with the cingula well developed. P3 and P4 have the same dimensions, not separated by a diastema. Posterior projection of P4 on the lingual side is reduced. M1 and M2 are of unequal size. M2 and M3 are not separated by a gap. Lower incisors are small, robust, bilobated, and not hypsondont. A wide gap separates the canines posterior-medially. Mandibular ramus is thin and straight. Coronoid process is projected forward. Coronoid fossa is deep and hollow. Angular process appears poorly developed in lateral view and does not extend beyond the mandibular condyle.

Ecological Notes. Finca San José is a private property consisting of secondary-growth forest that, at the time of collecting the holotype, was being deforested. As other areas surrounding San Lorenzo town, the vegetation is typical from the southern border of the Chocó region. Gentry (1986) and Baker et al. (2004) provide information and references on the plant community structure in the area. The holotype was collected in a mist net stretched under a narrow bridge above an active stream. Among the species collected at Finca San José are *Artibeus planirostris*, *Carollia castanea*, *Lonchophylla mordax*, *Micronycteris hirsuta*, *Platyrrhinus dorsalis*, *Platyrrhinus* cf. *helleri*, *Rhinophylla alethina*, and *Sturnira lilium*. Other than the testes size (6 x 5 mm), no information on reproduction is available for the holotype.

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APPENDIX 1: SPECIMENS EXAMINED

List of specimens examined with respective museum catalog numbers and localities. Voucher specimens are housed in a mammal collection at the American Museum of

Natural History (AMNH), Museo de Historía Natural, Universidad Nacional Mayor de San Marcos, Peru (MUSM), Museo de Zoología of the Pontificia Universidad Católica del Ecuador (QCAZ), Museum of Texas Tech University, Natural Science Research Laboratory (TTU), National Museum of Natural History (USNM), or Texas Cooperative Wildlife Collection at Texas A&M University (TCWC).

Micronycteris giovanniae (1): ECUADOR — Esmeraldas: E. San Lorenzo (toward Lita), Finca San José (1° 3′ 32.1″N, 78° 37′ 20.7″W), QCAZ 7200 (holotype; previously catalogued as TTU 85445).

Micronycteris hirsuta (30): COSTA RICA — Puntarenas, TCWC 22521. ECUADOR — Esmeraldas: San Lorenzo, Estación Científica La Chiquita, TTU 85428–29, 85432 — E. San Lorenzo (toward Lita), Finca San José (1° 3′ 32.1″ N, 78° 37′ 20.7″ W), TTU 85452, TTU 85449 — Pichincha: Reserva Florística Río Guajalito, QCAZ 2758–59, 3438, 3442 — 47 km S Santo Domingo, Estación Científica, Río Palenque, USNM 528479–80. HONDURAS — El Paraiso, TCWC 21456–57 — Olancho: 10.3 mi. SSW Dulce Nombre de Culmi, TTU 13152–53. NICARAGUA — Matagalpa, TCWC 23729–30 — Rivas: 5 mi. N, 1 mi. W San Juan del Sur, TTU 13157–59 — Zelaya Sur: specific locality unknown, TCWC 34993 — 3 km NW Rama, TTU 13154–13155 — 9 mi. E. Rama, Dos Bocas, TTU 13156. TRINIDAD AND TOBAGO — Trinidad: Saint George Co.; Blanchisseuse, TTU 5449 — Saint George Co.; Las Cuevas, TTU 5410 — Mayaro Co.; Guayaguayare, TTU 5229, 10116. VENEZUELA — Sucre: specific locality unknown, TCWC 47811.

Micronycteris matses (8): PERU — Loreto: Nuevo San Juan, Rio Galvez, MUSM 15229, 15231; AMNH 272814, 273043–44, 273095, 273133, 273196.

Micronycteris megalotis (59): BRAZIL — Amazonas: Borba, Rio Madeiro, AMNH 91893 — Tahuapunta, Rio Waupes, AMNH 78648–49 — Aramanay, Rio Tapajoz, AMNH 94518–23, 95425–27, 94530–31 — Caxiricatuba, Rio Tapajoz, AMNH 94532–33 — Ilhado do Taiuna, Rio Tocantis, AMNH 97206, 97219. COLOMBIA — Cundinamarca: Mesitas del Colegio, AMNH 207775–77. ECUADOR — Esmeraldas: San Lorenzo, Estación Científica La Chiquita, TTU 85289, 85435–36 — E. San Lorenzo, Finca Bananera La Guarapera, TTU 85389. HONDURAS — La Flor, Archaga, AMNH 126213–17 — Humuya, La Paz, AMNH 126764 — Olancho: 10.3 mi. SSW Dulce Nombre de Culmi, TTU 13161. MEXICO — San Luis Potosí: 25 mi. W Cuidad Valles, TTU 35355. NICARAGUA — Rivas: 4.9 mi. E San Juan del Sur, TTU 13167 — 5 mi. N, 1 mi. W San Juan del Sur, TTU 13166 — Zelaya Sur: 9 mi. E Rama, Dos Bocas, TTU 13162 — 4.5 km NW Rama, TTU 13163 — 3 km NW Rama, TTU 13164. PANAMA — Cituro, AMNH 38147, 38149. PERU — Junin: Tarma; 2 km NW San Ramón, AMNH 230117 — Loreto: Puerto Indiana, Río Amazonas, AMNH 73497. TRINIDAD & TOBAGO — Trinidad: Nariva Co.; 5 mi. Marker, TTU 5275 — Mayaro Co.; Guayaguayare, TTU 10118 — Saint George Co.; Las Cuevas, TTU 5438, 5446, 9788 — Saint George Co.; Blanchisseuse, TTU 5495 — Saint George Co.; Carenage, AMNH 29708, 29713 — St. Andrew Co.; Heights of Orepouche, AMNH 31240. VENEZUELA — Auyan-tepui, AMNH 130628 — Ciudad Bolivar, AMNH 16119 — Bolivar, El Hacha, AMNH 32135 — Peru Mine, El Callao, AMNH 30679 — San Esteban, AMNH 31503 — San Julian, AMNH 16685 — La Trinidad, AMNH 69962 — Latal, AMNH 69966.

APPENDIX 2: TISSUES EXAMINED

List of tissues examined with respective tissue numbers and localities. Acronyms for tissue numbers are: KU, University of Kansas, Museum of Natural History; NK, Museum of Southwestern Biology, University of New Mexico; TK, Museum of Texas Tech University, Natural Science Research Laboratory. Acronyms for museums where voucher specimens are housed are: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; MUSM, Museo de Historía Natural, Universidad Nacional Mayor de San Marcos, Peru; QCAZ, Museo de Zoología of the Pontificia Universidad Católica del Ecuador; MSB, Museum of Southwestern Biology, University of New Mexico; TTU, Museum of Texas Tech University, Natural Science Research Laboratory, and ROM, Royal Ontario Museum. With 1 exception, 4 numbers are given for each specimen. In order, they are tissue number, museum voucher number, cytochrome-*b* GenBank accession number, and beta fibrinogen GenBank accession number (the latter 2 numbers in parentheses). The exception is *Micronycteris schmidtorum*, for which the cytochrome-*b* sequence is from one specimen (TK 70447) and the beta fibrinogen sequence from another (TK 82837).

Lampronycteris brachyotis: TRINIDAD AND TOBAGO — Trinidad: Mayaro Co.; Guayaguayare, TK 25239, CM 97174 (AY380748, DQ077431).

Micronycteris brosseti: GUYANA — Potaro-Siparuni: Inokrame Reserve, KU 155163, KU 155163 (AY380771, DQ077455).

Micronycteris giovanniae: ECUADOR — Esmeraldas: E. San Lorenzo (toward Lita), Finca San José (1° 3′ 32.1″ N, 78° 37′ 20.7″ W), TK 104673, QCAZ 7200 (AY380750, DQ077456).

Micronycteris hirsuta: ECUADOR — Esmeraldas: E. San Lorenzo (toward Lita), Finca San José (1° 3′ 32.1″ N, 78° 37′ 20.7″ W), TK 104677, TTU 85449 (DQ077410, DQ077448), TK 104680, TTU 85452 (DQ077412, DQ077449). PANAMA — Veraguas, Montijo; Corregimiento de Arenas, Portobelo, NK 101615, MSB 94372 (AY380769, DQ077445).

Micronycteris homezi: GUYANA — East Berbice: Dubulay Ranch (5° 40′ 91″ N, 57° 51′ 52″ W), TK 86643, USNM 582262 (AY380754, DQ077441).

Micronycteris matses: PERU — Loreto: Nuevo San Juan, Rio Galvez, TK 82756, AMNH 272814 (DQ077417, DQ077457).

Micronycteris megalotis: ECUADOR — Esmeraldas: San Lorenzo, Estación Científica La Chiquita, TK 104663, TTU 85435 (DQ077424, DQ077476). MEXICO — Chiapas: 8.2 mi. SE, 2.5 mi. E Tonala, Rio Ocuilapa, TK 20558, TTU 36534 (AY380764, DQ077472). PANAMA — Canal Zone, Gamboa (090600 N, 0794200 W), TK 16372, ROM 104195 (AY380765, DQ077468).

Micronycteris microtis: BRAZIL — Sao Paulo: Caetetus Ecological Station (222300 S, 049400 W), TK 16377, ROM 111099 (AY380755, DQ077463).
Micronycteris minuta: ECUADOR — Orellana: 30 km S Pompeya Sur, Parque Nacional Yasuní, TK 16371, ROM 104067 (AY380752, DQ077438).

Micronycteris schmidtorum: PERU — Cusco: La Convencion; Camisea, Armihuari, TK 70447, MUSM 13737 (AY380753). PERU — Loreto: Nuevo San Juan, Rio Galvez, TK 82837, AMNH 273169 (DQ077443).

Trachops cirrhosus: FRENCH GUIANA — Paracou, TK 18829, AMNH 267129 (DQ233669, DQ233670).

LITERATURE CITED

Albuja, L.
1999 Murciélagos del Ecuador: 2nd edicíon. Escuela Politécnica Nacional, Cicetrónic Cia. Ltda, Quito, Ecuador.

Alonso-Mejía, A., and R. A. Medellín
1991 *Micronycteris megalotis*. Mammalian Species 376:1–6.

Baker, R. J.
1967 Karyotypes of bats of the family Phyllostomatidae and their taxonomic implications. The Southwestern Naturalist 12:407–428.

1979 Karyology. Pp. 107-155 in Biology of the Bats of the New World Family Phyllostomidae, Part III (Baker, R. J., J. K. Jones, Jr., and D. C. Carter, eds.). Special Publications, Museum of Texas Tech University 16:1-441.

Baker, R. J., R. M. Fonseca, D. M. Parish, C. J. Phillips, and F. G. Hoffmann
2004 New bat of the genus *Lophostoma* (Phyllostomidae: Phyllostominae) from northwestern Ecuador. Occasional Papers, Museum of Texas Tech University 232: i+1–16.

Baker, R. J., H. H. Genoways, W. J. Bleier, and J. W. Warner
1973 Cytotypes and morphometrics of two phyllostomatid bats, *Micronycteris hirsuta* and *Vampyressa pusilla*. Occasional Papers of the Museum of Texas Tech University 17:1-10.

Baker, R. J., M. Hamilton, and D. E. Parish
2003b Preparations of mammalian karyotypes under field conditions. Occasional Papers, Museum of Texas Tech University 228: i+1–8.

Baker, R. J., S. R. Hoofer, C. A. Porter, and R. A. Van Den Bussche
2003a Diversification among New World leaf-nosed bats: An evolutionary hypothesis and classification inferred from digenomic congruence of DNA sequence. Occasional Papers, Museum of Texas Tech University 230: i+1–32.

Baker, R. J., C. A. Porter, J. C. Patton, and R. A. Van Den Bussche
2000 Systematics of bats of the family Phyllostomidae based on *RAG2* DNA sequences. Occasional Papers, Museum of Texas Tech University 202: i +1–16.

Bradley, R. D., and R. J. Baker
2001 A test of the Genetic Species Concept: Cytochrome-*b* sequences and mammals. Journal of Mammalogy 82:960–973.

Carter, D. C., and P. G. Dolan
1978 Catalogue of type specimens of Neotropical bats in selected European museums. Special Publications, The Museum, Texas Tech University 15:1–136.

Cerón, R., W. Palacios, R. Valencia, and R. Sierra
1999 Las formaciones naturales de la Costa del Ecuador. Pp. 55–78 in Propuesta Preliminar de un Sistema de Clasificación para el Ecuador Continental (Sierra, R., ed.). Proyecto INEFAN/GEF-BIRF y EcoCiencia, Quito, Ecuador. vi + 196 pp.

Debaeremaeker, K. R., and M. B. Fenton
2003 Basisphenoid and basioccipital pits in microchiropteran bats. Biological Journal of the Linnean Society 78:215–233.

Dobzhansky, T.
1950 Mendelian populations and their evolution. American Naturalist 74:312–321.

Dodson, C. H., and A. H. Gentry
1991 Biological extinction in western Ecuador. Annals of the Missouri Botanical Garden 78:273–295.

Felsenstein, J.
1985 Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.

Gentry, A. H.
1986 Species richness and floristic composition of Chocó region plant communities. Caldasia 15(71–75):71–91.

Gray, J. E.
1842 Description of some new genera and fifty unrecorded species of Mammalia. Annals and Magazine of Natural History, series 1, 10:255–267.

Hillis, D. M., and J. P. Huelsenbeck
1992 Signal, noise, and reliability in molecular phylogenetic analysis. Journal of Heredity 83:189–195.

Hoffmann, F. G., and R. J. Baker
2001 Systematics of bats of the genus *Glossophaga* (Chiroptera: Phyllostomidae) and phylogeography in *G. soricina* based on the cytochrome-*b* gene. Journal of Mammalogy 82:1092–1101.

Koopman, K. F.
1993 Order Chiroptera: Pp. 137–241 in Mammals Species of the World: A Taxonomic and Geographic Reference. Second edition. (Wilson, D. E., and D. M. Reeder eds.). Smithsonian Institution Press, Washington, D.C., USA.

Longmire, J. L., M. Maltbie, and R. J. Baker
1997 Use of "lysis buffer" in DNA isolation and its implication for museum collections. Occasional Papers, The Museum, Texas Tech University 163:1–3.

Maddison, W. P., and D. R. Maddison
2002 MacClade: analysis of phylogeny and character evolution. Version 4.0. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts, USA.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B da Fonseca, and J. Kent
2000 Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Oxford Molecular Group PLC
1998 AssemblyLIGN™ 1.0.9. Oxford Molecular Group PLC, Oxford, UK.

Porter, C. A., S. R. Hoofer, C. A. Cline, F. G. Hoffmann, and R. J. Baker (Submitted)
Molecular evidence for unrecognized biodiversity in the bat genus *Micronycteris* (Phyllostomidae), with descriptions of two new subgenera.

Rehn, J. A. G.
1904 A revision of the mammalian genus *Macrotus*. Proceedings of the Academy of Natural Sciences of Philadelphia 56:427–446.

Ridgway, R.
1912 Color Standards and Color Nomenclature: 1st ed. Privately published, Washington, D.C., USA.

Sanborn, C. C.
1949 Bats of the genus *Micronycteris* and its subgenera. Fieldiana: Zoology, 31:215–233.

Simmons, N. B.
1996 A new species of *Micronycteris* (Chiroptera: Phyllostomidae) from northeastern Brazil, with comments on phylogenetic relationships. American Museum Novitates 3158:1–34.

2005 Order Chiroptera. Pp. 312-529 in Mammal Species of the World. Third edition (Wilson, D. E., and D. M. Reeder, eds). Smithsonian Institution Press, Washington, D.C., USA.

Simmons, N. B., and R. S. Voss
1998 The mammals of Paracou, French Guiana: A Neotropical lowland rainforest fauna. Part 1. Bats. Bulletin of the American Museum of Natural History 237:1–219.

Simmons, N. B., R. S. Voss, and D. W. Fleck
2002 A new Amazonian species of *Micronycteris* (Chiroptera: Phyllostomidae) with notes on the roosting behavior of sympatric congeners. American Museum Novitates 3358:1–14.

Swofford, D. L.
2002 PAUP* phylogenetic analysis using parsimony (*and other methods). Version 4. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts, USA.

Tamura, K., and M. Nei
1993 Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Molecular Biology and Evolution 10:512–526.

Thompson, J. D., T. J. Gibson, F. Plewniak, F. Jean-mougin, and D. G. Higgins
1997 The CLUSTAL X windows interface: Flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Research 24:4876–4882.

Tirira, D.
1999 Mamíferos del Ecuador. Publicación Especial 2, Museo de Zoología, Centro de Biodiversidad y Ambiente. Pontifica Universidad Católica del Ecuador, Quito. 392 pp.

Wagner, J. A.
1855 Die Säugthiere in Abbildungen nach der Natur mit Beshreibungen von Dr. Johann Christian Daniel von Schreber. Supplementband. Fünfte Abtheilung: Die Affen, Zahnlüeker, Beutelthiere, Hufthiere, Insektenfresser und Handflüger. L. D. Weigel, Leipzig 5:1–810.

Wetterer, A. L, M. V. Rockman, and N. B. Simmons
2000 Phylogeny of phyllostomid bats (Mammalia: Chiroptera): Data from diverse morphological systems, sex chromosomes, and restriction sites. Bulletin of the American Museum of Natural History 248:1–200.

Wickliffe, J. K., F. G. Hoffmann, D. S. Carroll, Y. V. Dunina-Barkovskaya, R. D. Bradley, and R. J. Baker
2003 Intron 7 (Fgb-I7) of the fibrinogen, B beta polypeptide (Fgb): A nuclear DNA phylogenetic marker for mammals. Occasional Papers, The Museum, Texas Tech University 219:i+1–6.

A NEW SPECIES OF *THOMASOMYS* (CRICETIDAE: SIGMODONTINAE) FROM CENTRAL BOLIVIA

UNA NUEVA ESPECIE DE *THOMASOMYS* (CRICETIDAE: SIGMODONTINAE) DE BOLIVIA CENTRAL

Jorge Salazar-Bravo and Terry L. Yates

ABSTRACT

We describe a new species of *Thomasomys* from the eastern slopes of the central Bolivian Andes. This is a medium-size long-tailed rodent phenetically similar in external and cranial features to *Thomasomys notatus*, although genetically it appears most closely related to species in the *Thomasomys oreas* complex. Phylogenetic analyses of morphological and molecular data indicate that the new species presents a unique combination of characters. The new taxon inhabits the upper montane rain forest, and appears to be arboreal; it is known only from the type locality.

Key words: Yungas, Cochabamba, upper montane rain forest, Thomasomyini

RESUMEN

El género *Thomasomys* es uno de los complejos taxonómicos más interesantes de los Bosques Andinos sudamericanos. En este trabajo y utilizando evidencia morfológica y molecular describimos una especie de la región de Corani, en el bosque yungueño Cochabambino. Esta especie se parece a *Thomasomys notatus* en la coloración de la piel y algunos rasgos del cráneo pero parece estar más emparentada filogenéticamente con las especies del complejo *Thomasomys oreas*. La especie en cuestión se conoce solamente de dos especimenes que provienen de una sola localidad (la localidad típica) y parece ser arbórea.

Palabras claves: Yungas, Cochabamba, bosque pluvial montano, Thomasomyini

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Pp. 747-774 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The Quintessential Naturalist: Honoring the Life and Legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

INTRODUCTION

Between 1984 and 1993 a collaborative project between the American Museum of Natural History (AMNH, New York), the Colección Boliviana de Fauna (CBF, La Paz, Bolivia), the Museum "Noel Kempff Mercado" (MNKM, Santa Cruz de la Sierra, Bolivia), and the Museum of Southwestern Biology (MSB, New Mexico) conducted surveys of mammals and their ectoparasites in Bolivia (e.g., Anderson, 1997; Gardner, 1991; Dunnum et al., 2001; Salazar-Bravo et al., 2002a, 2002b; Cook and Salazar-Bravo, 2005). One new genus (*Tapecomys*), 2 new species (*Tapecomys primus* and *Carollia manu*) and 1 subspecies (*Andalgalomys pearsoni dorbignyi*) have been fully or partially based on the material collected as part of this project (e.g., Olds et al., 1987; Anderson and Yates, 2000; Pacheco et al., 2004).

In 1993 our team surveyed mammals across the eastern slopes of the Andes in central Bolivia between the cities of Cochabamba and Santa Cruz de la Sierra. There have been many biological inventories along this road, including those of Alcide d'Orbigny who between 1830 and 1832 collected the first known mammals for the country (Hershkovitz 1987). However, due to the inhospitable terrain, few expeditions have sampled the intermediate elevations between 2000 and 3500 m. The unstable slopes along the Bosques de Yungas render trapping difficult and areas in this elevation range often are undersampled or bypassed completely. It is no surprising then that most of the new records (e.g., *Rhagomys*, Villalpando et al. *in press*) or new species (*Marmosops creightoni*, Voss et al. 2004a) of mammals for the country come from these regions. Among the 23 species of cricetid rodents we found in the 8 localities visited along this transect we trapped 3 species of *Thomasomys* occurring sympatrically at a locality ca. 60 km east of the city of Cochabamba. Two of them (*Thomasomys australis* and *Thomasomys oreas*) had been trapped elsewhere, but the third species was sufficiently different to require further comparisons. Morphological and molecular analyses showed that the third species is distinct from other known members of the genus; below we describe and name it as a new species.

MATERIALS AND METHODS

To place the new taxon in the context of the genus *Thomasomys* our approach is 2-fold; first, we use over 100 discrete morphological characters to address its phylogenetic relationships to all known taxa in *Thomasomys* and its close allies. Second, molecular data (sequences of the mtDNA cytochrome *b* gene) are used to a) test the hypothesis that *Thomasomys* is a monophyletic clade, and b) address the phylogenetic relationships of the new taxon with other species in *Thomasomys* for which homologous data exist.

Morphologic Data Analyses

Terminology of external, cranial, and dental anatomy follows Carleton and Musser (1989), Voss (1993), Steppan (1995), Musser et al. (1998), Luna and Pacheco (2002), and Pacheco (2003). Capitalized color nomenclature follows Ridgway (1912). Standard measurements, including total length (TL), tail length (LT), hind foot length (HF) and ear length (Ear), were obtained from specimen labels. Head + body length (HBL) is TL minus LT. Cranial measurements used here are defined and illustrated by Voss (2003) and include: CIL, condylo-incisive length; LD, length of diastema; LM, occlusal length of the maxillary molar row; BM1, breadth of the first maxillary molar; LIF, length of left incisive foramen; BIF, breadth across both incisive foramina; BPB, breadth of the palatal bridge; BZP, breadth of the zygomatic plate; LIB, least interorbital breadth; ZB, zygomatic breadth; DI, depth of upper incisor; BIT, breadth across both upper incisor tips.

Phylogenetic Analyses of Discrete Morphological Characters

The 2 individuals known of the new taxon were scored for phylogenetic analysis of discrete morphological characters according to character descriptions and character-state coding in Pacheco (2003). Only 111 of his 145 characters were scored for the new taxon; the remaining 34 characters were scored as missing in the resulting data matrix because we lacked digestive and reproductive tracts, and because we could not score the lower molar row and some jaw characters. Pacheco's matrix includes 64 ingroup and 16 outgroup terminals (80 taxa total) and thus with the inclusion of the new taxon the final matrix contained 81 taxa. We restricted our analyses to the 111 characters that were available for the new taxon. This matrix was submitted to a Maximum Parsimony phylogenetic analysis in PAUP* 4.0b10 (Swofford 2002) with a heuristic search with 250 random addition replicates and TBR branch swapping. All characters were weighted equally and multistate transformations were ordered following the criteria presented by Pacheco (2003). Measures of clade support were assessed using parsimony jackknife (500 replicates, 10 random additions, 30% characters deleted per replication) and bootstrap (500 replicates, 10 random additions). Morphological synapomorphies were documented by examining PAUP* outputs and visualized using MacClade 4 (Maddison and Maddison, 2002). In the diagnosis and description of the new taxon we used only those character changes which were unambiguously optimized irrespective of the type of character transformation used.

Molecular Data Analyses

DNA was isolated with the use of DNAeasy kits (Qiagen) from either frozen or ethanol-preserved tissues. Mitochondrial cytochrome *b* gene (cyt *b*) sequences were obtained using a combination of primers and protocols slightly modified from the literature (e.g., Smith and Patton, 1999; Salazar-Bravo et al., 2001). In all cases, both heavy and light DNA strands were sequenced and compared. Alignment, visualization and translation of obtained sequences were performed with modules in Lasergene for Windows (DNASTAR, 2003).

The entire cytochrome *b* gene sequence of the 2 specimens of the new taxon were obtained and added to a database of cyt *b* sequences of species of *Thomasomys* and various outgroups. Because the cytochrome *b* gene sequences of sigmodontine taxa vary in length (Smith and Patton, 1999; D'Elia, 2003), we restricted our analyses to the first 1134 base pairs of the sequence, following the criteria presented by D'Elia et al. (2003). We attempted to obtain molecular data for all known Bolivian species of *Thomasomys*; additionally, we included as many homologous sequences as possible from Peruvian (mostly from GenBank) and Ecuadorian taxa (generated by us). Our complete matrix included 15 taxa in *Thomasomys* plus multiple representatives of various tribes and "unique lineages" in the Sigmodontinae and in essence is the same one used by D'Elia et al. (2003), except that in our case we did not include representatives of any of the other cricetid (sensu Steppan et al. 2004) subfamilies (namely Arvicolinae, Cricetinae, Neotominae, or Tylomyinae). All analyses were rooted with homologous sequences of 4 species of *Sigmodon*.

This dataset was submitted to a phylogenetic analysis using the criteria of Maximum Parsimony in PAUP* with heuristic searches (250 random sequence additions) and TRB branch swapping. As measures of clade support we used parsimony jackknife (500 replicates, 10 random additions, 30% characters deleted per replication) and bootstrap (500 replicates, 10 random additions). Uncorrected sequence divergences among haplotypes and groups of haplotypes (i.e., average haplotype distances) were calculated with PAUP*. Sequences obtained for this work have been deposited in GenBank under Accession Nos. DQ914643 to DQ914654 .

Karyotypes

Chromosomal preparations for the 2 individuals of the new taxon were obtained following Anderson et al. (1987). Metaphase cells were photographed and scored to determine the diploid and fundamental numbers; at least 10 metaphase plates from each individual were scored to verify the chromosomal counts. Nomenclature for chromosome morphology and fundamental number (FN) follows Patton (1967).

RESULTS

Phylogenetic Analysis of Morphological Characters

With all characters weighted equally and multistate transformations ordered in 40 characters, a total of 99 equally most parsimonious trees were resolved, each 1050 steps long (CI=0.1667 and RI=0.6280). Our consensus tree (Fig. 1) agrees with Pacheco's (2003) analysis of the Andean Thomasomyines in one fundamental way: based on the phylogenetic analysis of discrete morphological characters, *Thomasomys* is polyphyletic. Our results, however, suggest several clades incongruous with Pacheco (2003). Among these: a) *Abrawayaomys ruschii* forms a sister taxa relationship with *Chilomys*, b) *Rhipidomys* does not form a monophyletic group, c) *Thomasomys notatus* is not the sister taxon to a clade formed by *Thomasomys oreas -- Thomasomys gracilis*, and d) there is at least weak evidence for a clade of Atlantic Rainforest taxa (i.e., *Juliomys*, *Wiedomys*, *Wilfredomys*, *Delomys*, and *Phaeonomys*).

Only 5 clades in the consensus tree received support values (either jackknife or bootstrap) above the cutoff level of 50%. Most of these were terminal clades that represented closely related species within a genus, for example *Rhagomys*, *Chilomys*, and *Delomys*. The only group in *Thomasomys* that received any level of support above the 50% cutoff value was the *Thomasomys oreas* complex, which included the nominal species plus 2 unnamed species (*Thomasomys* sp8 and *Thomasomys* sp9), and *T. gracilis* with a bootstrap value of 69%, but no jackknife support above 50%. The only basal node with >50% jackknife support was that defining the Atlantic Rainforest taxa as sister to the remaining ingroup taxa at 58% bootstrap support.

In the strict consensus tree, the new taxon appears in an unresolved polytomy with respect to the remaining *Thomasomys* species, as are *Thomasomys baeops*, *Thomasomys*

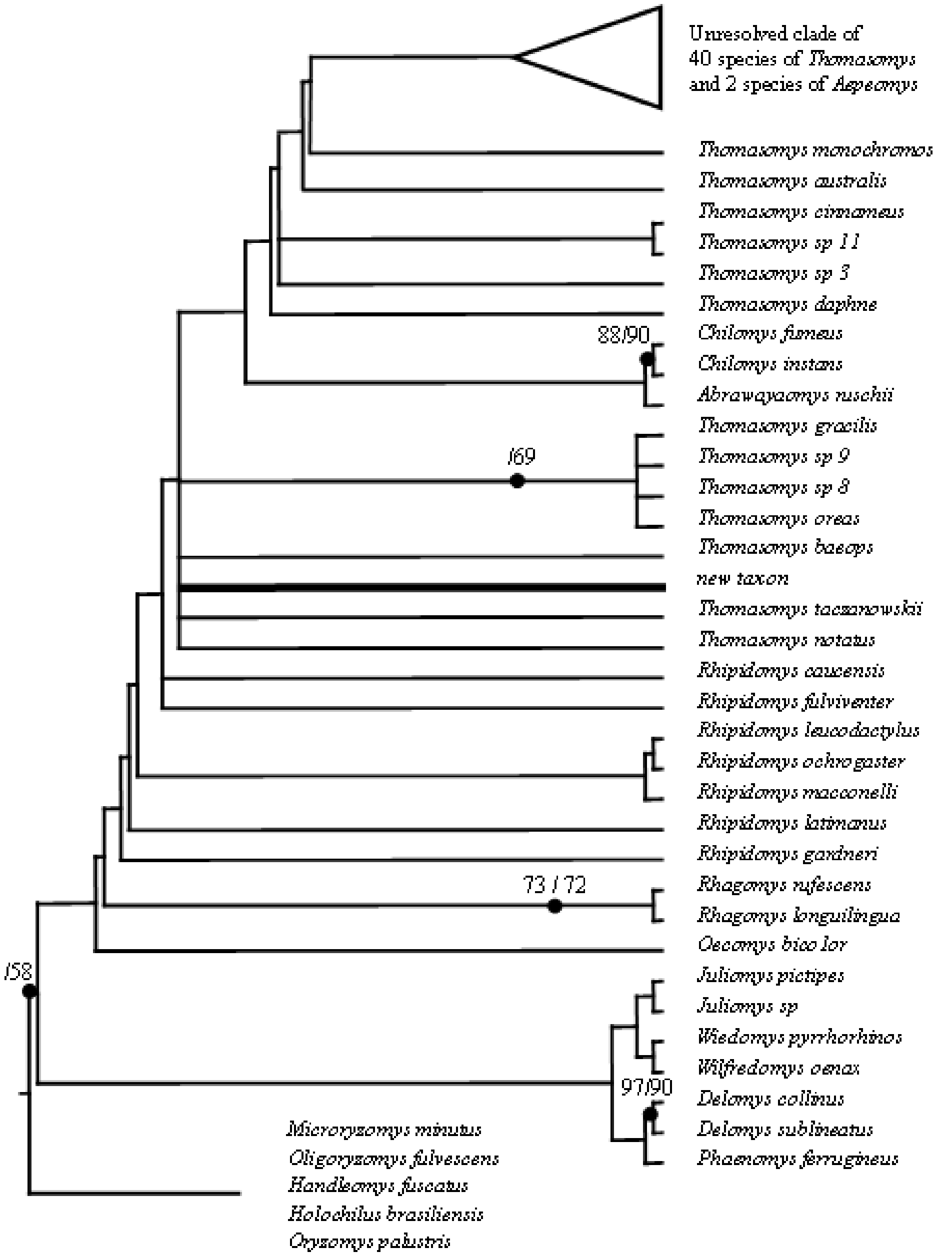

Figure 1. Strict consensus tree of the 91 shortest trees (length 1050, CI = 0.1667, RI = 0.6280) obtained on a heuristic search of phylogenetic analysis using Maximum Parsimony of 81 taxa and 111 discrete morphological characters from members of the genus *Thomasomys*, its close allies and several outgroup taxa. Numbers above branches indicate parsimony jackknife (left of the diagonal) and bootstrap (right of the diagonal) values for each basal node. Only values above 50% are reported. Notice the unresolved position of the new taxon (branch and name in bold) with respect to other species in *Thomasomys*.

notatus, and *Thomasomys taczanowski*.

Phylogenetic Analysis of Molecular Characters

We obtained from 403 to 1140 base pairs (bp) of the cytochrome *b* gene for species of *Thomasomys* sequenced for this work, including the entire sequence for both the holotype and the paratype. The dataset analyzed phylogenetically had 669 variable characters of which 553 were parsimony informative. Two shortest trees were found, each 7664 steps long. Despite the high level of homoplasy in the dataset (CI=0.1567 and RI=0.401) the strict consensus tree shows a good level of resolution with only 2 polytomies, both in groups outside *Thomasomys*. In this region of the tree the topology of the consensus tree is similar to that presented in D'Elia et al. (2003). The consensus tree (Fig. 2) shows strong jackknife support (91%) for the monophyly of this group but only moderate bootstrap support (75%). Like D'Elia et al. (2003) we found that *Chilomys* is the sister taxon to *Thomasomys*, although with low levels of support (jackknife support of 57%). In the tree, the new taxon is more closely related to species of the *Thomasomys oreas* complex with moderately high levels of support (jackknife, 90%; bootstrap, 70%). With the exception of the sister taxa relationships of the following pairs of species (*T. baeops* – *T. taczanowskii* and *T. australis* – *T. daphne*), all other phylogenetic hypothesis were only weakly supported.

Sequence Divergence

As quantified by uncorrected sequence divergence (p-distances, Table 1), the new taxon is markedly different from other species of *Thomasomys*, and is phenetically most similar to *T. oreas* (mean p-distance of 12.7%), and most dissimilar from Peruvian *T. notatus* (mean p-distance of 17%). In this arrangement of taxa, intraspecific comparisons varied from 0.1% divergence between individuals of *T. ladewi* from the same locality, to 2.9% divergence between individuals of *T. daphne* from localities separated by approximately 286 km in Bolivia and Peru. The average sequence divergence among species in *Thomasomys* is 12.9%; the lowest level was 6.4% divergence between *T. taczanowskii* and *T. baeops*.

In summary, phylogenetic analyses of morphological and molecular characters failed to provide robust hypotheses of relationships among the species of *Thomasomys* included. What is clear, however, is that both genetic distance and phylogenetic placement indicate equal uniqueness of the specimens of the new taxon in comparison to other taxa currently recognized as species, and thus we name it as follows:

Thomasomys andersoni, new species
(Figures 3-9)

Holotype. AMNH 268734, young adult female (Fig. 3), collected 30 July 1993 by Jorge Salazar–Bravo (original number JSB 659) in an elfin forest near the headquarters of the Corani hydroelectric plant (17° 12′ 43″ S, 65° 52′ 09″ W, GPS coordinates, map datum WGS 84) at 2,630 m, Department of Cochabamba, Bolivia (Fig. 4). The holotype is a standard skin with cranium (mandible missing, probably lost during cleaning of skull) and partial skeleton, in good condition; chromosome slides and cell suspensions housed at the Museum of Southwestern Biology (NK 30587); heart, liver and kidney tissue, originally preserved in liquid nitrogen, maintained at –76°C in the frozen collection of

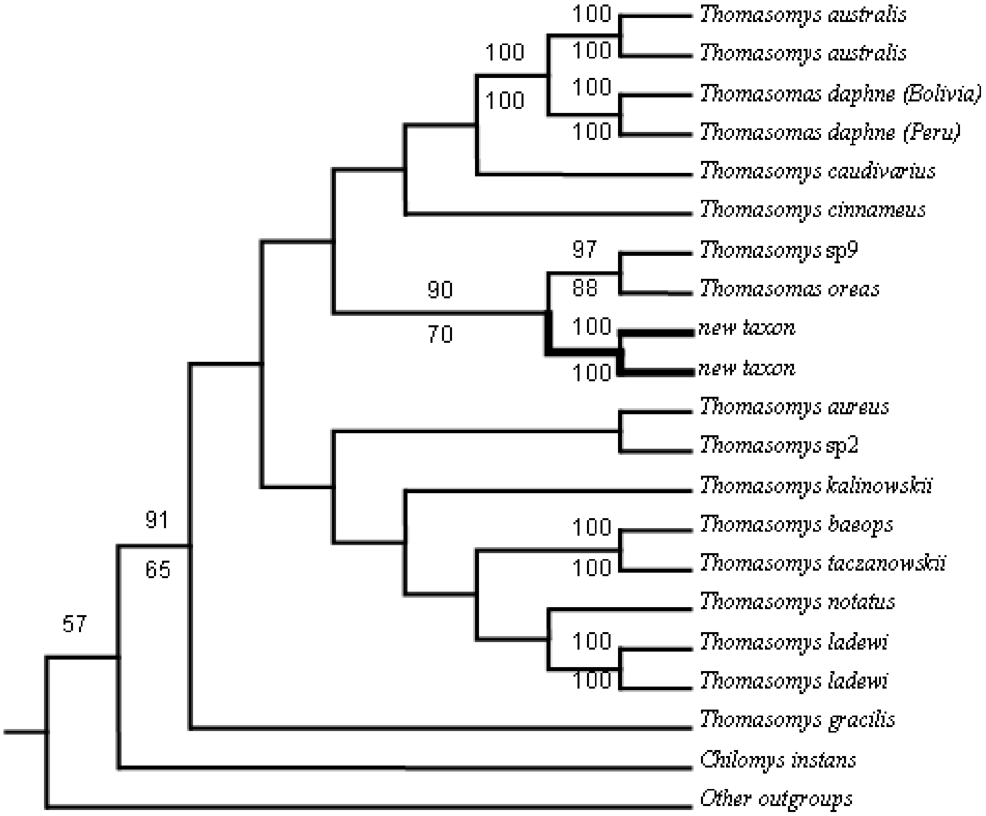

Figure 2. Strict consensus tree of the 2 shortest trees (length 7664, CI=0.1567, RI=0.401) obtained on a heuristic search (250 replicates of randomly added taxa) of phylogenetic analysis using Maximum Parsimony of variable length sequences, from 403 to 1134 base pairs, from the mitochondrial cytochrome *b* gene sequence data for 88 taxa. The tree is rooted with 1 sequence each of 4 species in the genus *Sigmodon*. Parsimony jackknife and bootstrap values are respectively indicated above or below the branches. Notice the position of the new taxon (name and branch in bold) as the sister group to a clade of species of the *Thomasomys oreas* complex.

the Division of Genomic Resources of the Museum of Southwestern Biology.

Paratype. Only 1 other specimen (standard skin with cranium, jaw and partial skeleton, plus associated frozen tissues, cell suspension, and cell spreads bearing number NK 30588) is known and is hereby designated as paratype (Fig. 5). This old adult female was trapped 30 July 1993 by Jorge Salazar-Bravo (original field number JSB 660), and is cataloged in the Museum of Southwestern Biology (MSB 146437).

Etymology. Named for Dr. Sydney Anderson, Curator Emeritus of the American Museum of Natural History and author of the first "Mammals of Bolivia" (Anderson 1997); his interest in Bolivian mammals spanned 4 decades culminating in several field trips from the mid 1980s to early 1990s; the species herein described was collected on

Table 1. Uncorrected percent sequence divergence (x100) within and among cytochrome *b* haplotypes from 15 species of *Thomasomys* and outgroups.

		new taxon	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1.	new taxon	0.2															
2.	*T. aureus*	16.3	-														
3.	*T. australis*	14.7	12.2	0.5													
4.	*T. baeops*	15.9	11.9	10.7	-												
5.	*T. caudivarius*	15.4	14.3	12.0	13.1	-											
6.	*T. cinnameus*	14.4	13.3	12.0	11.7	10.8	-										
7.	*T. daphne*	14.0	14.9	7.9	12.4	12.5	12.6	2.9									
8.	*T. gracilis*	16.3	16.3	12.9	13.1	11.8	12.3	13.7	-								
9.	*T. kalinowskii*	15.3	12.3	11.6	10.8	11.7	10.2	13.2	12.2	-							
10.	*T. ladewi*	13.4	11.5	11.4	11.6	12.2	10.4	13.0	12.1	9.9	0.1						
11.	*T. notatus*	17.0	14.1	13.9	11.9	13.6	13.3	14.7	14.1	13.2	11.3	-					
12.	*T. oreas*	12.7	13.2	12.5	12.2	13.6	12.7	14.2	12.5	12.4	10.5	12.9	-				
13.	*T. taczanowskii*	16.7	12.6	11.9	6.4	13.5	12.9	13.6	13.9	12.0	11.6	13.9	12.2	-			
14.	*T.* sp2	15.2	12.3	12.3	12.5	13.0	13.0	13.5	14.4	11.7	11.1	12.7	14.1	12.1	-		
15.	*T.* sp9	15.3	14.5	14.8	12.7	13.4	12.7	15.6	13.4	15.3	12.2	15.9	7.5	14.9	13.8	-	
	outgroups	19.2	18.6	18.6	17.3	18.0	16.9	18.3	18.2	18.0	17.7	18.7	17.8	18.3	18.1	19.2	18.8

Figure 3. Cranium and occlusal view of the upper molar row of the holotype of *Thomasomys andersoni* (female, AMNH 268734). Scale bar equals 5 mm for the cranium and 1.25 mm for the molar row.

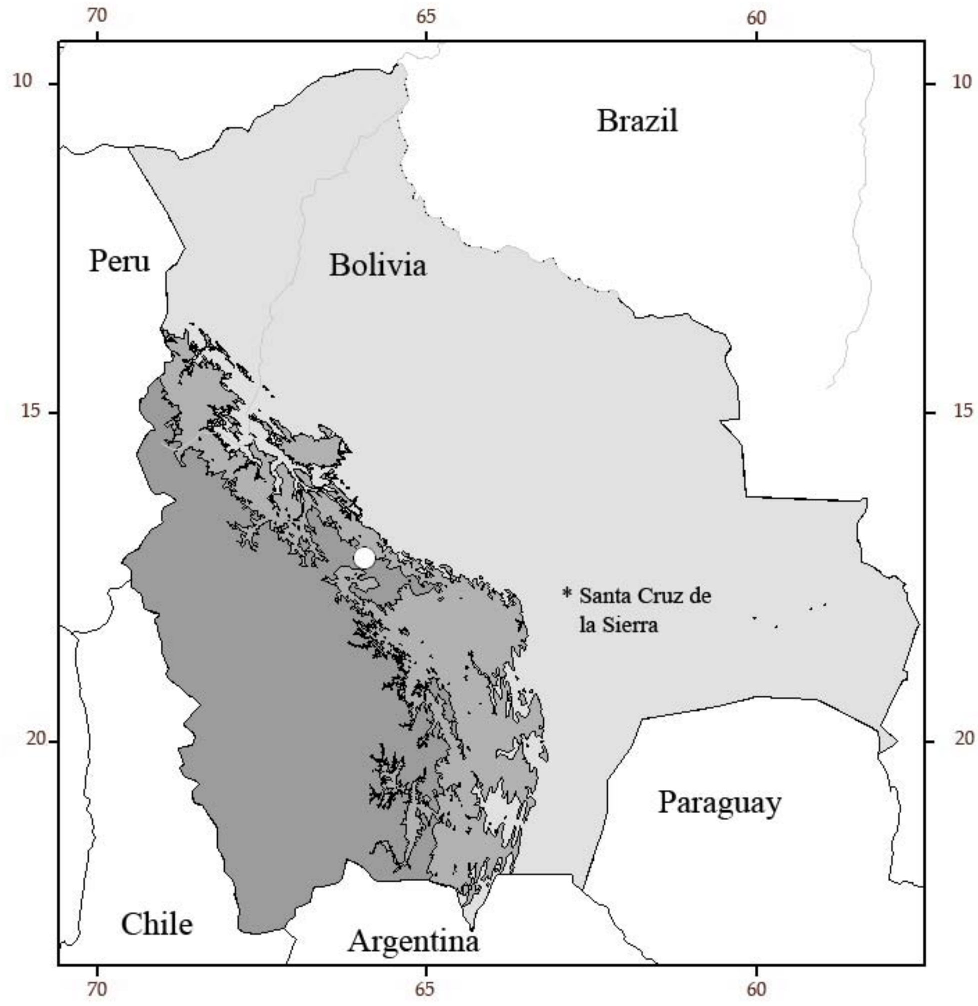

Figure 4. Map of Bolivia. Areas in light gray are above 1000 m, those in dark gray are above 3000 m. The open circle denotes the type locality (2,630 m) of *Thomasomys andersoni*, new species.

Figure 5. Cranium of the paratype of *Thomasomys andersoni* (female, MSB 146437). Scale bar equals 5 mm.

one of these trips. An undeterred champion of Bolivian collections of natural history, he has been instrumental in the academic formation of Bolivian personnel, including that of the senior author.

Diagnosis. A species of the subfamily Sigmodontinae (sensu Reig, 1980), diagnosable by the following combination of characters: medium-size (HBL=109 mm, CIL=27.21), dorsal coloration dull Brownish Olive, ventral coloration Olive Buff with a yellowish tinge and a distinct Strotian Yellow pectoral marking; moderately long mystacial vibrissae; tail slightly longer than head and body; interorbital region with rounded supraorbital margins, without ridges; straight fronto-nasal profile; broad and vertically oriented zygomatic plate; zygomatic arches convergent anteriorly; orbicular apophysis of malleus small, not basally constricted; parietal-supraoccipital suture narrow; bunodont and brachydont molars with weak labial cingula; accessory labial root of M1 present; orthodont yellowish upper incisors; short hallux (first phalange not extending beyond metatarsal of digit II) and long digit V of pes (claw of digit V extending about half the length of phalange 2 of digit IV). Analyses of the cytochrome *b* gene sequence data suggest several potential molecular synapomorphies which we do not list because molecular data are available for only a few species in *Thomasomys*.

Description

External Morphology: *Thomasomys andersoni* is a medium-sized mouse with soft, dense, and long dorsal fur (average length = 11 mm). Body pelage with a conspicuous demarcation between the dorsal and ventral pelage. Dorsal pelage dull Brownish Olive turning to Ochraceous Tawny on the sides; guard hairs uniformly dark. Ventral pelage Olive Buff, with hairs grayish at base, dull whitish mixed in with Buffy Yellow at tips; thoracic region with a distinct Strotian Yellow pectoral marking. Genal, mystacial, superciliary, and carpal vibrissae present; mystacial vibrissae long, extending posteriorly to just behind the pinnae. Pinnae proximally covered with short blackish hairs, about the same color as of the hairs covering the head. Metacarpals and digits of manus whitish; metatarsals chocolate brown, but digits of pes white; claws on manus ventrally closed at base. Digits in both manus and pes with ungual tufts of silvery hairs, more conspicuous in pes. Hind feet relatively short and broad; progression of size in digits IV, III, II, V, I, with IV, III, and II progressively smaller. Claw of digit V nearly reaching the base of claw of digit IV. Plantar pads large and fleshy; no gap between the thenar and hypothenar pads (in pes); soles of feet naked. Tail about as long as head and body (46–53% of total length), uniformly brown, without any trace of white, and covered with short thick hairs, scales large; distinctly penicillate (last 8-10 mm).

Cranium and Mandible: Rostrum of moderate proportions, not long but narrow and with shallow zygomatic notches. Interorbital region narrow (LIB ca. 28% of ZB; see Voss (2003)) with smooth sides and hourglass-shaped (not beaded, ridged or squared). Zygomatic arches convergent anteriorly and widest at the roots. Lateral view of the skull flattened from mid-frontals to tips of nasal bones; zygomatic plate broad (BZP ca. 8.2% of CIL; see Voss (2003)) with anterior margin sloping slightly backwards from base. Incisive foramina long (averaging 79% of diastema length), extending posteriorly to but not between molar alveoli, widest just behind the premaxillary/maxillary suture. Palate broad and short (as defined by Hershkovitz (1962)) and smooth, with

2 to 3 pairs of conspicuous posteropalatal foramina, but posterolateral palatal pits small, simple, and generally inconspicuous. Mesopterygoid fossa long and broadly U-shaped, with anterior margin smooth; not perforated dorsally by sphenopalatine vacuities (at least in the only 2 specimens known). Parapterygoid fossa (=lateral pterygoid plates) narrow, concave but shallow and perforated (in the older specimen) by pits between the pterygoid and sphenoid part of the plate as well as by the posterior end of the alisphenoid canal. Posterior opening of alisphenoid canal large and oval-shaped. Alisphenoid strut present; carotid circulation characterized by the presence of conspicuous sphenofrontal and stapedial foramina and squamosal-alisphenoid groove (pattern 1 of Voss (1988)). Postglenoid foramen and subsquamosal fenestra of about the same size, the latter slightly larger in the holotype, separated by a narrow hamular process (= post-tympanic hook) of the squamosal which sits on the periotic and reaches the mastoid. Tegmen tympanic overlapping the posterior suspensory process of squamosal across the middle lacerate foramen. Stapedial spine of bulla free (not appressed against bulla), ovoid in cross-section and almost reaching alisphenoid. As in other species of *Thomasomys* the carotid canal is small and bounded by the basioccipital and the ectotympanic portions of the auditory bullae. Auditory bullae uninflated and nearly flask-shaped, with bony eustachian tube differentiated from the capsular region of the bulla, extending and reaching the pterygoid lobes. Orbicular apophysis of malleus enlarged and wide at base (not constricted).

Upper incisors large, orthodont, and colored light-yellow; molar rows in parallel series composed of small, pentalophodont and brachydont teeth. As in other species of the genus, interpenetration of labial and lingual folds is only to toothrow axis with paraflexus and metaflexus bending posteriorly around the paracone and metacone, respectively. Antercone of M1 divided by an anteromedian flexus which defines subequal anterolabial and anterolingual conules. Anterolophs and mesolophs well developed in M1 and M2 fusing lingually with the mesostyle. Enterostyle present as a low stylar cusp.

In the paratype, the coronoid process is well developed and falciform, subequal in height to the mandibular condyle and defining a deep sigmoid notch. Angular notch noticeably excavated and angular process located almost even yet anterior to the condyloid process. Lower incisor capsule small relative to the size of the dentary and not projecting far upward. Lower incisors thin and with light yellow (almost white) pigmented faces.

Post-cranial Skeleton: The 2 known individuals of this species have 13 ribs, 19 thoracicolumbar vertebrae, 4 sacral vertebrae, 33 caudal vertebrae and an enlarged neural spine on their second thoracic vertebrae. The sternum of the paratype contains 5 sternebrae and a long xiphoid process (at least twice as long as sternebra I).

Karyotype: The 2 individuals of *Thomasomys andersoni* have a diploid complement of 44 all acrocentric chromosomes (2n=44, FNa=42); the X chromosomes appear to be acrocentric as well although they could not be identified unequivocally due to the lack of males in the sample.

Morphological Comparisons. Based on the phylogenetic analyses of discrete morphological characters presented in Fig. 1, we cannot unequivocally associate *Thomasomys andersoni* to any taxon currently recognized in the genus. *Thomasomys baeops* and *T. taczanowskii* share a number of morphological and molecular synapomorphies and appear as sister taxa in the phylogenetic analysis of molecular data with high levels of support (100% jackknife and bootstrap values). These species are currently restricted to the northern Peruvian (*T. taczanowskii*) and the Ecuadorian Andes (*T. baeops*).

Two species of *Thomasomys* are sympatric with *T. andersoni* at its type locality: *T. oreas* and *T. australis*. The latter is easily distinguishable from *T. andersoni* by its smaller body size, shorter ears, longer tail, short, narrow and chisel-like upper incisors and the lack of pelage countershading. *Thomasomys andersoni* merits further comparisons with *T. oreas* and *T. notatus*, the latter an allopatric taxon, currently known only from eastern Peru; as with various other species of small mammals however, it is possible that *T. notatus* will also be found in similar environments in western Bolivia.

Thomasomys andersoni and *Thomasomys oreas* have distinct countershading in body pelage, approximate similar tail length, and dark patches on top of the hind feet which contrast with paler toes and sides. They can be distinguished from each other because the dorsal pelage in *T. andersoni* is dull olive brown as opposed to rich yellowish brown (Prout's brown) in *Thomasomys oreas*; patterns of face coloration also serve to tell these species apart: the eye ring in *Thomasomys oreas* is darker that in *Thomasomys andersoni*, while the cheeks in the former are brighter (and more like the gular area) than in the latter. The ventral pelage in *Thomasomys andersoni* has a greenish/yellowish hue which becomes a yellowish pectoral shield whereas in *Thomasomys oreas* the ventral coloration is warm pinkish buff over plumbeous black. The skull of *Thomasomys andersoni* is larger than that of *T. oreas* for animals of about the same age. The rostrum in *T. oreas* is narrow, pointed, and tapers forward (Fig. 6); by contrast, the rostrum in *T. andersoni* is comparatively wider, longer, and presents a distinct straight fronto-nasal profile (Fig. 7). The auditory bullae in *T. oreas* are large and conspicuously inflated, to the point that the Eustachian tubes are indistinct, giving the bullae a globe-like shape. By contrast, the tympanic bullae in *T. andersoni* are uninflated and flask-shaped (Fig. 8)

Thomasomys andersoni and *Thomasomys notatus* overlap in all external and craniodental measurements (with the exception of Least Interorbital Breadth, Table 2) and require more detailed comparisons. They share many qualitative traits in common: both have genal vibrissae and moderately long mystacial hairs, body pelage distinctly countershaded; pencil-tipped tails; similarly proportioned hind feet with dark metatarsal patches, broad palates; broad and vertically oriented zygomatic plates, alisphenoid strut; and complete carotid arterial circulation.

However, *Thomasomys andersoni* and *T. notatus* differ in other points of comparison in external or cranial characters. Pelage in *T. andersoni* is similar to that of *T. notatus*, but darker, more ochraceous and longer dorsally (mean = 11 vs. 6 to 7 mm in *notatus*). By contrast *T. notatus* is more grayish and has a well-defined blackish streak down the middle of the back, from withers to rump, not present in *T. andersoni*. Ventrally, the pelage in *T. andersoni* is grayish tinged with buffy tips and presents a pectoral shield, whereas the undersurface in *T. notatus* is soiled whitish and has no pectoral markings. Ears are on average longer in *T. andersoni* (mean = 20.5 mm) than in *T. notatus* (mean = 19), but may overlap in some individuals. Insofar as the sample size permits, the only discriminant morphometric variable between *T. andersoni* and *T. notatus* is that of the Least Interorbital Breadth (LIB, Table 2), in which *T. andersoni* is comparatively and absolutely larger (≥ 4.44 mm), although that of *T. notatus* ranges up to 4.38 mm.

In a dorsal cranial view, *T. andersoni* is distinguishable by having a narrower, slightly longer rostrum and a broader, rounder, and smoother interorbital region

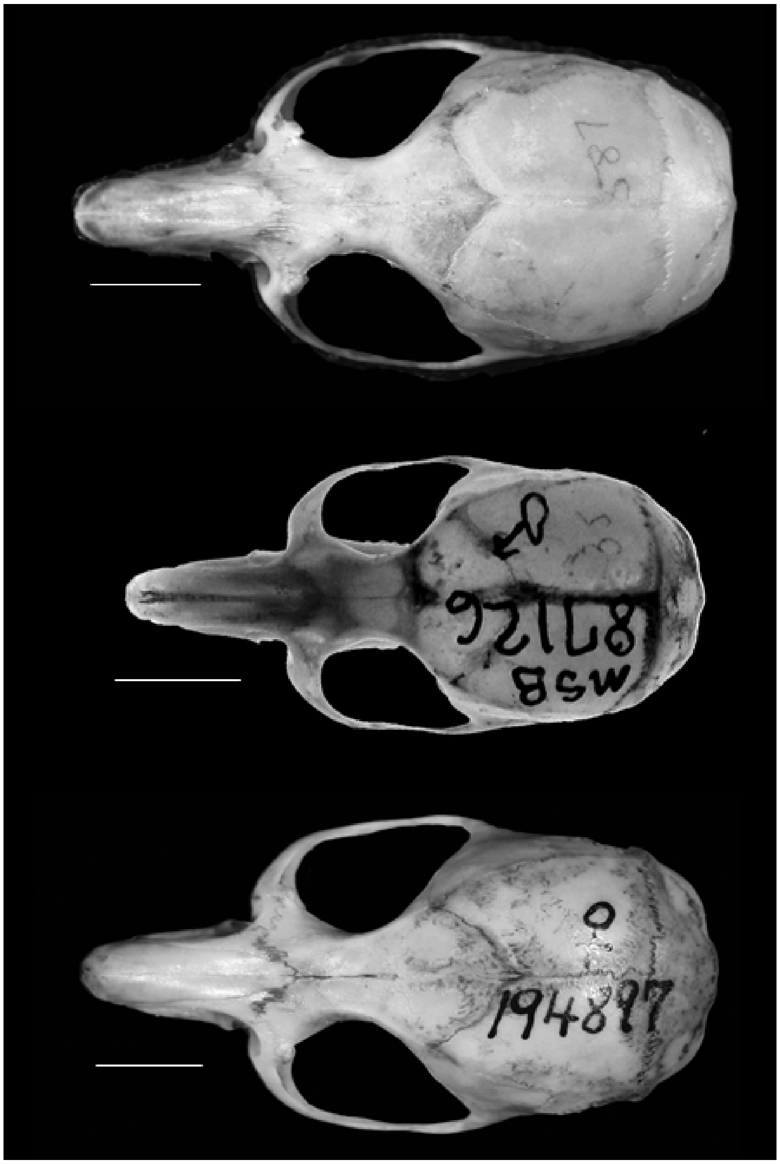

Figure 6. Dorsal view of crania of 3 species of *Thomasomys*, from top to bottom: *T. andersoni* (holotype), *T. oreas* (male, MSB 87126), and *T. notatus* (female, USNM 194897). Scale bar equals 5 mm.

Figure 7. Lateral view of crania, same specimens as in Fig. 6. Scale bar equals 5 mm.

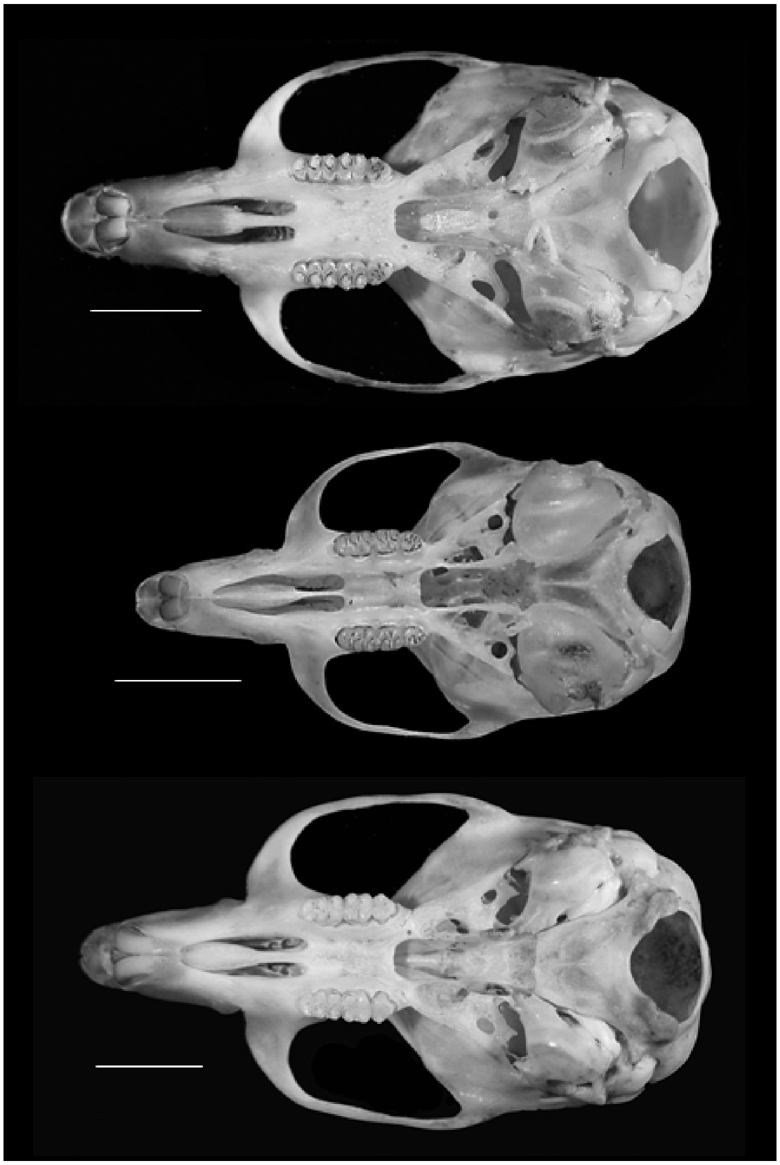

Figure 8. Ventral view of crania; same specimens as in Fig. 6. Scale bar equals 5 mm.

Table 2. Some measurements for *Thomasomys andersoni* and *Thomasomys notatus* from Perú. Measurements in mm and weight in grams. Weight in *Thomasomys notatus* is a mean of 7 individuals.

	Thomasomys andersoni		*Thomasomys notatus*		
	AMNH 268734	MSB 146437	Type (USNM 194548)	Mean (*N* = 9)	Range
TL	230	238	283	236.55	215-257
LT	122	128	155	126.56	100-144
HBL	108	110	128	110	92-130
HF	22	26	27	25.78	24-28
Ear	20	21	18.5	18.83	17.5-20
GLS	30.14	31.13	33	29.09	27.07-31.85
CIL	26.48	27.93	30	26.14	24.18-28.57
LD	7.53	8.17	na	7.40	6.86-8.25
LM	4.62	4.6	4.6	4.34	4.13-4.51
BM1	1.26	1.32	na	1.26	1.22-1.29
LIF	5.95	6.29	7.1	5.84	5.18-6.46
BIF	2.05	2.02	na	1.95	1.73-2.14
BPB	3.34	3.11	na	2.98	2.62-3.35
BZP	2.21	2.24	na	2.23	1.78-2.56
LIB	4.55	4.44	4.2	4.23	3.94-4.38
ZB	15.41	15.9	17.4	14.98	13.99-15.67
DI	1.53	1.47	na	1.56	1.28-1.78
BIT	1.79	1.79	na	1.68	1.28-2.82
Weight	35	38	na	36.14	23-52

(Fig. 6). By contrast, the rostrum of *T. notatus* is proportionally wider and shorter, and possesses a narrower interorbital region with slightly raised edges forming low supraorbital ridges. The upper incisors of *T. andersoni* are narrow, weakly pigmented, and orthodont, while those of *T. notatus* are comparatively wider and opisthodont (Fig. 7).

The premaxilla in *T. andersoni* is long, extending posterior to the nasals, whereas in *T. notatus* the premaxillae is only moderately long and terminates at the same level as nasals. Although difficult to quantify, the tympanic bullae in *Thomasomys andersoni* is slightly larger and less flask-shaped than that of *Thomasomys notatus*. These species also differ in the shape of the orbicular apophysis of the malleus; in *T. andersoni* this presents a bony structure with the proximal portions wider than the distal portion, whereas in *T. notatus* the body is proximally constricted rendering it bulb-shaped (Fig. 9)

Thomasomys andersoni and *T. notatus* have similar upper molars, both species

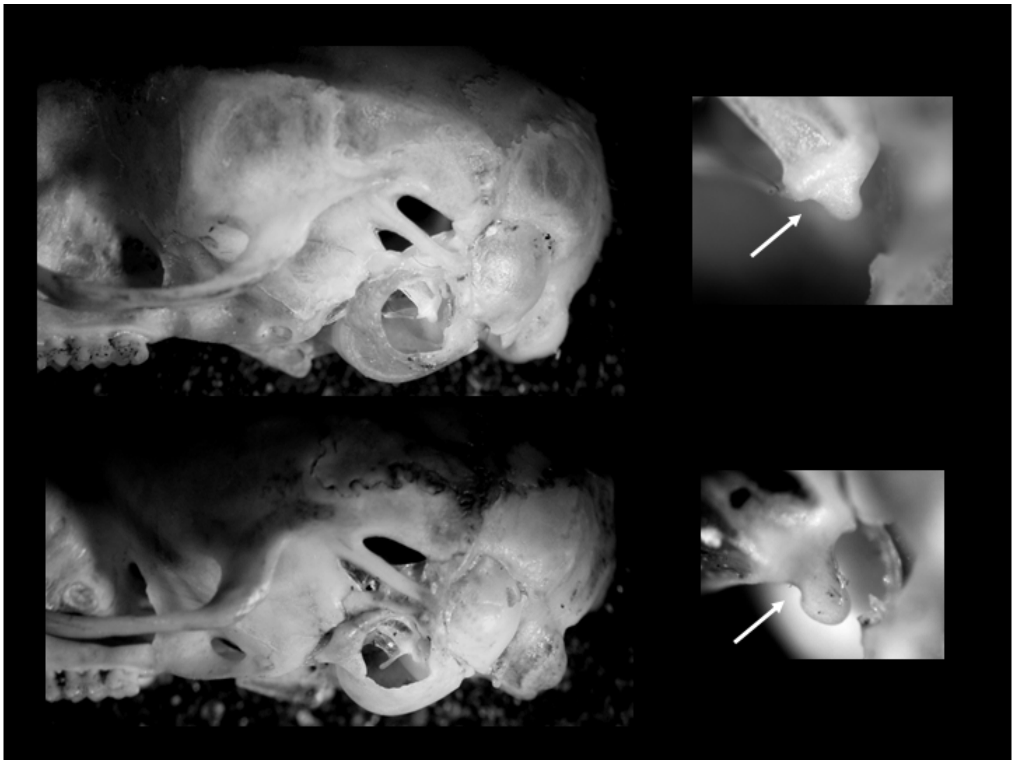

Figure 9. Crania of *Thomasomys andersoni* (holotype; above) and *Thomasomys notatus* (USNM 194547; below). Notice the ventral development of the tympanic bullae (slightly larger in *T. andersoni* than in *T. notatus*) and the structure of the orbicular apophysis of the malleus in the same 2 specimens (right panes). This structure is not basally constricted in *T. andersoni* (top right, arrow), while it is knob shaped in *T. notatus* due to a basal constriction (bottom right, arrow).

presenting distinct M1–M2 paralophules; however, the labial cingulum at the end of the anteroloph and mesoloph is more conspicuous in *Thomasomys notatus*. M2 presents a distinct protoflexus in *Thomasomys notatus* that is not present in andersoni and M3 in *Thomasomys andersoni* is somewhat larger and more rounded in general shape, whereas it is more triangular-shaped in *T. notatus*. These comparisons apply to only 1 individual *T. andersoni* (the holotype) because the paratype is so old that the occlusal surfaces are heavily worn. Moreover, these comparisons may be further enhanced when new material of the species herein described is obtained.

Natural History: The 2 specimens of *Thomasomys andersoni* were collected the same day at the type locality; attempts to secure more individuals of this species were unfruitful, although the site was populated with traps for several consecutive nights, and again 3 weeks later. The climate of the region is very humid, with daily fog and mist and low temperatures; biogeographically, the type locality is in the Province of the Bolivian-Peruvian Yungas, one of 5 in the Andean Biogeographic Region of Navarro and Maldonado (2002). According to these authors, the type locality of *Thomasomys andersoni* has a flora dominated by the species *Ocotea jelskii* (Lauracea), and *Podocarpus oleifolius* (Podocarpaceae). Data on the structure, ecology, and floristic composition of a forest near the type locality can be found in Zarate et al. (1999).

The 2 specimens of the new species were trapped at the base of the crown (at ca. 2 m above ground) in a short tree at the bottom of a small ravine. This tree (max height <6 m) had a short trunk and a wide crown. The base of the crown was fairly wide (ca. 20 cm), and covered with litter (depth of ca. 5 cm). We also collected 7 other species of rodents at the general site, including *Thomasomys australis*, *Thomasomys oreas*, *Rhipidomys austrinus*, *Akodon fumeus*, *Akodon mimus*, *Oryzomys levipes*, and an undescribed species of *Oligoryzomys* ("spB" of the *flavescens* group of Carleton and Musser 1989); however, only the 2 known specimens of *T. andersoni* were trapped on the tree, all the other species came from traps set on the ground. Because of this, we suggest that *Thomasomys andersoni* is at least partially arboreal, a fact also supported by the structure of the hind feet, which are short and broad.

DISCUSSION

A better understanding of the genus *Thomasomys* and its phylogenetic relationships is beginning to emerge, although there is still much room for improvement. Whereas the morphological data compiled by Pacheco (2003) -- a portion of which was used herein in the context of *T. andersoni* -- indicates that *Thomasomys* may be polyphyletic, molecular data appear to contradict the validity of more than 1 genus for this assemblage of species. However, sequence data is available for only a few taxa, and thus a compelling case to support either contention cannot be made. The apparent contradiction between a well-supported hypothesis on morphological grounds and the lack of support of such hypothesis based on the analysis of gene sequences has been already reported in the literature for South American sigmodonts (e.g., Smith and Patton, 1999; D'Elia, 2003). The sister taxa relationship found between *Thomasomys* and *Chilomys* is proposed on the basis of phylogenetic analysis of mitochondrial gene sequences alone. *Chilomys* has yet to be included in any phylogenetic analysis of nuclear sequences conducted in the context of the phylogeny of the Sigmodontinae (e.g., D'Elia, 2003; Weksler, 2003) and thus, until further studies are conducted, this hypothesis cannot be tested independently.

With respect to *Thomasomys*, the tree in Fig. 2 lacks strong support for most clades based on the phylogenetic analysis of cytochrome *b* gene sequences. We suggest this is due to poor taxonomic coverage, as our analyses included only 15 species (named and unnamed) of *Thomasomys*, while Pacheco (2003) recognized over 50. A lack of support in phylogenetic analyses may be the result of long branches, themselves artifacts of extinction or sparse taxon sampling (Horovitz 1999). An elegant example of increased congruence in phylogenetic analysis by the inclusion of "missing links" is presented in Voss et al. (2004b). We predict therefore, that increased taxonomic and geographic sampling will augment resolution in the phylogenetic hypothesis of *Thomasomys*, although it is unclear whether the lack of congruence between Pacheco's (2003) morphology-based hypothesis and 1 based on molecular data will be reconciled.

Our results strongly support the sister taxa relationship between *Thomasomys baeops* and *T. taczanowskii*, based on the phylogenetic analyses of molecular characters.

To our knowledge this relationship has been reported only by Pacheco (2003), who suggested the erection of a new genus (his "New Genus B") to include these 2 species. Based on the analyses of molecular data, *T. cinnameus* from the Paramos of El Cajas National Park in Ecuador is only distantly related to *T. gracilis*, a taxon with which it was historically synonymized (see for example, Musser and Carleton, 1993). In this respect, we concur with Voss (2003) that these species (*T. cinnameus* and *T. gracilis*) are separate taxonomic entities deserving specific status.

Data compiled in Table 1 indicate that species of *Thomasomys* included in these analyses range in sequence divergence from 6.17% to 16.87%, with an average of 12.7%. As expected, the same hierarchical pattern of phenetic divergence has been found, with the same gene, for other taxa of South American sigmodonts (e.g., Smith and Patton 1993; D'Elia 2003).

The karyotype of *Thomasomys andersoni* (2n = 44, FN = 42) is similar both in number and in structure (mostly acrocentric elements) to the karyotypes of several species of *Thomasomys* from Colombia, Peru, and Ecuador (Table 3), but it is most phenetically similar to that of *Thomasomys aureus* in that both species have fully acrocentric complements. Interestingly, only 1 species of *Thomasomys* (*Th. niveipes*) differs from the generalized pattern of 2n = 40-44 which appears to be the norm for the genus; in this species the karyotype (2n=24, FN=42) is composed of mostly biarmed elements which resemble the condition in *Aepeomys lugens*. To what extent these phenetic similarities reflect evolutionary history must wait for the availability of molecular data for the latter, as cladistic analysis of morphological data were inconclusive (Fig. 1, and Pacheco, 2003).

With *Thomasomys andersoni* the number of native mammals known to occur in Bolivia is 358, suggesting a rate of increase since 1980 of about 7.4 species per year (Salazar-Bravo et al., 2003). This rate is close to the average of 8 species per year calculated for the Neotropics by Patterson (2000). Elsewhere, we predicted that new species and records for Bolivia will come from areas poorly represented in faunistic

Table 3: Known diploid (2N) and fundamental (FNa) numbers of species of *Thomasomys*.

Species name*	2N	FN	Reference
T. niveipes	24	42	Gómez-Laverde et al. 1997
T. laniger	40, 42	40	Aguilera et al. 2000, Gómez-Laverde et al. 1997
T. monochromos	42	42	Gardner and Patton 1976
T. aureus	42	42	Gardner and Patton 1976
T. sp.	44	42	Gardner and Patton 1976
T. vestitus	44	42	Aguilera et al. 2000
T. andersoni	44	42	this contribution
T. kalinowskii	44	44	Gardner and Patton 1976
T. notatus	44	44	Gardner and Patton 1976
T. taczanowskii	44	44	Gardner and Patton 1976

*Identification of species valid at the time of publication.

inventories (Salazar-Bravo et al., 2003); notably, this new species comes from a geographic area that is readily accessible along a major road, and only 60 km from a major city (Cochabamba). It does come from a vegetation belt, however, which is usually bypassed or undersampled by faunistic inventories. As mentioned, this is quite likely the result of logistics, unstable terrain, and difficult field conditions; it clearly shows how much yet remains to be learned about the mammalian diversity and endemism in the eastern slopes of the Andes of Bolivia.

ACKNOWLEDGMENTS

This contribution is respectfully presented to honor O. P. Pearson. As serendipity would have it the type locality of *Thomasomys andersoni* is within 15 miles of places that Pearson visited in 1955 (e.g., 15 mi ENE Tiraque) while working on his revision of *Phyllotis* (Pearson 1958). We thank the following curators for allowing the use of specimens in their care: B. D. Patterson (FMNH); J. L. Patton and Chris Conroy (MVZ); M. D. Carleton and H. Kafka (USNM); Joe Cook, Bill Gannon, and Cindy Ramotnik (MSB); Eric Yensen (Orma Smith Museum of Natural History); Julieta Vargas M. (CBF). Several of the specimens reported herein were collected as part of a collaborative research grant to TLY and Sydney Anderson (BSR 9015454, and BSR 89200617). Special thanks are due to Dr. Victor Pacheco, for confirming our suspicion on the specific status of the species described herein, and for revising a group who many considered too complicated to work on. Our colleagues Jon Dunnum, Marcela Gómez-Laverde, Lucia Luna, Sergio Solari, and an anonymous reviewer read earlier versions of the manuscript providing several valuable comments.

APPENDIX 1: SPECIMENS EXAMINED

Acronyms for institutions are as follows: American Museum of Natural History (AMNH); Field Museum of Natural History (FMNH); Museum of Vertebrate Zoology (MVZ); United States National Museum (USNM), Colección Boliviana de Fauna (CBF), Division of Genomic Resources (DGR), Museum of Southwestern Biology (MSB). All NK numbers denote specimens stored in the Division of Genomic Resources of the MSB. Asterisks (*) indicate specimens measured and Pilcrow signs (¶) denotes specimens used in molecular analyses. For samples with fewer than the 1134 bp (see material and methods section), the number of unambiguous bases scored is given in brackets. Accession numbers for sequences obtained from GenBank in brackets.

Thomasomys aureus (1). Peru: Cuzco, 72 km NE (by road) Paucartambo, km 152 (MVZ 170076¶ [U03540])

Thomasomys andersoni (2). Bolivia: Cochabamba, Corani Hydroelectrical Plant (AMNH 268734 *¶, MSB 146437*¶)

Thomasomys australis (2). Bolivia: Cochabamba, Corani Hydroelectrical Plant (MSB 70447¶ [769bp], AMNH 268736¶ [1107bp])

Thomasomys baeops (2). Ecuador: Bolivar, Rio Tatahuazo (MSB 70704¶ [772bp], MSB 70705)

Thomasomys caudivarius (2). Ecuador: Bolivar, Rio Tatahuazo, 4 km E Cruz de Lizo (MSB 70712, MSB 70714¶ [749bp])

Thomasomys cinnameus (2). Ecuador: Azuay, Cajas (NK30922, NK30932¶ [783bp])

Thomasomys daphne (2). Bolivia: La Paz, Sayani (AMNH 268737¶[771bp]); Peru: Puno, 9 km N Limbani (MVZ 171502¶ [AF108673])

Thomasomys gracilis (6). Peru: Cuzco, Machu Picchu (USNM 194798, USNM 194800, USNM 194802), Ocobamba Valley (USNM 194807, USNM 194808), 90 km SE (by road) Quillabamba (MVZ 166668 [AF108674])

Thomasomys kalinowskii (1). Peru: Junin, 16 km NNE (by rd) Palca (MVZ 172598¶ [AF108678]; this species was identified as *Thomasomys* sp. by Smith and Patton 1999, but it was re-identified as *T. kalinowskii* by V. Pacheco [pers. com, June 2003])

Thomasomys ladewi (5). Bolivia: La Paz, Rio Aceromarca (AMNH 264779, AMNH 264980, MSB 68483 ¶ [734bp], MSB 68484¶ [761bp], MSB 68485)

Thomasomys notatus (11). Peru: Cuzco, Amambaya (MVZ 173968*, MVZ173969*, MVZ 173970*, MVZ 173971*), Paucartambo (MVZ 166706*¶ [AF108676] , MVZ 171503*, FMNH 172380*, FMNH 170696*), Torontoy (USNM 194897*, USNM 194547), Machu Picchu (USNM 194898*)

Thomasomys oreas (2). Bolivia: La Paz, Pelechuco (CBF 4041*), unknown locality (CBF 4954*); Bolivia: Cochabamaba, Corani Hydroelectrical Plant (MSB 87126¶ [403bp])

Thomasomys taczanowskii (5). Peru: Cajamarca, 35 km WNW Cajamarca (MVZ 137928, MVZ 137930, MVZ 137931), Rio Zaña (MVZ 182003; MVZ 181999¶ [AF108675]; the latter was identified as *Thomasomys ischyurus* by Smith and Patton, 1999, but it was re-identified as *T. taczanowskii* by V. Pacheco T. [pers. com., June 2003])

Thomasomys sp2 (1). Bolivia: Cochabamba, 28 km by road of Comarapa (AMNH 260422¶ [771bp])

Thomasomys sp9 (1). Peru: Cuzco, 32 km N Paucartambo (MVZ 166703¶; this species was identified as *Thomasomys oreas* by Smith and Patton, 1999, but it was re-identified as *Thomasomys* sp9 by V. Pacheco T. [pers. com., June 2003])

LITERATURE CITED

Aguilera, M. M., A. Pérez-Zapata, J. Ochoa, and P. Soriano
2000 Karyology of *Aepeomys* and *Thomasomys* (Rodentia: Muridae) from the Venezuelan Andes. Journal of Mammalogy 81:52-58.

Anderson, S.
1997 Mammals of Bolivia: taxonomy and distribution. Bulletin of the American Museum of Natural History 231:1-652.

Anderson, S., and T. L. Yates
2000 A new genus and species of phyllotine rodent from Bolivia. Journal of Mammalogy 81:37-51.

Anderson, S., T. L. Yates, and J. A. Cook
1987 Notes on Bolivian mammals 4: the genus *Ctenomys* (Rodentia, Ctenomyidae) in the eastern lowlands. American Museum Novitates 2891:1-20.

Carleton, M. D., and G. G. Musser
1989 Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): a synopsis of *Microryzomys*. Bulletin of the American Museum of Natural History 191:1-83.

Cook, J. A., and J. Salazar-Bravo
2005 Heterochromatin variation among the chromosomally diverse tuco tucos (Rodentia: Ctenomyidae) from Bolivia. Pp. 131-144 in Contribuciones Mastozoológicas en Homenaje a Bernardo Villa (Sánchez-Cordero, V., and R. A. Medellin, eds.). Instituto de Biologia & Instituto de Ecologia, UNAM and CONABIO, Mexico D.F.

D'Elia, G.
2003 Phylogenetics of sigmodontinae (Rodentia, Muroidea, Cricetidae), with special reference to the akodont group, and with additional comments on historical biogeography. Cladistics 19:307-323.

D'Elia, G., E. Gonzalez, and U. F. Pardiñas
2003 Phylogenetic analysis of sigmodontine rodents (Muroidea), with special reference to the akodont genus *Deltamys*. Mammalian Biology 68:351-364.

DNASTAR, Ltd.
2003 Lasergene: expert sequence analysis software. Version 5, Madison, Wisconsin, USA.

Dunnum, J. L., J. Salazar-Bravo, and T. L. Yates
2001 The Bolivian bamboo rat, *Dactylomys boliviensis* (Rodentia: Echimyidae), a new record for chromosome number in a mammal. Mammalian Biology 66:121-126.

Gardner, A. L., and J. L. Patton
1976 Karyotypic variation in oryzomyine rodents (Cricetinae) with comments on chromosome evolution in the neotropical cricetine complex. Occasional Papers, Museum of Zoology, Louisiana State University 49:1-48.

Gardner, S. L.
1991 Phyletic coevolution between subterranean rodents of the genus *Ctenomys* (Rodentia: Hystricognathi) and nematodes of the genus *Paraspidodera* (Heterakoidea: Aspidoderidae) in the Neotropics: Temporal and evolutionary implications. Zoological Journal of the Linnean Society 102:169-201.

Gómez-Laverde, M., O. Montenegro-Díaz, H. López-Arévalo, A. Cadena, and M. L. Bueno
1997 Karyology, morphology, and ecology of *Thomasomys laniger* and *T. niveipes* (Rodentia) in Colombia. Journal of Mammalogy 78:1282-1289.

Hershkovitz, P.
1962 Evolution of Neotropical cricetine rodents (Muridae) with special reference to the Phyllotine group. Fieldiana: Zoology 46:524.

1987 A history of the Recent mammalogy of the Neotropical region from 1492 to 1850. Fieldiana: Zoology, new series 39:11-98.

Horovitz, I.
1999 A phylogenetic study of living and fossil platyrrhines. American Museum Novitates 3269:1-40.

Luna, L., and V. Pacheco
2002 A new species of *Thomasomys* (Muridae: Sigmodontinae) from the Andes of southeastern Peru. Journal of Mammalogy 83:834-842.

Maddison, D. R., and W. P. Maddison
2002 MacClade 4. Analysis of phylogeny and character evolution, version 4.05. Sinauer Associates, Sunderland, Massachusetts, USA.

Musser, G. G., and M. D. Carleton
1993 Family Muridae. Pp. 501-756 in Mammal Species of the World (Wilson, D. E., and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C., USA.

Musser, G. G., M. D. Carleton, E. M. Brothers, and A. L. Gardner
1998 Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): diagnoses and distributions of species formerly assigned to *Oryzomys* "*capito*." Bulletin of the American Museum of Natural History 236:1-376.

Navarro, G., and M. Maldonado

2002 Geografia Ecológica de Bolivia: Vegetación y Ambientes Acuáticos. Editorial del Centro de Ecología Simon I. Patiño, Cochabamba, Bolivia

Olds, N., S. Anderson, and T. L. Yates

1987 Notes on Bolivian mammals 3: a revised diagnosis of *Andalgalomys* (Rodentia: Muridae) and the description of a new subspecies. American Museum Novitates 2890:1-17.

Pacheco, V. R.

2003 Phylogenetic Analyses of the Thomasomyini (Muroidea: Sigmodontinae) based on Morphological Data. Ph.D. Thesis, City University of New York, New York, USA. 397 pp.

Pacheco, V., S. Solari, and P. M. Velazco

2004 A new species of *Carollia* (Chiroptera: Phyllostomidae) from Peru and Bolivia. Occasional Papers, The Museum, Texas Tech University 236:1-15.

Patterson, B. D.

2000 Patterns and trends in the discovery of new Neotropical mammals. Diversity and Distributions 6:145-151.

Patton, J. L.

1967 Chromosome studies of certain pocket mice, genus *Perognathus* (Rodentia: Heteromyidae). Journal of Mammalogy 48:27-37.

Pearson, O. P.

1958 A taxonomic revision of the rodent genus *Phyllotis*. University of California Publications in Zoology 56:391-496.

Reig, O. A.

1980 A new fossil genus of South American cricetid rodents allied to *Wiedomys* with an assessment of the Sigmodontinae. Journal of Zoology 192:257-281.

Ridgway, R.

1912 Color standards and color nomenclature. Published by the author, Washington, D.C., USA.

Salazar-Bravo, J., J. W. Dragoo, M. D. Bowen, C. J. Peters, *T.* G. Ksiazek, and T. L. Yates

2002a Natural nidality in Bolivian hemorrhagic fever and the systematics of the reservoir species. Infection, Genetics and Evolution 1:191-199.

Salazar-Bravo, J., J. W. Dragoo, D. S. Tinnin, and T. L. Yates
2001 Phylogeny and evolution of the neotropical rodent genus *Calomys*: inferences from mitochondrial DNA sequence data. Molecular Phylogenetics and Evolution 20:173-184.

Salazar-Bravo, J., T. Tarifa, L. F. Aguirre, E. Yensen, and T. L. Yates
2003 Revised checklist of Bolivian mammals. Occasional Papers, The Museum, Texas Tech University 220:1-27.

Salazar-Bravo, J., T. L. Yates, and M. Zalles
2002b Mamíferos de Bolivia. Pp. 65-113 in Diversidad y Conservación de los Mamíferos de Neotropicales (Ceballos, G., and J. Simmonetti, eds.). CONABIO-UNAM, DF, México.

Smith, M. F., and J. L. Patton
1999 Phylogenetic relationships and the radiation of sigmodontine rodents in South America: Evidence from cytochrome *b*. Journal of Mammalian Evolution 6:89-128.

Steppan, S. J.
1995 Revision of the tribe Phyllotini (Rodentia: Sigmodontinae), with a phylogenetic hypothesis for the Sigmodontinae. Fieldiana: Zoology, new series 80: 1-112.

Steppan, S. J., R. M. Adkins, and J. Anderson
2004 Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. Systematic Biology 53:533-553.

Swofford, D. L.
2002 PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), version 4, Sinauer Associates, Sunderland, Massachusetts, USA.

Villalpando, G., J. Vargas, and J. Salazar-Bravo
In press First record of *Rhagomys* (Mammalia: Sigmodontinae) in Bolivia. Mastozoología Neotropical.

Voss, R. S.
1988 Systematics and ecology of ichthyomyine rodents (Muroidea): Patterns of morphological evolution in a small adaptive radiation. Bulletin of the American Museum of Natural History 188:259-493.

1993 A revision of the Brazilian muroid rodent genus *Delomys* with remarks on "thomasomyine" characters. American Museum Novitates 3073:1-44.

2003 A new species of *Thomasomys* (Rodentia: Muridae) from eastern Ecuador, with remarks on mammalian diversity and biogeography in the Cordillera Oriental. American Museum Novitates 3421:1-47.

Voss, R. S., A. L. Gardner, and S. A. Jansa
2004b On the relationships of "*Marmosa*" *formosa* Shamel, 1930 (Marsupialia: Didelphidae), a phylogenetic puzzle from the Chaco of northern Argentina. American Museum Novitates 3442:1-18.

Voss, R.S., T. Tarifa, and E. Yensen
2004a An introduction to *Marmosops* (Marsupialia: Didelphidae), with the description of a new species from Bolivia and notes on the taxonomy and distribution of other Bolivian forms. American Museum Novitates 3466:1- 40

Weksler, M.
2003 Phylogeny of Neotropical oryzomyine rodents (Muridae : Sigmodontinae) based on the nuclear IRBP exon. Molecular Phylogenetics and Evolution 29:331-349.

Zarate, M., D. Goitia, and G. Lazarte
1999 Estudio estructural y ecologico de los bosques relictos de tres especies de pinos de monte (*Podocarpus* spp., Podocarpaceae) en Cochabamba, Bolivia. Revista Boliviana de Ecología y Conservación Ambiental. 5:51-59.

A NEW SPECIES OF *PHYLLOTIS* (RODENTIA, CRICETIDAE, SIGMODONTINAE) FROM THE UPPER MONTANE FOREST OF THE YUNGAS OF NORTHWESTERN ARGENTINA

UNA NUEVA ESPECIE DE *PHYLLOTIS* (RODENTIA, CRICETIDAE, SIGMODONTINAE) DEL BOSQUE MONTANO SUPERIOR DE LAS YUNGAS DEL NOROESTE ARGENTINO

J. Pablo Jayat , Guillermo D'Elía[1], Ulyses F. J. Pardiñas, and Juan G. Namen

> *"When I returned from my first trip to the Andes in 1940, I found it impossible to identify many specimens of* Phyllotis *in accordance with the existing taxonomy… A revision of the genus therefore seemed desirable"*
> *Oliver P. Pearson (1958:394)*

ABSTRACT

We describe a new sigmodontine species of the genus *Phyllotis*. It was collected near Hualinchay, Tucumán, Argentina. The new species, which is a sister taxon to *P. osilae*, can be distinguished from other members of the genus by the following combination of traits: large size (slightly smaller than *P. osilae* and *P. xanthopygus*); dorsal color dark gray; light ochraceous belly; ears covered internally and externally by obscure brown hairs; manus with digits and distal dorsum covered with white hair, proximal dorsum of the manus and pes darker; tail slightly bicolored and slightly haired, not penicillate; incisors with white to yellowish-white enamel; noticeably hypsodont molars; and several molecular synapomorphies. The new species is an endemic from the alder forests of the upper Yungas. The low number of specimens captured, despite intensive trapping efforts, suggests that it is rare and restricted to this type of forest. Considering the rapid anthropogenic habitat loss in the Yungas, we argue that further intensive biodiversity studies and conservation plans are critical for this region

Keywords: Argentina, leaf-eared mouse, Muroidea, new species, Phyllotini, Sigmodontinae, taxonomy, Tucumán, Yungas

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RESUMEN

Se describe una nueva especie de sigmodontino del género *Phyllotis*. Esta fue colectada en las cercanías de Hualinchay, provincia de Tucumán, Argentina. La nueva especie, hermana de *P. osilae*, puede distinguirse del resto de los miembros del género por la siguiente combinación de caracteres: tamaño grande (apenas menor que el de *P. osilae* o *P. xanthopygus*); pelaje dorsal de coloración gris oscura; vientre de color ocre claro; orejas cubiertas externa e internamente por pelos de color marrón oscuro; dígitos y porción distal de las manos con pelos blancos; porción dorso proximal de las manos y pies oscura; cola apenas bicoloreada y escasamente peluda, sin pincel terminal; esmalte de los incisivos color blanco a blanco-amarillento; molares con notable hipsodoncia; numerosas sinapomorfías moleculares. La nueva especie es una forma endémica de los bosques de alisos del piso superior de las Yungas. El bajo número de ejemplares capturados, pese a los elevados esfuerzos de muestreo, sugiere que la nueva especie es poco común y restringida a este tipo de hábitat. Considerando el fuerte impacto antrópico que las Yungas argentinas están sufriendo, enfatizamos que la intensificaión de los estudios de biodiversidad y la aplicación de planes de conservación son críticos para esta ecoregión.

Palabras claves: Argentina, especie nueva, Muroidea, pericote, Phyllotini, Sigmodontinae, taxonomía, Tucumán, Yungas

INTRODUCTION

Northwestern Argentina is geographically and environmentally heterogeneous, and as such it is inhabited by around 40 species of sigmodontine rodents. In recent years intense work has resulted in a better knowledge of the regional sigmodontine community, including the description of new living (Mares and Braun, 1996; Díaz et al., 1999; Diaz and Barquez, this volume) and fossil taxa (Ortiz et al., 2000b) and contributions on the distribution, systematics, paleontology, and ecology of the different species (Mares et al., 1981; Ojeda and Mares, 1989; Bustos, 1995; Capllonch et al., 1997; Mares et al., 1997; Díaz, 1999; Díaz and Barquez, 1999, this volume; Ortíz et al., 2000a; Teta and Ortíz, 2002).

Phyllotis is one of the most diverse genera of the subfamily. This genus ranges along the Andes and nearby desert and semi-desert environments from the southern continental tip (Argentina and Chile) to Ecuador (Steppan, 1998; Kramer et al., 1999). The alpha taxonomy and phylogenetics of *Phyllotis* have been addressed with morphological (e.g., Pearson, 1958; Hershkovitz, 1962; Braun, 1993; Steppan, 1993, 1995, 1998), karyotypic (e.g., Pearson, 1972; Pearson and Patton, 1976; Spotorno, 1976; Walker et al., 1984), and molecular (Steppan, 1998; Steppan et al. this volume) evidence. Musser and Carleton (2005) recognize 13 species in the genus; these are *P. amicus, P. andium, P. bonaeriensis, P. caprinus, P. darwini, P. definitus, P. haggardi, P. limatus, P. magister, P. osgoodi, P. osilae, P. wolffsohni*, and *P. xanthopygus*. At the same time, Musser and Carleton (2005) place *P. gerbillus* in *Paralomys* (following, in part, the results of Braun, 1993); meanwhile Steppan and Ramirez (pers. comm.) retain this species in *Phyllotis* and transfer *wolffsohni* to the recently described *Tapecomys* (see also Steppan et al., this volume).

To date, 4 *Phyllotis* species have been reported for northwestern Argentina (Pearson, 1958; Hershkovitz, 1962; Díaz and Barquez, this volume). *P. xanthopygus* is represented by 3 subspecies: *P. x. rupestris*, in the east side of the Andes of the Province of Jujuy; *P. x. ricardulus* along the central and eastern Andes, from the northern provinces of Salta and Jujuy to Catamarca Province; and *P. x. vaccarum* in the latter province. Similarly, *P. osilae* presents 3 subspecies in the region: *P. o. osilae* and *P. o. nogalaris* in Jujuy Province, and *P. o. tucumanus* in the eastern side of the Andes in Catamarca and Tucumán provinces. *P. caprinus* inhabits the Province of Jujuy and has no described subspecies. Finally, *P. wolffsohni* was recently cited for the Province of Jujuy by Díaz and Barquez (this volume).

In the present paper we describe a new species of *Phyllotis* from the montane cloud forest of northwestern Argentina, based on both morphological and molecular evidence.

MATERIALS AND METHODS

The specimens of the new species were trapped with Museum Special and Sherman traps baited with oats. Voucher specimens (skin and skull plus complete skeleton) are deposited in the Colección Mamíferos Lillo (CML), Universidad Nacional de Tucumán, Tucumán, Argentina, and at the Colección de Mamíferos del Centro Nacional Patagónico (CNP), Puerto Madryn, Chubut, Argentina. Tissue samples (heart, liver, and kidney preserved in 70% ethanol) are deposited at the Colección de Tejidos del Laboratorio de Evolución, Facultad de Ciencias, Universidad de la República, Uruguay. Comparisons were made against the descriptions of each of the species and subspecies of *Phyllotis* presented by Pearson (1958). In addition, based in geographic distribution, and results of the phylogenetic analysis (see below), we studied series' of *Phyllotis caprinus*, *P. osilae osilae*, *P. o. nogalaris*, *P. o. tucumanus*, *P. xanthopygus rupestris, P. x. ricardulus*, and *P. x. vaccarum*. All specimens studied in this paper are listed in Appendix 1.

Morphologic Data Analyses.---Standard external measurements (HB: length of head and body; T: tail length; HF: length of hind foot with claw; E: ear length) and weight (W) were recorded in the field following Pearson (1958). Dental and cranial descriptions follow Reig (1977) and Steppan (1995), and Wahlert (1985), Voss (1988), and Abdala and Díaz (2000), respectively. In order to facilitate comparisons with other species of the genus we measured craniodental measurements following Myers et al. (1990). These included (measured with digital calipers to the nearest 0.01 mm): GLS (greatest length of skull), CIL (condyloincisive length), ZB (zygomatic breath), WBC (braincase breadth), IB (interorbital breadth), UTR (upper tooth row length), NL (nasal length), RW2 (mid-rostral width), DL (upper diastema length), IFL (incisive foramen length), OCW (occipital condyle width), BOL (basioccipital length), MFW (mesopterygoid fossa width), and ZP (zygomatic plate depth). In addition, we also recorded the greatest length of the mandible (excluding the incisor, ML), the alveolar length of the lower tooth row (LTR). Finally, we measured the depth (distance between greater and lesser curvatures) and width (measured across the enameled tip) of one upper incisor of the holotype (CML 6379).

Molecular Data Analyses.--- We sequenced 2 specimens (the holotype CML 6379 and the paratype CNP 736) of the new species for the first 801 base pairs of the gene that codes for cytochrome *b* (cyt *b*) following the protocol in D'Elía et al. (2003). Sequences were visualized, reconciled, and translated to proteins to proof for stop codons using Sequence Navigator (Applied Biosystems, 1994).

Cyt *b* sequences were analyzed by Steppan et al. (this volume) as part of their broad phylogenetic analysis of *Phyllotis*, where the new species appears as *Phyllotis* n. sp. 2. Details of phylogenetic analyses are provided therein.

Molecular synapomorphies were documented by examining outputs from PAUP* 4.0b10 (Swofford, 2000) and visualized using MacClade 3.05 (Maddison and Maddison 1992). Molecular transformations were optimized on the trees resulting from the maximum parsimony analysis of the cyt *b* matrix of Steppan et al. (this volume). Only those changes unambiguously optimized irrespective of the kind of character transformation used (i.e., accelerated, ACCTRAN, or delayed, DELTRAN) were taken into account.

RESULTS

Results of the phylogenetic analysis (see Steppan et al., this volume) indicate that the new species (there labeled as *Phyllotis* n. sp. 2) is a sister taxon to *P. osilae*. Therefore, we focused our morphological comparisons with *P. osilae*. We also compared the new species with other *Phyllotis* inhabiting the northwestern Argentina.

Phyllotis anitae, new species

Holotype.---CML 6379, adult female, collected by J. P. Jayat on 30 April 2003 (original field number JPJ 977), skin, skull, full skeleton, tissues in alcohol.

Type Locality.---ARGENTINA: Province of Tucumán, Department of Trancas, 10 km by road south of Hualinchay on the trail to Lara (26° 19′ 20.2″ S, 65° 36′ 45.5″ W, 2316 m) (Fig. 1).

Diagnosis.---A member of the genus *Phyllotis* (Sigmodontinae) distinguishable from all other species of the genus by the following combination of characters: size large; dorsal color dark gray; belly light ochraceous; ears covered internally and externally by dark brown hairs; manus with digits and distal dorsum covered with white hair, proximal dorsum of the manus and pes dark; tail slightly bicolored and haired, not penicillate; skull robust with short rostrum; zygomatic notches and nasolacrimal capsules inconspicuous; interorbital region narrow, hourglass-shaped and without overhanging borders; posteropalatal pits to the level of anterior border of mesopterygoid fossa; incisors white to yellowish-white; molars noticeably hypsodont; third upper molar simple, not "S" or "Z" shaped; the molecular synapomorphies listed in Table 1 (note that no sequences of *P. caprinus, P. definitus, P. gerbillus*, and *P. haggardi* were analyzed).

Paratypes.---Paratypes include 5 live-trapped specimens prepared as skins, skulls plus full skeletons, and tissues in alcohol: CNP 736, young male, collected by J. G. Namen on May 1 2002 (original field number JPJ 761); CNP 737, young female, collected by J. G.

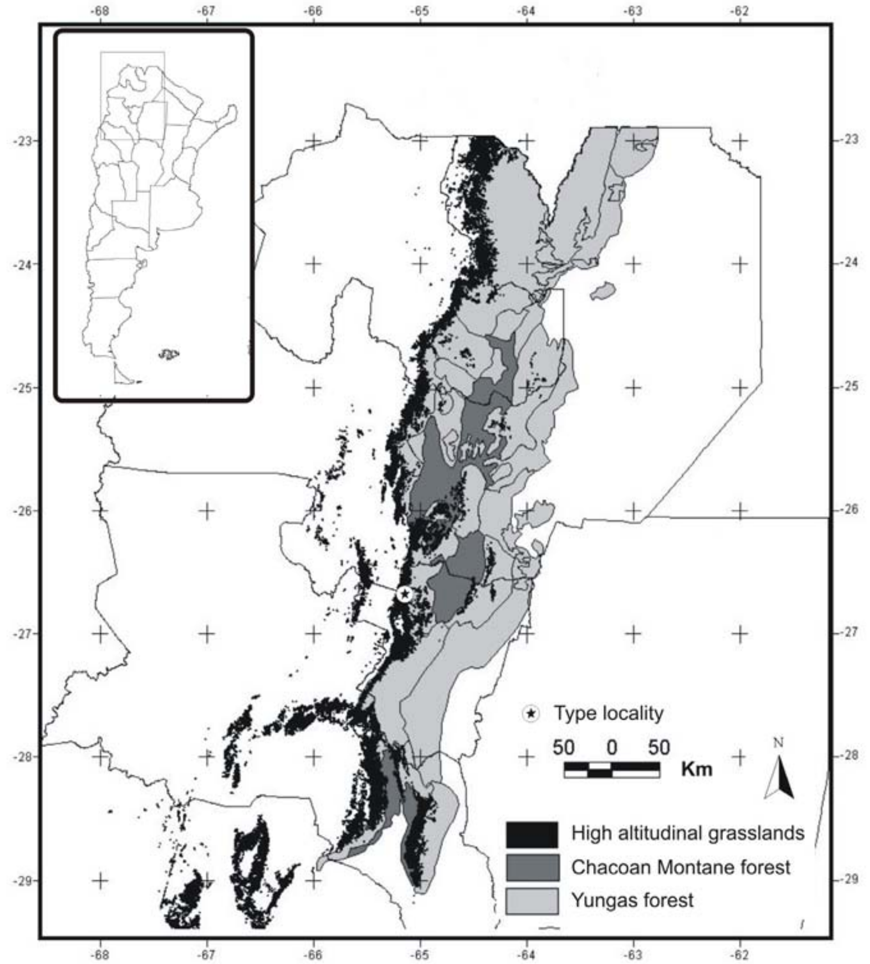

Figure 1.--- Map of northwestern Argentina and principal vegetation units occurring there; white areas to the east are the Chaco and those to the west are Prepuna, Puna, and High Andean biomes.

Namen on May 20 2001 (original field number JPJ 482); CNP 809, adult male, collected by J. P. Jayat on May 5 2004 (original field number JPJ 1124; CML 6380, young male, collected by J. P. Jayat on May 1 2003 (original field number JPJ 979); and CML 6381, young male, collected by J. P. Jayat on May 2 2003 (original field number JPJ 994).

Measurements of the Holotype.--- External measurements (in mm; see Table 3 for comparison with other species in *Phyllotis*): HB, 119; T, 124; HF, 29; E, 21; W, 37.5 g. Cranial measurements (in mm): GLS, 30.72; CIL, 27.80; ZB, 16.06; WBC, 14.10; IB, 4.02; UTR, 5.78; NL, 12.48; RW2, 5.00; DL, 7.80; IFL, 7.24; OCW, 7.04; BOL, 3.78; MFW, 1.68; breadth of zygomatic plate, 2.82; ML, 15.40; LTR, 5.70; upper incisor depth, 1.60; upper incisor width, 1.20. See Table 2 for paratypes measurements.

Etymology.---Dedicated to Anita Kelley Pearson and through her to Oliver P. Pearson,

Table 1.--- Molecular synapomorphies of *Phyllotis anitae* as revealed by maximum parsimony analysis of cyt b gene sequences (801 base pairs). Molecular transformations were optimized on a strict consensus tree of the 1764 most parsimonious trees (3310 steps; CI = 0.269) resulted from the analysis of the cyt b matrix of Steppan et al. (this volume). Twenty five fixed derived character states were found in *P. anitae*. Of these, 8 derived character states (indicated by asterisks) have not evolved independently in any species of *Phyllotis*. Some of these characters have a consistency index <1 because the character state present in 1 *P. anitae* also has evolved independently in at least 1 of the non-*Phyllotis* taxa included in the analysis. The remaining 17 derived character states of *P. anitae* have also secondarily appeared in at least 1 species of *Phyllotis*.

	Nucleotide position/ Codon position	Character State in *Phyllotis anitae*	Character Consistency Index
1	21/3	C	0.182
2	51/3*	T	1
3	96/3	T	0.333
4	123/3*	C	0.333
5	186/3*	G	1
6	189/3	T	0.167
7	222/3	C	0.067
8	240/3	T	0.222
9	255/3	T	0.100
10	282/3	G	0.125
11	294/3*	T	0.214
12	300/3	G	0.250
13	360/3*	T	0.167
14	427/1*	C	0.176
15	469/1	C	0.071
16	514/1	T	0.083
17	523/1	C	0.222
18	554/2	T	0.111
19	590/2*	T	1
20	593/2	T	0.111
21	625/1	G	0.600
22	655/1	T	0.111
23	691/1	G	0.333
24	769/1	C	0.200
25	791/2*	G	1

Table 2.-- Measurements of 5 paratypes (in mm) of *Phyllotis anitae* new species. Abbreviations as provided in text.

	CML 6381	CML 6380	CNP 736	CNP 737	CNP 809
HB	100	82	89	99	123
T	-	94	99	-	112
HF	30	27	30	30	31
E	21	18	19	20	21
W	28.5	20.5	21.0	25.0	50
GLS	28.66	26.56	27.38	28.20	31.26
CIL	25.54	23.30	24.42	25.46	28.26
ZB	14.64	14.08	14.02	14.36	16.26
WBC	13.80	13.26	13.50	13.42	13.96
IB	3.90	4.14	4.06	3.90	3.94
UTR	5.90	5.70	5.88	5.80	5.58
NL	10.76	9.44	9.92	10.72	12.58
RW2	4.62	4.36	4.26	4.62	5.26
DL	6.66	6.10	6.24	6.94	8.36
IFL	6.44	5.94	5.90	6.50	7.52
OCW	7.00	6.78	6.94	7.06	7.14
BOL	3.64	3.26	3.74	3.35	3.76
MFW	1.52	1.46	1.51	1.55	1.60
ZP	2.48	2.14	2.20	2.60	3.12
ML	14.48	13.90	14.30	14.84	16.26
LTR	6.22	5.68	6.00	5.82	6.00

who upon receiving his Doctorate Honoris Causa from the Universidad Nacional de La Plata, La Plata, Argentina (November 2000), expressed "yo solo soy un simple atrapador de ratones y nada hubiera sido posible sin Anita." It also is worth mentioning that in 1958 Oliver P. Pearson was the first author to review the genus *Phyllotis*.

Distribution.---Known only from the type locality.

Description.---The dorsal coloration is dark gray, spattered with ochraceous hairs. The holotype and the adult paratype (CNP 809) are slightly lighter than the remaining paratypes, which are all young individuals. Most of the dorsal hairs (hair length = 9 mm) are totally dark gray to black, with ochraceous tips. Some totally black hairs (length = 19 mm) also are present. Coloration of the sides and belly gradually blends to an ochraceous gray, without a sharp contrast between dorsal and ventral regions. The ventral hairs are basally gray and distally ochraceous. The throat and cheeks are lighter than the belly, including some hairs entirely white, but lacking a definite spot. The ears are moderate in size, internally and externally covered by dark brownish to almost black hairs.

Facial vibrissae are disposed in mystacial, submental, genal, and superciliary fields. The mystacials are abundant (although less so than in *P. xanthopygus*), some white and short, others black and long, extending beyond the posterior margins of the pinnae. The submental vibrissae are short and completely white. The genal and superciliary vibrissae are sparse (generally three and one, respectively), short, basally black and distally white.

Manus and pes are dark in general, covered by dense and short hairs. These hairs are drab with white tips. The dorsal coloration pattern of the manus is noticeable: the digits and distal dorsum show only white hair, contrasting with the darker coloration of the proximal carpus. The dorsal pes coloration is uniformly drab. The manus claws (length = 1.8 mm) are shorter than those of the pes (length = 3.7 mm), and in both fore and hind feet the ungual tufts surpass the end of the claws. These ungual tufts are white in the manus and are more abundant, larger, and more drab in the pes. In the manus, digits III and IV are the largest and are approximately subequal; digit II (with claw) surpasses the middle point of digits III and IV, and digit V is the shortest. Plantar pads include 3 small interdigitals and 2 metacarpals. Pes digits II, III, and IV are the largest; digit I is less than the 50% as long as digit II. There are 6 plantar pads, including 4 small interdigitals, 1 very small hypothenar, and 1 large thenar. The soles of both manus and pes are naked.

The tail is slightly bicolored and moderately hairless, with the ventral surface paler and more haired than the dorsal surface. The scales are readily visible to the naked eye.

Eight mammae are present in the holotype (the only known adult female), arrayed in 4 pairs: 1 pectoral, 1 postaxial, and 2 inguinal.

The skull of *P. anitae* is similar in general morphology to those of the *P. osilae* and *P. xanthopygus* (Figs. 2, 3). In lateral view, the dorsal profile is flat. The rostrum is moderately gracile and enlarged. The anterior one third of the nasal bones are expanded and surpass the anterior face of the upper incisors; posteriorly, the nasals terminate at the level of the lacrimal bones. The lacrimals are well developed. The zygomatic notches and the nasolacrimal capsules are inconspicuous in dorsal view. The premaxillo-maxillary suture is oriented nearly vertically with respect to the basal plane of the skull. The zygomatic plate is narrow and high, with a straight anterior border and a short, free upper border. The interorbital region is narrow, hourglass-shaped, and the frontal edges are smooth. The fronto-parietal suture is straight and the interparietal is large and wide. The braincase is rounded in dorsal view, without evident temporal and lambdoidal crests. In ventral view, the posterior ends of the incisive foramina surpass the anterior face of M1. The mesopterygoid fossa is wide and its hamular processes diverge posteriorly, similar to those of *P. osilae*, and it is wider than those of *P. xanthopygus*. The anterior border of the mesopterygoid fossa typically is U-shape, with a small median spinous process on the palatine. A pair of posterolateral palatal pits are present adjacent to the anterior margin of the mesopterygoid fossa. These pits are smaller than those of *P. xanthopygus*. The mesopterygoid roof is deeply excised. The parapterygoid fossae are well-developed and moderately excavated. The carotid circulation system includes stapedial and sphenofrontal foraminae, and a squamosal-alisphenoid groove. This is the common pattern for the genus (Steppan,

Figure 2. *Phyllotis anitae*, new species (holotype, CML 6379): skull in dorsal (upper, left) and ventral (upper, right) views, and skull and mandible in lateral view (bottom). Scale = 10 mm.

1995). The hamular process is delicate and distally attached to the mastoidal capsule, determining a large subsquamosal and a small postglenoid foramina. The tympanic tegmen contacts the squamosal. A strut of the alisphenoid is absent. The auditory bullae are moderately small with a short and tubular eustachian tube.

In the mandible (Fig. 2) the condyloid and coronoid processes are subequal in height. The former is moderately short, as is the angular process. The capsular projection is inconspicuous. The upper and lower masseteric crests are well developed, joining anteriorly at the level of the mental foramen. In the lingual side of the mandible, a well-developed mandibular foramen is present. The medioventral process of the mandibular ramus is weak.

The upper incisors are moderately narrow, opisthodont, and possess a long and straight dentine fissure. The anterior enamel is totally white in young individuals and yellowish-white in the holotype.

The upper tooth rows are parallel. Hypsodonty is noticeable (with respect to other species of *Phyllotis*) in both upper and lower molars, conferring a prismatic form particularly to the M1 (Figs. 2, 4). The primary cusps are slightly alternate. M1 has a well developed procingulum, which is anterior-posteriorly compressed, and with an

Figure 3.--- Dorsal (top), ventral (middle), and lateral (bottom) views of skulls in (from left to right) *Phyllotis anitae*, new species (holotype, CML 6379), *P. osilae* (JPJ 748), and *P. xanthopygus* (PEO 13). Scale = 10 mm.

anteromedian flexus reduced to a shallow notch. M2 shows a moderate 8-shape, with a deep and oblique mesoflexus. M3 is small and has a hypoflexus pinched off to form a lake; this condition is widespread in *Phyllotis* (see Steppan, 1995). In young individuals

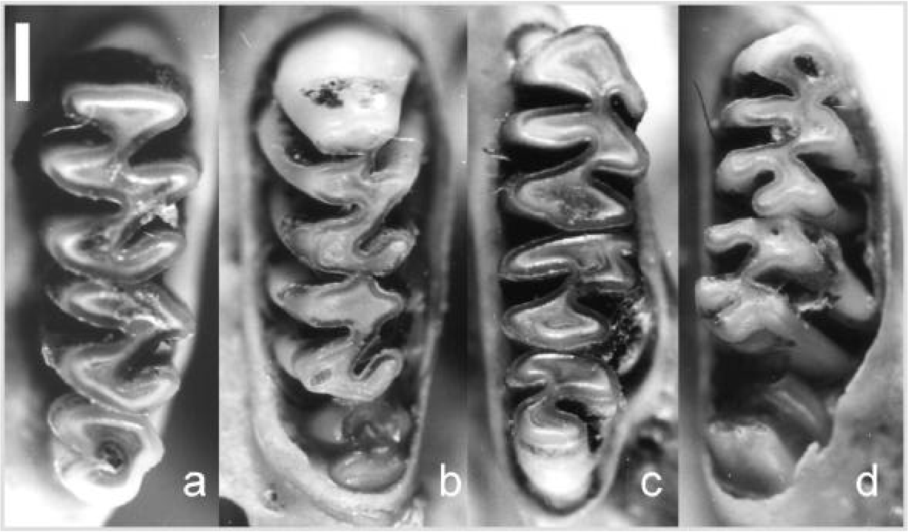

Figure 4. *Phyllotis anitae*, new species: Left upper and right lower molar rows in adult (a and c; holotype, CML 6379) and young specimens (b and d; paratype, CML 6380). Scale = 1 mm.

M2 displays a shallow anteroflexus and a persistent fossetus on the hypocone (Fig. 4).

The lower incisors are more delicate and paler than the upper ones. m1 has a trilophodont pattern in the holotype, but in young individuals this molar is tetralophodont, with both anteromedian flexid and anteromedian fossetid well developed. The anterolabial cingulum also is well developed and does not coalesce to the protoconid. The metalophid is oriented transversally, and the entolophid is fused with the posterolophid. m2 displays a bilophodont pattern in adults, with a wide hypoflexid. A persistent short anterolabial cingulum is also present. m3 is moderately large relative to m2.

Phyllotis anitae has 13 thoracic ribs and 7 cervical, 12-13 thoracic, 6 lumbar, and 28-36 caudal vertebrae (*N* = 3 specimens examined).

There are no chromosomal data on this species.

Two specimens of *P. anitae* were studied genetically, and carry the same cyt *b* haplotype.

Comparisons.---Several traditionally recognized species of *Phyllotis* are easily distinguishable from *P. anitae* by their small size. This is the case of *P. haggardi*, *P. amicus*, *P. gerbillus*, and *P. andium* (see Gyldenstolpe, 1932; Hershkovitz, 1962). Moreover, results of the phylogenetic analysis (Steppan et al., this volume) shows that *P. anitae* is not closely related to *P. amicus*, *P. andium*, or *P. gerbillus*. This analysis did not include *P. haggardi*. *P. wolffsohni* (transferred to *Tapecomys* by Steppan et al., this volume) displays trenchant skull and dental characters (e.g., frontals with divergent and sharp edges, M3 S- or Z-shaped) that easily differentiate it from *P. anitae*.

The only species of *Phyllotis* known to be sympatric to *P. anitae* is *P. osilae*. Despite the high morphologic variability of the latter species in northwestern Argentina (see Pearson, 1958; Hershkovitz, 1962), numerous features are useful to distinguish it from *P. anitae*. Although *P. osilae* specimens from humid regions are in general darker than those that inhabit dry ones (Pearson, 1958), *P. anitae* is always darker than *P. osilae*. Ventrally, *P. osilae* frequently present an ochraceous streak, absent in *P. anitae*. The manus and pes of *P. osilae* are covered by white hairs, contrasting with the generally dark hairs of *P. anitae*. In addition, the tail of *P. osilae* is clearly bicolored, and the ears are covered by whitish hairs. Differences between the 2 species also are present in skull and dental morphology (Fig. 3). The posterior extent of the nasals in *P. osilae* is longer than in *P. anitae*, surpassing the lacrimals. The nasolacrimal capsules of *P. osilae* are well inflated. The incisors have orange enamel, contrasting with the white or yellowish-white condition found in *P. anitae*. Finally, the molars in *P. osilae* are less hypsodont than those of *P. anitae*. *Phyllotis o. nogalaris* occupies similar habitat to *P. anitae*. Pearson (1958) characterized this form as a *P. osilae* with coarse pelage, dorsally brown and darker than *P. o. tucumanus*. Nine individuals trapped in the cloud grasslands of Sierra del Centinela (Jujuy Province; Appendix I) are in accordance with this description. These specimens present a lighter and richer coloration than *P. anitae*. They have a lateral ochraceous strip and a buffy belly with a pectoral ochraceous streak; their manus and pes are white and the tail bicolored and more haired than in *P. anitae*, and the hairs that covered the ears have an ochraceous tip. Additionally, *P. o. nogalaris* is, in almost all dimensions, larger than *P. anitae* (see Pearson, 1958; Table 3). Although somewhat variable, *P. o. osilae* is the subspecies with paler dorsal coloration in northwestern Argentina, and therefore, it is clearly separable from *P. anitae*. Díaz (1999) described this subspecies, based on specimens from Jujuy Province, as a form with an ochraceous strip crossing the venter, tail bicolored, and whitish manus and pes. A series from Bárcena (Jujuy Province; Appendix I), referred to *P. o. osilae*, has a yellowish dorsum with sparse black hairs, the manus and pes are white, and the tail is strongly bicolored. *Phyllotis o. tucumanus*, like *nogalaris*, is another dark subspecies. We examined several individuals of this form from Catamarca Province (Appendix I). These specimens are intermediate in dorsal coloration between *P. o. osilae* and *P. o. nogalaris*, and are, in general, lighter colored than *P. anitae*.

The widespread *P. xanthopygus* is morphologically similar to *P. anitae*. *P. xanthopygus* has a denser, softer, and noticeably lighter pelage than *P. anitae*. The dorsum of *P. xanthopugus* has fewer black hairs, and the venter is whiter, than *P. anitae*. Contrasting with *P. anitae*, the facial vibrissae in *P. xanthopygus* are long and distinctly colored, the ears are larger and less haired, both manus and pes are white, and the tail is strongly bicolored. Cranially, *P. xanthopygus* has larger posterolateral palatal pits that in specimens from northwestern Argentina are anterior to the mesopterygoid fossa (Fig. 3; see also Pearson, 1958). The incisor enamel is orange and molar hypsodonty is less developed than in *P. anitae*. *P. xanthopygus* inhabit desert and semi-desert environments, in general associated with stones or rock outcrops and scattered xerophytic vegetation (brush, tola, cacti). According to Pearson (1958), *P. x. rupestris* is a paler form with noticeably large ears, and it is therefore easily distinguishable from *P. anitae*. In northwestern Argentina, *P. x. rupestris* occupies Puna, Prepuna, and High-Andean regions, but not Yungas environments. Several specimens from Jujuy Province (Appendix I) have a light gray dorsal coloration, a whitish belly, ears covered by yellowish tipped hairs, pure white manus and pes, and a strongly bicolored tail. The molars of this form are much more delicate, smaller, and less hypsodont than those of *P. anitae*. *Phyllotis x. ricardulus* is another subspecies present in northwestern Argentina and has been characterized as a rich-colored form, with buff lateral and pectoral strips (Pearson, 1958). These traits are present in 5 specimens from Abra Pampa (Jujuy Province; Appendix I). In addition,

Figure 5. *Alnus* cloud forest habitat of *Phyllotis anitae* at Hualinchay (Tucumán province, Argentina).

the tail in this subspecies is more haired than in *P. anitae*, and the molar toothrow is, on average, longer (Table 3). *Phyllotis x. vaccarum* is a subspecies with light coloration, larger than *P. anitae* (Pearson, 1958). The same is true for *P. x. bonariensis*, an endemic form from central-eastern Argentina (Crespo, 1964).

Phyllotis caprinus has a distribution restricted to localities in the Puna and Prepuna of northwestern Argentina and Bolivia (Pearson, 1958). It can be distinguished from *P. anitae* by its larger size, general coloration (similar to that of *P. xanthopygus*), ears covered by yellowish hairs, interorbital region with divergent and sharp frontal edges, a V-shaped fronto-parietal suture, and orange incisors (Pearson, 1958).

Habitat and Natural History.---Hualinchay, the type locality of *P. anitae*, is in the ecotone between montane forest and high-altitude grasslands, in the upper altitudinal limit of the Yungas. This vegetation level is characterized by alder forests (*Alnus acuminata*) and grassland communities dominated by *Festuca hieronymi*, *Deyeuxia polygama*, and

Table 3.-- Measurements of various taxa of *Phyllotis*. For each measurement, we provide mean ± standard deviation, range (in parentheses), and sample size.

	P. anitae n. sp. Holotype	*P. o. osilae*	*P. o. nogalaris*	*P. o. tucumanus*	*P. x. rupestris*	*P. x. ricardulus*	*P. x. vaccarum*
HB	119	118±4.92 (108-124); 9	126±5.67 (116-137); 17	119±5.12 (111-123); 6	105±6.24 (100-112); 3	118±4.93 (115-124); 3	127±2.83 (125-129); 2
T	124	118±6.10 (111-130); 9	137±8.65 (118-148); 17	130±5.48 (122-136); 6	124±11.53 (112-135); 3	103±7.64 (95-110); 3	134±20.51 (119-148); 2
HF	29	30±0.71 (29-31); 9	30±1.69 (27-32); 18	30±1.27 (28-31); 7	25±1.00 (24-26); 3	20±1.53 (19-22); 3	26±0.71 (26-27); 2
E	21	22±1.01 (21-24); 9	22±1.20 (20-24); 18	23±2.14 (22-28); 7	25±0.58 (24-25); 3	20±4.00 (16-24); 3	28±5.66 (24-32); 2
W	37.5	41.5±5.85 (32.5-49); 9	56.8±11.36 (41-82); 18	52.4±11.99 (40-74); 7	41.5±4.09 (38-46); 3	---	58; 1
GLS	30.72	29.90±0.67 (28.94-30.68); 9	31.52±1.11 (29.60-33.46); 18	30.69±0.87 (29.42-31.80); 7	28.22±0.41 (27.78-28.58); 3	29.60±1.73 (28.38-30.82); 2	31.82±0.23 (31.66-31.98); 2
CIL	27.80	27.97±0.56 (26.88-28.54); 9	29.37±1.13 (27.46-31.34); 18	28.65±0.78 (27.80-30.12); 7	26.08±0.47 (25.56-26.48); 3	27.12±1.98 (25.72-28.52); 2	29.69±0.04 (29.66-29.72); 2
ZB	16.06	16.02±0.34 (15.60-16.60); 9	16.85±0.62 (15.86-18.80); 18	16.25±0.42 (15.62-16.82); 7	14.75±0.59 (14.12-15.30); 3	15.82; 1	16.10±0.14 (16.00-16.20); 2
WBC	14.10	13.55±0.28 (13.22-13.98); 9	13.99±0.43 (13.20-14.74); 18	13.72±0.29 (13.38-14.12); 7	13.42±0.36 (13.08-13.80); 3	12.93±0.02 (12.90-12.94); 3	13.52±0.17 (13.40-13.64); 2
IB	4.02	4.19±0.16 (3.90-4.38); 9	4.23±0.17 (3.90-4.50); 18	4.15±0.11 (3.98-4.26); 7	4.19±0.22 (4.04-4.44); 3	3.96±0.25 (3.70-4.20); 3	4.26±0.31 (4.04-4.48); 2

Table 3 (continued).

UTR	5.78	5.58±0.19 (5.38-5.82); 9	5.69±0.17 (5.38-6.00); 18	5.42±0.12 (5.24-5.56); 7	4.87±0.25 (4.60-5.10); 3	5.18±0.22 (4.96-5.40); 3	5.63±0.38 (5.36-5.90); 2
NL	12.48	12.44±0.69 (11.20-13.16); 9	13.26±0.71 (12.24-14.36); 18	13.23±0.46 (12.42-13.80); 7	11.87±0.56 (11.32-12.44); 3	13.29±1.20 (12.46-14.66); 3	13.37±0.04 (13.34-13.40); 2
RW2	5.00	5.23±0.20 (4.90-5.56); 9	5.57±0.26 (5.12-5.92); 18	5.30±0.09 (5.18-5.44); 7	4.96±0.27 (4.70-5.24); 3	5.14±0.20 (5.00-5.28); 2	5.18±0.31 (4.96-5.40); 2
DL	7.80	7.58±0.32 (6.94-8.06); 9	8.04±0.58 (7.20-9.18); 18	7.80±0.34 (7.38-8.42); 7	7.29±0.24 (7.10-7.56); 3	7.65±0.74 (6.84-8.30); 3	8.18±0.45 (7.86-8.50); 2
IFL	7.24	7.02±0.42 (6.36-7.58); 9	7.34±0.41 (6.70-8.34); 18	7.15±0.33 (6.74-7.72); 7	6.57±0.19 (6.36-6.74); 3	6.95±0.46 (6.58-7.46); 3	7.65±0.30 (7.44-7.86); 2
OCW	7.04	6.94±0.15 (6.66-7.10); 9	7.50±0.34 (6.08-7.50); 18	6.90±0.20 (6.60-7.24); 7	6.57±0.09 (6.46-6.64); 3	6.86; 1	7.06±0.20 (6.92-7.20); 2
BOL	3.78	4.05±0.11 (3.92-4.20); 9	4.42±0.27 (4.04-5.00); 18	4.34±0.26 (4.06-4.76); 7	4.31±0.08 (4.26-4.40); 3	4.15±0.35 (3.90-4.40); 2	4.49±0.13 (4.40-4.58); 2
MFW	1.68	1.60±0.20 (1.26-1.86); 9	1.64±0.17 (1.38-2.06); 17	1.52±0.13 (1.40-1.80); 7	1.17±0.06 (1.10-1.22); 3	---	1.52±0.11 (1.44-1.60); 2
ZP	2.82	3.18±0.14 (2.90-3.40); 9	3.32±0.24 (3.04-3.76); 18	3.14±0.07 (3.00-3.20); 7	2.83±0.06 (2.76-2.88); 3	3.15±0.60 (2.64-3.82); 3	3.27±0.04 (3.24-3.30); 2
ML	15.40	16.32±0.41 (15.86-16.98); 9	17.02±0.53 (16.14-17.82); 18	16.47±0.47 (15.94-17.26); 7	14.93±0.31 (14.74-15.28); 3	15.92±1.24 (14.50-16.80); 3	16.74±0.17 (16.62-16.86); 2
LTR	5.70	5.48±0.22 (5.18-5.80); 9	5.54±0.19 (5.14-5.80); 18	5.14±0.15 (5.00-5.40); 7	4.93±0.25 (4.74-5.22); 3	4.65±0.53 (4.04-4.96); 3	5.45±0.58 (5.04-5.86); 2

Stipa eriostachia (Grau and Veblen, 2000; Fig. 5). Specimens of *P. anitae* were trapped near isolated and large rocks. The soil, with a well-developed organic horizon, was covered by abundant leaf detritus. The climate in this region shows a bimodal pattern with precipitations concentrated during summer and early autumn. In the wet season (January to May) mean rainfall reaches 1500 mm, contrasting with <60 mm during the dry season. These dramatic changes in precipitation result in abrupt vegetation modifications, from dense development of grasses and ferns during the wet season to an almost naked soil during the dry season. An additional humidity input, in cloud form, characterizes this region year-through (Brown et al., 2001). Temperatures also vary seasonally, with an annual mean value of 11.9°C. Snow falls occasionally in winter.

Phyllotis anitae seems to be a rare and specialist taxon of the high-altitude *Alnus* forest. Of 350 small mammals trapped at the type locality surroundings (including 8 trapping sites between 1700 and 2800 m in grassland and montane forest environments) only 5 specimens belong to this species. All *P. anitae* individuals except 1 were captured at night. The holotype was a lactating female. Both the holotype female as well as the female paratype had closed vaginas, and the male paratypes had abdominal testicles.

Other small mammals trapped at Hualinchay were the sigmodontines *Abrothrix illuteus*, *Akodon lutescens caenosus*, *Akodon simulator*, *Akodon spegazzini tucumanensis*, *Andinomys edax*, *Phyllotis osilae*, and undetermined species of the genera *Akodon*, *Oligoryzomys*, *Oxymycterus*, and the didelphine *Thylamys*.

DISCUSSION

In contrast with other highly polytypical genus of sigmodontine rodents (such as *Akodon*, *Calomys*, *Oligoryzomys*, and *Oryzomys*), the alpha diversity of *Phyllotis* has not been augmented in recent decades. The last valid species erected was *P. caprinus*, with type locality in Tilcara, Jujuy Province (Pearson, 1958). Several years later Crespo (1964) described the subspecies *P. xanthopygus bonaerensis* (formerly, *P. darwini*) from the isolated system of Ventana in the eastern Pampean region of Buenos Aires Province, Argentina. Although this form has been considered as a valid species by several authors (Reig, 1978; Galliari et al., 1996; Musser and Carleton, 2005) its status at the species level has not been correctly assessed. The description of *P. anitae* indicates that the static scenario of *Phyllotis* alpha diversity can be attributed more fundamentally to the lack of collections in vast geographic areas of the Andean region, than to a stabilized and well-resolved alpha taxonomy.

As noted above, *Phyllotis anitae* is sister taxon to *P. osilae*. Both species are easily distinguishable at both morphological and molecular (cyt *b* gene) levels. For instance, *P. anitae* is more hypsodont, with white or yellowish-white incisors, a delicate rostrum, and a distinct coloration (see above for details). Similarly, cyt *b* haplotypes of *P. anitae* and *P. osilae* are very divergent; the lowest value of observed divergence between haplotypes of both species is 9.36%. Remarkably, this high value of observed divergence is the lowest observed between haplotypes recovered from *P. anitae* specimens and individuals of any other *Phyllotis* species. This fact, together with the morphological comparisons detailed in the previous section, clarifies that *P. anitae* is distinct to all other known species of *Phyllotis*.

Phyllotis generally inhabit open areas, mainly grasslands and xerophytic environments (Pearson, 1958). The exceptions to this pattern are *P. anitae* and *P. o. nogalaris*, which are the only known *Phyllotis* forms that inhabit the Yungas. The Yungas have a rich sigmodontine fauna, which has been poorly studied. In spite of the lengthy time period between the descriptions of the first species known from the region (e.g., Allen, 1901, Thomas, 1916, 1918, 1921a, 1921b, 1925) and recent contributions covering different aspects of the sigmodontine fauna (e.g., Barquez, 1976; Olrog, 1979; Barquez et al., 1980; Mares et al., 1981; Kajon et al., 1984; Ojeda and Mares, 1989; Mares et al., 1997; Díaz, 1999; Díaz and Barquez, 1999; Díaz et al., 1999; Ortíz et al., 2000a, 2000b; Ortíz and Pardiñas, 2001), knowledge of several species remains sparse. The Argentine part of the Yungas has, at least, 27 sigmodontine species, which are included in 12 genera.

In northwestern Argentina the Yungas reach their southern limit and become fragmented. The Yungas here are characterized by a strong altitudinal gradient, where climatic conditions vary strongly over short distances. This variation determines altitudinally structured vegetation zones (Brown et al., 2001). The upper montane forest, which is inhabited by *P. anitae*, constitutes a band from 1500 to 3000 meters above see level, distributed in patches, mainly on the eastern slopes of northwestern Argentina mountain chains. This band is highly heterogeneous, especially at the transition zone with the cloud grasslands (Brown et al., 2001).

Traditionally, mammalogists have concentrated their efforts at lower vegetation levels; meanwhile, the upper montane forest have received less attention. Of the 27 sigmodontines recorded for the Yungas, 18 have been observed in upper montane forests. The finding of *P. anitae* as well as other new taxa currently under study (e.g., a new *Oxymycterus*) indicates that this number is an underestimate of the local diversity.

Unfortunately, the Yungas are suffering substantial human impacts. Cattle raising, fire, and wood exploitation are among the main factors underlying the deterioration of the Yungas. As is the case for several unique South American biomes (e.g., Chaco), conservation strategies based on sound biological knowledge are lacking, and the effects of these stressors on the sigmodontine fauna, as well as in other small mammals, have not been assessed.

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APPENDIX 1: SPECIMENS EXAMINED

Specimens of *Phyllotis* used in this study are listed below. All specimens were used in morphological analysis; specimens used in molecular and quantitative analyses are indicated by ^{m} and ^{q}, respectively. Museum and Collection acronyms and personal field numbers are as follows: CML, Colección Mamíferos Lillo, Tucumán, Argentina; CNP, Colección de Mamíferos del Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina; MMP-Ma, Museo de Ciencias Naturales y Tradicional de Mar del Plata "Lorenzo Scaglia," Mar del Plata, Argentina; JPJ, field number of Jorge P. Jayat (to be deposited at CML); MMD, field number of M. Mónica Díaz (to be deposited at CML); and PEO, field number of Pablo E. Ortiz (to be deposited at CML).

Phyllotis anitae (5).---TUCUMÁN: 10 km by road south of Hualinchay on the trail to Lara (CML 6379^{mq} [holotype], CML 6380^{q}, CML 6381^{q}, CNP 736^{mq}, CNP 737^{q}, CNP 809^{m}).

Phyllotis caprinus (9).---JUJUY: Bárcena, 3 km S Ruta 9, 1808 m (JPJ 132, JPJ 624, JPJ 626, JPJ 640, JPJ 671); Chilcayoc, Puente Bailey, 2239 m (JPJ 130); Maimará, 2500 m (CML 98, CML 282); Tilcara (MMPMa 3073).

Phyllotis osilae nogalaris (9).---JUJUY: La Antena, Sierra del Centinela, al S de El Fuerte, 2350 m (JPJ 933^{q}, JPJ 936^{q}, JPJ 940^{q}, JPJ 955^{q}, JPJ 956, JPJ 958^{q}, JPJ 962^{q}, JPJ 969^{q}, JPJ 970).

Phyllotis osilae osilae (8).---JUJUY: Bárcena, aprox. 3 km al S, sobre Ruta Nacional N° 9, 1808 m (JPJ 632, JPJ 636, JPJ 637, JPJ 638, JPJ 639, JPJ 646, JPJ 655, JPJ 668).

Phyllotis osilae tucumanus (7).--- CATAMARCA: unión entre las rutas provinciales N° 9 y 18, 3,4 km al S, sobre Ruta Provincial N° 18, 1529 m (JPJ 19, JPJ 24, JPJ 31, JPJ 41, JPJ 1129, JPJ 1137, JPJ 1149).

Phyllotis osilae ssp. (103).---CATAMARCA: Aprox. 2 km al SE de Huaico Hondo, sobre Ruta Provincial N° 42, al E del Portezuelo, 1992 m (JPJ 412, JPJ 781, JPJ 790); El Rodeo, 1.5 km NE of Hwy 4, el. 4500 ft (CML 3448); km 33 de la Ruta Provincial N° 47, al S de Capillitas, 2500 m (JPJ 674, JPJ 676, JPJ 677, JPJ 680, JPJ 681, JPJ 685^{q}, JPJ 686, JPJ 688, JPJ 693, JPJ 695^{q}, JPJ 702^{q}, JPJ 703^{q}, JPJ 704^{q}, JPJ 705^{q}, JPJ 706^{q}, JPJ 707, JPJ 713^{q}, JPJ 715^{q}); Las Chacritas, aprox. 28 km al NNW de Singuil, sobre Ruta Provincial N° 1, 1888 m (JPJ 567, JPJ 568). JUJUY: Termas de Reyes, aprox. 15 km al N, sobre Ruta Provincial N° 4 (JPJ 291, JPJ 315); Termas de Reyes, mirador, sobre Ruta Provincial N° 4 (JPJ 122^{q}, JPJ 296, JPJ 324, JPJ 333, JPJ 334). SALTA: Abra de Ciénaga Negra, aprox. 3 km al SE, 3090 m (JPJ 722, JPJ 723, JPJ 727^{q}, JPJ 738^{q}); Aprox. 15 km al W de Escoipe, sobre Ruta Provincial N° 33, 2680 m (JPJ 51, JPJ 57, JPJ 60, JPJ 65, JPJ 68, JPJ 71, JPJ 74, JPJ 86, JPJ 1034, JPJ 1048, JPJ 1056, JPJ 1059); Campo Quijano aprox. 5 Km al NO, Km 30 de la ruta Nacional 51 (Quebrada del Toro), alt. aprox. 1600 msnm (JPJ 91, JPJ 92^{q}, JPJ 97^{q}, JPJ 98, JPJ 101, JPJ 102, JPJ 103, JPJ 104^{q}, JPJ 135, JPJ 136^{q}, JPJ 137, JPJ 140, JPJ 141, JPJ 142^{q}). TUCUMÁN: Aprox. 10 km al S de Hualinchay, sobre el camino a Lara, 2300 m (JPJ 435, JPJ 444^{q}, JPJ 451^{q}, JPJ 453^{q}, JPJ 456, JPJ 460, JPJ 461, JPJ 467, JPJ 469, JPJ 474, JPJ 476, JPJ 483, JPJ 487, JPJ 488, JPJ 771); Aprox. 16 km de Hualinchay, sobre el camino a Lara, 2750 m (JPJ 746, JPJ 748^{q}, JPJ 749, JPJ 751, JPJ 765, JPJ 767, JPJ 769^{q}, JPJ 776, JPJ 777^{q}); aprox. 7 km al NO de la finca de la familia Usandivara, Altos de Medina, 1717 m (JPJ 810, JPJ 831^{q}, JPJ 837, JPJ 839^{q}); Carapunco, km 81 de la Ruta Provincial N° 307, 2960 m (JPJ 1063, JPJ 1071); Hualinchay, sobre el camino a Cafayate, 1861 m (JPJ 173, JPJ 175, JPJ 176, JPJ 178, JPJ 183, JPJ 187, JPJ 189, 218, JPJ 220, JPJ 223, JPJ 227, JPJ 228).

Phyllotis xanthopygus ricardulus (5).---JUJUY: Abra Pampa (CML 1276^{q}, CML 1277, CML 1278^{q}, CML 1283); La Ciénaga, Abra Pampa (CML 1280^{q}).

Phyllotis xanthopygus rupestris (4).---JUJUY: 17 km al W de La Quiaca, sobre ruta provincial N° 5 y 3 km al S de la misma ruta (MMD 433, MMD 434^{q}, MMD 436^{q}, MMD 438).

Phyllotis xanthopygus vaccarum (3).---CATAMARCA: Chumbicha, 1 km NW by rd. from balneario, el. 2600 ft (CML 3451^{q}). SAN JUAN: Estancia Leoncito, 2 km E observatorio Astronómico (CML 3624); San Guillermo (CML 1080^{q}).

Phyllotis xanthopygus ssp. (7).---JUJUY: 4 km al O de Rinconada (PEO 11, 13); Avedrez (PEO 8); Curques, 24 km al N de Susques, sobre ruta 74 (MMD 291^{q}). TUCUMÁN: Cerro Bayo (CML 5563); Cerro Muños (CML 382); km 99 Ruta 307 (Tafí-Amaicha) (CML 5564).

LITERATURE CITED

Abdala, F., and M. M. Díaz
2000 Anatomía craneana de *Akodon albiventer* (Rodentia, Muridae, Sigmodontinae). Iheringia, Zoología 88:33-50.

Allen, J. A.
1901 New South American Muridae and a new *Metachirus*. Bulletin of the American Museum of Natural History 14:405-412.

Applied Biosystems, Inc.
1994 Sequence Navigator DNA and Protein Sequence Comparison Software. Perkin-Elmer Corporation, Foster City, California, USA.

Barquez, R. M.
1976 Nuevo registro de distribución de *Oxymycterus paramensis* (Mammalia, Rodentia, Cricetidae). Neotrópica 22:115.

Barquez, R. M., D. F. Williams, M. A. Mares, and H. H. Genoways
1980 Karyology and morphometrics of three species of *Akodon* (Mammalia: Muridae) from northwestern Argentina. Annals of Carnegie Museum of Natural History 49:379-403.

Braun, J. K.
1993 Systematic relationships of the Tribe Phyllotini (Muridae: Sigmodontinae) of South America. Special Publication, Oklahoma Museum of Natural History. 50 pp.

Brown, A. D., H. R. Grau, L. R. Malizia and A. Grau
2001 Argentina. Pp. 623-659 in Bosques Nublados del Neotrópico (Kappelle, M., and A. D. Brown eds.). Instituto Nacional de Biodiversidad (INBio), Costa Rica.

Bustos, M.
1995 Diversidad de micromamíferos terrestres durante una sucesión secundaria de selva montana. Pp. 115-122 In Investigación, Conservación y Desarrollo en Selvas Subtropicales de Montaña (Brown, A. D., and H. R. Grau, eds.). Laboratorio de Investigaciones Ecológicas de las Yungas (LIEY-UNT), Tucumán, Argentina.

Capllonch, P., A. G. Autino, M. M. Díaz, R. M. Barquez, and M. Goytia
1997 Los mamíferos del Parque Biológico Sierra de San Javier, Tucumán, Argentina: Observaciones sobre su sistemática y distribución. Mastozoología Neotropical 4:49-71.

Crespo, J. A.
1964 Descripción de una nueva subespecie de roedor filotino (Mammalia). Neotrópica 10:99-101.

D'Elía, G., E. González, and U. F. J. Pardiñas
2003. Phylogenetic analysis of sigmodontine rodents (Muroidea), with special reference to the akodont genus *Deltamys*. Mammalian Biology 68:351-364.

Díaz, M. M.
1999 Mamíferos de la Provincia de Jujuy: Sistemática, Distribución y Ecología. Ph.D. Dissertation, Doctoral Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina. 640 pp.

Díaz, M. M., and R. M. Barquez
1999 Contributions to the knowledge of the mammals of Jujuy province, Argentina. Southwestern Naturalist 44:324-333.

(This volume)
The Wild Mammals of Jujuy Province, Argentina: Systematics and Distribution. Pp. 417-578 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

Díaz, M. M., R. M. Barquez, J. K. Braun, and M. A. Mares
1999 A new species of *Akodon* (Muridae: Sigmodontinae) from northwestern Argentina. Journal of Mammalogy 80:786-798.

Galliari, C. A., U. F. J. Pardiñas, and F. J. Goin
1996 Lista comentada de los mamíferos argentinos. Mastozoología Neotropical 3:39-61.

Grau, H. R., and T. T. Veblen
2000 Rainfall variability, fire and vegetation dynamics in neotropical montane ecosystem in north-western Argentina. Journal of Biogeography 27:1107-1121.

Gyldenstolpe, N.
1932 A manual of Neotropical sigmodont rodents. Kungliga Svenska Vetenskapsakademiens Handlingar, Stockholm, Band 11, 3:1-164.

Hershkovitz, P.
1962 Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana: Zoology, 46:1-524.

Kajon, A. E., O. A. Scaglia, C. Horgan, C. Velazquez, M. S. Merani, and O. A. Reig
1984 Tres nuevos cariotipos de la tribu Akodontini (Rodentia, Cricetidae). Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigación de las Ciencias Naturales, Zoología 13:461-469.

Kramer, K. M., J. A. Monjeau, E. C. Birney, and R. S. Sikes
1999 *Phyllotis xanthopygus*. Mammalian Species 617:1-7.

Maddison, W. P., and D. R. Maddison
1992 MacClade. Analysis of Phylogeny and Character Evolution. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Mares, M. A., and J. K. Braun
1996 A new species of phyllotine rodent, genus *Andalgalomys* (Muridae: Sigmodontinae), from Argentina. Journal of Mammalogy 77:928-941.

Mares, M. A., R. A. Ojeda, J. K. Braun, and R.M. Bárquez
1997 Systematics, distribution, and ecology of the mammals of Catamarca Province, Argentina: Pp. 89-141 in Life Among the Muses: Papers in Honor of James S. Findley (Yates, T. L., W. L. Gannon, and D. E. Wilson, eds.). Special Publication, The Museum of Southwestern Biology, The University of New Mexico, Albuquerque, New Mexico, USA.

Mares, M. A., R. A. Ojeda, and M. P. Kosco
1981 Observations on the distribution and ecology of the mammals of Salta Province, Argentina. Annals of Carnegie Museum of Natural History 50:151-206.

Musser, G. M., and M. D. Carleton
2005 Superfamily Muroidea. Pp. 894-1531 in Mammal Species of the World: A Taxonomic and Geographic Reference. Third ed. (Wilson, D. E., and D. M. Reeder, eds.). Johns Hopkins University Press, Baltimore, Maryland, USA.

Myers, P., J. L. Patton, and M. F. Smith
1990 A review of the *boliviensis* group of *Akodon* (Muridae: Sigmodontinae) with emphasis on Peru and Bolivia. Miscellaneous Publications, Museum of Zoology, University of Michigan 177:1-89.

Ojeda, R. A., and M. A. Mares
1989 A biogeographic analysis of the mammals of Salta Province, Argentina. Patterns of species assemblage in the neotropics. Special Publications, The Museum, Texas Tech University 27:1-66.

Olrog, C. C.
1979 Los mamíferos de la Selva Húmeda, Cerro Calilegua, Jujuy. Acta Zoológica Lilloana 33:9-14.

Ortiz, P. E., S. Cirignoli, D. H. Podesta, and U. F. J. Pardiñas
2000a New records of sigmodontine rodents (Mammalia: Muridae) from high-Andean localities of northwestern Argentina. Biogeographica 76:133-140.

Ortíz, P. E., and U. F. J. Pardiñas
2001 Sigmodontinos (Mammalia: Rodentia) del Pleistoceno tardío del valle de Tafí (Tucumán, Argentina): taxonomía, tafonomía y reconstrucción paleoambiental. Ameghiniana. 38:3-26.

Ortiz, P. E., U. F. J. Pardiñas, and S. J. Steppan
2000b A new fossil phyllotine (Rodentia: Muridae) from northwestern Argentina and relationships of the *Reithrodon* Group. Journal of Mammalogy 81:37-51.

Pearson, O. P.
1958 A taxonomic revision of the rodent genus *Phyllotis*. University of California Publications in Zoology 56:391-496.

1972 New information on ranges and relationships within the rodent genus *Phyllotis* in Peru and Ecuador. Journal of Mammalogy 53:677-686.

Pearson, O. P., and J. L. Patton
1976 Relationships among South American phyllotine rodents based on chromosome analysis. Journal of Mammalogy 57:339-350.

Reig, O. A.
1977 A proposed unified nomenclature for the enameled components of the molar teeth of the Cricetidae (Rodentia). Journal of Zoology (London) 181:227-241.

1978 Roedores cricétidos del Plioceno superior de la Provincia de Buenos Aires (Argentina). Publicaciones del Museo Nacional de Ciencias Naturales de Mar de Plata "Lorenzo Scaglia" 2:164-190.

Spotorno, A. O.
1976 Análisis taxonómico de tres especies altiplánicas del género *Phyllotis* (Rodentia: Cricetidae). Anales del Museo de Historia Natural de Valparaíso 9:141-161.

Steppan, S. J.
1993 Phylogenetic relationships among Phyllotini (Rodentia: Sigmodontinae) using morphological characters. Journal of Mammalian Evolution 1:187-213.

1995 Revision of the tribe Phyllotini (Rodentis: Sigmodontinae), with a phylogenetic hypothesis for the Sigmodontinae. Fieldiana: Zoology, new series 80:1-112.

1998 Phylogenetic relationship and species limits within *Phyllotis* (Rodentia: Sigmodontinae): Concordance between MTDNA sequence and morphology. Journal of Mammalogy 79:573-593.

Steppan, S. J., O. Ramirez, J. Banbury, D. Huchon, V. Pacheco, L. Walker, and A. O. Spotorno (This volume)
A molecular reappraisal of the systematics of the leaf-eared mice *Phyllotis* and their relatives Pp. 799-826 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

Swofford, D. L.
2000 PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, MA.

Teta, P., and P. E. Ortíz
2002 Micromamíferos andinos holocénicos del sitio arqueológico Inca Cueva 5, Jujuy, Argentina: tafonomía, zoogeografía y reconstrucción paleoambiental. Estudios Geologicas 58:117-135.

Thomas, O.

1916 Two new species of *Akodon* from Argentina. Annals and Magazine of Natural History, ser. 8, 18:334-336.

1918 On small mammals from Salta and Jujuy collected by Mr. E. Budin. Annals and Magazine of Natural History, ser. 9, 1:186-193.

1921a New *Rhipidomys*, *Akodon*, *Ctenomys*, and *Marmosa* from the Sierra Santa Barbara, S. E. Jujuy. Annals and Magazine of Natural History, ser. 9, 7:183-187.

1921b On a further Collection of Mammals from Jujuy obtained by Sr. Budin. Annals and Magazine of Natural History, ser. 9, 8:608-617.

1925 On some Argentine mammals. Annals and Magazine of Natural History, ser. 9, 15:582-586.

Voss, R. S.

1988 Systematics and ecology of Ichthyomyine rodents (Muroidea): Patterns of morphological evolution in a small adaptative radiation. Bulletin of the American Museum of Natural History 188:259-493.

Wahlert, J. H.

1985 Cranial foramina of rodents. Pp. 311-332 in Evolutionary Relationships among Rodents: A Multidisciplinary Analysis (Luckett, W. P., and J. L. Hartenberger, eds.). Plenum Press, New York, New York, USA.

Walker, L. I., A. E. Spotorno, and J. Arrau

1984 Cytogenetic and reproductive studies of two nominal subspecies of *Phyllotis darwini* and their experimental hybrids. Journal of Mammalogy 65:220-230.

A MOLECULAR REAPPRAISAL OF THE SYSTEMATICS OF THE LEAF-EARED MICE *PHYLLOTIS* AND THEIR RELATIVES

UNA RE-EVALUACIÓN MOLECULAR DE LA SISTEMÁTICA DEL GÉNERO *PHYLLOTIS* Y SUS GRUPOS HERMANOS

Scott J. Steppan, O. Ramirez, Jenner Banbury, Dorothée Huchon,
Víctor Pacheco, Laura I. Walker, and Angel E. Spotorno

ABSTRACT

The tribe Phyllotini includes the ecologically abundant and well studied leaf-eared mice *Phyllotis*. We report on phylogenetic analyses of both mitochondrial (1,185 bp of the complete cytochrome *b* gene (cyt *b*) and flanking tRNA) and nuclear (1,300 bp of the nuclear recombination activating gene 1, RAG1) DNA for 13 species of *Phyllotis*, including 2 undescribed species. We also include published and new sequences for 19 other phyllotine species. Sampling within species is relatively high, with 5 of the species represented by 7 to 17 individuals each. The results clarify relationships among phyllotine genera, test monophyly of *Phyllotis*, resolve some relationships within *Phyllotis*, and confidently resolve the position of the newly discovered species. Notably, we confirm previous cyt *b* results, but in contrast to morphological hypotheses, that *Graomys* and *Andalgalomys* are not closely related. Relationships near the base of Phyllotini are poorly supported by cyt *b* but receive somewhat better support from the more slowly evolving RAG1. *Graomys* and *Eligmodontia* do not appear to be members of a clade that includes *Phyllotis* and *Auliscomys*. *Phyllotis wolffsohni* should be removed from *Phyllotis* and placed in *Tapecomys*. The data do not support recognition of *Paralomys* because the type species (*Phyllotis gerbillus*) is closely related to 3 other northwestern species (*andium, amicus*, sp. nov. 1) that together fall within *Phyllotis*. A second undescribed species, from Argentina, appears to be the sister species to *P. osilae*, and together these are the sister-group to all other *Phyllotis* s. s. The *darwini* species-group is supported by cyt *b* data, and within that group, the widespread species *P. xanthopygus* is characterized by deep divergences, high genetic diversity, and paraphyly with respect to at least 2 morphological species, *limatus* and *bonariensis*. Two or 3 possible cryptic species are revealed by the phylogenies. Problematic sequences from GenBank are identified. Finally, with respect to molecular clock estimates of divergence dates, our application of different calibrations and methods suggests that phyllotine divergence dates estimated by Salazar-Bravo et al. (2001) may be too old.

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Key words: *Phyllotis*, cytochrome *b*, RAG1, phylogenetics, biogeography, cryptic species

RESUMEN

La tribu Phyllotini incluye a los ecológicamente abundantes y bien estudiados ratones orejones del género *Phyllotis*. En este trabajo, presentamos un análisis filogenético basado en secuencias del genoma mitocondrial (1,185 pb del gen completo del citocromo *b* (cyt *b*) y el adyacente RNAt) y nuclear (1,300 pb del gen nuclear activante de recombinación 1, RAG 1), incluyendo a 13 especies de *Phyllotis*, 2 de ellas aún no descritas. Además, hemos incluído nuevas secuencias y otras previamente publicadas para otras 19 especies de filotinos. La muestra dentro del nivel de especie fue relativamente alta, 5 de las especies estuvieron representadas con un número que varió entre 7 y 17 individuos. Los resultados resuelven las relaciones filogenéticas entre los géneros de filotinos, prueban la monofília de *Phyllotis*, resuelven algunas relaciones dentro de *Phyllotis*, y resuelve la posición de las nuevas especies descubiertas. Notablemente, confirmamos los resultados previos basados en secuencias del cyt *b* pero es incongruente con la hipótesis, basada en datos morfológicos, que *Graomys* y *Andalgalomys* no están cercanamente relacionados. Las relaciones cercana a la base del clado Phyllotini son pobremente soportadas por el cyt *b* pero reciben un mejor soporte del RAG1, cuya tasa de mutación es más lenta. *Graomys* y *Eligmodontia* no parecen ser miembros del clado que incluye a *Phyllotis* y *Auliscomys*. *Phyllotis wolffsohni* debería ser removido de *Phyllotis* y ubicado en *Tapecomys*. Los datos no apoyan el reconocimiento de *Paralomys* debido a que la especie tipo (*Phyllotis gerbillus*) está cercanamente relacionada a otras 3 especies del noroeste (*andium, amicus,* sp. nov. 1) que juntas forman parte del clado de *Phyllotis*. Una segunda aún no descrita especie de Argentina, parece ser la especie hermana de *P. osilae*, y juntas son el grupo hermano de todas las otras especies de *Phyllotis* s. s. El grupo de especies *darwini* está soportado por los datos provenientes del cyt *b*, y dentro de este grupo, *P. xanthopygus*, la especie de más amplia distribución geográfica, se caracterizó por profundas divergencias, alta diversidad genética, y parafília con respecto a 2 especies morfológicas, *limatus* y *bonaerensis*. Dos o 3 especies crípticas se observan en las filogénias. Se han identificado secuencias problemáticas de GenBank. Finalmente, con respecto a la antigüedad de las divergencias estimadas por reloj molecular, nuestra aplicación de diferentes calibraciones y métodos sugiere que Salazar-Bravo et al. (2001) las ha sobrestimado.

Palabras claves: *Phyllotis*, citocromo *b*, RAG1, filogenética, biogeografía, especies crípticas

INTRODUCTION

The genus *Phyllotis* (Rodentia: Sigmodontinae) has had a long systematic history and captured the attention of some of the leading mammalogists, starting with the original collection of 2 species by Charles Darwin on the voyage of the *Beagle*, followed by their subsequent description by Waterhouse (1837) and later revisionary studies by Pearson (1958) and Hershkovitz (1962). Members of the genus are widespread throughout the

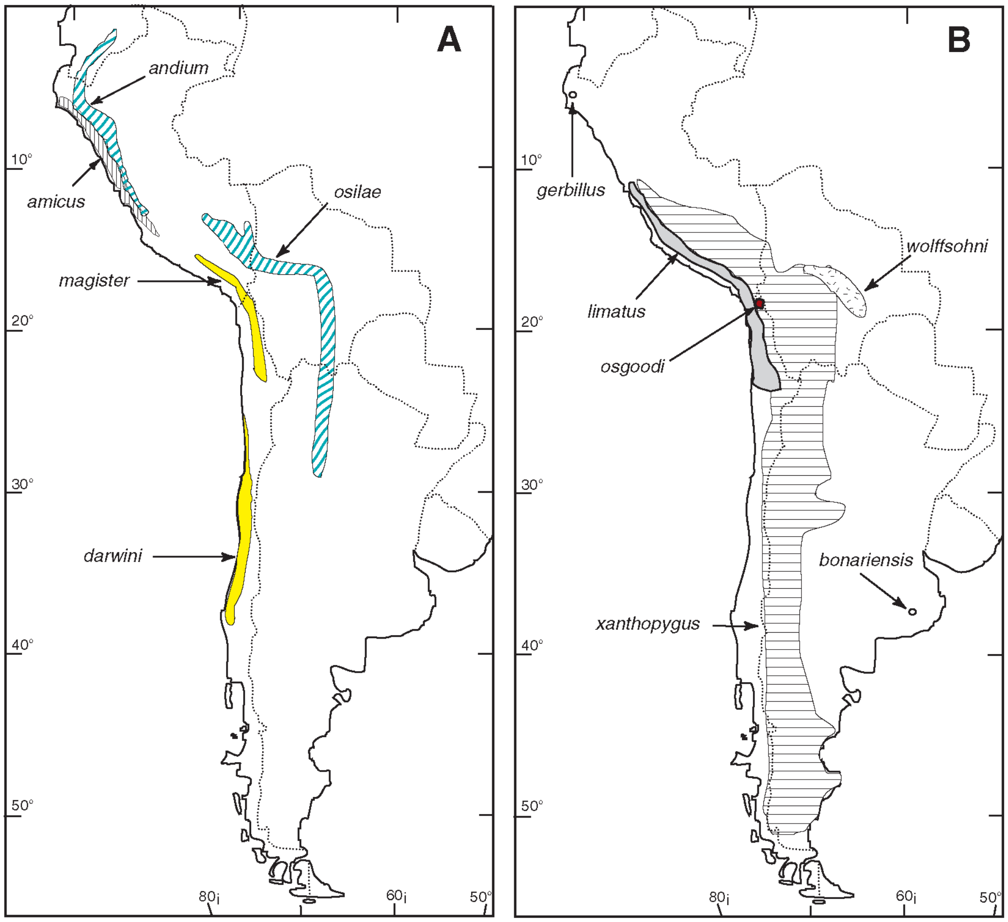

Figure 1. Distribution of *Phyllotis* species included in this study. Panels A and B separate species with overlapping distributions for visual clarity.

central and southern Andes (Fig. 1) and often are the most abundant mammal at a location. Their appearance, ecology, and taxonomic complexity led Pearson to describe them as the South American equivalent of *Peromyscus* (1958:391). Group membership has varied considerably in different treatments, including the more recent studies by Pearson and Patton (1976), Olds and Anderson (1989), Braun (1993), and Steppan (1993, 1995, 1998).

The primary objective of this study is to assess the monophyly of *Phyllotis*, its placement within Phyllotini, and to provide a phylogenetic hypothesis for the genus. These objectives are best achieved by thorough taxonomic sampling within putative members as well as among phyllotines in general, so that monophyly can be tested exhaustively. We have therefore examined all available phyllotine species for which sequences of cytochrome *b* (cyt *b*) have been reported and combined those with 61 new cyt *b* and 85 new recombination activating gene 1 (RAG1) sequences we generated. Relationships within the *P. darwini* species group are very complex, and a detailed phylogeographic study is being conducted separately (Albright et al., in prep). We include here selected exemplars of the major clades in the *darwini* species group.

The secondary objective is to provide phylogenetic hypotheses for 2 newly discovered species from Peru and Argentina. Remarkably, after the 2 revisions by Pearson (1958) and Hershkovitz (1962), only 1 other new species has been described (*P. bonariensis*; Crespo, 1964), until now. The complete descriptions of these species will be published elsewhere (Pacheco et al., unpubl. ms.; Jayat et al., This volume).

Morphological studies have largely agreed on the composition of Phyllotini; *Andalgalomys, Andinomys, Auliscomys, Calomys, Chinchillula, Eligmodontia, Euneomys, Galenomys, Graomys, Irenomys, Loxodontomys, Neotomys,* and *Phyllotis*. Two more recently described genera, *Salinomys* (Braun and Mares, 1995) and *Tapecomys* (Anderson and Yates, 2000), both appear to be well supported as members of this tribe. The inclusion of the Puna mouse (*Punomys*) in Phyllotini has been much more unsettled, with Olds and Anderson (1989) including it and Steppan (1995) excluding it. Nearly all have also included *Reithrodon*, although Vorontsov (1959) created the Reithrodontini for this genus. Inclusion of *Reithrodon* was strengthened when Olds and Anderson (1989) proposed the *Reithrodon* group for *Reithrodon, Euneomys*, and *Neotomys*, all with sigmoidal or nearly sigmoidal molars. Steppan (1995) concurred and added some supporting characters, such that the *Reithrodon* group was possibly the best supported clade within the phyllotines. New fossil finds appeared to provide additional support to the *Reithrodon* group, presenting possible transitional forms between an *Auliscomys/Loxodontomys*-like ancestor and the extant members of the group (Steppan and Pardiñas, 1998; Ortiz et al., 2000). However, molecular data have strongly refuted several of these hypotheses. *Reithrodon* was found to be unrelated to phyllotines, arising from an unresolved basal radiation of sigmodontines, based on mitochondrial (cyt *b* -- Smith and Patton 1999; D'Elia, 2003) and nuclear genes (IRBP -- D'Elía, 2003; Weksler, 2003; RAG1, GHR, c-myc -- Steppan et al., 2004a). *Euneomys* has been found to be neither a phyllotine nor member of a *Reithrodon* group (IRBP -- D'Elia 2003; RAG1, GHR, c-myc -- Steppan et al., unpubl. data). No molecular data are yet available for *Neotomys*, but given the results regarding the other 2 genera, it likely is not a phyllotine either. Furthermore, *Andinomys* (Smith and Patton, 1999; Steppan et al., 2004a) and *Irenomys* (Smith and Patton, 1999; D'Elía, 2003; Steppan et al., 2004a) appear to be additional "unique lineages" of sigmodontines, not closely related to other tribes. Therefore, all of these genera are removed from Phyllotini. There is molecular support for the inclusion of most of the remaining genera, and among these 11 (*Auliscomys, Andalgalomys, Calomys, Chinchillula, Eligmodontia, Galenomys, Graomys, Loxodontomys, Phyllotis, Salinomys, Tapecomys*) those with published sequences or available tissues are included here. For this study, we lack data only for *Galenomys* and *Chinchillula*.

Morphological data (predominantly dental and cranial) have not resulted in any strongly supported hypotheses among genera within Phyllotini (Steppan and Sullivan, 2000), and few even within genera. Steppan (1995) analyzed 98 morphological characters for all recognized genera and found only 2 intergeneric clades with greater than 80% bootstrap support; the *Reithrodon* group and *Graomys* plus *Andalgalomys*. Both of these clades have subsequently been refuted by molecular data (e.g., Smith and Patton, 1999; Anderson and Yates, 2000), although not thoroughly tested. A subsequent reanalysis of Steppan's (1995) morphological data with faster computers, more thorough search strategies, and some additional taxa resulted in lower bootstrap scores for these clades (Steppan and Sullivan, 2000) and in fact, most intergeneric clades had less than 10%

bootstrap support and only the *Reithrodon* group displayed greater than 30% bootstrap support. The morphological study by Braun (1993) also failed to demonstrate any strongly supported clades. To date, morphological data have not been very informative about phyllotine phylogeny, other than to suggest that internal branches might be short.

Similarly, morphological data have been equivocal regarding monophyly of *Phyllotis*. Braun (1993) found that *Phyllotis* was not monophyletic and she resurrected *Paralomys* for the grouping of *amicus* and *gerbillus,* although her *Paralomys* was also paraphyletic. Steppan (1995) found these species to form a clade in the bootstrap consensus tree, although notably not in any of the most parsimonious trees. *P. wolffsohni* appeared to be well outside *Phyllotis*, but again, intervening nodes were not well supported. Therefore, morphological data suggested that *Phyllotis* as then construed likely was paraphyletic and that *wolffsohni, amicus, gerbillus*, and *andium* might all need to be removed (Braun 1993; Steppan 1995). Within *Phyllotis*, only one moderately well-supported clade appeared, that of the *darwini* species group: *P. darwini*, *P. xanthopygus*, *P. caprinus*, and *P. limatus* (Steppan and Sullivan, 2000). *P. magister* and *P. definitus* might be sister to that group but support was again weak (*P. bonariensis* was not examined).

Molecular Studies

No published molecular studies have expressly targeted phyllotines although several have included a variety of phyllotines (e.g., Salazar-Bravo et al., 2001). DNA hybridization indicated that *Phyllotis* was more closely related to *Loxodontomys* than either were to *Calomys, Graomys*, or *Eligmodontia* (Dickerman, 1992). Several studies agree that *Calomys* is the sister group to all other phyllotines, including mitochondrial (Engel et al., 1998; Smith and Patton, 1999) and nuclear data (Steppan et al., 2004a). Anderson and Yates (2000) showed that *Andalgalomys* was not closely related to *Graomys*, contra Steppan (1993; 1995) and Braun (1993).

Within *Phyllotis*, Steppan (1998) found that cyt *b* was equivocal regarding the inclusion of *P. wolffsohni*. *Phyllotis andium* and *P. amicus* appeared to be sister taxa and within the genus, although outgroup sampling was too limited for a definitive test of the validity of *Paralomys* sensu Braun (1993). A *darwini* species group was supported, including *P. darwini* and *P. magister* as sister species and a genetically diverse *P. xanthopygus* that was paraphyletic with respect to *P. limatus*. More detailed sampling confirmed that *P. limatus* was a very recent offshoot from *P. xanthopygus* (Kuch et al., 2002).

Several hypotheses can be drawn from these morphological and the limited cyt *b* data: 1) *P. amicus* and *P. gerbillus* are sister species and are not members of a strict *Phyllotis* clade, 2) *Phyllotis* includes *amicus, andium,* and *gerbillus*, but not *wolffsohni*, 3) *Phyllotis* does not include *wolffsohni*, *amicus*, or *gerbillus*, 4) *Phyllotis* does not include those 3 plus *andium*, 5) the *darwini* species group comprises *P. darwini, P. caprinus, P. xanthopygus*, and *P. limatus*, to the exclusion of *P. magister* and *P. definitus* (except in a more inclusive clade), 6) *Graomys* and *Andalgalomys* form a clade.

In 1958, Pearson remarked that he preferred to focus on the taxonomic questions of species, subspecies, and their delimitation rather than more inclusive genus-level questions because it is there that “one deals with more tangible, less subjective evidence” (Pearson, 1958, p. 385). With the advent of cladistic methods and DNA sequence data on the one hand and the proliferation of species concepts (and a growing recognition of the amorphous nature of species) it seems that the situation is now reversed. Thus the subject of this paper is the more tangible delimitation of phylogenetic relationships among species and a reassessment of generic-level systematics of the genus *Phyllotis* and its phyllotine relatives.

Objectives

We assess the systematics of *Phyllotis* and its place within the phyllotines by analyzing new sequences for mitochondrial cyt *b* and nuclear RAG1. Using genes from both genomes, we achieve a less biased estimate of the phylogeny than might be achieved using mitochondrial data alone — mitochondria reflect maternal lines of inheritance only. We combine our new data with previously published cyt *b* sequences available from GenBank.

METHODS

Specimens Sequenced

We sequenced 101 specimens for cytochrome *b*, including 65 specimens representing 13 species (one of them undescribed) in the genus *Phyllotis*. In addition, 2 sequences of another undescribed species were contributed by Jayat et al. (This volume). Eighteen phyllotine species were added to clarify relationships within the tribe Phyllotini, including 5 species of the designated outgroup, *Calomys*. Locality information and GenBank accession numbers are listed in Appendix 1. We downloaded all available cyt *b* sequences for phyllotines (Steppan, 1998; Smith and Patton, 1999; Anderson and Yates, 2000; Salazar-Bravo et al., 2001; Catanesi et al., 2002; Kuch et al., 2002), but excluded some from this study in an effort to reduce computational time: only a partial survey of *Calomys* sequences were included because it would replicate analyses of Salazar-Bravo et al. (2001); there was little variation among *Graomys centralis* and *G. griseoflavus* from Catanesi et al. (2002); samples of *Auliscomys boliviensis* (AF387810) and *Andalgalomys olrogi* (AY070231) were identical and not closely related to congeners in either genus and thus their identity is questionable.

Sixty-nine specimens were sequenced for nuclear RAG1, representing 10 recognized species of *Phyllotis* and 2 undescribed species. Nine other phyllotine species, including 3 species of *Calomys*, were added in hopes of clarifying the relationships within the tribe Phyllotini.

DNA Extraction, Amplification, and Sequencing

Complete genomic DNA was extracted from frozen or EtOH-preserved tissue according to standard phenol/chloroform extraction techniques (Sambrook et al., 1989). We amplified the entire cytochrome *b* (cyt *b*) gene using polymerase chain reaction (PCR) with primers P484 and P485 (Steppan et al., 1999) or MVZ05 and MVZ14 (Smith and Patton 1999). This resulted in 1185 nucleotides, including 1144 in cyt *b* and 41 in the 3′ flanking tRNA. *Phyllotis osgoodi* was amplified in a small fragment from an extraction derived from a dried skin using primers L14925 and H15052 (Kuch et al., 2002), yielding a 127 bp fragment. DNA amplification was performed at 50μl reaction volumes containing 1 ng/μl whole genomic extract, 5 μl of 10X buffer, 3 μM $MgCl_2$, 2.5 μM of DMSO, 0.3 mM of dNTP, 2.5 μM of each primer and 0.03 U/μl of Amplitaq Gold (Perkin-Elmer) in buffer supplied by the manufacturer. Typical cycling conditions were initial denaturation at 94°C for 15 minutes followed by 40-45 cycles of denaturation (45s at 94°C), primer annealing (45s at 51°C), DNA extension (1 min 15s at 72°C), and a final extension for 6 min at 72°C. Five μl of amplification product for each sample were electrophoresed on a 1% TBE agarose gel, stained by ethidium bromide, and visualized with UV light. The products were purified by precipitation with polyethylene glycol (PEG) in saline (NaCl) and re-suspended in 25μL deionized water. DNA concentration was measured by UV absorption.

Sequencing was performed on double-stranded templates with ABI Big-dye terminator sequencing chemistry on ABI (Perkin Elmer) 373A and 3100 automated sequencers. All individuals were sequenced completely in both directions for the entire cyt *b* gene with the amplification primers and the following sequencing primers: B12p (Steppan, 1998), and P1185 (Steppan et al., 1999). Sequences were aligned with Sequencher 4.1 (Genecodes). There were no insertions or deletions (indels) allowing unambiguous alignment by eye.

We amplified a 1,000 or 1,300 base pair (bp) segment in the 5′ region of RAG1 using PCR techniques using 2 primer pairs S70/S105 (Steppan et al., 2004b) and S116/142 (AGATGTTTAGGGTGMGATCC and GAGGAAGGTRTTGACACGGATG, respectively). The smaller fragment falls entirely within and the larger fragment falls primarily within the more variable divergent domain (Fugmann et al., 2000; Steppan et al., 2004b). This divergent domain constitutes approximately the first 1,000 bp of these fragments, comprising the 5′ end. DNA amplification was performed at 50μl reaction volumes containing 2ng/μl whole genomic extract, 4mM $MgCl_2$, 2.5μM of DMSO, 0.3mM of dNTP, 2.5μM of each primer and 0.03 U/μl of Amplitaq Gold (Perkin-Elmer) in 1X Gold buffer supplied by the manufacturer. Typical cycling conditions were initial denaturation at 94°C for 12 min followed by 40 cycles of denaturation (45s at 94°C), primer annealing (45s at 52°C), DNA extension (1 min 30s at 72°C), and a final extension for 6 min at 72°C. Purification and sequencing for RAG1 were as for cyt *b* with one exception. When multiple polymorphic sites were detected in a sample (as evidenced on chromatograms by superimposed pairs of peaks, typically half-height, and confirmed by sequencing in both directions), PCR products were cloned using the pCR 2.1-TOPO vector. Three to 8 clones for each sample were sequenced with clone primer M13F. Alternative haplotypes were then determined. For sequences with only 1 heterozygous site, haplotypes were designated as the 2 alternative resolutions. Direct sequencing of PCR products used the amplification primers and internal primers S102 and S106 (Steppan et al., 2004b). Alignment of RAG1 was done by eye with reference to the protein sequence because RAG1 has no introns. One indel, consisting of a single amino acid, was detected.

Phylogenetic Analyses

Phylogenetic analyses were conducted on nucleotide sequences with equally weighted maximum-parsimony (MP), maximum likelihood (ML), and Bayesian methods. *Calomys* was designated as the outgroup based on prior mitochondrial (Engel et al., 1998; Smith and Patton, 1999), nuclear DNA (Steppan et al., 2004a), and morphological studies (Braun, 1993; Steppan, 1995). Individuals with identical haplotypes were consolidated into single OTUs for phylogenetic analyses. Maximum-parsimony and ML methods were conducted using the program PAUP* (Swofford, 2002). All MP analyses used heuristic searches with tree bisection-reconnection (TBR) branch swapping and 20 random-addition replicates. A sequential optimization approach (Swofford et al., 1996; Fratti et al., 1997) was used to estimate the cyt *b* ML phylogeny. Initial trees were generated by MP. The ML parameter values were estimated under a nested array of substitution models for the MP tree (Swofford et al., 1996; Fratti et al., 1997) as implemented in ModelTest 3.04 (Posada and Crandall, 1998). When reconstructing a phylogenetic tree, adding new parameters is not always justified and can lead to erroneous results (Nei and Kumar, 2000). For this reason it is important to choose the model for which each parameter contributes significantly to explain the data. Fourteen different nucleotide substitution models were evaluated for among-site variation under equal rates, a portion of the sites assumed to be invariable (I), rates among all sites assumed to vary according to a gamma distribution (Γ; Yang, 1994), and a combination of invariable sites and gamma-distributed rates. Because each of the models can be considered a special case of the most general, GTR + I + Γ, likelihood-ratio tests (LRT) can be used to test for significant differences in the contributions of each model parameter to explaining the data (Yang et al., 1995). Both the LRT and the Akaike Information Criterion (an alternative model selection method) selected the same model. The GTR + I + Γ was a significantly better fit for cyt *b* than simpler models. We then conducted a ML search using the preferred model with parameters fixed at the values estimated on the MP tree. Heuristic searches were conducted with 20 random-addition replicates and TBR branch swapping. Model parameters were re-estimated from the initial ML tree, and the process repeated until the topology of the re-estimated tree matched that of the tree from the previous search, never requiring more than one iteration.

Robustness of the results for both MP and ML was estimated by means of 200 bootstrap replicate searches (Felsenstein, 1985). MP bootstrap was limited to 400 maxtrees. Due to computational demands, the ML bootstrap analysis was done on a 40-processor cluster of computers using Condor job management, stepwise addition with 5 random addition sequence for each replicate, TBR branch-swapping, and each addition sequence replicates restricted to a 3,000 rearrangement limit.

Bayesian analyses were conducted with MrBayes 3.01 (Huelsenbeck and Ronquist, 2003). Bayesian analysis used the GTR + I + Γ model as in the ML analyses. We conducted a Metropolis-Coupled Markov chain Monte Carlo (MCMC) analysis with 4 chains, with a heating parameter of 0.2, for 7,000,000 generations, sampling trees every 100 generations. The likelihood converged on a stable value by 50,000 generations and clade frequencies, examined in successive 200,000 generation bins, stabilized by 1 million generations. We excluded the first 2 million generations from the sampling (as the "burn-in" period).

For RAG1, we followed the procedures for cyt *b* with the following differences. The HKY85 + I model (unequal base-frequencies, different transition and transversion rates) was a significantly better fit for RAG1 than simpler models, and more complicated models would result in over-parameterization of the data. Bootstrapping with maximum likelihood used 3 random addition sequence replicates and a 2,000 rearrangement limit. Bayesian analysis used the HKY85 + I model as in the ML analyses. We ran 4 MCMC chains, with a heating parameter of 0.2, for 10,000,000 generations, partitioning the data by codon position (i.e., each codon position had parameters estimated separately), sampling trees every 300 generations. The likelihood converged on a stable value by 50,000 generations, and we excluded the first 2 million generations from the sampling (as the "burn-in" period).

The mitochondrial and nuclear data sets were analyzed separately and not combined because many individuals were heterozygous for RAG1. Given some evidence of possible introgression or incomplete lineage sorting (see Results), cyt *b* and RAG1 must be viewed as independently assorting loci that would be expected to have different evolutionary histories. The assumption of phylogenetic methods that operational taxonomic units (OTUs, in this case individuals) are monophyletic would be violated for RAG1 as would be the assumption that characters coded for OTUs share identical genealogies (i.e., OTUs not hybrids), making it invalid to concatenate the data from the 2 genes.

RESULTS

Phyllotine Phylogenetics

As expected, the mitochondrial data were much more variable than the nuclear. For cyt *b*, 478 of 1185 characters were parsimony informative whereas only 68 out of 1334 were so for RAG1. After the divergence of *Calomys*, the basal split among the phyllotines sampled here, based on cyt *b* sequences, are the clade of *Graomys* and *Eligmodontia* on one branch and remaining phyllotines on the other. Support for these 2 clades was weak, with only 31/35% ML and 42/41% MP bootstrap values on the respective branches (Figs. 2 and 3). Bayesian analysis gave a slightly different picture, providing little support for the *Graomys*/*Eligmodontia* clade (the group was most likely paraphyletic because *Eligmodontia* is the sister-group to the remaining phyllotines with 0.55 posterior probability (pp)), but somewhat surprisingly, monophyly of the second clade was strongly supported (pp = 1.00). In either case, cyt *b* data did not support a close relationship between *Graomys* and *Andalgalomys*. The RAG1 data were equivocal regarding the latter point, yielding a polytomy for this region of the tree (Fig. 4) but supporting a *Graomys*/*Andalgalomys* clade in 55% of MP bootstrap replicates. We lacked RAG1 data for several key taxa, including *Eligmodontia* and *Salinomys*, and their inclusion could easily break up the *Graomys*/*Andalgalomys* clade. RAG1 data provided support for a *Phyllotis* group that included *Auliscomys*, *Loxodontomys*, and *"P." wolffsohni* (see comment below) with 75% ML bootstrap. Bootstrap values for RAG1 were higher than for cyt *b* in the deeper regions of the tree, while much lower near the tips.

The cyt *b* data weakly supported a monophyletic *Auliscomys*, with ML and Bayesian trees showing *A. pictus* and *A. sublimis* as sister taxa (Fig. 2; 61%, 0.95 pp) whereas MP separated them (Fig. 3). Although the optimal cyt *b* trees place *Loxodontomys* close to *Auliscomys* (or just to *A. pictus*), in agreement with traditional arrangements, that support was very weak and the clade was not present in the RAG1 tree (Fig. 4). The same lack of support for intergeneric relationships was seen throughout the basal portions of the phyllotine tree. The one well-supported clade was that consisting of *Tapecomys* and *"P." wolffsohni*. Based on cyt *b* (*Tapecomys primus* was not sequenced for RAG1) this clade received 100% bootstrap and posterior probabilities in all analyses. The placement of the *Tapecomys*/*P. wolffsohni* clade was relatively unstable as well, being associated either with *Auliscomys*/*Loxodontomys* (cyt *b* ML, Fig. 2), *Andalgalomys*/

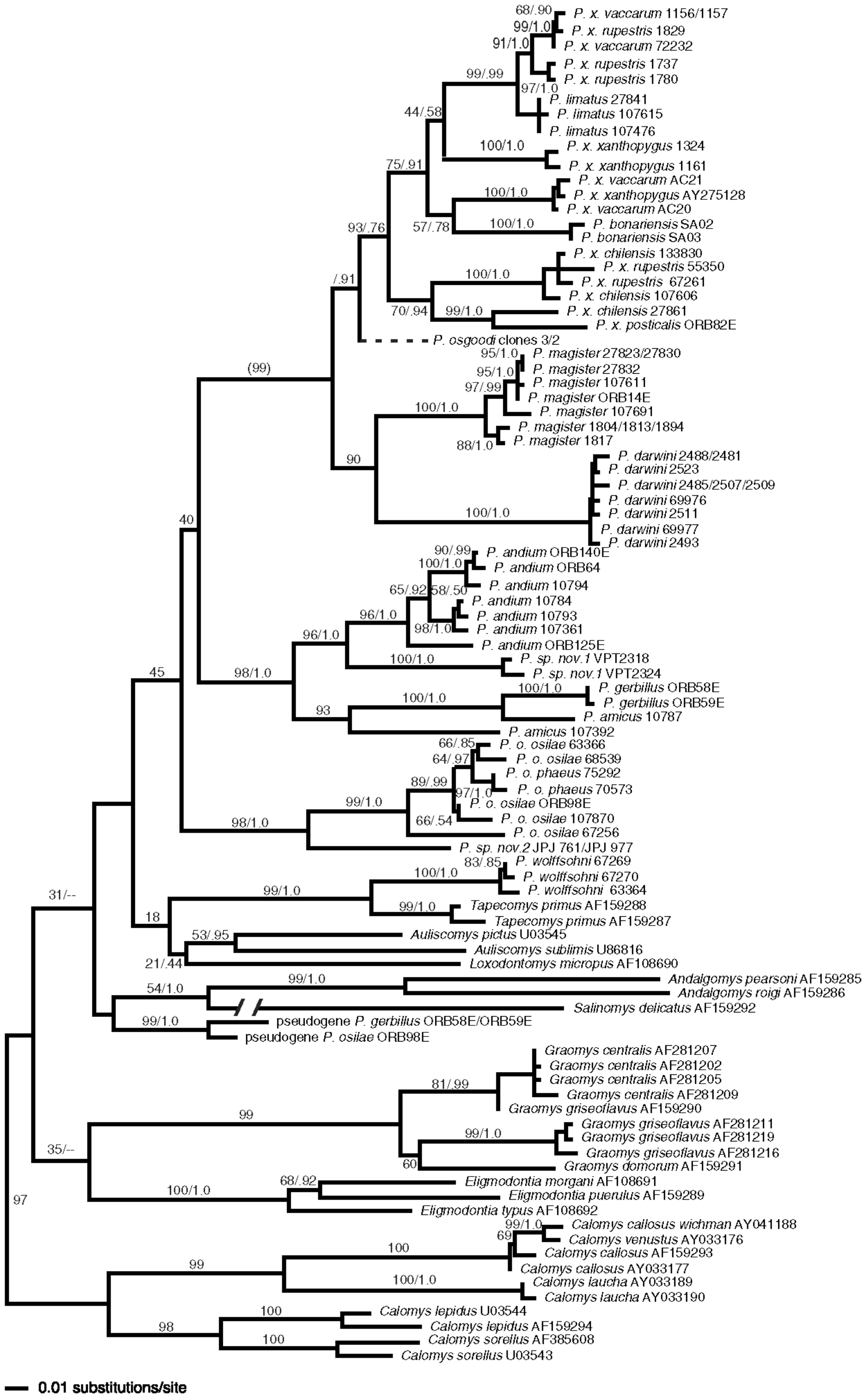
68/.90
P. x. vaccarum 1156/1157
99/1.0
P. x. rupestris 1829
91/1.0
P. x. vaccarum 72232
P. x. rupestris 1737
99/.99
P. x. rupestris 1780
97/1.0
P. limatus 27841
44/.58
P. limatus 107615
P. limatus 107476
100/1.0
P. x. xanthopygus 1324
75/.91
P. x. xanthopygus 1161
P. x. vaccarum AC21
100/1.0
P. x. xanthopygus AY275128
P. x. vaccarum AC20
100/1.0
P. bonariensis SA02
93/.76
57/.78
P. bonariensis SA03
P. x. chilensis 133830
100/1.0
P. x. rupestris 55350
/.91
P. x. rupestris 67261
P. x. chilensis 107606
70/.94
99/1.0
P. x. chilensis 27861
P. x. posticalis ORB82E
P. osgoodi clones 3/2
95/1.0
P. magister 27823/27830
(99)
95/1.0
P. magister 27832
P. magister 107611
97/.99
P. magister ORB14E
100/1.0
P. magister 107691
P. magister 1804/1813/1894
88/1.0
P. magister 1817
P. darwini 2488/2481
90
P. darwini 2523
P. darwini 2485/2507/2509
P. darwini 69976
40
100/1.0
P. darwini 2511
P. darwini 69977
P. darwini 2493
90/.99
P. andium ORB140E
100/1.0
P. andium ORB64
P. andium 10794
65/.92
58/.50
P. andium 10784
96/1.0
P. andium 10793
98/1.0
P. andium 107361
96/1.0
P. andium ORB125E
100/1.0
P. sp. nov.1 VPT2318
45
98/1.0
P. sp. nov.1 VPT2324
100/1.0
P. gerbilus ORB58E
100/1.0
P. gerbilus ORB59E
93
P. amicus 10787
P. amicus 107392
66/.85
P. o. osilae 63366
64/.97
P. o. osilae 68539
P. o. phaeus 75292
89/.99
P. o. phaeus 70573
99/1.0
97/1.0
P. o. osilae ORB98E
98/1.0
66/.54
P. o. osilae 107870
P. o. osilae 67256
P. sp. nov.2 JPJ 761/JPJ 977
83/.85
P. wolffsohni 67269
100/1.0
P. wolffsohni 67270
31/--
99/1.0
P. wolffsohni 63364
99/1.0
Tapecomys primus AF159288
18
Tapecomys primus AF159287
53/.95
Auliscomys pictus U03545
Auliscomys sublimis U86816
21/.44
Loxodontomys micropus AF108690
99/1.0
Andalgomys pearsoni AF159285
54/1.0
Andalgomys roigi AF159286
Salinomys delicatus AF159292
99/1.0
pseudogene P. gerbilus ORB58E/ORB59E
pseudogene P. osilae ORB98E
Graomys centralis AF281207
Graomys centralis AF281202
Graomys centralis AF281205
81/.99
Graomys centralis AF281209
Graomys griseoflavus AF159290
99
Graomys griseoflavus AF281211
99/1.0
Graomys griseoflavus AF281219
35/--
Graomys griseoflavus AF281216
60
Graomys domorum AF159291
68/.92
Eligmodontia morgani AF108691
100/1.0
Eligmodontia puerulus AF159289
97
Eligmodontia typus AF108692
99/1.0
Calomys callosus wichman AY041188
69
Calomys venustus AY033176
100
Calomys callosus AF159293
99
Calomys callosus AY033177
100/1.0
Calomys laucha AY033189
Calomys laucha AY033190
100
Calomys lepidus U03544
98
Calomys lepidus AF159294
100
Calomys sorellus AF385608
Calomys sorellus U03543
0.01 substitutions/site

Figure 2 (facing page). Maximum likelihood phylogram of cyt b sequences using the GTR+Γ+I model of evolution. *Calomys* is designated the outgroup. The branch leading to *Salinomys* has been shortened to precisely 1/2 the actual length for visual clarity. Numbers above branches are bootstrap percentages and Bayesian posterior probabilities. The bootstrap percentage in parentheses was estimated from analyses excluding the short *P. osgoodi* sequence; the provisional nature of the placement of that sequence is indicated by the dashed branch leading to *P. osgoodi*. Taxon names are followed by specimen or accession number. Numbers beginning in "AF," "AY," or "U" are GenBank accessions. Some bootstrap values less than 50% or posterior probabilities less than 0.50 are deleted.

Salinomys (cyt *b* MP, Fig. 3), or near the base of Phyllotini (as represented by *wolffsohni*, RAG1, Fig. 4). After exclusion of *wolffsohni*, the remaining species of *Phyllotis* formed a moderately supported clade (42% ML and 36% MP bootstrap but 1.00 pp).

We detected a presumptive nuclear pseudogene copy (numt) of a portion of cyt *b* in *P. osilae* and both individuals of *P. gerbillus* as evidenced by the presence of internal stop codons, a frame shift deletion, high proportion of non-synonymous substitutions, and very short branches on the ML tree. The placement of this pseudogene clade at the base of the "*Phyllotis* group" and the ratio of terminal to internal branch lengths indicate that transfer of a copy to the nucleus occurred early in phyllotine history. Therefore, other species in that generic group likely contain the pseudogene as well. The pseudogene was preferentially amplified in these 2 taxa when using the primer pair P484/P1185 but was never amplified using the cyt *b* flanking pair P484/P485.

Relationships within *Phyllotis*

Relationships within genera generally were better supported than those among genera. Within *Phyllotis* sensu stricto 3 major cyt *b* clades were evident: an *osilae* group that includes the undescribed species from Argentina (*Phyllotis* sp. nov. 2), an *andium*/*amicus* group that includes *P. gerbillus* and the undescribed species from Peru (*Phyllotis* sp. nov. 1), and the *darwini* species group. Monophyly of each of these 3 groups was well supported (67-93% MP bootstrap, 76-98% ML bootstrap, 0.91-1.00 pp). Support values for the *darwini* group were moderate when the short (127 bp) *P. osgoodi* sequence was included but high when it was excluded (e.g., MP bootstrap rises from 67% to 100%).

Within the *andium* group there appear to be 2 species pairs: *P. gerbillus* with *P. amicus* and *P. andium* with *Phyllotis* sp. nov. 1. Monophyly of both species pairs was moderately to well supported. *Phyllotis amicus* appears to be paraphyletic based on both cyt *b* and RAG1. Specimens of *P. amicus* from Lima, Peru (MUSN 10787, MUSN 10789) are much more closely related to *P. gerbillus* than to *P. amicus* (FMNH 107392). After re-examination, all voucher specimens appear to have been properly identified (*P. amicus (*FMNH 107392) from Arequipa, Peru was not re-examined for this study) and the 2 Lima *P. amicus* specimens clearly are not *P. gerbillus*, although specimen MUSN 10789 has relatively small incisors more similar to *P. gerbillus* than typical *amicus*. RAG1 optimal trees did not include a monophyletic *andium* group but all members of that group shared a single amino acid insertion that is the only insertion or deletion among phyllotines and was not seen in any of the other 140 muroid rodent species we have sequenced (Steppan et al., 2004a, unpublished data).

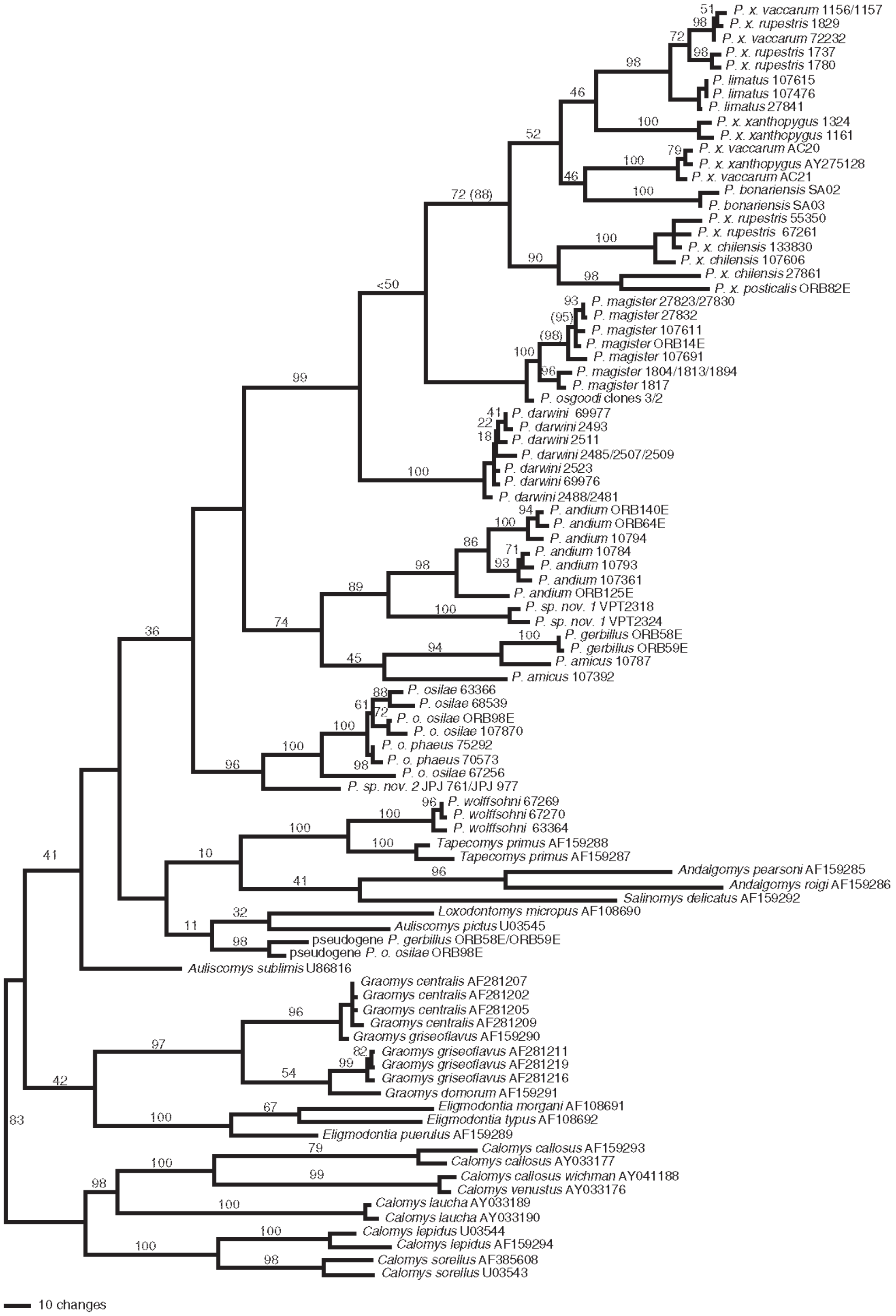
51
P. x. vaccarum 1156/1157
98
P. x. rupestris 1829
72
P. x. vaccarum 72232
98
98
P. x. rupestris 1737
P. x. rupestris 1780
P. limatus 107615
P. limatus 107476
P. limatus 27841
46
100
P. x. xanthopygus 1324
P. x. xanthopygus 1161
52
79
P. x. vaccarum AC20
100
P. x. xanthopygus AY275128
46
P. x. vaccarum AC21
100
P. bonariensis SA02
72 (88)
P. bonariensis SA03
P. x. rupestris 55350
100
P. x. rupestris 67261
P. x. chilensis 133830
90
P. x. chilensis 107606
98
P. x. chilensis 27861
<50
P. x. posticalis ORB82E
93
P. magister 27823/27830
(95)
P. magister 27832
P. magister 107611
(98)
P. magister ORB14E
100
P. magister 107691
96
P. magister 1804/1813/1894
99
P. magister 1817
P. osgoodi clones 3/2
41
P. darwini 69977
22
P. darwini 2493
18
P. darwini 2511
P. darwini 2485/2507/2509
100
P. darwini 2523
P. darwini 69976
P. darwini 2488/2481
94
P. andium ORB140E
100
P. andium ORB64E
P. andium 10794
86
71
P. andium 10784
93
P. andium 10793
98
P. andium 107361
89
P. andium ORB125E
100
P. sp. nov. 1 VPT2318
74
P. sp. nov. 1 VPT2324
36
100
P. gerbillus ORB58E
94
P. gerbillus ORB59E
45
P. amicus 10787
P. amicus 107392
88
P. osilae 63366
61
P. osilae 68539
72
P. o. osilae ORB98E
100
P. o. osilae 107870
100
P. o. phaeus 75292
P. o. phaeus 70573
96
98
P. o. osilae 67256
P. sp. nov. 2 JPJ 761/JPJ 977
96
P. wolffsohni 67269
100
P. wolffsohni 67270
100
P. wolffsohni 63364
41
100
Tapecomys primus AF159288
10
Tapecomys primus AF159287
96
Andalgomys pearsoni AF159285
41
Andalgomys roigi AF159286
Salinomys delicatus AF159292
32
Loxodontomys micropus AF108690
11
Auliscomys pictus U03545
98
pseudogene P. gerbillus ORB58E/ORB59E
pseudogene P. o. osilae ORB98E
Auliscomys sublimis U86816
Graomys centralis AF281207
Graomys centralis AF281202
96
Graomys centralis AF281205
Graomys centralis AF281209
Graomys griseoflavus AF159290
97
82
Graomys griseoflavus AF281211
99
Graomys griseoflavus AF281219
42
54
Graomys griseoflavus AF281216
Graomys domorum AF159291
67
Eligmodontia morgani AF108691
83
100
Eligmodontia typus AF108692
Eligmodontia puerulus AF159289
79
Calomys callosus AF159293
100
Calomys callosus AY033177
99
Calomys callosus wichman AY041188
98
Calomys venustus AY033176
100
Calomys laucha AY033189
Calomys laucha AY033190
100
Calomys lepidus U03544
100
Calomys lepidus AF159294
98
Calomys sorelius AF385608
Calomys sorelius U03543
10 changes

Figure 3 (facing page). Maximum parsimony phylogram of cyt b sequences, one random tree of 970 equally parsimonious trees, each 3330 steps long. The only nodes to collapse in the strict consensus are within tip local-population level clades within species. Numbers above branches are bootstrap proportions. Numbers in parentheses were estimated from analyses excluding the short *P. osgoodi* sequence.

The *darwini* species group was well supported by cyt *b* (99% MP bootstrap, 99% ML bootstrap) but not directly by RAG1 (Fig. 4). Based on cyt *b*, it includes *P. darwini, P. magister, P. osgoodi,* the geographically widespread *P. xanthopygus*, and 2 peripheral species that are embedded in a *xanthopygus* complex, *P. limatus* and *P. bonariensis*. Parsimony and likelihood disagreed regarding the relationships among some of the species. Parsimony placed *P. magister* (plus *P. osgoodi*) as the sister group to the *xanthopygus* complex (Fig. 3), rather than as the sister species to *P. darwini*, as did ML (Fig. 2) and RAG1 (Fig. 4). The ML RAG1 tree indicated that 2 specimens of *P. darwini* (LCM 2493, 27558) possessed an allele that was otherwise characteristic of *P. magister*, suggesting introgression, but this result was not stable. MP did not resolve the relationship of this allele to either species (forming a trichotomy) and the allele in question was placed in a *P. darwini* clade in 52% of ML bootstrap replicates. *Phyllotis osgoodi*, for which we have only 127 bp of cyt *b* sequence, is closely related to either the *xanthopygus* complex (ML) or to *P. magister* (MP).

The *xanthopygus* complex is very diverse genetically, with up to 19% sequence divergence for cyt *b* among populations (GTR+Γ+I ML distances). *Phyllotis darwini* and *P. magister* exhibited very little diversity in contrast (1.4% and 3.35% maximum ML sequence divergence respectively), and *P. andium* and *P. osilae* exhibited intermediate genetic diversity (6.3% and 9.1% maximum ML sequence divergence respectively). Two groups were evident within the *xanthopygus* complex based on both genes -- a northern/altiplano group comprised of *P. xanthopygus posticalis, P. x. chilensis,* and some *P. x. rupestris*, and a widespread, lower elevation clade comprised of *P. limatus, P. bonariensis, P. x. xanthopygus, P. x. vacarrum,* and some *P. x. rupestris*.

DISCUSSION

Phyllotine Systematics

Data from cytochrome *b* appears to be insufficient to resolve many of the branching events within Phyllotini. The data from the nuclear gene RAG1 corroborate some of the cyt *b* findings but weakly conflict in other areas, suggesting that some of the internal branches are short enough that differential lineage sorting may have occurred, resulting in incongruence between gene trees and species trees. We thus interpret the results in these regions with greater caution than the support values would themselves suggest. The balance of evidence suggests that there is a *Phyllotis* group that contains *Auliscomys, Loxodontomys*, probably *Tapecomys*, and possibly the *Andalgalomys/Salinomys* clade. Previous molecular studies have clearly demonstrated that, contrary to morphological studies by Steppan and coworkers (Steppan, 1995; Steppan and Pardiñas, 1998; Ortiz et al., 2000), *Reithrodon* and *Euneomys* (and probably *Neotomys* as well) do not belong in this group (Engel et al., 1998; Smith and Patton, 1999; D'Elía, 2003; Weksler, 2003;

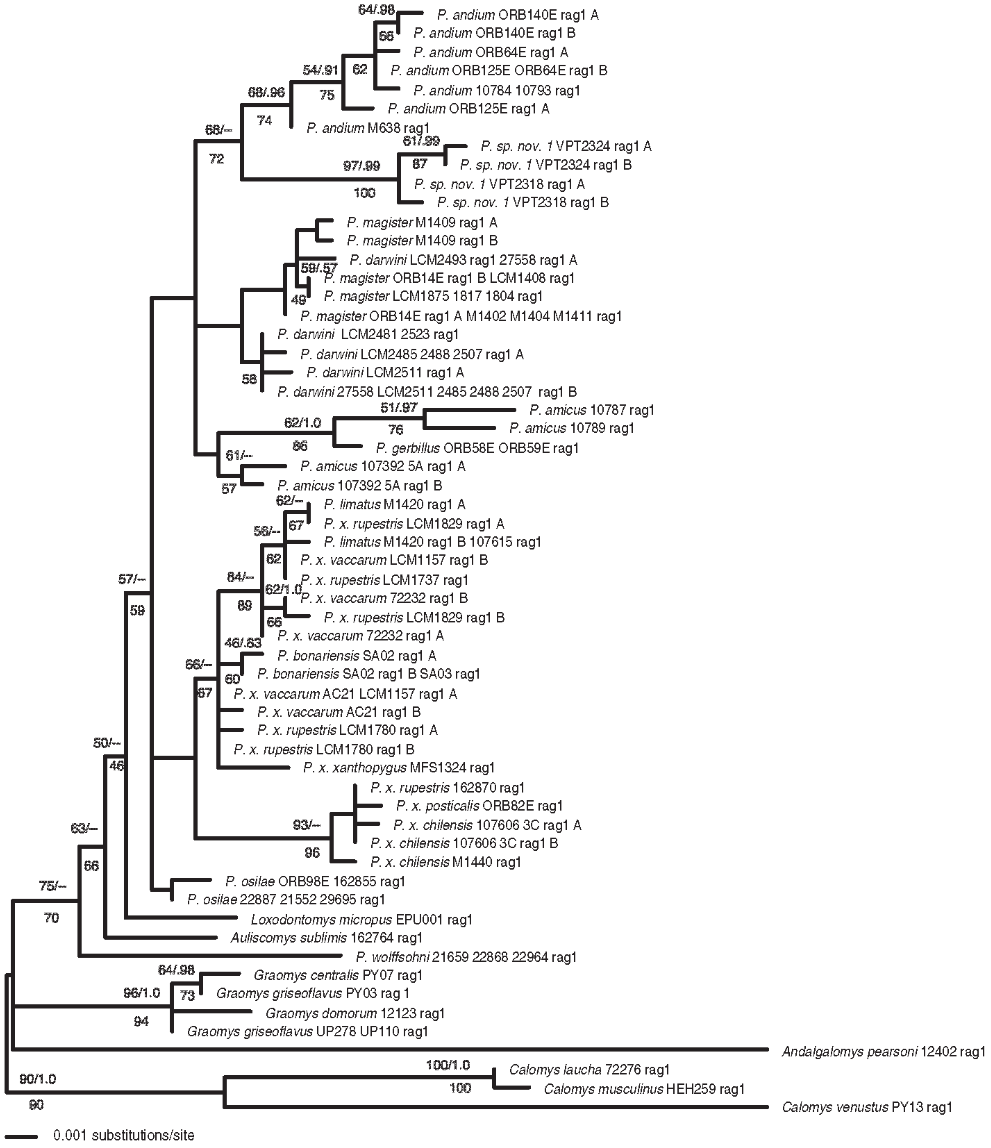

Figure 4. Maximum likelihood phylogram of RAG1 sequences, one of 4 trees with -L = 3055.77. Differences among the optimal trees are limited to rearrangements within *P. magister*. "A" and "B" refer to the 2 alleles when individuals are heterozygous. Numbers above branches are bootstrap proportions (>50%) and Bayesian posterior probabilities (>0.50). Numbers below branches are MP bootstrap proportions.

Steppan et al., 2004a). *Graomys* does not appear to be a member of the *Phyllotis* group and may be most closely related to *Eligmodontia*. It also does not appear to be most closely related to *Andalgalomys*, contrary to the morphological results of Braun (1993) and Steppan (1993; 1995; but cf. Steppan and Sullivan, 2000).

Perhaps the strongest conclusion from these results is that *wolffsohni* should be removed from *Phyllotis* and placed in *Tapecomys*. The monophyly of this clade is strongly supported in all analyses. Although we lack RAG1 data for *Tapecomys primus*, *wolffsohni* still falls well outside a *Phyllotis* clade. The association between these 2 species is not that surprising. They share several derived morphological features (e.g., ridged and posteriorly divergent interorbital region) but more significantly, they have nearly identical karyotypes that are distinct from all other phyllotines. Anderson and Yates (2000) noted this but attributed the similarity to convergence. Evidence that the 2 taxa are distinct species comes from their reciprocal monophyly, genetic distances similar to other species pairs, and the fact that they were clearly distinguishable in a morphological phylogeny (*Tapecomys primus* was listed as *species nova* in Steppan, 1993).

After removal of *wolffsohni*, *Phyllotis* appears monophyletic. There is no support for *Paralomys*, either consisting of *amicus* and *gerbillus* (Braun, 1993; Nowak, 1999) or *gerbillus* alone (Cabrera, 1961). Recognition of *Paralomys* would require removal of *andium* from *Phyllotis* as well as elevation of the *osilae* clade to generic status.

Systematics of *Phyllotis*

We included 2 undescribed species in this study, one of which is closely related to *P. andium* and the other closely related to *P. osilae*. Notably, *Phyllotis* sp. nov. 1 from Peru has a long branch for RAG1, and the 2 individuals are distinguished from *P. andium* by 6 apomorphic changes (4 unique synapomorphies for *Phyllotis.* sp. nov. 1 and 2 unique synapomorphies shared by all *P. andium*), providing evidence that this is not just a local population of *P. andium*. Even after the removal of *wolffsohni*, the number of species in *Phyllotis* increases to at least 15. There may be additional "cryptic" species in *Phyllotis*, that is, taxa recognized first by DNA and for which we have not yet identified phenotypic differences. The possible paraphyly of *P. amicus* suggests one case and the deep divergences within the paraphyletic *xanthopygus* complex suggest another. It is notable that the genetic differences between *P. gerbillus* and 2 of the *P. amicus* (which come from Lima within previous estimates of the known range) is less than that seen within most species, and the location of the other *P. amicus* (FMNH 107392) is in Arequipa Province, nearly 400 km SE of the previously known southern limits of *P. amicus* (Hershkovitz, 1962). This raises the possibility that FMNH 107392 is a new species and that the marked pelage and dental characters that make *P. gerbillus* the most derived species in the genus (and formed the basis for removal to its own genus *Paralomys*) have evolved only recently, perhaps within the last 1 MY. The issue involving the *xanthopygus* complex will be analyzed in more detail elsewhere (Albright et al., unpubl. ms.).

The systematics of *P. gerbillus* have been particularly uncertain. Our results suggest that this specialized coastal desert species is derived from the nearby and similar sized *P. amicus*. Together these 2 species are the sister group to another northern species pair, *P. andium* and *Phyllotis* sp. nov. 1.

Our data are unable to resolve the basal relationships within the *darwini* species group. Maximum likelihood for cyt *b* and RAG1 favor a close relationship between *P. darwini* and *P. magister*, both Pacific slope species from central Chile and northern Chile to central Peru, respectively (Fig. 1). Both of these species exhibit little genetic diversity, even though the geographic sampling is fairly extensive. For *P. magister*, we have samples spanning nearly the entire latitudinal range, covering 800 km. The genetic diversity within *P. magister* or *P. darwini* is much less than that seen in *P. xanthopygus*.

Problematic Sequences

We identified several sequences on GenBank that seemed out of place phylogenetically or had unusual characteristics. The cyt *b* sequence for *Salinomys* was divergent and was estimated by likelihood to have a very long branch leading to it (Fig. 2). The branch leading to *Salinomys* appears to have 3-5 times the average amino acid substitution rate for phyllotines and is the only sequence included in this study to have an unusually long branch (unpubl. analysis). Given that this mouse lives around salt flats (Braun and Mares, 1995), a very unusual and physiologically demanding environment for rodents, it would be interesting to determine whether the unusual sequence characteristics were caused by adaptation or sequencing errors. We cannot exclude the alternative possibility that this sequence might be a numt (nuclear copy of a mitochondrial gene), although in that case we would expect a short terminal branch because of a reduced rate of third-position substitutions.

Our analyses also detected a probable taxonomic problem with *Graomys* that likely is due to changing taxonomy and the separation of *G. centralis* from *G. griseoflavus*. The Bolivian *G. griseoflavus* sequence from Anderson and Yates (2000) groups closely with Argentine specimens that Catanesi et al. (2002) elevated to *G. centralis* based on karyotype differences. Interestingly, the *G. domorum* of Anderson and Yates (2000) is more closely related to the *G. griseoflavus* of Catanesi et al. (2002) than to their own "*griseoflavus*," but diverges near the base of the genus. This suggests that the old concept of *G. griseoflavus* may have been composite. Unfortunately, Catanesi et al. (2002) did not make morphological comparisons of their 2 karyotype groups to museum specimens or the type specimens, and Anderson and Yates (2000) did not report their karyotypes, so the resolution of this question awaits further study. These data do support the presence of at least 3 species in *Graomys*.

Finally, re-sequencing the specimens from Steppan (1998) detected errors in several published sequences. Most of these were minor random errors that did not affect the topology, and updates have been submitted to GenBank. However, the published sequence for *P. osgoodi*, amplified from a dried skin fragment, was found to be a composite of 2 contaminating sequences; a *P. osilae* and a *P. limatus*. The hybrid nature of the sequence resulted in a most parsimonious placement of "*osgoodi*" in an intermediate basal position on the tree, not far from where the new cloned sequences suggest it might actually belong. However, our sequence is still very short and should be confirmed with fresh tissue samples. Although the unstable resolution of *A. sublimis* (which was not re-sequenced) suggests that it might contain sequencing errors, data from several nuclear genes and another individual indicate that the uncertainty from cyt *b* may correctly reflect the absence of many synapomorphies because of very short internodes (Steppan and Adkins, unpubl. data).

Biogeography and Dating

Phylogenetic relationships among genera are too uncertain to confidently propose biogeographic patterns. Within *Phyllotis*, the 3 primary clades are distributed on the eastern slopes of the Andes (*P. osilae* and *Phyllotis* sp. nov. 2), northwestern Peru (*andium*/*gerbillus* clade), and the more widespread *darwini* group, absent only from the northern areas. It is unclear whether *P. darwini* and *P. magister* represent sequential Pacific-slope sister-groups to the *xanthopygus* complex. If they were sequential sister-groups, that would support a "bathtub" model of peripheral-isolate speciation in the clade. In that model, successive range expansions of the ancestral *xanthopygus* complex would result in sequential colonization of the Pacific-slope region followed by speciation and eventual reciprocal monophyly between the Pacific-slope isolate and the widespread ancestor. The bathtub metaphor suggests *P. xanthopygus* "spilling over" the confining Andes.

We have not employed a tree-wide molecular clock despite failing to reject a clock model for cyt *b* (after excluding *Salinomys*; $-L_{\text{clock}} = 14{,}261.2$, $-L_{\text{unconstrained}} = 14{,}185$; $p_{(d.f.\ 176)} \approx 0.1$) because we are not confident that fossil calibrations using sigmodontines can be placed accurately enough on the phylogeny to avoid overconfidence in and over-interpretation of the resulting dates. Salazar-Bravo et al. (2001) used an *Auliscomys*/*Loxodontomys* divergence of 4 Mya (based on the first fossil occurrence of *Auliscomys formosus*) and a global clock to derive a time scale of *Calomys* evolution. They estimated that *Calomys* radiated around 8 Mya, and diverged from other phyllotines at 10-12 Mya (i.e., *A. formosus* is 33-40% of the age of the phyllotines). These estimates are somewhat at odds with a nuclear gene-based estimate that would place the *Calomys*/phyllotine split between 4.0-5.5 (the range of molecular clock and relaxed-clock estimates ± 1 sd, based on a revised *Mus-Rattus* divergence at 9.5 Mya; Steppan et al., 2004a) and the earlier South American radiation of sigmodontines at 7.6 Mya. We caution that there do not appear to be definitive apomorphies that place *A. formosus* in a clade with extant *Auliscomys*, nor that would unequivocally place it in a more-inclusive clade along with *Loxodontomys*. Thus, the common ancestor of *Auliscomys* and *Loxodontomys* could have lived several My before or after *A. formosus*. We also note that the *Auliscomys*/*Loxodontomys* clade has relatively short branches, suggesting that lower evolutionary rates there may result in overestimating divergence dates when extrapolated elsewhere on the tree. The *Mus-Rattus* calibration used by Steppan et al. (2004a) is much better constrained, although possibly too distant phylogenetically to apply to cyt *b* data with confidence. Using a *Mus-Rattus*-based ML rate for cyt *b* of 7.3% divergence per My (Steppan et al., 2003), we approximate the following divergences: basal split in Phyllotini at 4.8-7.4 Mya (minimum-maximum point estimates), basal split in *Calomys* at 4.5 Mya (mean), *A. pictus*/*Loxodontomys* at 3.0 Mya, *Tapecomys primus* vs. *wolffsohni* at 1.5 Mya (mean), basal split in *Phyllotis* at 3.0-5.1 Mya (range), basal split in *P. xanthopygus* at 1.6-2.3 Mya (range). Thus a revised *Mus-Rattus* calibration yields dates in Phyllotini that are younger than estimated by Salazar-Bravo et al. (2001), and with a slightly different distribution (e.g., the *Auliscomys-Loxodontomys* split is 41-62% as old as the ancestral phyllotine rather than 33-40%). Each of these dates should be viewed as having considerable errors associated with them and a tree-based bayesian approach yielded older dates (unpubl. data). Clearly, better fossil calibrations are needed.

CONCLUSIONS

Our analyses based on both mitochondrial and nuclear genes have clarified some relationships among phyllotine genera and refined our concept of *Phyllotis*. Notably, *Graomys* and *Eligmodontia* do not appear to be members of a clade that includes *Phyllotis* and *Auliscomys*, and *wolffsohni* should be removed from *Phyllotis* and placed in *Tapecomys*. The data do not support recognition of *Paralomys* because the type (*P. gerbillus*) is closely related to 3 other northwestern species (*andium, amicus*, sp. nov. 1) that together fall within *Phyllotis*. The *darwini* species-group is supported by cyt *b* data, and within that group, the widespread species *xanthopygus* is characterized by deep divergences, large genetic diversity, and paraphyly with respect to at least 2 morphological species, *limatus* and *bonariensis*. The data allow us to place 2 undescribed species fairly precisely. Finally, our application of different calibrations and methods suggests that phyllotine divergence dates estimated by Salazar-Bravo et al. (2001) may be too old.

ACKNOWLEDGMENTS

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APPENDIX 1: SPECIMEN LOCALITIES

Abbreviations: FMNH, Field Museum of Natural History; LCM, Laboratorio de Citogenética de Mamíferos, Universidad de Chile; LSUMZ, Louisiana Sate University, Museum of Zoology; MFS, collection of Margaret F. Smith, Museum of Vertebrate Zoology, University of California. MSB, Museum of Southwestern Biology, University of New Mexico; MUSN, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Perú; ORB, collection of Oswaldo Ramirez-Baca; UWBM, University of Washington, Burke Museum; UP, PY, EUP, SA, AC, JPJ, collections of U. F. J. Pardiñas; VPT, collection of Victor Pacheco-Torres. Accession numbers in parentheses are for nuclear psuedogenes.

Species Name	Voucher Information	Locality	cyt *b* GenBank Accession#	rag1 GenBank Accession#
Andalgomys pearsoni	MSB 55245	BOLIVIA. Santa Cruz: 29.5 km W Roboré.		AY963176
Auliscomys sublimis	FMNH 162764	BOLIVIA. Oruro: Escuela Seccional Villa Ventilla, 181 km S Oruro.		AY963182
Calomys laucha	UWBM 72276	ARGENTINA. Buenos Aires: 30 km SW La Plata, Punta Blanco.		AY963173
Calomys musculinus	UWBM 72233	ARGENTINA. Mendoza: 49.2 km N central Mendoza.		AY963175
Calomys venustus	PY 13	ARGENTINA. San Luis: Papagayos.		AY963174
Graomys centralis	PY 07	ARGENTINA. San Luis: Papagayos.		AY963177
Graomys domorum	MSB 55291	BOLIVIA. Santa Cruz.		AY963178
Graomys griseoflavus	UP 110	ARGENTINA. San Luis: San Francisco del Monte de Oro.		AY963180
Graomys griseoflavus	UP 278	ARGENTINA. Chubut: Playa Fracasso.		AY963179
Graomys griseoflavus	PY 03	ARGENTINA. San Luis: Papagayos.		AY963181
Loxodontomys micropus	EUP001	ARGENTINA. Neuquen: Laguna Epulaufquen.		AY963183
Phyllotis amicus	FMNH 107392	PERU. Arequipa: Caraveli, 1 km SW Atiquipa.	U86817	AY963209/ AY963210
Phyllotis amicus	MUSN 10787	PERU. Lima: R.N. Chancay, Lachay, Quebrada Teatrino.	AY956708	AY963207
Phyllotis amicus	MUSN 10789	PERU. Lima: R.N. Chancay, Lachay, Quebrada Teatrino.		AY963208

Phyllotis andium	MUSN 10784	PERU. Lima: Canta, Sachaqui.	AY956705	AY963203
Phyllotis andium	MUSN 10793	PERU. Lima: Huarochiri, Bosque de Zarate.	AY956706	AY963204
Phyllotis andium	MUSN 10794	PERU. Lima: Oyon, Oyon.	AY956704	
Phyllotis andium	FMNH 107361	PERU. Lima: Lima, Santa Eulalia Canyon, 1/2 mile NNE of Huinco.	U86818	
Phyllotis andium	LSUMZ 26949	PERU. Piura: Cruz Blanca, 33 km SW Huancabamba.		AY963202
Phyllotis andium	ORB 64	PERU. Ancash: Macate.	AY956703	AY963196/ AY963199
Phyllotis andium	ORB 125	PERU. Cajamarca: Cumbemayo.	AY956707	AY963197/ AY963198
Phyllotis andium	ORB 140	PERU. Ancash: Recuay.	AY956702	AY963200/ AY963201
Phyllotis bonariensis	SA 02	ARGENTINA. Buenos Aires: Parque Provincial Ernesto Tornquist, Abra de la Ventana.	AY956731	AY963250/ AY963251
Phyllotis bonariensis	SA 03	ARGENTINA. Buenos Aires: Parque Provincial Ernesto Tornquist, Abra de la Ventana.	AY956732	AY963252
Phyllotis darwini	MSB 69976	CHILE. Coquimbo: Limari, Parque Nacional Fray Jorge.	U86819	AY963217/ AY963219
Phyllotis darwini	MSB 69977	CHILE. Coquimbo: Limari, Parque Nacional Fray Jorge.	U86820	
Phyllotis darwini	LCM 2481	CHILE. Coquimbo: Petorca, Los Molles.	AY956723	AY963211
Phyllotis darwini	LCM 2485	CHILE. Coquimbo: Petorca, Los Molles.	AY956724	AY963213/ AY963221
Phyllotis darwini	LCM 2488	CHILE. Coquimbo: Petorca, Los Molles.	AY956722	AY963214/ AY963222

Phyllotis darwini	LCM 2493	CHILE. Coquimbo: Petorca, Los Molles.	AY956727	AY963216
Phyllotis darwini	LCM 2507	CHILE. Coquimbo: Petorca, Los Molles.	AY956725	AY963215/ AY963223
Phyllotis darwini	LCM 2509	CHILE. Coquimbo: Petorca, Los Molles.	AY956726	
Phyllotis darwini	LCM 2511	CHILE. Atacama: Huasco, Parque Nacional Llanos de Challe.	AY956728	AY963218/ AY963220
Phyllotis darwini	LCM 2523	CHILE. Metropolitana: Maipu, Quebrada de la Plata.	AY956729	AY963212
Phyllotis gerbillus	ORB 58	PERU. Piura: Sechura.	AY956712/ (AY956710)	AY963205
Phyllotis gerbillus	ORB 59	PERU. Piura: Sechura.	AY956713/ (AY956709)	AY963206
Phyllotis limatus	FMNH 107476	CHILE. Tarapacá: Parincota, Arica, 72 km E Chapiquina, 10 km S Putre.	U86822	
Phyllotis limatus	FMNH 107615	PERU. Moquegua: Mariscal Nieto, 16 km NE Torata.	U86821	AY963237
Phyllotis limatus	LSUMZ 27841	PERU. Arequipa: 38 km E Arequipa.	AY956740	AY963235/ AY963236
Phyllotis magister	LCM 1804	CHILE. Antofagasta: El Loa, Ojo Opache, Calama II.	AY956716	AY963234
Phyllotis magister	LCM 1813	CHILE. Antofagasta: El Loa, Ojo Opache, Calama II.	AY956717	
Phyllotis magister	LCM 1817	CHILE. Antofagasta: El Loa, Ojo Opache, 2 km W Calama	AF484213	AY963233
Phyllotis magister	LCM 1875	CHILE. Antofagasta: El Loa, Ojo Opache, Calama II.		AY963232
Phyllotis magister	LCM 1894	CHILE. Antofagasta: El Loa, Ojo Opache III.	AY956718	

Phyllotis magister	LSUMZ 27823	PERU. Arequipa: 35 km E Arequipa.	AY956719	AY963225
Phyllotis magister	LSUMZ 27825	PERU. Arequipa: 35 km E Arequipa.		AY963226
Phyllotis magister	LSUMZ 27829	PERU. Arequipa: 35 km E Arequipa.		AY963229
Phyllotis magister	LSUMZ 27830	PERU. Arequipa: 35 km E Arequipa.	AF484214	AY963230/ AY963231
Phyllotis magister	LSUMZ 27832	PERU. Arequipa: 35 km E Arequipa.	AY956721	AY963227
Phyllotis magister	ORB 14	PERU. Tarata: Tacna.	AY956720	AY963224/ AY963228
Phyllotis magister	FMNH 107691	PERU. Arequipa: Caylloma, 5 km NNE Chivay.	U86823	
Phyllotis magister	FMNH 107611	PERU. Tacna: Tarata, 3 km NE Tarata.	U86824	
Phyllotis osgoodi	LCM 638	CHILE. Tarapacá: Parinacota.	U86825	
Phyllotis osilae osilae	MSB 68539	BOLIVIA. La Paz: Mina Lourdes.	U86828	
Phyllotis osilae osilae	MSB 67256	BOLIVIA. Tarija: Serrania Sama.	U86829	
Phyllotis osilae osilae	MSB 63366	BOLIVIA. Chuquisaca: 2 km N, 3 km E Tarabuco.	U86827	AY963190
Phyllotis osilae osilae	FMNH 107870	PERU. Puno: Chucuito, 35 km S, 5 km W Llave.	U86826	
Phyllotis osilae osilae	FMNH 162855	BOLIVIA. Tarija: Abra Condor, 2 km W Junacas.		AY963188
Phyllotis osilae osilae	ORB 98	PERU. Cuzco: Quenko.	AY956699/ (AY956711)	AY963187
Phyllotis osilae osilae	MSB 67272	BOLIVIA. Cochabamba: 17 km E Totora.		AY963189
Phyllotis osilae phaeus	MSB 75292	BOLIVIA. La Paz: Zongo, Laguna Viscachani.	AY956700	
Phyllotis osilae phaeus	MSB 70573	BOLIVIA. La Paz.	AY956701	AY963191

Phyllotis sp. nov. 1	VPT 2318	PERU.	AY956714	AY963192/ AY963193
Phyllotis sp. nov. 1	VPT 2324	PERU.	AY956715	AY963194/ AY963195
Phyllotis sp. nov. 2	JPJ 761	ARGENTINA. Tucuman.	AY627299	
Phyllotis sp. nov. 2	JPJ 977	ARGENTINA. Tucuman.	AY627298	
Tapecomys wolffsohni	MSB 67269	BOLIVIA. Santa Cruz: 17 km S Quiñe.	AY956698	AY963186
Tapecomys wolffsohni	MSB 67270	BOLIVIA. Santa Cruz: 17 km S Quiñe.	U86834	AY963185
Tapecomys wolffsohni	MSB 63364	BOLIVIA. Tarija: Serrania Sama.	U86835	AY963184
Phyllotis xanthopygus chilensis	FMNH 107606	PERU. Tacna: Tarata, 5 km NE Tarata.	U86830	AY963255/ AY963256
Phyllotis xanthopygus chilensis	FMNH 133830	PERU. Tacna: Tarata, 5 km NE Tarata.	U86831	
Phyllotis xanthopygus chilensis	LSUMZ 27861	PERU. Arequipa: 53 km E Arequipa.	AF484212	AY241466
Phyllotis xanthopygus posticalis	ORB 82	PERU. Lima: Huarochiri, Casapalca.	AY956730	AY963254
Phyllotis xanthopygus rupestris	LCM 1737	CHILE. Antofagasta: Tocopilla, Desembocadura Rio Loa.	AY956739	AY963244
Phyllotis xanthopygus rupestris	LCM 1780	CHILE. Antofagasta: Toconao, Quebrada de Jerez.	AF484211	AY963245/ AY963246
Phyllotis xanthopygus rupestris	LCM 1829	CHILE. Antofagasta: Provincia El Loa: Talabre, Toconao arriba.	AF484210	AY963247/ AY963248
Phyllotis xanthopygus rupestris	FMNH 162870	BOLIVIA. Oruro: Escuela Seccional Villa Ventilla, 181 km S Oruro.		AY963249

Phyllotis xanthopygus rupestris	MSB 55350	BOLIVIA. Oruro: 1 km W Huancaroma.	AY956738	
Phyllotis xanthopygus rupestris	MSB 67261	BOLIVIA. Tarija: 4.5 km E Iscayachi.	U86832	
Phyllotis xanthopygus vaccarum	AC 20	ARGENTINA. Córdoba: Pampa de Achala.	AF484209	
Phyllotis xanthopygus vaccarum	AC 21	ARGENTINA. Córdoba: Pampa de Achala.	AY956733	AY963238/ AY963240
Phyllotis xanthopygus vaccarum	LCM 1156	CHILE. Región Metropolitana: El Yeso.	AY956735	
Phyllotis xanthopygus vaccarum	LCM 1157	CHILE. Región Metropolitana: El Yeso.	AY956736	AY963239/ AY963241
Phyllotis xanthopygus vaccarum	UWBM 72232	ARGENTINA. Provincia de Mendoza: 49.2 km N central Mendoza.	AY956734	AY963242/ AY963243
Phyllotis xanthopygus xanthopygus	LCM 1161	CHILE. Aisén: Chile Chico.	AY956737	
Phyllotis xanthopygus xanthopygus	MFS 1324	ARGENTINA. Rio Negro: Comallo.	U86833	AY963253

LITERATURE CITED

Anderson, S., and T. L. Yates
2000 A new genus and species of phyllotine rodent from Bolivia. Journal of Mammalogy. 81: 18-36.

Braun, J. K.
1993 Systematic relationships of the tribe Phyllotini (Muridae: Sigmodontinae) of South America. Special Publication, Oklahoma Museum of Natural History, Norman, Oklahoma, USA. 50 pp.

Braun, J. K., and M. A. Mares
1995 A new genus and species of phyllotine rodent (Rodentia: Muridae: Sigmodontini: Phyllotini) from South America. Journal of Mammalogy. 76:504-521.

Cabrera, A. L.
1961 Catálogo de los mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia." Ciencias Zoológicas 4:309-732.

Catanesi, C. I., L. Vidal-Rioja, J. V. Crisci, and A. Zambelli
2002 Phylogenetic relationships among Robertsonian karyomorphs of Graomys griseoflavus (Rodentia, Muridae) by mitochondrial cytochrome *b* DNA sequencing. Hereditas 136:130-136.

Crespo, J. A.
1964 Descripción de una nueva subespecie de roedor filotino. Neotrópica 10:99-101.

D'Elía, G.
2003 Phylogenetics of sigmodontinae (Rodentia, Muroidea, Cricetidae), with special reference to the akodont group, and with additional comments on historical biogeography. Cladistics 19:307-323.

Dickerman, A. W.
1992 Molecular Systematics of Some New World Muroid Rodents. Ph.D. Dissertation, University of Wisconsin-Madison, Wisconsin, USA.

Engel, S. R., K. M. Hogan, J. F. Taylor, and S. K. Davis
1998 Molecular systematics and paleobiogeography of the South American sigmodontine rodents. Molecular Biology and Evolution 15:35-49.

Felsenstein, J.
1985 Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783-791.

Fratti, F., C. Simon, J. Sullivan, and D. L. Swofford
1997 Evolution of the mitochondrial cytochrome oxidase II gene in Collembola. Journal of Molecular Evolution 44:145-158.

Fugmann, S. D., A. I. Lee, P. E. Shockett, I. J. Villey, and D. G. Schatz
2000 The rag proteins and V(D)J recombination: complexes, ends, and transposition. Annual Reviews of Immunology 18:495-527.

Hershkovitz, P.
1962 Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana: Zoology, 46:1-524.

Huelsenbeck, J. P., and F. Ronquist.
2003 MrBayes: a program for the Bayesian inference of phylogeny, 3.0. Rochester, New York, USA.

Jayat, J. P., G. D'Elía, U. F. J. Pardiñas, and J. G. Namen (This volume)
A New Species of *Phyllotis* (Rodentia, Cricetidae, Sigmodontinae) from the Upper Montane Forest of the Yungas of Northwestern Argentina / Una Nueva Especie de *Phyllotis* (Rodentia, Cricetidae, Sigmodontinae) del Bosque Montano Superior de las Yungas del Noroeste Argentino. Pp. 775-798 in Kelt, D. A., E. P. Lessa, J. Salazar-Bravo, and J. L. Patton (eds.). 2007. The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson. University of California Publications in Zoology 134:1-981.

Kuch, M., N. Rohland, J. Betancourt, C. Lattore, S. J. Steppan, and H. N. Poinar
2002 Molecular analysis of a 11,700-yr old rodent midden from the Atacama Desert Chile. Molecular Ecology 11:913-924.

Nei, M., and S. Kumar
2000 Molecular Evolution and Phylogenetics. Oxford University Press, New York, New York, USA. 333 pp.

Nowak, R. M.
1999 Walker's Mammals of the World. Sixth ed. Johns Hopkins University Press, Baltimore, Maryland, USA. 1936 pp.

Olds, N., and S. Anderson
1989 A diagnosis of the tribe Phyllotini (Rodentia, Muridae). Pp. 55-74 in Advances in Neotropical Mammalogy (Redford, K. H. and J. F. Eisenberg, eds.). Sandhill Crane Press, Gainesville, Florida, USA.

Ortiz, P. E., U. F. J. Pardiñas, and S. J. Steppan
2000 A new fossil phyllotine (Rodentia: Muridae) from northwestern Argentina and relationships of the Reithrodon group. Journal of Mammalogy. 81:37-51.

Pearson, O. P.
1958 A taxonomic revision of the rodent genus *Phyllotis*. University of California Publications in Zoology 56:391-477.

Pearson, O. P., and J. L. Patton
1976 Relationships among South American phyllotine rodents based on chromosome analysis. Journal of Mammalogy 57:339-350.

Posada, D., and K. A. Crandall
1998 Modeltest: testing the model of DNA substitution. Bioinformatics 14:817-818.

Salazar-Bravo, J., J. W. Dragoo, D. S. Tinnin, and T. L. Yates
2001 Phylogeny and evolution of the Neotropical rodent genus *Calomys*: inferences from mitochondrial DNA sequence data. Molecular Phylogenetics and Evolution 20:173-184.

Sambrook, E., F. Fritsch, and T. Maniatis
1989 Molecular Cloning: A Laboratory Manual. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, New York, USA.

Smith, M. F., and J. L. Patton
1999 Phylogenetic relationships and the radiation of sigmodontine rodents in South America: evidence from cytochrome *b*. Journal of Mammalian Evolution 6: 89-128.

Steppan, S. J.
1993 Phylogenetic relationships among the Phyllotini (Rodentia: Sigmodontinae) using morphological characters. Journal of Mammalian Evolution 1:187-213.

1995 Revision of the tribe Phyllotini (Rodentia: Sigmodontinae), with a phylogenetic hypothesis for the Sigmodontinae. Fieldiana: Zoology, new series 80:1-112.

1998 Phylogenetic relationships and species limits within *Phyllotis* (Rodentia: Sigmodontinae): concordance between mtDNA sequence and morphology. Journal of Mammalogy. 79:573-593.

Steppan, S. J., R. M. Adkins, and J. Anderson
2004a Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. Systematic Biology 53:533-553.

Steppan, S. J., M. R. Akhkverdyan, E. A. Lyapunova, D. G. Fraser, N. N. Vorontsov, R. S. Hoffmann, and M. J. Braun
1999 Molecular phylogeny of the marmots (Rodentia: Sciuridae): tests of evolutionary and biogeographic hypotheses. Systematic Biology 48:715-734.

Steppan, S. J., and U. F. J. Pardiñas
1998 Two new fossil muroids from the Early Pleistocene of Argentina: phylogeny and paleoecology. Journal of Vertebrate Paleontology 18:640-649.

Steppan, S. J., B. L. Storz, and R. S. Hoffmann
2004b Nuclear DNA phylogeny of the squirrels (Mammalia: Rodentia) and the evolution of arboreality from c-myc and RAG1. Molecular Phylogenetics and Evolution 30:703-719.

Steppan, S. J., and J. Sullivan
2000 The emerging statistical perspective in systematics: a comment on Mares and Braun. Journal of Mammalogy. 81:260-270.

Steppan, S. J., C. Zawadzki, and L. R. Heaney
2003 Molecular phylogeny of the endemic Philippine rodent *Apomys* (Muridae) and the dynamics of diversification in an oceanic archipelago. Biological Journal of the Linnean Society 80:699-715.

Swofford, D. L.
2002 PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), 4.0bv.10. Sinauer Associates, Sunderland, Massachusetts, USA.

Swofford, D. L., G. J. Olsen, P. J. Waddell, and D. M. Hillis
1996 Phylogenetic inference. Pp. 407-514 in Molecular Systematics (Hillis, D. M., C. Moritz, and B. K. Mable, eds.). Sinauer Associates, Sunderland, Massachusetts, USA.

Vorontsov, N. N.
1959 Sistema khomiakov (Cricetinae) mirovoi fauny i ikh filogeneticheskie sviazi. Biuletin Moskovkogo Obshtschestva Ispitately Prirody, Otdel Biologia 44:134-137.

Weksler, M.
2003 Phylogeny of Neotropical oryzomyine rodents (Muridae: Sigmodontinae) based on the nuclear IRBP exon. Molecular Phylogenetics and Evolution 29:331-349.

Yang, Z.
1994 Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: approximate methods. Journal of Molecular Evolution 39:306-314.

Yang, Z., N. Goldman, and A. Friday
1995 Maximum likelihood trees from DNA sequences: a peculiar statistical problem. Systematic Biology 44:384-399.

MOLECULAR PHYLOGENETICS AND DIVERSIFICATION OF SOUTH AMERICAN GRASS MICE, GENUS *AKODON*

LA FILOGENÉTICA MOLECULAR Y LA DIVERSIFICACIÓN DE LOS RATONES CAMPESTRES DE SUDAMÉRICA DEL GENERO *AKODON*

Margaret F. Smith and James L. Patton

We dedicate this paper to Oliver P. Pearson, our friend, colleague, and fellow mouse-trapper, with whom both of us shared experiences in the field and museum while struggling to comprehend the diversity of South American rodents. From our many interactions over more than 3 decades we remain grateful for what he taught us about science, scholarship, inquisitiveness, and simply living life.

ABSTRACT

We examine variation in the mitochondrial cytochrome *b* gene for 30 of the approximately 40 species of South American grass mice, genus *Akodon*. Phylogenetic analyses encompassing both maximum parismony and Bayesian methods consistently identified 4 clades, but each with varying levels of support: (1) The "*varius*-group" from eastern Bolivia, western Paraguay, and Argentina, which forms a consistent clade structure of (*A. iniscatus* + *nucus* (*A. dayi* (*A. toba* (*A. dolores* + *A. molinae*)))). (2) The "*boliviensis*-group", a set of 7 species from the high Andean and Sub-Andean grasslands that form a common phylogenetic order in most of the analyses of (((*A. kofordi* + *A. fumeus*) *A. juninensis*)((*A. boliviensis* + *A. spegazzinii*)(*A. subfuscus* + *A. lutescens*))). (3) The "*aerosus*-group", an assemblage of 8 species, including *A. aerosus*, *A. affinis*, *A.* cf. *budini*, *A. mollis*, *A. orophilus*, *A. siberiae*, and *A. torques* from the forested Andean slopes plus *A. albiventer* from the Altiplano from southern Peru south to northern Argentina. The species in this group do not display a consistent internal phylogenetic structure. And (4), the "*cursor*-group", from the coastal regions of Brazil south to Argentina, that includes 2 subclades in most analyses consisting of (*cursor* + aff. *cursor*) and (*montensis* (*reigi* (*mystax* + *paranaensis*))). The affinities of 4 additional species (*A. lindberghi*, *A. azarae*, *A. mimus*, and *A. serrensis*) remain unclear. In fact, *A. serrensis* is so divergent that it may not even belong in the genus *Akodon*. The geographic distributions of sister-species pairs suggest allopatric divergence as the major mode of speciation in the group. While the genus *Akodon* stems from the Pliocene, most speciation events

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leading to the extant taxa appear of moderate age at best, and many are quite recent.

Key words: *Akodon*, grass mice, mitochondrial DNA, phylogeny, speciation

RESUMEN

Examinamos la variación del gen mitocondrial citocromo *b* en 30 de las aproximadamente 40 especies de ratones campestres del género *Akodon*. Los análisis filogenéticos, tanto por máxima parsimonia como por métodos bayesianos, identificaron cuatro clados de manera consistente, aunque con grados de apoyo variables: (1) El "grupo *varius*" del este de Bolivia, oeste de Paraguay y Argentina, con una estructura de clado consistente: (*A. iniscatus* + *nucus* (*A. dayi* (*A. toba* (*A. dolores* + *A. molinae*)))). (2) El "grupo *boliviensis*", un conjunto de 7 especies de las praderas andinas y subandinas, con un orden filogenético común en la mayoría de los análisis: (((*A. kofordi* + *A. fumeus*) *A. juninensis*)((*A. boliviensis* + *A. spegazzinii*)(*A. subfuscus* + *A. lutescens*))). (3) El "grupo *aerosus*", un ensamble de 8 especies, incluyendo *A. aerosus*, *A. affinis*, *A.* cf. *budini*, *A. mollis*, *A. orophilus*, A. *siberiae*, y *A. torques* de las laderas boscosas de los Andes, más *A. albiventer* del Altiplano, desde el sur de Perú hasta el norte de Argentina. Las especies en este grupo no muestran una estructura filogenética interna consistente. Y (4), el "grupo *cursor*", desde las regiones costeras del Brasil hasta la Argentina, que en la mayoría de los análisis incluye 2 subclados, consistentes de (*cursor* + aff. *cursor*) y (*montensis* (*reigi* (*mystax* + *paranaensis*))). Las afinidades de 4 especies adicionales (*A. lindberghi*, *A. azarae*, *A. mimus*, y *A. serrensis*) siguen siendo inciertas. De hecho, *A. serrensis* es tan divergente que puede no pertenecer al género *Akodon*. Las distribuciones geográficas de pares de especies hermanas sugieren a la divergencia alopátrida como el principal modo de especiación en el grupo. Aunque el género *Akodon* surgió en el Plioceno, la mayor parte de los eventos de especiación que generaron la diversidad actual en el género son de edad moderada en el mejor de los casos, y muchos pueden ser bastante recientes.

Palabras claves: *Akodon*, ratones campestres, ADN mitocondriál, filogenía, especiación

INTRODUCTION

Grass mice of the genus *Akodon* constitute one of the most speciose and broadly distributed genera of the South American Sigmodontinae (Smith and Patton, 1993). Musser and Carleton (2005) list 41 species of *Akodon*, but note that the genus "stands at the nexus of a host of specific- and generic-level taxonomic problems" (pg. 1091). Recent hypotheses based primarily on sequences from mitochondrial and nuclear genes have either removed several genus-level taxa that have been historically linked to the confusing taxonomic history of *Akodon* (e.g., *Abrothrix*, *Bolomys*, *Chroeomys*, *Deltamys*, *Necromys*, *Thalpomys*, and *Thaptomys*) or placed others in synonymy (*Chalcomys*, *Hypsimys*, *Microxus*) (Musser and Carleton, 2005). For example, *Abrothrix* and *Chroeomys* belong to a clade quite distinct from the genus *Akodon*, one that also includes *Chelemys*, *Notiomys*, *Geoxus*, and *Pearsonomys* (Smith and Patton, 1991, 1993, 1999). *Thaptomys* and *Necromys* (= *Bolomys*) appear to be sister taxa to the genus *Akodon* (Smith and Patton, 1993, 1999). *Deltamys* and *Thalpomys* usually are placed outside of the restricted *Akodon* (D'Elía, 2003, D'Elía et al., 2003), a view supported by morphological studies of both genera (Hershkovitz, 1990a; Bianchini and Delupi, 1991 [1994]); González and Massoia, 1995). *Chalcomys*, as represented by the type species *aerosus*, is nested among species usually placed in the nominate subgenus *Akodon*. *Hypsimys*, based on the assignment of *siberiae* along with the type species, *budini*, to this taxon (Myers and Patton, 1989a), likewise is nested within *Akodon*. The placement of *Microxus*, as represented by the type species *mimus*, remains unresolved, although most molecular data suggest that it is nested within *Akodon* (e.g., Smith and Patton, 1991, 1993; D'Elía, 2003).

As a result of these studies, of the 45 species of *Akodon* listed in Musser and Carleton (1993), 9 are now assigned to *Abrothrix*, 1 to *Necromys*, 1 to *Deltamys*, and 1 to *Thaptomys* (Musser and Carleton, 2005). However, the 41 species now placed in the genus by Musser and Carleton's latest compilation is by no means likely to be the final count. For example, *Akodon serrensis* appears to fall outside of *Akodon sensu stricto* (D'Elía, 2003, D'Elía et al., 2003; this study). New species have been formally described in recent years (e.g., González et al., 1998; Hershkovitz, 1998; Díaz et al., 1999; Braun et al., 2000; Christoff et al., 2000; Pardiñas et al., 2005) and others have been informally identified (e.g., Silva and Yonenaga-Yassuda, 1998; Geise et al., 2001). The affinities of those species for which data are missing obviously still need to be documented. For example, *A. bogotensis* and *A. latebricola*, northern Andean endemics, differ from typical *Akodon* by a number of characters and may merit separate nomenclatural recognition (Voss, 2003; Musser and Carleton, 2005). And, finally, the status of the 21 names listed by Musser and Carleton (2005) in synonymy of the species of *Akodon* they do recognize may well change with additional study.

We use sequence data from the mtDNA cytochrome *b* gene (cyt *b*) to examine relationships within the genus *Akodon*, explore the possibility that some groupings of taxa are linked to geographic regions and habitat types, and consider what these data suggest about the timing and biogeographic history of the genus. Data are available for 28 of the 41 species listed by Musser and Carleton (2005).

MATERIALS AND METHODS

Whole genomic extracts of DNA were made following the sodium dodecyl sulfate-proteinase K/phenol/RNAse method (Maniatis et al., 1982, pp. 458-462), by salt extraction (Medrano et al., 1990), by using Chelex (Walsh et al., 1991), or with the use of the DNAeasy Tissue Kit (Qiagen Inc.). One South American sigmodontine, *Chroeomys jelskii*, has been shown to carry a nuclear copy of a portion of the mitochondrial genome that includes part of the cyt *b* gene (Smith et al., 1992). Smith and Patton (1999) also reported encountering nuclear copies of cyt *b* in the genus *Delomys*. Therefore, when frozen liver tissue was available, purified mitochondrial DNA was obtained using cesium chloride-ethidium bromide gradient centrifugation (Lansman et al., 1981) or by a more rapid method based on an alkaline lysis procedure, using a Promega Wizard Minipreps kit (Beckman et al., 1993).

Smith and Patton (1999) describe amplification and manual sequencing methods, following procedures in Smith and Patton (1991). Sequences were also obtained with an Applied Biosystems model 377 slab gel and with a 3730 capillary automated DNA sequencer using the Taq FS, dRhodamine, and Big Dye terminator cycle sequencing kits. Additional sequencing primers used on the automated sequencers included light strand primers MVZ 103 and MVZ 17 (Smith and Patton, 1999) and heavy strand primer MVZ 14 (Smith and Patton, 1993). Sequences were edited using the Sequence Navigator software (Applied Biosystems, Inc., 1994).

Sequence data were available for the first 801 bp of cyt *b* from various akodontines (Smith and Patton, 1991, GenBank accession numbers M35691-M35716; Smith and Patton, 1993, U03524-U03550; Geise et al., 2001, AF184049-AF184058). For the most part, specimens were assigned to species based on comparison (by ourselves or others) to appropriate museum materials, or based on our own revisionary work on various groups of *Akodon* (e.g., Myers and Patton, 1989a, 1989b; Myers et al., 1990). Assignment of the names *Akodon cursor*, *A.* aff. *cursor*, *A. montensis*, *A. lindberghi*, *A. mystax*, and *A. serrensis* follows Geise et al. (2001). Additional sequence was obtained from representative individuals in the earlier samples to complete the cyt *b* gene (ca. 1140 bp). Complete cyt *b* sequence was obtained for *Akodon affinis* (AY196164), *A. albiventer* (AY494838), *A.* cf. *budini* (AY605060), *A. dayi* (AY605059), *A. fumeus* (AY605061), *A. iniscatus* (AY273917), *A. iniscatus nucus* (AY605062), *A. molinae* (AY494839), and *A. spegazzinii* (AY196165). The complete cyt *b* sequence was available for representatives of *Thaptomys*, *Necromys* (formerly *Bolomys*), and *Oxymycterus* (Smith and Patton, 1999, AF108666-AF108709), and *Juscelinomys* (Emmons, 1999, AF133667). Additional cyt *b* sequences were provided by G. D'Elía, including *Akodon dolores* (AY273904), *Akodon paranaensis* (AY195866), *Akodon reigi* (AY195865), *Deltamys kempi* (AY195860), and *Thalpomys cerradensis* (AY273916). Sample localities and museum catalog numbers of voucher specimens are listed in the Appendices to Smith and Patton (1999) and Geise et al. (2001). Additional localities are listed below. Acronyms refer to GenBank accession numbers, or to collector's personal catalog numbers (LHE, Louise H. Emmons; JLP, James L. Patton; UP, Ulyses Pardiñas) or museum accession numbers (FMNH, Field Museum of Natural History; LSU, Louisiana State University; MVZ, Museum of Vertebrate Zoology).

Akodon affinis (J. A. Allen, 1912)—Colombia: Depto. Risaralde, Municipio Pereira, Corregimiento La Florida, vereda La Pastora, camino a Las Cascadas, PRN Ucumarí. (Instituto de Ciencias Naturales in Bogotá 16547 [JLP 16684]).

Akodon cf. *budini* (Thomas, 1918)—Bolivia: Depto. Chuquisaca, Rinconada del Bufete, 20° 49.81′ S; 64° 22.47′ W; el 2,000 m. (LHE 1260). This specimen comes from the Bosque Tucumano-Boliviano, part of the tendril of moist forest that extends along the eastern slope of the Andes for nearly 700 km from the Yungas in Bolivia south to Jujuy, Argentina (see Emmons, 1997). Given the geographic proximity to the type locality of *A. budini* in Jujuy, we tentatively assign this specimen to that taxon.

Akodon dayi Osgood, 1916—Bolivia: Depto. Santa Cruz, El Refugio, Parque Nacional Noël Kempff Mercado (LHE 1268).

Akodon dolores Thomas, 1916—Argentina: Prov. San Luis, Papagallos (AY273904).

Akodon fumeus Thomas, 1902—Bolivia: Depto. Chuquisaca, Rinconada del Bufete, 20°

49.81′ S; 64° 22.47′ W; el 2,000 m (LHE 1262).

Akodon molinae Contreras, 1968 (new details on the locality, not included in Smith and Patton, 1999)—Sample was from a mouse colony whose original stock was captured in Ñacuñán MaB Reserve, Depto. Santa Rosa, Prov. Mendoza, Argentina (see Yunes and Castro-Vázquez, 1990).

Akodon iniscatus nucus Thomas, 1926—Argentina: Prov. Neuquen, Estáncia La Porteña, Sierra de Cuchillo Curá, Las Lajas (UP 442).

Akodon paranaensis Christoff, Fagundes, Sbalqueiro, Mattevi, and Yonenaga-Yassuda, 2000—Brazil: Estado do Rio Grande do Sul, Venancio Aires (see D'Elía et al., 2003).

Akodon reigi González, Langguth, and Oliveira, 1998—Uruguay: Depto. Lavalleja, Paso Averías (see D'Elía et al., 2003).

Akodon spegazzinii Thomas, 1897—Argentina: Prov. Córdoba, Pampa de Achala, Repetidora La Posta (AY168165).

We employed both maximum parsimony (MP), using PAUP* 4.0b10 (Swofford, 2002), and Bayesian inference (reviewed in Huelsenbeck et al., 2001; Lewis, 2001), using MrBayes 3.0 (Ronquist and Huelsenbeck, 2003), to examine phylogenetic relationships among the 30 species of *Akodon* for which data are available. Parsimony reconstructions were done with all sites weighted equally and with transversions weighted 5 times as much as transitions, based on the empirical ratio of 5.3 for transitions/transversions, with 200 random orders of addition. Support for the nodes was assessed in separate MP bootstrap analyses with 1,000 pseudoreplicates, with 5 random orders of addition for each replicate. An initial Bayesian analysis used the most general, parameter rich model of evolution, GTR with a gamma parameter and a proportion of invariable positions. A second Bayesian analysis used the same GTR model, but with site-specific rate variation partitioned by codon position, so that substitution rates were estimated separately for first, second, and third codon positions, in keeping with a protein-coding gene. Bayesian analyses were initiated with random starting trees and run for 1,000,000 generations. The Markov chains were sampled every 100 generations. Of the resulting 10,001 trees, 2500 were discarded as "burn-in", and the remaining 7501 trees were summarized in 50% majority rule consensus trees. Support for nodes in the Bayesian analyses is based on posterior probabilities. All analyses were rooted by comparison to the genera *Oxymycterus* and *Juscelinomys*, which are phyletically outside an *Akodon-Necromys-Thaptomys-Thalpomys-Deltamys* clade (see Smith and Patton, 1999; Hoffman et al., 2002; D'Elía, 2003).

Kimura 2-parameter distances (Kimura, 1980) were calculated using MEGA version 2.1 (Kumar et al., 2001). We used this model of sequence evolution to provide direct comparisons to our earlier study (Smith and Patton, 1999). For the 4 clades within *Akodon*, within-group mean K2-p distances and standard errors, estimated by the bootstrap method, were obtained from MEGA2. Estimates of observed proportional sequence divergence (p-distance) were plotted against corrected sequence divergence (K2-p) values for pairwise comparisons, obtained from MEGA2, to examine whether nucleotide substitutions were saturated. A UPGMA tree based on third-position transversions was produced in MEGA2 to provide a framework for estimating times of divergence using fossil dates to set the scale, as discussed in Smith and Patton (1999).

RESULTS AND DISCUSSION

Sequence Variation

Of the first 1134 aligned nucleotide positions, 637 (56%) were constant, 79 (7%) were parsimony uninformative, and 418 (37%) were parsimony informative. The data fit the pattern of a mitochondrial, protein-coding gene, with a low frequency of G (mean base frequencies A = 0.29, C = 0.29, G = 0.13, and T = 0.30), and most changes occurring at the third position. The overall number of differences (transitions plus transversions) at first positions averaged 22.8 (16%), at second positions 7.4 (5%), and at third positions 114.4 (79%). Plots of p-distances versus K2-p distances are generally linear for both first and second positions, but distinctly curvilinear for third positions (Fig. 1), suggesting that some saturation has occurred at the third position across the set of ingroup and outgroup taxa examined herein. Corrected sequence divergence values (Kimura 2-parameter distances; Table 1) among all of the species of *Akodon* we examined are relatively modest, averaging 0.13, including *A. serrensis*, or 0.12 if *A. serrensis* is excluded (ranging from 0.005 [*A. iniscatus* – *A. iniscatus nucus*] to 0.19 [*A. dolores* – *A. serrensis*, or 0.17 for *A. azarae* – *A. siberiae*]). Within the clades identified below, average corrected distances range from 0.07 to 0.09. Distances between species of *Akodon* and the closely related akodontine genera *Deltamys* and *Thaptomys* average 0.16. *Akodon serrensis* likewise differs from members of a restricted genus *Akodon* by an average K2-p distance of 0.16, a level of divergence almost as great as that between a restricted group of *Akodon* species and *Thalpomys* (average K2-p distance of 0.17). Species of *Akodon* differ more from *Necromys* (0.18), from *Brucepattersonius* and *Blarinomys* (0.19), from *Oxymycterus*, *Juscelinomys*, *Bibimys*, and *Lenoxus* (0.20), and from *Scapteromys* and *Kunsia* (0.22).

Phylogenetic Analysis

Our analyses were not designed to test the monophyly of *Akodon* to the exclusion of other taxa, such as *Thaptomys*, *Thalpomys*, *Necromys*, and *Deltamys*, that have been varyingly grouped as subgenera of a more inclusive *Akodon* or as genera apart from a more exclusive *Akodon*. That question has been addressed in our earlier, more taxon dense papers (Smith and Patton, 1993, 1999), as well as by the recent analyses of D'Elía (2003). However, the trees generated by each of the various methods we employed with the data set examined here do provide good support for a monophyletic *Akodon* to the exclusion of *Thaptomys*, *Thalpomys*, and *Necromys* (Figs. 2 and 3). "*Akodon*" *serrensis* falls outside of *Akodon*, except in the transversion weighted MP analysis. The molecular uniqueness of "*Akodon*" *serrensis* was noted in previous analyses in which this species was included (e.g., Geise et al., 2001; D'Elía, 2003; D'Elía et al., 2003). Clearly, this taxon needs additional attention from both a morphological and molecular perspective. The monotypic *Deltamys* falls within the inclusive taxon *Akodon* in some of our analyses. Thus, some of our analyses here are at odds with the evidence

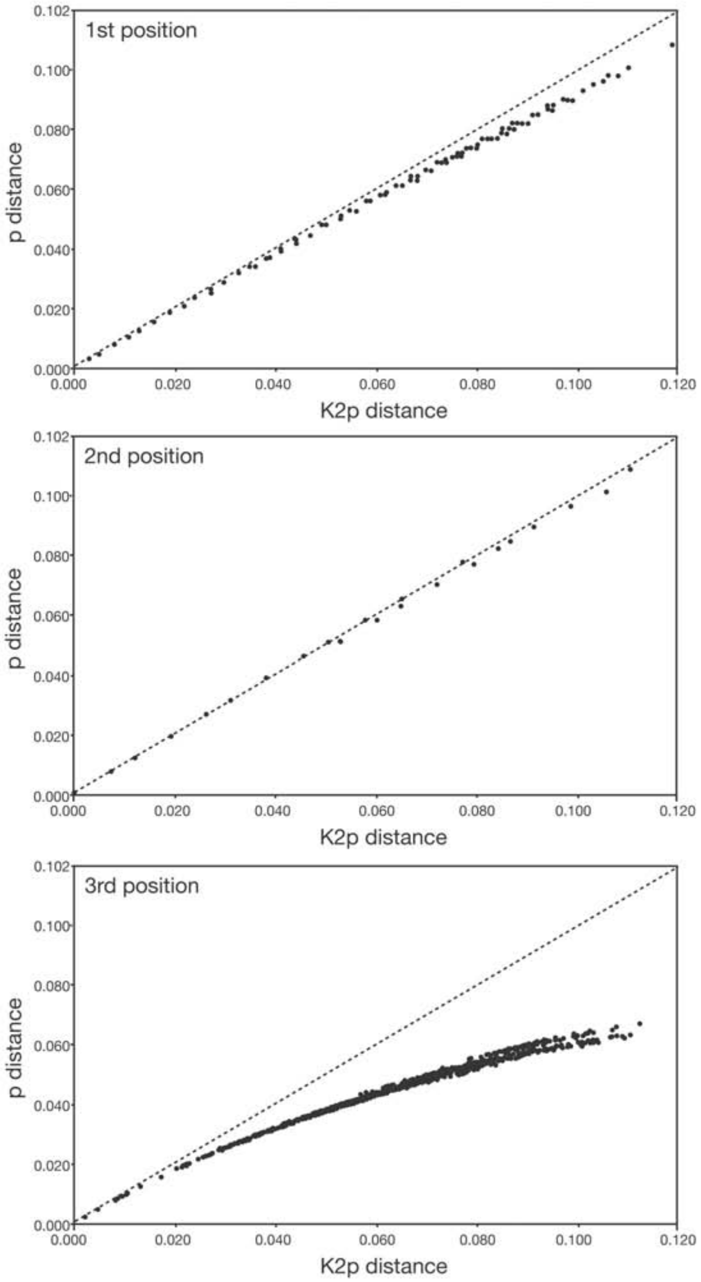


Figure 1. Bivariate plots of p-distances (Y-axis) and Kimura 2-parameter distances (X-axis) for all substitutions at 1st, 2nd, and 3rd positions in the cytochrome *b* gene sequences of akodontine rodents examined in this report.

Table 1. Matrix of Kimura 2-parameter distances among all cytochrome *b* sequences analyzed in this study.

		1	2	3	4	5	6	7	8	9	10	11	12
[1]	*Akodon subfuscus*												
[2]	*Akodon lutescens*	0.054											
[3]	*Akodon boliviensis*	0.093	0.071										
[4]	*Akodon spegazzinii*	0.092	0.072	0.051									
[5]	*Akodon juninensis*	0.098	0.079	0.095	0.092								
[6]	*Akodon kofordi*	0.091	0.073	0.081	0.085	0.076							
[7]	*Akodon fumeus*	0.094	0.077	0.084	0.090	0.080	0.028						
[8]	*Akodon cursor*	0.115	0.095	0.099	0.106	0.103	0.111	0.108					
[9]	*Akodon aff. cursor*	0.133	0.108	0.117	0.128	0.119	0.119	0.120	0.044				
[10]	*Akodon montensis*	0.116	0.103	0.104	0.111	0.103	0.102	0.102	0.103	0.109			
[11]	*Akodon mystax*	0.117	0.105	0.120	0.115	0.104	0.107	0.110	0.100	0.100	0.084		
[12]	*Akodon paranaensis*	0.113	0.099	0.111	0.107	0.102	0.101	0.103	0.096	0.101	0.086	0.023	
[13]	*Akodon reigi*	0.095	0.079	0.103	0.097	0.089	0.090	0.095	0.094	0.104	0.082	0.058	0.059
[14]	*Akodon azarae*	0.128	0.115	0.127	0.119	0.128	0.114	0.123	0.136	0.136	0.124	0.118	0.120
[15]	*Akodon lindberghi*	0.118	0.095	0.110	0.115	0.104	0.108	0.108	0.112	0.117	0.109	0.106	0.103
[16]	*Akodon toba*	0.141	0.128	0.142	0.127	0.145	0.145	0.147	0.143	0.146	0.148	0.151	0.144
[17]	*Akodon dayi*	0.131	0.125	0.135	0.130	0.134	0.127	0.132	0.141	0.151	0.144	0.140	0.140
[18]	*Akodon molinae*	0.139	0.138	0.145	0.129	0.143	0.134	0.137	0.139	0.144	0.141	0.144	0.139
[19]	*Akodon dolores*	0.147	0.141	0.148	0.132	0.144	0.141	0.146	0.143	0.148	0.147	0.149	0.143
[20]	*Akodon iniscatus*	0.144	0.121	0.152	0.134	0.131	0.143	0.138	0.141	0.146	0.146	0.145	0.141
[21]	*Akodon iniscatus nucus*	0.144	0.121	0.150	0.134	0.133	0.143	0.136	0.140	0.145	0.144	0.140	0.137
[22]	*Akodon torques*	0.129	0.112	0.132	0.128	0.129	0.126	0.121	0.121	0.131	0.142	0.131	0.125

Table 1 (continued).

		1	2	3	4	5	6	7	8	9	10	11	12
[23]	*Akodon orophilus* (MVZ 173057)	0.133	0.110	0.139	0.134	0.124	0.125	0.132	0.125	0.136	0.141	0.118	0.112
[24]	*Akodon mollis*	0.135	0.111	0.128	0.123	0.114	0.128	0.126	0.122	0.131	0.129	0.124	0.124
[25]	*Akodon affinis*	0.145	0.128	0.149	0.138	0.139	0.149	0.147	0.137	0.145	0.165	0.135	0.137
[26]	*Akodon aerosus baliolus*	0.138	0.131	0.143	0.134	0.129	0.145	0.138	0.133	0.150	0.161	0.133	0.131
[27]	*Akodon aerosus* (MVZ 172870)	0.153	0.133	0.147	0.136	0.142	0.155	0.152	0.142	0.157	0.165	0.131	0.135
[28]	*Akodon aerosus* (MVZ 171679)	0.138	0.129	0.143	0.147	0.136	0.148	0.148	0.134	0.149	0.143	0.137	0.140
[29]	*Akodon orophilus* (FMNH 129234)	0.153	0.133	0.151	0.149	0.143	0.139	0.140	0.127	0.145	0.148	0.126	0.126
[30]	*Akodon orophilus* (LSU 27957)	0.139	0.121	0.139	0.140	0.131	0.132	0.139	0.129	0.134	0.151	0.140	0.135
[31]	*Akodon albiventer*	0.148	0.128	0.137	0.146	0.140	0.147	0.150	0.146	0.152	0.152	0.144	0.147
[32]	*Akodon siberiae*	0.159	0.144	0.149	0.156	0.145	0.143	0.139	0.149	0.156	0.157	0.150	0.148
[33]	*Akodon cf. budini*	0.158	0.141	0.148	0.149	0.144	0.146	0.148	0.150	0.158	0.158	0.145	0.148
[34]	*Akodon mimus*	0.149	0.115	0.121	0.132	0.125	0.125	0.125	0.139	0.146	0.157	0.136	0.142
[35]	*Akodon serrensis*	0.158	0.132	0.146	0.147	0.155	0.150	0.152	0.164	0.167	0.166	0.166	0.162
[36]	*Deltamys kempi*	0.182	0.155	0.158	0.162	0.169	0.169	0.162	0.157	0.166	0.162	0.159	0.165
[37]	*Thaptomys nigrita*	0.174	0.148	0.153	0.156	0.149	0.157	0.152	0.154	0.161	0.156	0.169	0.162
[38]	*Thalpomys cerradensis*	0.172	0.166	0.164	0.173	0.173	0.174	0.171	0.167	0.168	0.173	0.162	0.159
[39]	*Necromys lasiurus*	0.175	0.169	0.170	0.189	0.167	0.180	0.179	0.167	0.174	0.171	0.166	0.169
[40]	*Necromys amoenus*	0.180	0.181	0.181	0.189	0.173	0.167	0.169	0.171	0.177	0.183	0.173	0.172
[41]	*Necromys urichi*	0.169	0.156	0.161	0.155	0.158	0.162	0.164	0.159	0.150	0.155	0.158	0.166
[42]	*Necromys temchuki*	0.173	0.168	0.175	0.188	0.172	0.183	0.185	0.168	0.178	0.174	0.168	0.174
[43]	*Oxymycterus paramensis*	0.196	0.182	0.193	0.194	0.193	0.197	0.197	0.199	0.211	0.201	0.190	0.191
[44]	*Juscelinomys huanchacae*	0.196	0.189	0.190	0.186	0.184	0.189	0.196	0.192	0.200	0.201	0.192	0.197

Table 1 (continued).

	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
[1]																
[2]																
[3]																
[4]																
[5]																
[6]																
[7]																
[8]																
[9]																
[10]																
[11]																
[12]																
[13]																
[14]	0.108															
[15]	0.091	0.126														
[16]	0.130	0.124	0.130													
[17]	0.122	0.137	0.136	0.070												
[18]	0.126	0.130	0.139	0.032	0.064											
[19]	0.131	0.135	0.138	0.027	0.070	0.012										
[20]	0.134	0.132	0.128	0.097	0.109	0.100	0.100									
[21]	0.130	0.130	0.131	0.097	0.109	0.099	0.100	0.005								
[22]	0.116	0.138	0.113	0.124	0.131	0.130	0.135	0.124	0.121							

Table 1 (continued).

	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
[23]	0.115	0.139	0.120	0.130	0.135	0.136	0.140	0.124	0.119	0.054						
[24]	0.108	0.137	0.104	0.128	0.128	0.132	0.139	0.122	0.122	0.067	0.079					
[25]	0.119	0.147	0.120	0.137	0.146	0.152	0.150	0.133	0.130	0.077	0.077	0.079				
[26]	0.120	0.149	0.123	0.140	0.147	0.136	0.144	0.139	0.134	0.070	0.086	0.078	0.054			
[27]	0.127	0.155	0.131	0.150	0.159	0.157	0.163	0.142	0.137	0.090	0.085	0.089	0.065	0.065		
[28]	0.117	0.154	0.118	0.122	0.130	0.134	0.138	0.124	0.124	0.084	0.090	0.084	0.082	0.087	0.085	
[29]	0.120	0.152	0.126	0.124	0.140	0.133	0.139	0.125	0.120	0.069	0.072	0.078	0.080	0.075	0.082	0.071
[30]	0.114	0.153	0.120	0.126	0.134	0.139	0.142	0.124	0.120	0.073	0.084	0.081	0.083	0.093	0.093	0.082
[31]	0.137	0.145	0.137	0.128	0.153	0.149	0.152	0.136	0.132	0.106	0.106	0.100	0.101	0.101	0.112	0.108
[32]	0.141	0.173	0.147	0.150	0.162	0.153	0.163	0.144	0.137	0.106	0.113	0.120	0.114	0.117	0.119	0.118
[33]	0.138	0.169	0.146	0.152	0.164	0.161	0.163	0.149	0.144	0.108	0.119	0.120	0.116	0.125	0.122	0.124
[34]	0.132	0.152	0.127	0.155	0.155	0.146	0.158	0.143	0.143	0.114	0.126	0.111	0.126	0.118	0.137	0.131
[35]	0.146	0.176	0.173	0.173	0.167	0.183	0.194	0.173	0.168	0.149	0.145	0.153	0.165	0.159	0.163	0.144
[36]	0.165	0.160	0.166	0.165	0.155	0.165	0.171	0.163	0.158	0.153	0.147	0.147	0.161	0.150	0.163	0.157
[37]	0.149	0.156	0.168	0.164	0.164	0.167	0.168	0.167	0.169	0.150	0.146	0.148	0.156	0.159	0.163	0.158
[38]	0.155	0.171	0.169	0.173	0.175	0.171	0.176	0.176	0.173	0.174	0.165	0.154	0.178	0.175	0.187	0.175
[39]	0.162	0.183	0.162	0.170	0.171	0.171	0.180	0.186	0.186	0.177	0.180	0.167	0.182	0.189	0.200	0.172
[40]	0.164	0.177	0.170	0.201	0.188	0.197	0.205	0.189	0.184	0.178	0.167	0.183	0.177	0.166	0.190	0.176
[41]	0.156	0.161	0.164	0.172	0.170	0.175	0.184	0.180	0.177	0.174	0.168	0.166	0.169	0.167	0.185	0.166
[42]	0.160	0.182	0.168	0.166	0.175	0.168	0.176	0.191	0.191	0.176	0.176	0.176	0.178	0.187	0.196	0.167
[43]	0.181	0.198	0.201	0.202	0.187	0.204	0.207	0.193	0.193	0.188	0.192	0.186	0.192	0.197	0.211	0.197
[44]	0.188	0.201	0.194	0.204	0.211	0.202	0.211	0.208	0.211	0.200	0.190	0.189	0.189	0.189	0.200	0.200

Table 1 (continued).

	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
[23]																
[24]																
[25]																
[26]																
[27]																
[28]																
[29]																
[30]	0.066															
[31]	0.114	0.113														
[32]	0.101	0.101	0.134													
[33]	0.111	0.102	0.129	0.036												
[34]	0.119	0.128	0.132	0.127	0.134											
[35]	0.158	0.153	0.155	0.158	0.173	0.164										
[36]	0.152	0.157	0.160	0.155	0.166	0.145	0.172									
[37]	0.160	0.163	0.166	0.160	0.170	0.156	0.161	0.175								
[38]	0.184	0.189	0.179	0.186	0.193	0.186	0.184	0.177	0.162							
[39]	0.181	0.183	0.182	0.187	0.204	0.169	0.191	0.177	0.170	0.166						
[40]	0.173	0.179	0.174	0.163	0.181	0.174	0.177	0.177	0.164	0.161	0.146					
[41]	0.170	0.169	0.181	0.176	0.180	0.168	0.163	0.180	0.151	0.175	0.137	0.133				
[42]	0.185	0.188	0.183	0.193	0.206	0.174	0.191	0.189	0.172	0.170	0.021	0.146	0.143			
[43]	0.199	0.201	0.190	0.199	0.212	0.190	0.210	0.193	0.194	0.203	0.207	0.198	0.205	0.214		
[44]	0.200	0.201	0.198	0.206	0.232	0.180	0.210	0.196	0.183	0.194	0.182	0.181	0.190	0.185	0.112	

provided by D'Ellía (2003) and D'Elía et al. (2003), who supported the generic status of *Deltamys* based, weakly, on molecular grounds (bootstrap support for an *Akodon* node excluding *Deltamys* in the D'Elía et al., 2003 analysis was <50%, and in D'Elía 2003 jackknife support for the *Akodon* node was 58%). The phylogenetic resolution of *Deltamys* relative to *Akodon* thus remains somewhat ambiguous, a circumstance that may be corrected with the inclusion of data from additional taxa and more genes, both mitochondrial and nuclear. We do not comment on this difference further.

The various tree-building methods we used do not recover the exact same topology, yet consistencies are apparent in groups of taxa identified as clades within the genus *Akodon*. We discuss 4 clades, each with varying levels of presence and support across our analyses. We then focus on 4 species whose phylogenetic placement remains ambiguous: *A. lindbergi*, *A. azarae*, *A. mimus*, and *A. serrensis*. The MP analysis with all sites weighted equally resulted in 3 shortest trees (length = 2515 steps) in 1 island. The 3 trees had identical arrangements of the *Akodon* species, and differed only in the placement of 1 outgroup taxon, *Thalpomys*. For simplicity, we present only 1 MP tree [a strict consensus tree based on the 3 trees in 1 island from the equally weighted MP analysis (Fig. 2)], as well as 1 Bayesian [B] tree [from the site-specific analysis with rates estimated separately at the 3 codon positions (Fig. 3)], but discuss the differences among all trees obtained in our various analyses with regard to the placement of taxa and/or support of specific nodes in the discussion below. Support values (Table 2) are given for each node numbered in Fig. 2. The 4 clades identified in the trees, with equivalent or variable levels of support and inclusion are the following:

Clade 1: The Akodon varius *Group*.—The most strongly and consistently supported clade is the grouping of *A. toba*, *A. dolores*, *A. molinae*, *A. dayi*, and *A. iniscatus* (including *nucus*, which has been variously treated as a subspecies of *A. iniscatus* or as a separate species). Not only is this set of taxa strongly supported as a monophyletic lineage (bootstrap values = 99 and 98 in equally weighted and transversion weighted MP; posterior probabilities = 100 in both Bayesian analyses), but an internal clade structure of (*iniscatus* + *nucus* (*dayi* (*toba* (*dolores* + *molinae*)))) is also consistently present in all analyses, with bootstrap and posterior probability support of 96% or higher at each node (Table 2, nodes 15, 16, 17, 18). Sequence differences among the included taxa are the lowest for any of the groups of species we discuss, with a mean Kimura 2-parameter distance of 0.073 (standard error 0.006; range 0.005 to 0.109). Excluding *A. iniscatus* and *nucus*, the degree of interspecific differentiation is low, ranging from 0.012 (between the sister-species pair of *A. molinae* and *A. dolores*) to a maximum of 0.070 (between *A. dayi* and *A. toba,* or *A. dayi* and *A. dolores*). Clearly this is a closely related and relatively recent group of species. The sample of *nucus*, which has been variously treated as a subspecies of *A. iniscatus* (Barros et al., 1990; Pearson, 1995 ; Musser and Carleton, 2005) or as a separate species (Reig, 1987; Hershkovitz, 1990b; Galliari et al., 1996), differs from *A. iniscatus* by only 0.005. Others (e.g., Bradley and Baker, 2001) have used such low values of sequence divergence to support conspecificity of taxa, a phenetic view to which we do not subscribe. Rather, since we believe that speciation can be both a rapid and recent event, additional data will be required to establish the species status of *nucus* relative to *A. iniscatus*.

Four of these species are included in Myers' (1989) "*Akodon varius* group," a set of large-bodied taxa inhabiting the eastern slopes of the Andes and adjacent lowlands from Bolivia, Paraguay, and northern and central Argentina, with a squared or beaded

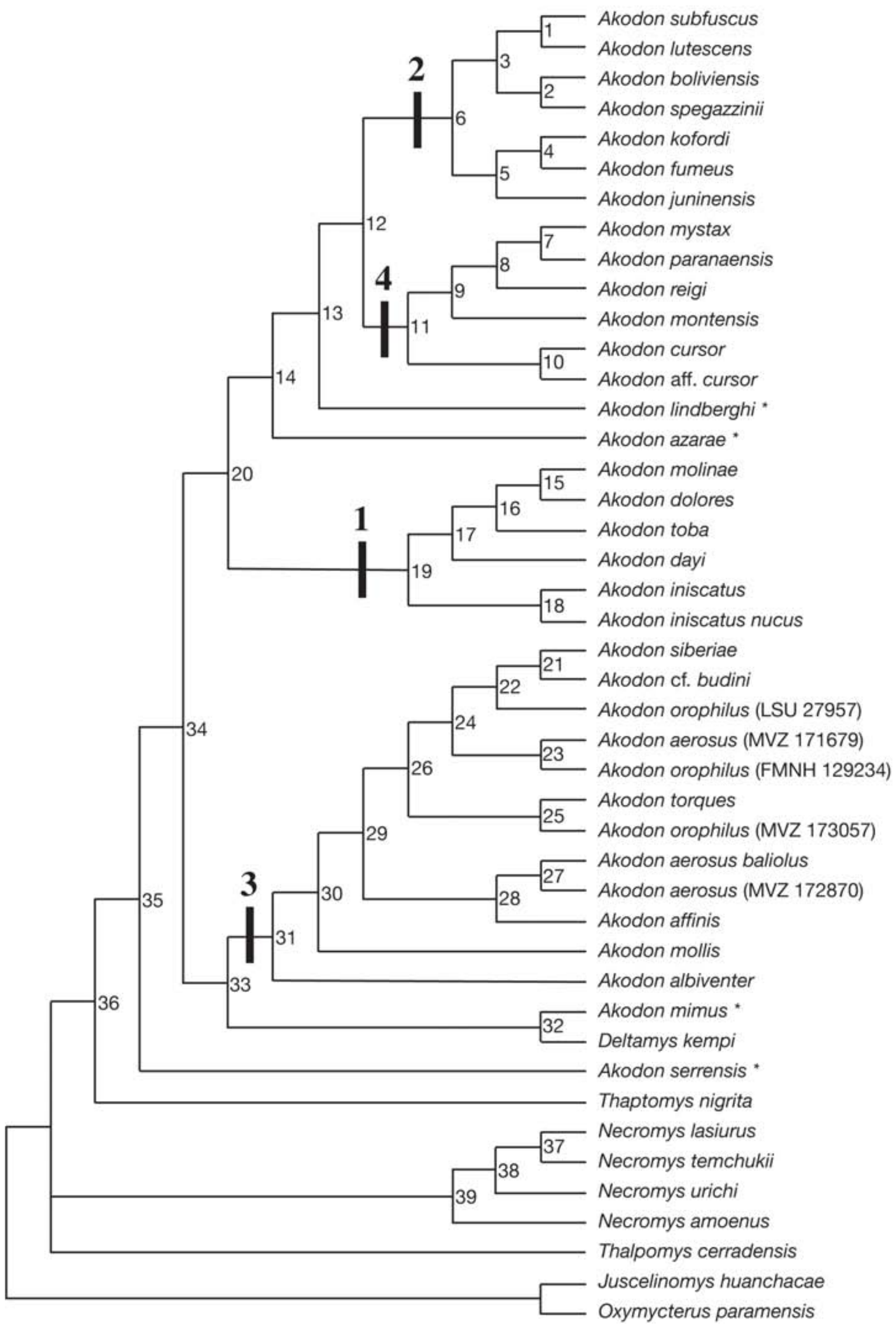


Figure 2. Maximum Parsimony - strict consensus of 3 trees in one island of shortest trees, based on equal weighting of complete cytochrome *b* sequences (tree lengths = 2,515 steps; CI = 0.290; RI = 0.499, and HI = 0.710). Node numbers 1-39 correspond to the nodes in Table 2. The 4 major clades are identified numerically. The 4 "unique" species are marked with asterisks.

supraorbital region and a short rostrum. In this group Myers included *A. varius*, *A. simulator* (with *glaucinus* and *tartareus* as valid subspecies), *A. toba*, *A. dayi*, *A. neocenus*, *A. dolores*, and *A. molinae*, but he stressed (Myers, 1989:35) that his grouping was "explicitly based on the overall similarity of the taxa and their apparently contiguous geographic distributions." Our analyses lend phylogenetic support to his admittedly phenetic grouping, and there seems little doubt that Myers' concept of a "*varius* group", while based on overall morphological similarity, does, in fact, represent a phylogenetic clade within *Akodon*. It remains to be established where the remaining taxa in Myers' group (*varius, simulator*, *glaucinus*, *tartareus*, and *neocenus*) fit with respect to this clade, but we are confident that future studies will confirm their close phyletic affinity with the group of taxa we have examined here, and we thus use Myer's terminology of the "*varius* group" even though we have no sequence data for *A. varius* itself as yet. It also remains to be determined if the recently described *A. oenos* (Braun et al., 2000) from north-central Argentina belongs to this assemblage of species, as hypothesized by those authors. According to Ulyses Pardiñas (personal communication, April 2004), the samples identified as *A. neocenus* in Apfelbaum and Reig (1989) are in fact *A. oenos*. Their allozyme data suggest a linkage between *A. iniscatus* and what is therefore presumably *A. oenos*, as well as with *A. molinae*, but in addition a link with *A. boliviensis* (the sample was actually *A. spegazzinii*, according to Ulyses Pardiñas, personal communication, April 2004), although the taxon sampling in the analysis by Apfelbaum and Reig (1989) was too limited to be definitive.

The close relationship between *A. dolores* and *A. molinae* is well supported by a wealth of karyotypic (e.g., Merani and Lizarralde, 1980), allozyme (Apfelbaum and Blanco, 1984), and DNA characterization data (Vidal-Rioja et al., 1979, 1982). Described karyotypes for species in the *varius* group range from 2n=34 to 2n=42, with a more consistent FN of 40 to 44 (Myers, 1989). Myers (1989) did not recognize the well-corroborated relationship of *A. iniscatus* + *nucus* to his "*varius* group" that we recovered in our sequence analyses (Figs. 2 and 3) (see also D'Elía, 2003), as these taxa are smaller in body size and have differently proportioned cranial components. Cranially, *A. iniscatus* is more similar to *A. azarae* (Pardiñas and Galliari, 1999). Nevertheless, the cyt *b* data strongly link *iniscatus* + *nucus* to Myers' "*varius* group" and, thus, expand that concept accordingly.

Clade 2: The Akodon boliviensis *Group*.—All of our analyses, except for 1 of the 2 islands of transversion-weighted MP trees, recovered a monophyletic assemblage of 7 small-bodied Andean species that includes *A. boliviensis*, the type species of the genus *Akodon*, along with *A. spegazzinii*, *A. subfuscus*, *A. lutescens*, *A. juninensis*, *A. kofordi*, and *A. fumeus*. As a unit, this group is weakly supported in the MP analyses (bootstrap values of 54 and <50 % for equally-weighted and transversion-weighted analyses, respectively) but strongly supported in both Bayesian analyses (posterior probabilities of 100) (Figs. 2 and 3). Within this clade, the species pairs *A. subfuscus* + *A. lutescens* (node 1) and *A. boliviensis* + *A. spegazzinii* (node 2) each associate with strong bootstrap (97 to 99%) and high Bayesian posterior probabilities (100% in both analyses). These 2 groups form sister lineages (node 3) with weak bootstrap support (55 and 59%) but strong Bayesian posterior probabilities (99 to 100%). The species pair *A. fumeus* and *A. kofordi* (node 4) has strong support (100% in all cases), and *A. juninensis* joins this pair (node 5) in most analyses (equally weighted MP analysis bootstrap of 62%, and Bayesian support of 87 or 90%). Together this trio is at the base of the ((*boliviensis*

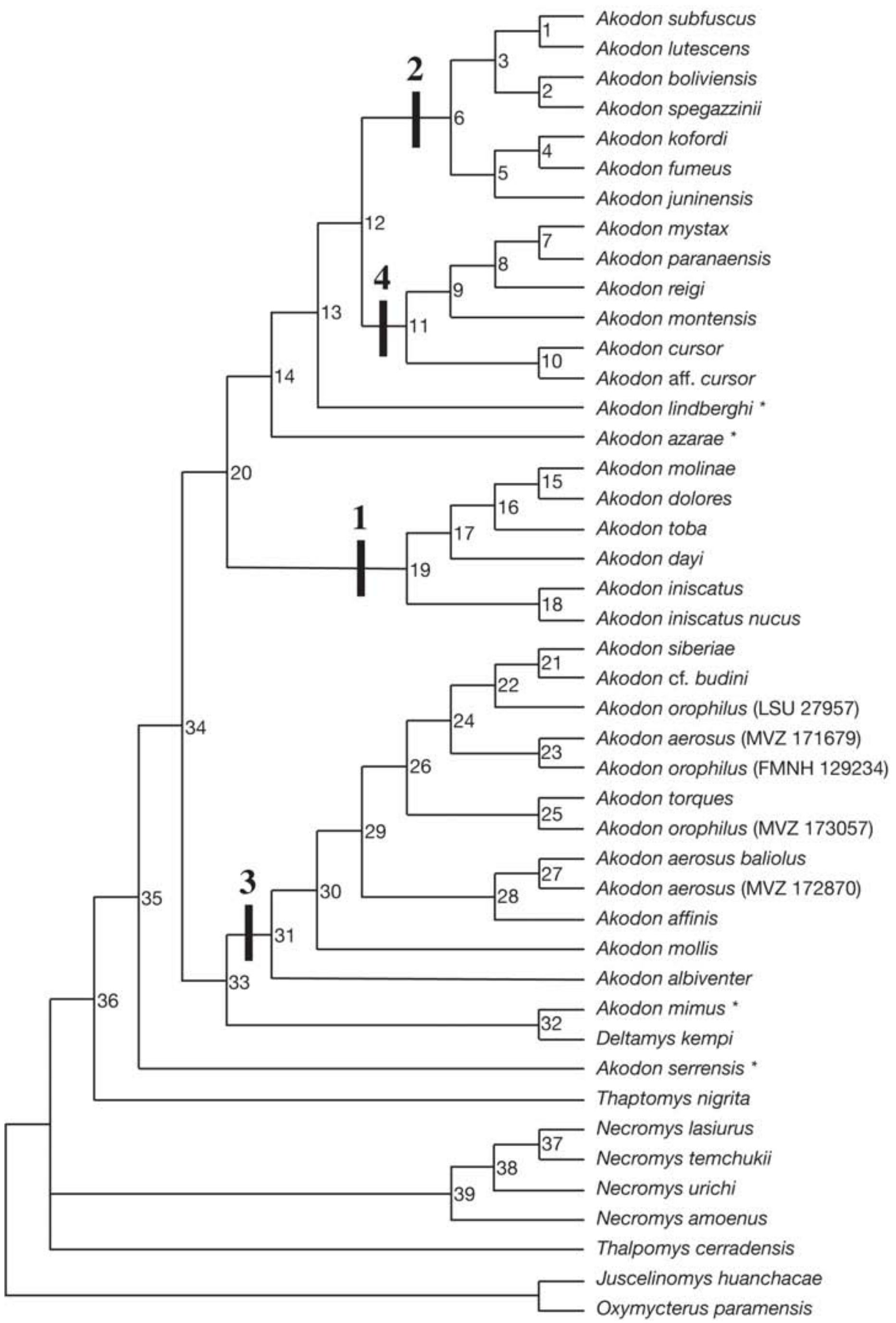


Figure 3. Bayesian tree from the analysis with site-specific rate variation partitioned by codon position, with the 4 major clades identified numerically. Nodes in common with those of the maximum parsimony analysis are numbered as in that tree (Fig. 2), and posterior probabilities are given in Table 2. The 4 "unique" species are marked with asterisks.

+ *spegazzinii*)(*subfuscus* + *lutescens*)) clade. Hence, a pattern of (((*kofordi* + *fumeus*) *juninensis*)((*boliviensis* + *spegazzinii*)(*subfuscus* + *lutescens*))) is recovered in almost all analyses. While Myers et al. (1990) did not examine *fumeus, spegazzinii,* or *kofordi*, their electrophoretic analyses did support the topology of (*juninensis* (*boliviensis* (*subfuscus* + *lutescens*))) that is obtained by our cyt *b* analyses here. The karyotype is quite uniform across all taxa of our concept of the *boliviensis* group, with 2n=40 and FN=40-42 where such data are available (Bárquez et al., 1980; Myers and Patton, 1989b; Myers et al., 1990). Kimura 2-parameter distances across this set of species average 0.079 (standard error = 0.005, range 0.028 [*kofordi* to *fumeus*] to 0.098 [*subfuscus* to *juninensis*]).

Two relatively recent papers have grouped species of *Akodon* into a "*boliviensis* group" (Hershkovitz, 1990b; Myers et al., 1990), although the basis for such a grouping as well as its respective membership differs radically between these treatments. Hershkovitz (1990b) simply divided the genus *Akodon* into 2 size classes, placing in a "small-bodied" assemblage that he termed the "*boliviensis* group" 13 named taxa (*alterus*, *azarae*, *boliviensis*, *caenosus*, *iniscatus*, *lindberghi*, *lutescens*, *nucus*, *pacificus*, *puer*, *subfuscus*, *tucumanensis*, and *sanctipaulensis*). Our cyt *b* data do not support this set of taxa as a monophyletic lineage, even though all taxa placed within it have not yet been examined. Specifically, *iniscatus* and *nucus* appear closely related to other members of our "*varius* clade" (see above) while both *lindberghi* and *azarae* are of uncertain placement but without direct association with any of the other species in Hershkovitz's list. The remaining forms in Hershkovitz's "*boliviensis* group" for which data are available do group phylogenetically as our Clade 2, the assemblage of species recognized by Myers et al. (1990) as related. These authors used a combination of allozymic, karyotypic, qualitative morphology, and morphometric analyses to tease apart an assortment of named forms that had previously resided as synonyms of *A. boliviensis*, separating *lutescens* [= *puer* in their analysis] and *subfuscus* at the species level while describing *juninensis* as a new species. They also argued that Argentinian *spegazzinii*, while sufficiently distinct from *boliviensis* to warrant species status, at least until geographically intervening samples from Bolivia had been assembled and adequately examined, was closely related to that species. Their concept of a "*boliviensis* group" was thus an assemblage of taxa that shared multiple characters, had contiguous to slightly overlapping ranges through the Altiplano from central Peru south to Argentina, and, at least partly, were joined in a phyletic analysis of allozymes (see also Patton et al., 1989).

This grouping of 5 species is corroborated by the cyt *b* sequence data we present here. In addition, our analyses indicate that *A. kofordi*, from the upper edge of the elfin forest in southeastern Peru, and *A. fumeus*, from the Yungas of Bolivia, are likewise members of this group. Myers and Patton (1989b) placed both species in a "*fumeus*-species group" and suggested a close relationship to *A. mollis*. The cyt *b* data, however, unambiguously align *kofordi* and *fumeus* with the core of Myers et alia's (1990) "*boliviensis* group" and not with *A. mollis* and its relatives (see below, and Figs. 2 and 3). The inclusion of *kofordi* with the "*boliviensis* group" of Myers et al. (1990) is also supported by data from the mitochondrial Control Region (Hoekstra and Edwards, 2000). Sequence data would help to determine the status of the poorly known *A. aliquantulus*, considered by Díaz et al. (1999) to be a member of the *boliviensis* group of Myers et al. (1990) and similar to *spegazzinii* and *lutescens caenosus*.

Clade 3: The Akodon aerosus *Group*.—This clade comprises nearly all of the species

Table 2. Support values for specific nodes in each of the 4 phylogenetic analyses (bootstrap values are provided for maximum parsimony trees and posterior probabilities for Bayesian analyses). Nodes are identified numerically as in the topology of Figure 2.

Node	MP – equal weights	MP – 5:1 transversion weighted	Bayesian	Bayesian – 3 positions
1	97	98	100	100
2	99	99	100	100
3	55	59	99	100
4	100	100	100	100
5	62	--	87	90
6	54	--	100	100
7	100	100	100	100
8	72	89	99	96
9	58	--	incl. *azarae*, 84	incl. *azarae*, 74
10	100	100	100	100
11	--	--	incl. *azarae*, 58	--
12	--	--	incl. *azarae*, 92	incl. *azarae*, 87
13	58	--	incl. *azarae*, 96	incl. *azarae*, 99
14	--	51	96	99
15	96	97	100	100
16	100	100	100	100
17	100	100	100	100
18	100	100	100	100
19	99	98	100	100
20	--	--	--	--
21	100	100	100	100
22	--	--	--	--
23	--	56	54	61
24	--	--	--	--
25	90	62	98	96
26	--	--	--	--
27	--	--	50	74
28	89	96	100	100
29	--	--	--	--
30	--	--	--	--
31	55	57	98	100

Table 2 (continued).

Node	MP – equal weights	MP – 5:1 transversion weighted	Bayesian	Bayesian – 3 positions
32	--	--	--	--
33	--	--	--	--
34	--	--	61	--
35	--	62	100	100
36	--	--	71	75
37	100	100	100	100
38	--	--	61	--
39	75	59	52	93

of *Akodon* that inhabit the elfin and upper tropical forests on the eastern slopes of the Andes, or extend onto the western slope, from southern Bolivia to Colombia, including *A. aerosus*, *A.* cf. *budini*, *A. affinis*, *A. mollis*, *A. orophilus*, *A. siberiae*, and *A. torques*. This series of species replace one another from south to north along the Andes, as well as, in some cases, elevationally within more restricted geographic regions (see, for example, Patton and Smith, 1992a, for mapped distributions of those species occurring in Peru). The only member of this apparent clade whose range is above the elfin forests is *A. albiventer*, which is found above tree-line from southern Peru across the Altiplano to Chile and northern Argentina. The clade is weakly supported in the MP analyses (bootstrap values of 55% for the equally weighted analysis and 57% for the transversion weighted analysis), but strongly supported in the Bayesian analyses (98 and 100% posterior probabilities in the overall, and the site-specific codon position analyses, respectively).

The various geographic samples of *A. aerosus* and *A. orophilus* are not monophyletic within the named species, suggesting either that lineage sorting has been incomplete, that more than 1 taxon is represented within each of these currently recognized species, and/or that the similar morphologies implied by current species allocations resulted from parallel or convergent evolution. Internally, however, 3 clusters of species/geographic localities are well supported, and a fourth is weakly supported. These include: (1) cf. *budini* + *siberiae* (node 21), 2 taxa traditionally linked in the subgenus *Hypsimys* that are grouped with 100% bootstrap or 100% posterior probability in all analyses; (2) an unresolved trichotomy containing *aerosus baliolus* + *aerosus* (MVZ 172870 from Depto. Junín, Peru) + *affinis* (node 28), a triad that is strongly supported with bootstrap values ranging from 89 to 96 in the MP analyses and posterior probabilities of 100 in both Bayesian analyses; (3) *torques* + *orophilus* (MVZ 173057, Depto. Junín, Peru) (node 25), which is supported by MP bootstrap values of 90 and 62% and Bayesian posterior probabilities of 98 and 96%; and, (4) (*orophilus* [LSU 27957, Depto. Huanuco, Peru] (*orophilus* [FMNH 129234, Depto. Amazonas, Peru] + *aerosus* [MVZ 171679, Depto. Cusco, Peru])), which is recovered in the transversion-weighted MP and the Bayesian analyses (tv weighted MP bootstrap value <50%; Bayesian posterior probabilities 83 and 88%). None of these subclades have geographic continuity, as each includes samples that are widely distributed, with individuals of other subclades geographically interspersed. Based on the limited chromosome data that are available for the *A. aerosus* group, karyotypic diversity is extreme, with 2n ranging broadly both within and among taxa (from 22 to 26 in *torques*, 22 to 40 in *aerosus*, and 22 to 38 in *mollis*); data for *A. orophilus* are as yet unavailable (Patton and Smith, 1992a; unpubl. data). The karyotype of *A. albiventer* is 2n=40 and that of both *A. budini* and *A. siberiae* is 2n=38 (Myers and Patton, 1989a). This assemblage of species exhibits the highest mean among-species Kimura 2-parameter distance of 0.093 (standard error = 0.005), with pairwise distances across all sequences, regardless of the species or population, ranging from 0.054 [*torques* to *orophilus*-Junín or *affinis* to *aerosus baliolus*] to 0.134 [*albiventer* to *siberiae*].

The best working hypothesis is that *A. albiventer* is a high elevation relative of a lineage that is otherwise distributed on the flanks of the Andes. To our knowledge, a formal association of *A. albiventer* with other species of *Akodon* has not previously been proposed; indeed, some earlier authors have associated *albiventer* with *Bolomys* (=*Necromys*), not *Akodon* (see Musser and Carleton, 1993). A geographically coherent phylogenetic unit of *Akodon* species from the forested Andean slopes is appealing on biogeographic grounds, although this "*aerosus* group" had not been recognized as a potential lineage until now. Interestingly, the taxonomically limited Control Region data of Hoekstra and Edwards (2000) also support a portion of taxa as a monophyletic lineage, as their analysis identified a group composed of ((*aerosus* + *aerosus baliolus*)(*orophilus* (*torques* + *mollis*))). While data are as yet unavailable, *A. surdus* (from the cloud forests in the vicinity of Machu Picchu in southern Peru) is likely a member of this group, either as a distinct species or perhaps conspecific with *aerosus* (Patton and Smith, 1992a).

Clade 4: The Akodon cursor *Group*.—The fourth grouping of species present in our analyses includes 6 species ranging through the coastal forests of Brazil, Paraguay, Uruguay, and Argentina, namely *A. cursor*, *A.* aff. *cursor*, *A. montensis*, *A. mystax*, *A. reigi*, and *A. paranaensis*. This collective group is, however, resolved only in the equally-weighted MP analysis, and only with support <50%. In 1 of the tv weighted MP analyses the clade includes *A. lindberghi*, and in the other *montensis* joins in a polytomy with the *cursor* group and the *boliviensis* group, again with support <50%. The overall Bayesian analysis included *A. azarae* in the clade (posterior probability of only 58%). Thus, the general validity of this grouping needs to be tested seriously with additional data. Within the group, however, are 2 strongly to moderately corroborated subclades. One subclade links *A. cursor* with *A.* aff. *cursor* (node 10) at bootstrap and posterior probabilities of 100% in all analyses. A second subclade, found in the MP analyses, links the other 4 species at increasingly well-supported nodes, as (*montensis* (*reigi* (*mystax*, *paranaensis*))), with bootstrap values of 58 and <50% in the MP analyses for the node joining *montensis* to the other 3 species. In the Bayesian analyses *A. azarae* is also part of this subclade (support 84 and 74). All of the analyses support the node linking *reigi* to *mystax* + *paranaensis* (bootstrap support of 72 and 89%, and posterior probabilities of 99 and 96%), and the *mystax* + *paranaensis* linkage (bootstrap and posterior probabilities of 100%). This group has an average Kimura 2-parameter distance of 0.083 (standard error = 0.006) with a range between species pairs of 0.023 (between *mystax* and *paranaensis*) to 0.109 (between aff. *cursor* and *montensis*).

An association of species occupying forested areas of coastal Brazil was first recognized by Rieger et al. (1995) as an "*Akodon cursor* group" based on the electrophoretic similarity among *A. cursor*, *A. montensis*, and an allopatric chromosomal variant referred to as *A.* aff. *cursor*. *Akodon cursor* is karyotypically variable, with 2n=14 or 15; *A.* aff. *cursor* differs with 2n=16; and *A. montensis* has 2n=24 or 25. The grouping was expanded to include *A. mystax* (2n=44) and possibly *A. lindberghi* (2n=42) by Geise et al. (2001) based on cyt *b* sequences. The close relationship between *reigi*, *mystax*, and *paranaensis*, all with 2n=44, was not recognized by the authors who described these species despite the high degree of similarity in the individual descriptions, since their work was done at approximately the same time (González et al., 1998; Hershkovitz, 1998; and Christoff et al., 2000, respectively). Rather, González et al. (1998) and Christoff et al. (2000) compared *A. reigi* and *A. paranaensis*, respectively, primarily to *A. serrensis* and made no assignment of either species to any species group. Pardiñas et al. (2003) pointed out the similarity, based on karyotypes and cyt *b* sequences, of *mystax*, *paranaensis*, *reigi*, and a fourth 2n=44 specimen (previously referred to *A. serrensis*, see Liascovich & Reig, 1989) from Misiones, Argentina. M. J. Silva et al. (personal communication, January 2004) have confirmed a clade composed of *mystax*, *montensis*, *cursor*, and aff. *cursor*, along with a 2n=10 form from central Brazil related to *cursor* + aff. *cursor*, based on both chromosomal banding and cyt *b* sequences. Cyt *b* sequence is not available for another potential member of the *cursor* group, *A. sanctipaulensis*, described from a very restricted geographic area in southeastern São Paulo state, Brazil (Hershkovitz, 1990b).

The 4 "unique" species of Akodon.—As mentioned above, the placement of 4 of the 30 taxa of *Akodon* we have included in this analysis is ambiguous. *Akodon lindbergi* was originally described from a locality in the drier Cerrado biome (Hershkovitz, 1990b), but has subsequently been reported from forested areas in southeastern Brazil (Geise et al., 1996). It is placed at the base (node 13) of Clade 2 (the "*Akodon boliviensis* group") and Clade 4 (the "*Akodon cursor* group") in almost all of the analyses, including the equally-weighted MP analysis, 1 of the 2 tv weighted MP islands, and both Bayesian analyses, and it is at the base of the *cursor* group in the other tv weighted MP island. Support for the placement of *lindberghi* varies widely. For example, the bootstrap value for node 13 in the equally weighted MP analysis is only 58% while the Bayesian analyses provide high posterior probabilities for this node, including *azarae* (96 and 99%, respectively, for the general and the site-specific codon position analyses). These data at least provide some support for a hypothesis linking *lindberghi* to 2 other lineages of *Akodon*. Note added in proof: Pardiñas et al. (2005) described a new species, *A. philipmyersi*, from Misiones, Argentina, which, based on cytochrome *b* sequences, is sister to *A. lindberghi*, although this relationship is distant (10.1% Kimura 2-parameter distance) and weakly supported in their phylogenetic analyses. This pair of species is placed at the base of our *Akodon cursor* and *Akodon boliviensis* groups in their analyses.

Akodon azarae is widely distributed in central and northeastern Argentina, eastern Paraguay, Uruguay, and southern Brazil. Its phylogenetic position fluctuates across our analyses, linking to Clade 2 (the "*Akodon boliviensis* group") plus Clade 4 (the "*Akodon cursor* group") plus *lindberghi* (node 14) in the equally weighted MP and 1 of the 2 islands in the tv weighted MP analysis (but with very weak support of <50% and 51%, respectively), or within Clade 4, as part of the subclade containing *montensis, reigi, mystax*, and *paranaensis* in both Bayesian analyses (84 and 74% posterior probabilities for the general and the site-specific codon position analyses, respectively). The Control Region analyses of Hoekstra and Edwards (2000) suggested a relationship with our

Clade 2, as *azarae* appears as the sister to *boliviensis*, within our Clade 2, with reasonably strong support (bootstrap = 81). This species must continue to be considered enigmatic in its phylogenetic relationships. Perhaps the inclusion of data from additional species (such as *A. sylvanus* from northwestern Argentina that Cabrera [1961], based on Thomas [1927], considered a synonym, and other species, some undescribed [Pardiñas et al., 2003; description in progress]), and additional subspecies (e.g., *A. a. bibianae* and *A. a. hunteri*) will help stabilize its placement.

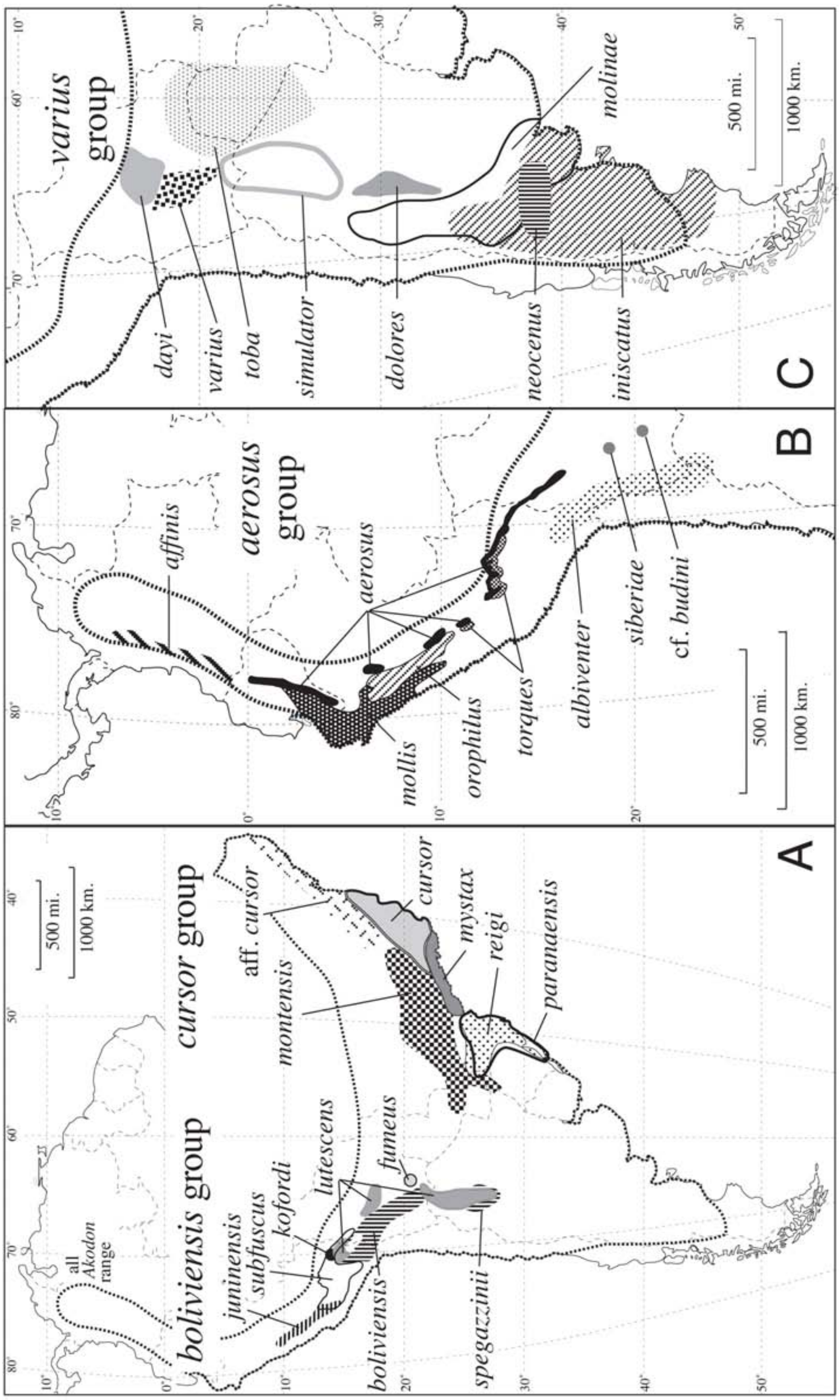
The range of *A. mimus* extends along the fringe of elfin forest from southeastern Peru to northern Bolivia. It is the type species of *Microxus*, which has been varyingly treated historically as a separate genus, a subgenus of *Akodon*, or a simple synonym of *Akodon* (see Musser and Carleton, 2005). Our earlier analyses (Patton et al., 1989; Smith and Patton, 1991, 1993), using both allozyme and mtDNA markers, firmly supported the inclusion of *mimus* within an inclusive *Akodon*. The exact phylogenetic position of this species within *Akodon*, however, remains uncertain. *Akodon mimus* is paired with *Deltamys kempi* as sister to Clade 3 (the "*Akodon aerosus* group") in the equally weighted MP analysis, singly as sister to Clade 3 in 1 tv weighted island of trees, and in a cluster with *Deltamys kempi* and "*Akodon" serrensis*, joining a basal *Akodon* polytomy, in the other island of tv weighted trees, with support <50% in all MP analyses. *Akodon mimus* joins in a polytomy with Clade 1, Clade 3, and *Deltamys kempi* in the general Bayesian analysis (support for that entire grouping is 71%), and is sister to Clade 1 in the site-specific Bayesian analysis (support 63%). D'Elía et al. (2003), in their review of the generic status of *Deltamys*, found no association between that species and *A. mimus*, a view we share since the bootstrap linking those taxa is low. The best we can suggest with available data is that *A. mimus* appears to have ties to Clade 1 (the "*Akodon varius* group") and Clade 3 (the "*Akodon aerosus* group").

Akodon serrensis occurs in mixed rainforest in southern Brazil and morphologically resembles members of Clade 4 (the "*Akodon cursor* group"). However, we reiterate our comment above that the status of *A. serrensis* should be thoroughly reviewed, as all of our analyses except the tv weighted MP analyses place this species outside a more restricted *Akodon*, with the strongest support as the sister to *Akodon*, including *Deltamys* (posterior probability 99%, general Bayesian analysis), or as the sister to *Deltamys* outside of *Akodon* (posterior probability 73% for the *serrensis* - *Deltamys* pair, and support of 100% for that pair as sister to *Akodon*, in the site-specific Bayesian analysis).

Speciation and Timing of Diversification

The lack of strong support for many nodes in the trees generated by both sets of analyses limits our ability to define biogeographic units and hypothesize modes of diversification in this complex of mice. However, nodal support for many sister-species

Figure 4 (facing page): Approximate geographic ranges of species in each of the 4 species groups identified by the analyses presented herein. The stippled boundary in each depicts the range limits of the entire genus, as currently understood. Note that ranges of the 4 species of ambiguous phylogenetic affinity are not mapped, and that the "*varius*-group" includes those species assigned to the group by Myers (1989) even though not all have been sequenced as yet.


A
boliviensis group
cursor group
all *Akodon* range
500 mi.
1000 km.
juninensis
subfuscus
kofordi
lutescens
fumeus
boliviensis
spegazzinii
montensis
aff. *cursor*
cursor
mystax
reigi
paranaensis
B
aerosus group
affinis
aerosus
mollis
orophilus
torques
albiventer
siberiae
cf. *budini*
500 mi.
1000 km.
C
varius group
dayi
varius
toba
simulator
dolores
neocenus
iniscatus
molinae
500 mi.
1000 km.

pairs is strong, and their pattern of geographic distribution suggests that speciation has been largely, if not exclusively, allopatric. For example, 8 pairs of sister-species with Bayesian posterior probabilities of 94% or greater and MP bootstrap support of 86% or greater (Figs. 2 and 3, Table 2) are geographic replacements of one another, a geographic pattern that is consistent with allopatric, but not sympatric, divergence (Lynch, 1989): from Clade 2, *A. boliviensis* + *A. spegazzinii*, *A. subfuscus* + *A. lutescens*, and *A. fumeus* + *A. kofordi* (Fig. 4A; Myers and Patton, 1989b; Myers et al., 1990); from Clade 3, *A. aerosus* + *A. affinis*, *A. orophilus* + *A. torques*, and *A.* cf. *budini* + *A. siberiae* (Fig. 4B; Myers and Patton, 1989a; Patton and Smith, 1992a, 1992b); and from Clade 4, *A. mystax* + *A. paranaensis* and *A. cursor* + *A.* aff. *cursor* (Fig. 4A). Those species within specific clades that have more broadly overlapping ranges are, in each case, not sisters, suggesting that their current ranges have developed subsequent to divergence. Examples of this pattern are *A. boliviensis* and *A. lutescens* in Clade 2 and *A. montensis*, *A. mystax*, and *A. cursor* in Clade 4 (Fig. 4A). The parapatric distribution of many species, especially of sister-pairs, could suggest a process of diversification across ecological gradients, but on the eastern slope of the Andes where this hypothesis has been explicitly examined, this mode of speciation has been falsified for members of the "*aerosus* group" (Clade 3) (Patton and Smith, 1992b). A caveat to this type of argument about speciation mode based on geographic distributions is necessary, as the argument assumes that the respective species' ranges have remained largely constant since divergence. However, as Pardiñas (1999; see also Ortiz and Pardiñas, 2001) notes, fossil faunas often are "non-analogue assemblages" (*sensu* Barnosky, 1993) relative to those of today, and he provides evidence of earlier sympatry between presently allopatric species, such as the subtropical *Akodon* cf. *A. cursor* and Patagonian-central Argentinian *Akodon* cf. *A. iniscatus* in the Ensenadan (Early-Middle Pleistocene) of Buenos Aires Province, Argentina.

The time of divergence of *Akodon* and its member species can be roughly estimated by the rate of change in third-position transversions in cyt *b*, which are argued to change linearly with time (Irwin et al., 1991), an approach we used in our earlier analyses of the larger sigmodontine radiation (Smith and Patton, 1999: Fig. 10). If the split between *Mus* and *Rattus* at about 10 mya is used to set the scale, then the base of the radiation of the genus *Akodon* is approximately 2.46 mya. A second calibration takes the date of the occurrence of a fossil *Necromys* (called *Bolomys* in our 1999 paper) as the date of the split between *Necromys*, *Thaptomys*, *Deltamys*, and *Akodon*. The holotype of *Necromys formosus* was collected in bank 3 of the Monte Hermoso formation (Pardiñas and Tonni, 1998). In Smith and Patton (1999) we used a date of 3.5 mya for this fossil. More recent studies give a date for the Monte Hermoso formation as around 4-5 mya (Cione and Tonni, 2001), or 5.33 mya (Schultz et al., 2002). If we choose a *Necromys* fossil date of 5 mya, the radiation of the genus *Akodon* would be at around 2.5 mya, fairly close to the estimate based on the *Mus*/*Rattus* scale. The range of dates for the *Necromys* fossil, from 4 to 5.33 mya, would give a range of estimates for the *Akodon* radiation from 2 to 2.65 mya. These estimates are slightly younger than the earliest known fossil assigned to *Akodon sensu stricto*, represented by the species †*A. lorenzinii* from the Vorohuean Age/Stage of the latest Pliocene (Reig, 1987), which has a minimal age of approximately 2.8 mya (Cione and Tonni, 1995). Three points should be made from these dating considerations: first, the genus *Akodon* is reasonably old, certainly dating from the Pliocene. Thus, both accumulating fossil and molecular based ages affirm a substantial age to the sigmodontine radiation itself (see Reig, 1987; Engel et al., 1998; Smith and Patton, 1999; D'Elía, 2003; Pardiñas et al., 2003 (2002)). Second, the timing of sister-species divergence ranges from moderate age to quite recent. If one simply apportions sequence divergence evenly beginning with the date of the base of the genus (an approximate K2p average distance of 0.124, excluding *A. serrensis*; Table 1), then species pairs such as *A. boliviensis* + *A. spegazzinii* (K2p distance of 0.051), *A. subfuscus* + *A. lutescens* (0.054), or *A. torques* + *A. orophilus* (0.054) are relatively old, approximately 1 mya. Alternatively, species pairs such as *A. molinae* + *A. dolores* appear much more recently derived, approximately only 200 kya, based on a K2p distance of 0.012 (Table 1). And, third, the relatively deep ages only reinforce the necessary recognition that current range distributions likely have been established subsequent to speciation itself, which makes an understanding of important issues, such as "centers of original differentiation" (e.g., Reig, 1984) as well as modes of speciation (above) difficult, at best, to establish.

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LITERATURE CITED

Apfelbaum, L. I., and A. Blanco
1984 Genetic similarity between species of *Akodon* (Rodentia, Cricetidae). Journal of Experimental Zoology 229:1-5.

Apfelbaum, L. I., and O. A. Reig
1989 Allozyme genetic distances and evolutionary relationships in species of akodontine rodents (Cricetidae: Sigmondotinae). Biological Journal of the Linnean Society 38:257-280.

Applied Biosystems, Inc.
1994 Sequence Navigator DNA and Protein Sequence Comparison Software. Perkin-Elmer Corporation, Foster City, California.

Barnosky, A. D.
1993 Faunal response to glacial-interglacial transitions in the western United States. VI International Theriological Congress. Abstracts: 14. Sydney.

Bárquez, R. M., D. F. Williams, M. A. Mares, and H. H. Genoways

1980 Karyology and morphometrics of three species of *Akodon* (Mammalia: Muridae) from northwestern Argentina. Annals of Carnegie Museum 49:379-403.

Barros, M. A., R. C. Liascovich, L. Gonzalez, M. S. Lizarralde, and O. A. Reig

1990 Banding pattern comparison between *Akodon iniscatus*, and *Akodon puer* (Rodentia, Cricetidae). Zeitschrift für Säugetierkunde 55:115-127.

Beckman, K. B., M. F. Smith, and C. Orrego

1993 Purification of mitochondrial DNA with Wizard Minipreps DNA purification system. Promega Notes 43:10-13.

Bianchini, J. J., and L. H. Delupi

1991 (1994) Consideraciones sobre el estado sistemático de *Deltamys kempi* Thomas, 1917 (Cricetidae, Sigmodontinae). Physis 49:27-35.

Bradley, R. D., and R. J. Baker

2001 A test of the genetic species concept: cytochrome-*b* sequences and mammals. Journal of Mammalogy 82:960-973.

Braun, J. K., M. A. Mares, and R. A. Ojeda

2000 A new species of grass mouse, genus *Akodon* (Muridae: Sigmodontinae), from Mendoza Province, Argentina. Zeitschrift für Säugetierkunde 65:216-225.

Cabrera, A.

1961 Catálogo de los mamíferos de America del Sur. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia." Ciencias Zoológicas 4(2): v-xxii + 309-732.

Christoff, A. U., V. Fagundes, I. J. Sbalqueiro, M. S. Mattevi, and Y. Yonenaga-Yassuda

2000 Description of a new species of *Akodon* (Rodentia: Sigmodontinae) from southern Brazil. Journal of Mammalogy 81:838-851.

Cione, A. L., and E. P. Tonni

1995 Chronostratigraphy and "Land-mammal ages" in the Cenozoic of southern South America: Principles, practices and the "Uquian" problem. Journal of Paleontology 69:135-159.

2001 Correlation of Pliocene to Holocene southern South American and European vertebrate-bearing units. Bollettino della Societá Paleontologica Italiana 40(2):167-173.

D'Elía, G.

2003 Phylogenetics of Sigmodontinae (Rodentia, Muroidea, Cricetidae), with special reference to the akodont group, and with additional comments on historical biogeography. Cladistics 19:307-323.

D'Elía, G., E. M. González, and U. F. J. Pardiñas

2003 Phylogenetic analysis of sigmodontine rodents (Muroidea) with special reference to the akodont genus *Deltamys*. Mammalian Biology 68:351-364

Díaz, M. M, R. M. Bárquez, J. K. Braun, and M. A. Mares

1999 A new species of *Akodon* (Muridae: Sigmodontinae) from northwestern Argentina. Journal of Mammalogy 80:786-798.

Emmons, L. H.

1997 Mammals of the Río Urucuti Basin, south central Chuquisaca, Bolivia. Pp. 31-33 in A Rapid Assessment of the Humid Forests of South Central Chuquisaca, Bolivia. RAP Working Papers 8, Conservation International.

1999 Two new species of *Juscelinomys* (Rodentia: Muridae) from Bolivia. American Museum Novitates 3279:1-15.

Engel, S. R., K. M. Hogan, J. F. Taylor, and S. K. Davis

1998 Molecular systematics and paleobiogeography of the South American sigmodontine rodents. Molecular Biology and Evolution 15:35-49.

Galliari, C., U. F. J. Pardiñas, and F. J Goin

1996 Lista comentada de los mammíferos argentinos. Mastozoología Neotropical 3:39-61.

Geise, L., R. Cerqueira, and H. N. Seuánez

1996 Karyological characterization of a new population of *Akodon lindberghi* (Rodentia, Sigmodontinae) in Minas Gerais state (Brazil). Caryologia 49:57-63.

Geise, L., M. F. Smith, and J. L. Patton

2001 Diversification in the genus *Akodon* (Rodentia: Sigmodontinae) in southeastern South America: Mitochondrial DNA sequence analysis. Journal of Mammalogy 82:92-101.

González, E. M., A. Langguth, and L. F. de Oliveira

1998 A new species of *Akodon* from Uruguay and southern Brazil (Mammalia: Rodentia: Sigmodontinae). Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo 12:1-6.

González, E. M., and E. Massoia

1995 Revalidación del género *Deltamys* Thomas, 1917, con la descripción de una nueva subespecie de Uruguay y Sur del Brasil (Mammalia, Rodentia: Cricetidae). Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo 12:1-8.

Hershkovitz, P.

1990a The Brazilian rodent genus *Thalpomys* (Sigmodontinae, Cricetidae), with a description of a new species. Journal of Natural History, 24:777-783.

1990b Mice of the *Akodon boliviensis* size class (Sigmodontinae, Cricetidae), with the description of two new species from Brazil. Fieldiana: Zoology, new series 57:1-35.

1998 Report on some sigmodontine rodents collected in southeastern Brazil with descriptions of a new genus and six new species. Bonner zoologische Beiträge 47:193-256.

Hoekstra, H. E., and S. V. Edwards

2000 Multiple origins of XY female mice (genus *Akodon*): phylogenetic and chromosome evidence. Proceedings of the Royal Society of London, B, 267:1825-1831.

Hoffmann, F. G., E. P. Lessa, and M. F. Smith

2002 Systematics of *Oxymycterus* with description of a new species from Uruguay. Journal of Mammalogy 83:408-420.

Huelsenbeck, J. P., F. Ronquist, R. Nielsen, and J. P. Bollback

2001 Bayesian inference of phylogeny and its impact on evolutionary biology. Science 294:2310-2314.

Irwin, D. M., T. D. Kocher, and A. C. Wilson

1991 Evolution of the cytochrome *b* gene of mammals. Journal of Molecular Evolution 32:128-144.

Kimura, M.

1980 A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequence. Journal of Molecular Evolution 16:111-120.

Kumar, S., K. Tamura, I. B. Jakobsen, and M. Nei

2001 MEGA2: Molecular Evolutionary Genetics Analysis software. Bioinformatics 17:1244-1245.

Lansman, R. A., R. O. Shade, J. F. Shapira, and J. C. Avise

1981 The use of restriction endonucleases to measure mitochondrial DNA sequence relatedness in natural populations. III. Techniques and potential applications. Journal of Molecular Evolution 17:214-226.

Lewis, P.

2001 Phylogenetic systematics turns over a new leaf. Trends in Ecology and Evolution 16:30-37.

Liascovich, R. C., and O. A. Reig
1989 Low chromosomal number in *Akodon cursor montensis* Thomas and karyologic confirmation of *A. serrensis*. Journal of Mammalogy 70:391-396.

Lynch, J. D.
1989 The gauge of speciation: on the frequencies of modes of speciation. Pp. 527-553 in Speciation and Its Consequences (Otte, D., and J. A. Endler, eds.). Sinauer Associates, Sunderland, Massachusetts, USA.

Maniatis, T., E. F. Fritsch, and J. Sambrook
1982 Molecular Cloning. A Laboratory Manual, Cold Spring Harbor, New York, USA.

Medrano, J. F., E. Aasen, and L. Sharrow
1990 DNA extraction from nucleated red blood cells. Biotechniques 8:43.

Merani, S., and M. S.Lizarralde
1980 *Akodon molinae* (Rodentia: Cricetidae), a new laboratory animal: breeding, management, and reproductive performance. Laboratory Animals 14:129-131.

Musser, G. M., and M. D. Carleton
1993 Family Muridae. Pp. 501-756 in Mammal Species of the World: A Taxonomic and Geographic Reference. Second ed. (Wilson, D. E., and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D. C., USA.

2005 Superfamily Muroidea. Pp. 894-1531 in Mammal Species of the World: A Taxonomic and Geographic Reference. Third ed. (Wilson, D. E., and D. M. Reeder, eds.). Johns Hopkins Univerfsity Press, Baltimore, Maryland, USA.

Myers, P.
1989 A preliminary revision of the *varius* group of *Akodon* (*A. dayi*, *dolores*, *molinae*, *neocenus*, *simulator*, *toba*, and *varius*). Pp. 5-54 in Advances in Neotropical Mammalogy (Eisenberg, J. F., and K. H. Redford, eds.). The Sandhill Crane Press, Gainesville, Florida, USA.

Myers, P., and J. L. Patton
1989a A new species of *Akodon* from the cloud forests of eastern Cochabamba Department, Bolivia (Rodentia, Sigmodontinae). Occasional Papers of the Museum of Zoology, The University of Michigan 720:1-28.

1989b The *Akodon* of Peru and Bolivia -- Revision of the "*fumeus* group" (Rodentia: Sigmodontinae). Occasional Papers of the Museum of Zoology, The University of Michigan 721:1-35.

Myers, P., J. L. Patton, and M. F. Smith
1990 A review of the *boliviensis* group of *Akodon* (Muridae: Sigmodontinae) with emphasis on Peru and Bolivia. Miscellaneous Publications, Museum of Zoology, University of Michigan 117, ii-104.

Ortiz, P. E., and U. F. J. Pardiñas
2001 Sigmodontinos (Mammalia: Rodentia) del Pleistoceno tardío del valle de Tafí (Tucumán, Argentina): Taxonomía, tafonomía y reconstrucción paleoambiental. Ameghiniana 38:3-26.

Pardiñas, U. F. J.
1999 Fossil murids: Taxonomy, palaeoecology, and palaeoenvironments. Quaternary of South America and the Antarctic Peninsula 12:225-254.

Pardiñas, U. F. J., G. D'Elía, and S. Cirignoli
2003 The genus *Akodon* (Muroidea: Sigmodontinae) in Misiones, Argentina. Mammalian Biology 68:129-143.

Pardiñas, U. F. J., G. D'Elía, S. Cirignoli, and P. Suánez
2005 A new species of *Akodon* (Rodentia, Cricetidae) from the Northern Campos grasslands of Argentina. Journal of Mammalogy 86:462-474.

Pardiñas, U. F. J., G. D'Elía, and P. E. Ortiz
2003 (2002) Sigmodontinos fósiles (Rodentia, Muroidea, Sigmodontinae) de América del Sur: estado actual de su conocimiento y prospectiva. Mastozoología Neotropical, 9:209-252.

Pardiñas, U. F. J., and C. A. Galliari
1999 La presencia de *Akodon iniscatus* (Mammalia: Rodentia) en la provincia de Buenos Aires (Argentina). Neotrópica 45 (113-114):115-117, La Plata.

Pardiñas, U. F. J., and E. P. Tonni
1998 Procedencia estratigráfica y edad de los más antiguos muroideos (Mammalia, Rodentia) de América del Sur. Ameghiniana 35:473-475.

Patton, J. L., P. Myers, and M. F. Smith
1989 Electromorphic variation in selected South American Akodontine rodents (Muridae: Sigmodontinae), with comments on systematic implications. Zeitschrift für Säugetierkunde 54:347-359.

Patton, J. L., and M. F. Smith
1992a Evolution and systematics of akodontine rodents (Muridae: Sigmodontinae) of Peru, with emphasis on the genus *Akodon*. Pp. 83-103 Biogeografía, Ecología, y Conservación del Bosque Montano en el Perú (Valencia, N., and K. Young, eds.). Memorias del Museo de Historia Natural, Lima, Peru.

1992b mtDNA phylogeny of Andean mice: a test of diversification across ecological gradients. Evolution. 46:174-183.

Pearson, O. P.
1995 Annotated keys for identifying small mammals living in or near Nahuel Huapi National Park or Lanín National Park, Southern Argentina. Mastozoología Neotropical 2:99-148.

Reig, O. A.
1984 Distribução geográfica e historia evolutiva dos reodores muroideos sulamericanos (Cricetidae: Sigmodontinae). Revista Brasileira do Genética 7:333-365.

1987 An assessment of the systematics and evolution of the Akodontini, with the description of new fossil species of *Akodon* (Cricetidae: Sigmodontinae). Fieldiana: Zoology, new series 39:347-399.

Rieger, T. T., A. Langguth, and T. A. Waimer
1995 Allozymic characterization and evolutionary relationships in the Brazilian *Akodon cursor* species group (Rodentia-Cricetidae). Biochemical Genetics 33(9/10):283-295.

Ronquist, F., and J. P. Huelsenbeck
2003 MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572-1574.

Schultz, P. H., M. A. Zarate, W. Hames, J. King, C. Heil, C. Koeberl, P. R. Renne, and A. Blasi
2002 Argentine impact record. Geological Society of America Abstract Program 34 (2002) 401.

Silva, M.J. de J., and Y. Yonenaga-Yassuda
1998 Karyotype and chromosomal polymorphism of an undescribed *Akodon* from Central Brazil, a species with the lowest diploid chromosome number in rodents. Cytogenetics and Cell Genetics 81:46-50.

Smith, M. F., and J. L. Patton
1991 Variation in mitochondrial cytochrome *b* sequence in natural populations of South American akodontine rodents (Muridae: Sigmodontinae). Molecular Biology and Evolution 8:85-103.

1993 The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. Biological Journal of the Linnean Society 50:149-177.

1999 Phylogenetic relationships and the radiation of sigmodontine rodents in South America: Evidence from cytochrome *b*. Journal of Mammalian Evolution 6:89-128.

Smith, M. F., W. K. Thomas, and J. L. Patton

1992 Mitochondrial DNA-like sequence in the nuclear genome of an akodontine rodent. Molecular Biology and Evolution 9:204-215.

Swofford, D. L.

2002 PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts, USA.

Thomas, O.

1927 On a further collection of mammals made by Sr. E. Budin in Neuquen, Patagonia. Annals and Magazine of Natural History, ser. 9, 19:650-658.

Vidal-Rioja, V., N. O. Bianchi, A. Catala, and L. Semorile

1982 DNA of *Akodon* (Rodentia, Cricetidae). II. Molecular hybridization of repetitive DNA sequences. Canadian Journal of Genetics and Cytology 24:601-609.

Vidal-Rioja, V., L. Semorile, and N. O. Bianchi

1979 DNA of *Akodon* (Rodentia-Cricetidae). I. Biophysical characterization. Biochemical Genetics 17:297-303.

Voss, R. S.

2003 A new species of *Thomasomys* (Rodentia: Muridae) from eastern Ecuador, with remarks on mammalian diversity and biogeography in the Cordillera Oriental. American Museum Novitates 3421:1-47.

Walsh, P. S., D. A. Metzger, and R. Higuchi

1991 Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. Biotechniques 10:506-513.

Yunes, R. M. F., and A. Castro-Vázquez

1990 An unusual pattern of copulatory behavior in a South American cricetid rodent: *Akodon molinae*. Journal of Comparative Psychology 104:263-267.

PHYLOGEOGRAPHY OF THE TUCO-TUCO *CTENOMYS PEARSONI*: MTDNA VARIATION AND ITS IMPLICATION FOR CHROMOSOMAL DIFFERENTIATION

FILOGEOGRAFIA DEL TUCO-TUCO *CTENOMYS PEARSONI*: VARIACIÓN EN EL MTADN Y SUS IMPLICACIONES PARA LA DIFERENCIACIÓN CROMOSÓMICA

Ivanna H. Tomasco and Enrique P. Lessa

We dedicate this paper to Oliver P. Pearson, who inspired us and many other South Americans to devote our work to the study of mammals in general and, naturally, tuco-tucos in particular.

ABSTRACT

Classical models propose that chromosomal speciation occurs when a population becomes fixed for 1 or more negatively heterotic chromosomal rearrangements. This can only happen under restrictive conditions, namely in small and isolated populations. Such conditions are presumed to characterize tuco-tucos (*Ctenomys*), which show extensive chromosomal variation. *C. pearsoni* is an excellent system in which to test this hypothesis: it has the largest range of diploid number variation in the genus, with limited associated morphological or behavioral variation. Our analysis of variation in the mitochondrial control region of this species throughout the distribution of *C. pearsoni* shows that all variable populations and chromosomal forms are polyphyletic in their mitochondrial DNA. These results are incompatible with scenarios that entail the fixation by drift of negatively heterotic chromosomal rearrangements in this species because, under such scenarios, the monophyly of mitochondrial DNA of different chromosomal forms is expected. *C. pearsoni* shows a broad pattern of isolation by distance and no consistent indications of possible departures from neutrality or historical demographic change. This suggests that the species has occupied its current distribution for considerable time. This regional stability may have been retained in spite of reported Holocene transgressions and other perturbations of the species distribution. Gene flow and divergence time estimations between kariomorphs suggest a more recent colonization of the eastern part of the distribution, in line with paleogeographical data regarding changes of the Atlantic coast during the Holocene. We conclude that all populations included in this study represent a single species, *C. pearsoni*.

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Key words: Control region, population genetics, speciation, subterranean rodents

RESUMEN

Los modelos clásicos proponen que la especiación cromosómica ocurre al fijarse uno o más rearreglos cromosómicos con heterosis negativa en una población. Esto puede suceder sólo en limitadas condiciones, como poblaciones pequeñas y aisladas. Se presume que estas condiciones caracterizan a los tuco-tucos (*Ctenomys*), que presentan una variación cromosómica extraordinariamente alta. Un excelente sistema para evaluar esta hipótesis es *C. pearsoni*: presenta el mayor grado de variación en el número diploide del género sin una asociación aparente con la variación morfológica o comportamental. Nuestro análisis de la variación en la región control del ADN mitocondrial de *C. pearsoni* a lo largo de su distribución muestra que todas las poblaciones y formas cromosómicas son polifiléticas en su ADN mitocondrial. Estos resultados son incompatibles con escenarios de fijación por deriva de rearreglos cromosómicos con heterosis negativa en la especie porque, bajo tales escenarios, se espera la monofilia del ADN mitocondrial de las diferentes formas cromosómicas. *C. pearsoni* muestra un amplio patrón de aislamiento por distancia y no hay indicaciones consistentes de apartamientos de la neutralidad o cambios demográficos históricos. Esto sugiere que la especie ha ocupado su distribución actual por un tiempo considerable. Esta estabilidad regional se ha mantenido a pesar de las transgresiones holocénicas y otras perturbaciones de la distribución de la especie. Las estimaciones de flujo génico y de tiempos de divergencia entre cariomorfos sugieren una colonización más reciente del Este de la distribución, coincidiendo con datos paleogeográficos sobre cambios de la costa atlántica durante el Holoceno. Concluimos que todas las poblaciones incluidas en este estudio representan una única especie, *C. pearsoni*.

Palabras claves: Región de control, genética de poblaciones, especiación, roedores subterráneos

INTRODUCTION

Speciation is a central theme in evolutionary biology (Berlocher, 1998). During the second half of the 20th century, the frequent observation of chromosomal differences among related species suggested that chromosomal changes may play a central role in the speciation process (White, 1968, 1978). Classically, it has been proposed that individuals heterozygous for particular rearrangements may be partly sterile (underdominant) and that chromosomal changes may act as genetic barriers to gene flow between populations fixed for different rearrangements and thus, facilitate reproductive isolation. However, if underdominance were strong, it would be very unlikely that new rearrangements would become established, unless their frequencies increase by meiotic drive or by genetic drift in small and isolated populations. Paradoxically, rearrangements that are neutral or weakly underdominant are more easily fixed by genetic drift alone in populations, but they will be ineffective as reproductive barriers. In spite of some recent support (reviewed by King, 1993), classical chromosomal speciation is not currently favored by most evolutionists (e.g., Spirito, 1998; Rieseberg, 2001). However, the debate about the role of chromosomal change in speciation is still open; new and promising models have been proposed (Rieseberg and Livingstone, 2003) and their predictions have been tested with exiting results (Navarro and Barton, 2003).

Subterranean rodents, particularly South American tuco-tucos (genus *Ctenomys*), have been of special interest in the literature on speciation, precisely by virtue of their patchy distributions, low vagility, territoriality, and extensive karyotypic variation (e.g., Reig and Kiblisky, 1969; Nevo, 1979; Reig et al., 1990). They are still often thought to be eloquent examples of "chromosomal speciation" (e.g., Massarini et al., 1991; Ortells, 1995; Bidau et al., 1996; Contreras and Bidau, 1999). *Ctenomys* exhibits high chromosomal variation (Cook et al., 1990), with diploid numbers varying from 10 (Anderson et al., 1987) to 70 (Kiblisky et al., 1977; Contreras and De Contreras, 1984). The genus comprises more than 56 species (Reig et al., 1990) and has been considered one of the most rapidly speciating mammalian lineages (Reig and Kiblisky, 1969; Reig, 1970; Reig et al., 1990; Cook et al. 2000). Traditionally, the age of the genus has been estimated to be approximately 1.8 million years (Reig et al., 1990). More recently, however, Verzi (2002, see also Schultz et al., 1998) reported *Ctenomys* fossils >3 million years old. The idea that highly structured populations might have facilitated the fixation of new homokaryotypes and hence the production of new species is widely accepted by students of *Ctenomys*, but critical evidence concerning the actual effect of chromosomal rearrangements or their fixation by drift alone is lacking (reviewed by Lessa, 2000).

Several approaches are necessary to tackle the possible relationship between chromosomal change and speciation in *Ctenomys*. Recent research has focused in the relationship between satellite copy number and chromosomal evolution in tuco-tucos (Slamovits et al., 2001). Also, several studies have detailed chromosomal polymorphism (e.g., Massarini et al., 1995; Freitas, 1997, 2001; Braggio et al., 1999; García et al., 2000) or examined breeding patterns in contact zones between different chromosomal races (e.g., Gava and Freitas, 2002, 2003). Here, we attempt to test one of the predictions of classical models of chromosomal speciation, namely that it entails the fixation by drift of negatively heterotic chromosomal changes. The expected time for lineage sorting to reciprocal monophyly is 4-fold longer for neutral, diploid chromosomal rearrangements than for mtDNA. That difference should be at least maintained if rearrangements are negatively heterotic. Therefore, if fixation was due to drift alone the monophyly of mtDNA would be expected. Mitochondrial DNA monophyly should accompany the fixation of chromosomal rearrangements. Thus, at least derived, if not all, karyomorphs should be monophyletic in their mtDNA.

To examine this prediction, we carried out a study of mitochondrial DNA variation in the chromosomally polytypic *Ctenomys pearsoni* (Fig. 1). This species inhabits the coastal plains of southern Uruguay by the Río de la Plata and the Atlantic Ocean, although there are also some populations in Argentina (García et al., 2000). Among tuco-tucos, this species is especially interesting for our purpose, because it has the largest range of diploid numbers in the genus (2n=56 to 2n=70; Kiblisky et al., 1977; Novello and Lessa, 1986; Novello et al., 1990, 1996; Villar, 2000; Novello and Altuna, 2002). C and G banding patterns surveys have uncovered 7 karyomorphs (although some share the same diploid number of 2n=70, see Fig. 2, Table 1) with limited associated morphological or behavioral differences (Lessa and Langguth, 1983; Altuna and Lessa, 1985; Altuna et al., 1992, 1993; Francescoli, 2002). As in other species of the

Figure 1. Pearson's tuco-tuco (*Ctenomys pearsoni*). Photograph by Daniel Rueda.

genus, intrapopulational variation has also been reported (Novello et al., 1990).

The pattern of mtDNA variation also sheds light on the systematics of the Uruguayan species of the genus, particularly regarding the taxonomic status of chromosomal races of *C. pearsoni.* Since their description by Kiblisky et al. (1977), fixed chromosomal differences between coastal populations have raised doubts about their species status. All the karyotypic forms (except 2n=70a in Fig. 2 and Table 1) used in the description of the species have been called collectively the "*C. pearsoni* complex" (Altuna and Lessa, 1985). Recent work identifies some of these chromosomally distinct forms as yet undescribed species (e.g., Altuna et al., 1999; González, 2001).

MATERIALS AND METHODS

We analyzed 103 individuals, 98 belonging to populations of *C. pearsoni*, 1 of *C. rionegrensis* and 4 of *C. torquatus* (see Appendix 1). Tissues and standard voucher specimens are deposited in the collection of the Laboratorio de Evolución, Facultad de Ciencias, Universidad de la Republica, Montivideo, Uruguay. We designed our geographic sampling within *C. pearsoni* to cover the geographical range and known chromosomal variation of the species in Uruguay. Populations studied are shown in Fig. 2 and their corresponding sample sizes (geographical coordinates and Department in parenthesis) were as follows: Limetas (34° 09′ 00′′ S, 58° 05′ 30′′ W, Colonia), $N = 8$; Arazatí (34° 33′ 00′′ S, 57° 00′ 00′′ W, San José), $N = 9$; Penino (34° 68′ 00′′ S, 56° 25′ 00′′ W, San José), $N = 7$; Carrasco (34° 53′ 00′′ S, 56° 02′ 00′′ W, Montevideo), $N = 10$; Roosevelt (34° 51′ 18′′ S, 56° 02′ 38′′ W, Canelones), $N = 11$; Cuchilla Alta (34° 47′ 06′′

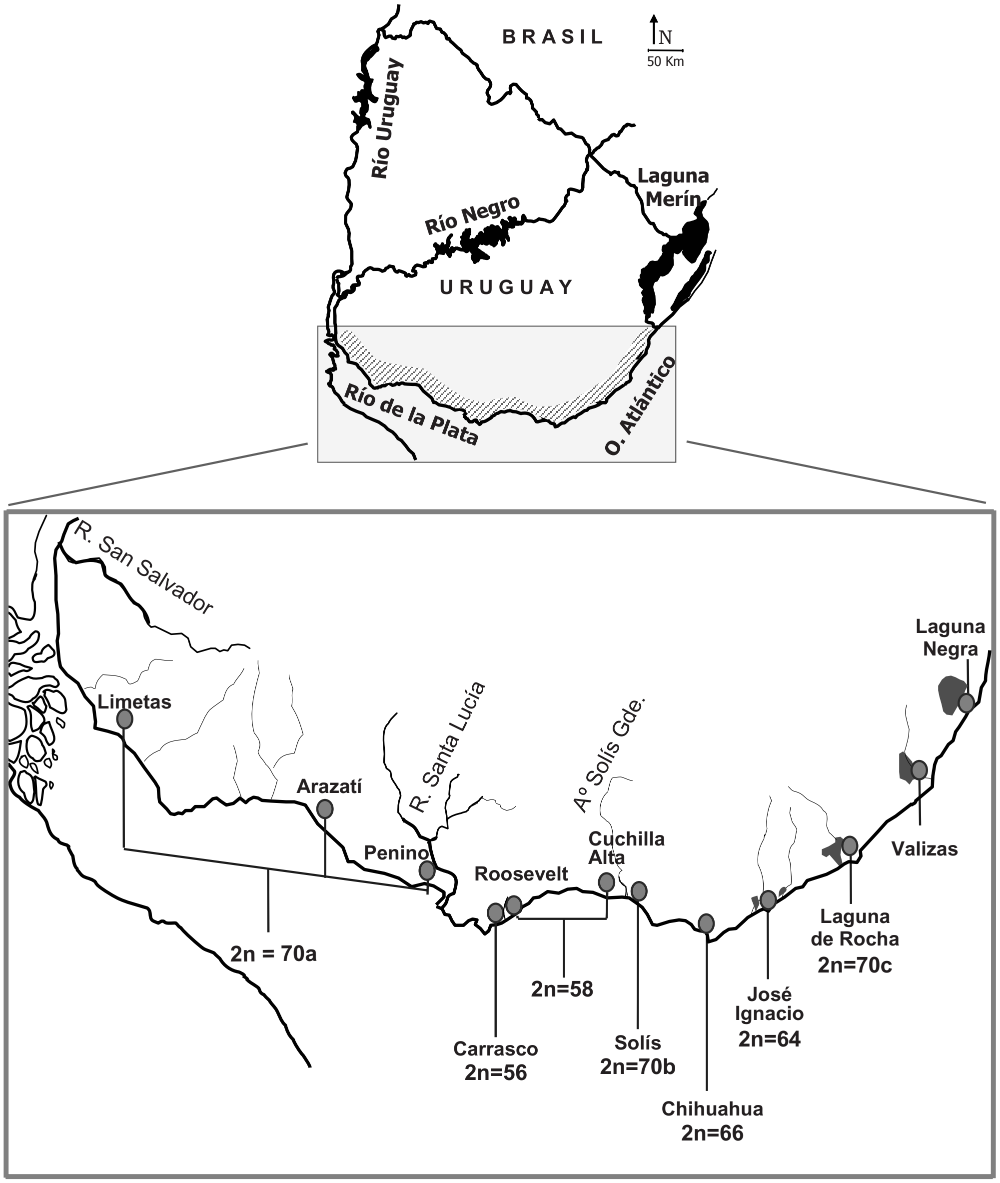

Figure 2. Distribution of *C. pearsoni* in Uruguay, with sample localities and known diploid numbers. Geographically separate forms with 2n=70 are labeled differently for clarity.

S, 55° 29′ 55′′ W, Canelones), $N = 10$; Solís (34° 47′ 00′′ S, 55° 23′ 00′′ W, Maldonado), $N = 10$; Chihuahua (34° 56′ 44′′ S, 54° 56′ 47′′ W, Maldonado), $N = 9$; José Ignacio (34° 50′ 22′′ S, 54° 38′ 52′′ W, Maldonado), $N = 10$; Laguna de Rocha (34° 37′ 21′′ S, 54° 15′ 27′′ W, Rocha), $N = 3$; Valizas (34° 21′ 06′′ S, 53° 50′ 30′′ W, Rocha), $N = 8$ and Laguna Negra (37° 75′ S, 59° 60′ W, Rocha), $N = 1$. The specimen from Laguna Negra and was

Table 1. Reported karyomorphs in *C. pearsoni*: diploid number (2n), fundamental number (FN), total number of studied localities and individuals that have been karyotyped, and references. Documented intrapopulational variation is indicated in parenthesis. Three geographically separated forms with 2n=70 are labeled 70a, 70b, and 70c for clarity.

		Total number of studied		
2n	FN	localities	individuals	References
70a (68)	80	3	35	Kiblisky et al. 1977 Novello and Lessa 1986 Novello et al. 1990 Novello et al. 1996 Villar 2000
56	78 (77, 79)	1	18	Novello and Lessa 1986 Novello et al. 1990
58	78	7	53	Kiblisky et al. 1977 Novello et al. 1996 Novello and Altuna 2002
70b	80	3	29	Novello et al. 1996 Novello and Altuna 2002
66	78	2	14	Villar 2000
64	76	2	22	Kiblisky et al. 1977 Villar 2000
70c	80	1	20	Novello com. pers.

included in phylogenetic reconstruction, but not in population genetic estimations.

Total DNA extractions were made with SDS/proteinase K/NaCl/alcohol precipitation (modified from Miller et al., 1988) from liver preserved in 95% ethyl-alcohol. A fragment of approximately 470 base pairs of the Control Region of mtDNA was amplified by PCR (Polymerase Chain Reaction) from all specimens using the primers TucoPro (5´ TTC TAA TTA AAC TAT TTC TTG - 3´) and TDKD (5´- CCT GAA GTA GGA ACC AGA TG -3´, Kocher et al., 1989). Amplification was carried out in a total volume of 12.5 µl containing the following constituents: 6.25 µl of DNA (0.4 µg/ml) used as a template, 1X Taq Polymerase Buffer, 240 µM of each dNTP, 240 nM of each primer, 0.5 units of Taq Polymerase and 4 mM of $MgCl_2$. PCR amplifications were performed in a Rapidcycler™ (Idaho Technology) by an initial denaturation of 1 min at 94 °C, followed by 30 cycles of 30 sec. of denaturation at 94°C, 30 sec. of annealing at 47 °C and 30 sec. of extension at 72 °C, and a final extension of 5 min. at 72 °C. PCR products were purified by chromatography (Sephadex G50 fine, Pharmacia Biotech AB) performed following the guidelines of suppliers and sequenced using a Perkin-Elmer ABI Prism 377 automated sequencer (Perkin Elmer, Foster City, CA) with the terminal primers used in PCR.

The sequences were aligned using *CLUSTALX* (Thompson et al., 1997) with default options and distinct sequences reported in this paper were deposited in GenBank under the accession numbers AY755438 to AY755461. The phylogenetic relationships among haplotypes were estimated using *PAUP* 4.0b10 (Swofford, 2000) by unweighted Maximum Parsimony (Fitch, 1971) using 200 replicates of heuristic searches (tree bisection and reconnection) following stepwise addition of haplotypes. Support for these nodes was tested with 1,000 bootstrap replicates (Felsenstein, 1985). The analysis included 4 specimens (2 haplotypes) from *C. torquatus* which is thought to be the sister species to *C. pearsoni*, and 1 *C. rionegrensis*, considered to be an outgroup to that pair (D´Elía et al., 1999; Slamovits et al., 2001). Nucleotide variation was estimated as π (the average number of pairwise difference between haplotypes, which estimates $\theta = 2N_{ef}\mu$) and θ_w, an estimate of θ based on the number of segregating sites (Watterson, 1975). Tajima´s *D* (Tajima, 1989) and Fu´s F_s (Fu, 1997) tests of neutrality were performed for each population using Arlequin (Schneider et al., 2000). A Mantel test (Mantel, 1967) was performed to assess if the data were consistent with a pattern of isolation by distance. The mean number of migrants per generation was estimated as $Nm = (1 - F_{st}) / (2 F_{st})$ and the distance matrix from geographic coordinates using the program ´´How far is it?´´ (http://www.indo.com/distance).

In order to investigate the existence of hierarchical levels of population structure an AMOVA (Analysis of Molecular Variance) was performed considering genetic distances between haplotypes and their frequencies, using Arlequin (Schneider et al., 2000). We grouped populations with similar karyotypes as follows (Fig. 2): 1) Limetas, Arazatí, and Penino, all 2n=70a; 2) Carrasco with 2n=56, Roosevelt and Cuchilla Alta, with 2n=58; 3) Solís with 2n=70b; 4) Chihuahua, with 2n= 64, and José Ignacio, 2n=68; and finally 5) Laguna de Rocha 2n=70c and Valizas with unknown karyotype.

Estimates of times of divergence between chromosomally distinct regions (as defined by the AMOVA above) were estimated using M-DIV (Nielsen and Wakeley, 2001). We used the Hasegawa-Kishino-Yano model of nucleotide substitution (Hasegawa et al., 1985) and the options suggested by the authors (length of Markov Chain, 5,000,000; "burn-in time", 500.000; maximum value of migration rate, 10; maximum value for divergence time, 20 N generations).

RESULTS

We analyzed a 438 bp sequence from the first hypervariable region of mtDNA control region, adjacent to Pro-tRNA. Base composition (14.3% G, 23.5% C, 27.9% T, 34.21% A) and the observed transition bias (observed transition:transversion ratio = 2.33) did not differ from the pattern found in mtDNA of *Ctenomys* (D´Elía, 1996; Lessa and Cook, 1998) and mammals in general (Irwin et al., 1991). Of the 51 variable sites, 26 were parsimony informative. We identified 21 haplotypes among *C. pearsoni*, 2 among *C. torquatus* (1 for each locality analyzed), and 1 for *C. rionegrensis*. The haplotypes of *C. pearsoni* varied from 1 to 16 copies; 8 haplotypes were shared between populations and 13 were exclusive (Table 2). The most variable population was Solís, with 5 haplotypes, 3 of which were shared with other populations. Only 1 population (Cuchilla Alta) was monomorphic, but its single haplotype was shared with Solís. Numbers of nucleotide differences between pairs of haplotypes ranged from 1 to 27 changes (0.002 to 0.057 %). These were 16 to 27 observed differences (0.037 to 0.057 divergence) between *C. pearsoni* and *C. rionegrensis*, and from 8 to 21 differences between the former and *C.*

Table 2. Haplotypes found in *C. pearsoni*, their frequencies and values of θ_w, π, D (Tajima, 1989) and F_s (Fu 1997) per population. Underlined haplotypes are shared among populations.

Populations	Haplotypes	Frequencies	θ_w	π	D	F_s
Limetas	H18, H20	0.10, 0.90	1.41	0.80	-1.67 *	1.74 ns
Arazatí	H15, H17, H19	0.78, 0.11, 0.11	3.68	2.89	-1.00 ns	2.73 ns
Penino	H2, H16, H17	0.14, 0.71, 0.14	4.08	2.86	-1.61 *	2.09 ns
Carrasco	H12, H13, H14	0.10, 0.20, 0.70	0.71	0.67	-0.18 ns	-0.27 ns
Roosevelt	H10, H13, H14	0.09, 0.18, 0.73	1.71	1.05	-1.46 ns	0.69 ns
Cuchilla Alta	H9	1	---	---	---	---
Solís	H6, H9, H11, H14, H21	0.10, 0.10, 0.60, 0.10, 0.10	5.66	5.76	0.08 ns	1.95 ns
Chihuahua	H7, H10, H21	0.44, 0.11, 0.44	4.42	4.78	0.39 ns	4.31 ns
José Ignacio	H1, H5	0.90, 0.10	0.35	0.20	-1.11 ns	-0.34 ns
Lag Rocha	H1, H2	0.33, 0.67	0.67	0.67	0 ns	0.20 ns
Valizas	H3, H4	0.50, 0.50	1.54	2.29	2.10 **	3.93 ns
Laguna Negra	H8	1	---	---	---	---

*, $p < 0.05$; **, $p < 0.01$; ns, not significant

torquatus. Maximum divergence among haplotypes of *C. pearsoni* was 16 nucleotide substitutions (0.037 %) between haplotypes H11 and B8.

Fu and Tajima's tests suggested no consistent pattern of departures from neutrality in all populations analyzed (Table 2). An excess of low-frequency haplotypes was suggested by Tajima's test in Limetas and Penino, and the opposite was found in Valizas, although those were not supported by Fu's test.

A total of 22 trees of 72 steps were found (Consistency Index = 0.79) and their Majority Rule consensus is shown in Fig. 3 together with Bootstrap support values. All trees show *C. pearsoni* as a monophyletic clade and *C. torquatus* as paraphyletic with respect to that clade. However, only 1 step was required to enforce the reciprocal monophyly of *C. torquatus* and *C. pearsoni*. Within *C. pearsoni* 2 major clades of haplotypes, formed by haplotypes H1 to H8 and H9 to H20, were supported (Fig. 3). However, all regions and chromosomal races were polyphyletic, as were all local populations except Cuchilla Alta (2n=58). The haplotype found in the latter locality, however, was shared with Solís (2n=70b).

We determined geographical distance and estimated gene flow between pairs of populations, and a Mantel test indicated a significant and negative correlation ($p <$

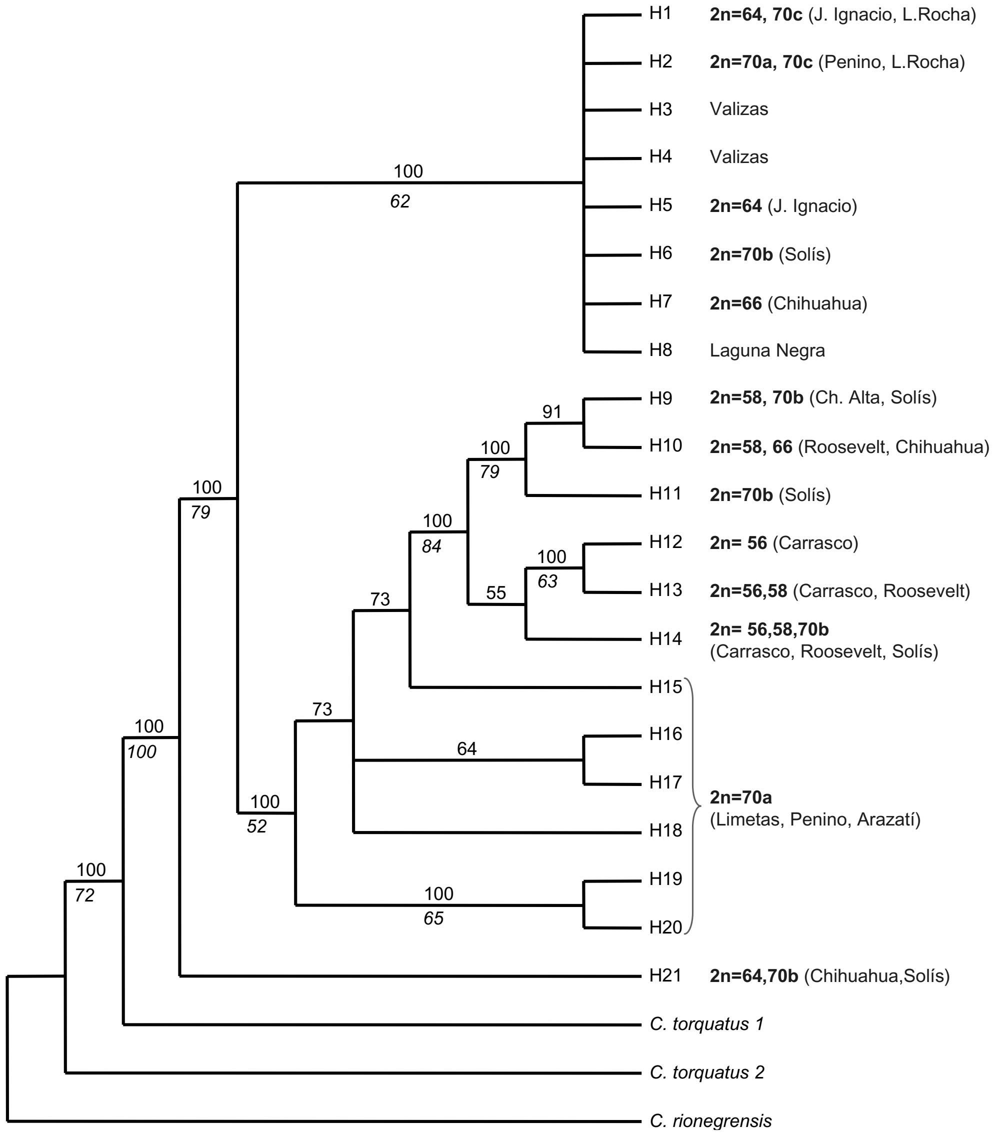

Figure 3. Majority rule consensus tree from 6 most parsimoniosus trees. Consensus and bootstrap support are given above and below branches, respectively.

0.015) between both matrices. This, coupled with the plots of pairwise estimates of *Nm* and geographic distances (Fig. 4), suggested a broad pattern of isolation by distance (Slatkin, 1993). Most estimations of gene flow are much less than 1 (data not shown), with the exception of the pair Carrasco-Roosevelt, which behaves as a single, panmictic unit, and some pairs from the eastern part of the distributions, with values near 1.

The AMOVA showed that variation was evenly distributed among hierarchical levels, namely within populations (31.75%), among populations within regions (34.31%), and among regions (33.94%). All these components of variance were highly significant (Table 3).

Values of divergence time estimated between pairs of chromosomally distinct regions ranged from 3.96 $2N_{ef}$ to 0.48 x $2N_{ef}$ generations (Fig. 5). The lower comparisons correspond to pairs from the eastern part of the range of distribution analyzed, namely karyomorphs 2n=64 and 66 (Chihuahua and José Ignacio) with 2n=70c (Laguna de Rocha).

DISCUSSION

Mitochondrial DNA variation within *Ctenomys pearsoni*, and between this and related species, offers insights into several pending issues, namely: a) the significance of chromosomal variation and the likelihood of classical chromosomal speciation; b) population structure and geographic differentiation of tuco-tucos in a changing coastal environment; and c) the systematics of Uruguayan species of *Ctenomys*. We discuss each of these issues below.

Chromosomal Speciation?

Although this survey was based on single locus estimations, our results are at odds with the hypothesis of chromosomal speciation which states that new, negatively heterotic chromosomal rearrangement are fixed solely by drift in small, inbred populations (White, 1978). Under neutrality, the expected time for lineage sorting to achieve reciprocal monophyly in isolated populations is 4 times longer for nuclear loci, as well as for chromosomal rearrangements, than for mtDNA. Therefore monophyly of mtDNA is expected, at least in derived karyomorphs. However, every population and karyomorph studied, with the exception of Cuchilla Alta (which was monomorphic), were polyphyletic in their mtDNA. Nevertheless, the exclusive haplotypes presented in some populations denote some degree of population differentiation.

The absence of monophyly in mtDNA is unlikely under the assumptions of negative heterosis or neutrality of chromosomal rearrangements. One possible solution is to invoke additional mechanisms, such as meiotic drive, that promote the fixation of certain rearrangements (King, 1993). These processes are yet to be examined in the case of *C. pearsoni*, but would increase the probability of fixation of rearrangements and could account for the observed pattern. Centric fusions/fissions may also

Table 3. Results from AMOVA showing the distribution of genetic variation among hierarchical levels of *C. pearsoni*.

	d.f.	Sums of squares	Variance components	Percentage of variation
Among regions	4	187,43	1,640	33,94 **
Among populations within regions	6	94,81	1,658	34,31 ***
Within populations	86	131,93	1,534	31,75 ***
Total	96	414,17	4,832	

d.f. = degrees of freedom; **, $p < 0.01$; ***, $p < 0.005$.

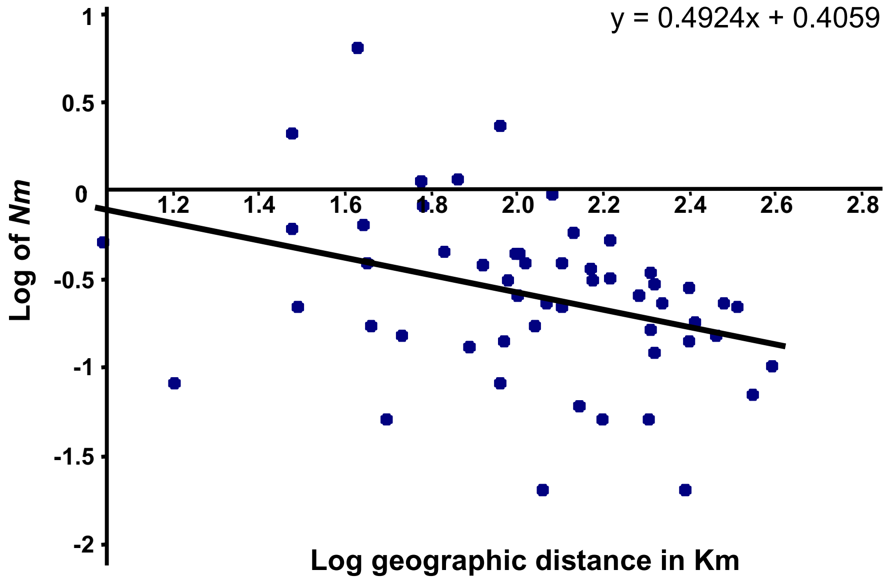

Figure 4. Log of Nm plotted against log of geographic distances between pairs of populations of *C. pearsoni*. Least squares regression line is represented.

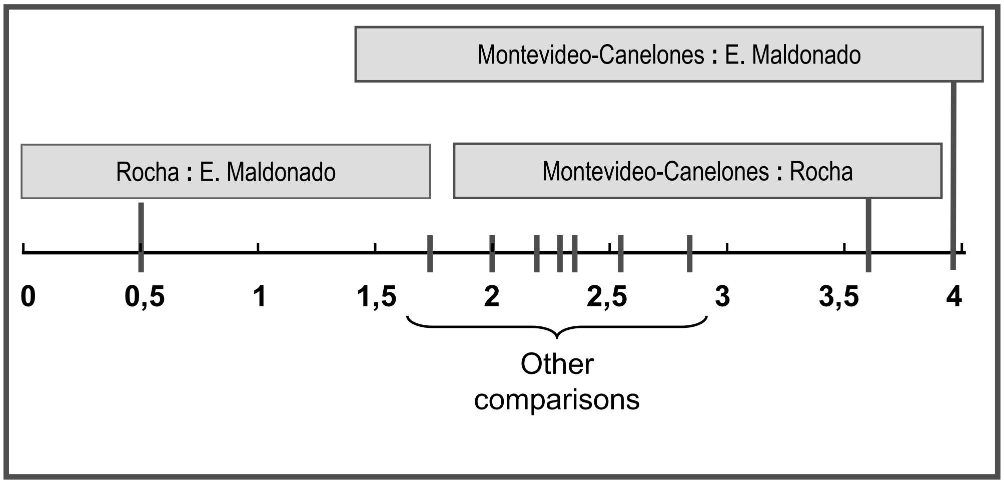

Figure 5. Divergence times estimated beween paris of kariomorphs, scaled in units of 2Nef generations. See text for details.

become fixed with little or no negative heterosis but their accumulation may result in mutually incompatible, derived chromosomal forms (e.g., Capanna, 1982; Baker and Bickham, 1986). For this idea to be tested, a detailed study of chromosomal homology among different karyomorphs of *C. pearsoni* and of their meiotic consequences is needed. Another possibility is to invoke an alternative role for chromosomal change in speciation. Recently, models that avoid the difficulties of underdominant rearrangements, which have rendered classic models weak and unconvincing, have been proposed (Spirito, 1998; Rieseberg, 2001). One of them postulates that chromosomal changes are strong genetic barriers because they reduce recombination in heterokaryotypes, and not because of underdominance (Rieseberg and Livingstone, 2003). Reduced recombination favors the fixation of alternative adaptive alleles in different chromosomal races. Testing this model requires the estimation of rates of synonymous and nonsynonymous substitutions in regions of the genome within rearranged chromosomes, and contrasting these with comparable data for regions not affected by chromosomal rearrangements (Navarro and Barton, 2003). Finally, it would be worthwhile to question whether rearrangements are negatively heterotic in the first place.

A careful reading of the limited literature available suggests that *C. pearsoni* is not an isolated case in the genus *Ctenomys*. Other surveyed species of tuco-tucos characterized by high karyotypic variation fail to show the expected patterns of mitochondrial DNA monophyly (Mascheretti et al., 2000; Giménez et al., 2002). In addition, the chromosomal literature shows a growing number of chromosomal polymorphisms that fail to cause sterility in heterozygous individuals, as well as several hybrid zones that show no evidence of negative heterosis (Freitas, 1997; Braggio et al., 1999; Gava and Freitas, 2002, 2003). Moreover, some studies have shown the absence of allozymic (Apfelbaum et al., 1991; Ortells and Barrantes, 1994; Villar, 2000), nucleotide (Mascheretti et al., 2000; Giménez et al., 2002; this work), and morphological (Ortells et al., 1990) differentiation among populations and named species with different karyotype. Therefore, it seems that fixation of new rearrangements is frequent in tuco-tucos and may not be hampered by negative heterosis.

Population Structure and Genetic Differentiation

The AMOVA demonstrated that genetic variation is evenly distributed within populations, both among populations within regions (defined by geographic location and chromosomal similarity) and between regions. A broad pattern of isolation by distance (namely that genetic differentiation increases with geographic distance) is observed in plots of *Nm* estimates against geographic distances between pairs of populations (Fig. 4), and is confirmed by a Mantel test ($p < 0.015$). A species with restricted dispersal will exhibit this pattern if it has remained in a stable migration regime of local differentiation under low levels of gene flow for a long enough time to approach equilibrium (Slatkin, 1993). Estimation of *Nm* from F_{st} can be problematic (e.g., Whitlock and McCauley, 1999), especially in the absence of equilibrium between migration and local drift. Here, however, we are only interested in broad patterns of geographic structure, rather than in specific point estimates of gene flow. Furthermore, a pattern of isolation by distance, such as the one observed here, suggests stability and an equilibrium between migration and drift. Additional evidence of stability comes from Fu's and Tajima's neutrality tests, which can detect demographic change, genetic hitchhiking, and background selection, but differ in their statistical properties: Fu's test is more powerful for detecting the first 2 processes than is Tajima's test, and vice versa (Fu, 1997). There were very few significant results (Table 2), indicating neither strong departures from neutrality nor strong changes in population sizes. One interesting departure is a significant D in Valizas, a population with 2 divergent haplotypes in equal proportion. This may be due recent local admixture.

Finally, high *Nm* estimations corresponded to the Carrasco-Roosevelt comparison (for details see Tomasco, 2003). These 2 populations together seem to behave as a single population despite their karyotypic differences. Relatively high values of gene flow (*Nm*>1) were also obtained comparing pairs of population from the eastern region of our study area, namely Chihuahua, José Ignacio, Laguna de Rocha, and Valizas. As discussed below, the particular history of the eastern part of the species distribution may be the cause of these observations.

All of this information taken together suggests the following scenario for the geographic differentiation of *C. pearsoni*. The species has occupied its range and maintained a stable regime of differentiation by genetic drift under limited gene flow for some time. The isolation by distance pattern reflects such overall stability. Furthermore, estimates of divergence times (Fig. 5) are moderate to high in population genetic terms. Thus, populations exhibit considerable genetic differentiation but fail to be monophyletic.

Locally, however, populations may have shifted in response to sea-level changes. In particular, a well documented Holocene marine transgression occurred approximately 5,000 to 6,000 years before present (BP), with sea levels about 5 m above current values (Cavallotto et al., 1999; García-Rodríguez, 2002; García-Rodríguez and Witkowski, 2003). The eastern part of the species distribution consists of sand dunes along the Atlantic coast, interspersed with coastal lagoons and wetlands, which were most strongly affected by the aforementioned marine transgression. Consistent with this scenario, we found lower divergence times and higher values of gene flow between populations / karyomorphs from eastern Maldonado and Rocha (Fig. 5). At a smaller geographical scale, it appears that the populations of Roosevelt and Carrasco were (or still are) strongly connected by gene flow, in an area of coastal sand dunes.

Available paleogeographical studies support this interpretation. Since the last Holocene marine transgression, sea level has progressively declined to the present level in the western part of the species' range (Cavallotto et al., 1999), whereas along the eastern Atlantic coast a more complex coastal dynamic has been reported. In the latter region, sea level was 0.7 m above modern values approximately 3,900 to 3,600 years BP (García-Rodríguez, 2002; García-Rodríguez and Witkowski, 2003). A series of high frequency oscillations of sea level in some lagoons of the region and 2 minor transgressions during the last 3,000 years have been documented. Finally, during the last transgression sea level rose 2.5 m above the present level (García-Rodríguez, 2002).

The scenario proposed for *C. pearsoni* contrasts with that found in *C. rionegresis*, another species of the genus for which population-level molecular data are available. *C. rionegrensis* appears to have undergone a recent range expansion, and thus shows no pattern of isolation by distance in allozymes, mitochondrial cytochrome *b* sequences, or microsatellites (D´Elía et al., 1998, Wlasiuk et al., 2003). Wlasiuk et al. (2003) suggested that this species expanded into its current geographic range from a more restricted area at a relatively recent time in the past and has subsequently differentiated in near isolation such that many contemporary populations comprise distinct genetic entities. Despite these rather different recent histories, both species of tuco-tucos appear to be characterized by very low levels of current gene flow.

The nearly linear, 1-dimensional distribution of *C. pearsoni* in Uruguay greatly simplifies the interpretation of the isolation by distance pattern. However a multilocus approximation with independent loci would be needed to refine and complement this survey (Beerli and Felsenstein 1999). Microsatellites loci have been successfully developed in recent years (Lacey et al., 1999; Lacey, 2001), and successfully used across species (Lacey, 2001; Wlasiuk et al., 2003), including *C. pearsoni* (Tomasco, pers. obs.).

Systematic Implications

Haplotypes of *C. pearsoni* formed a strongly supported monophyletic group. Although *C. torquatus* haplotypes appear to be paraphyletic with respect to *C. pearsoni* in the most parsimonious trees (Fig. 3), a single additional step is required to enforce reciprocal monophyly of these 2, closely related species. This point requires additional research, but the possible paraphyly of *C. torquatus* relative to *C. pearsoni* is weakly supported. The highest observed divergences correspond to comparisons of either species with *C. rionegrensis*. These observations are consistent with morphological analyses: *C. rionegrensis* differs from *C. torquatus* in numerous skull characteristics (Langguth and Abella, 1970), whereas *C. pearsoni* and *C. torquatus* are very similar morphologically (Lessa and Langguth, 1983; Freitas and Lessa, 1984; Altuna and Lessa, 1985). Furthermore, molecular phylogenetic analyses consistently relate *C. torquatus* to *C. pearsoni* (D´Elía et al. 1999; Slamovits et al. 2001) and place *C. rionegrensis* within the "*mendocinus*" species group (Rossi et al., 1995; D´Elía et al., 1999; Slamovits et al. 2001).

The status of the chromosomal races identified along the Uruguayan coast of the Río de la Plata and Atlantic Ocean (with diploid numbers ranging from 2n=56 to 2n=70) has remained uncertain since its original description by Kiblisky et al. (1977). At the time, all of these forms were assigned to *C. torquatus*. Subsequent work separated the coastal tuco-tuco as a distinct species, *C. pearsoni* (Lessa and Langguth, 1983), and restricted *C. torquatus* to the 2n=44 and 2n=46 forms found through much of the rest of Uruguay and parts of southern Brazil (Lessa and Langguth, 1983; Freitas and Lessa, 1984; Altuna and Lessa, 1985). Fixed chromosomal differences between coastal populations raised doubts about their status. The western race (2n=70a, see Fig. 2) is the typical form for the species (Lessa and Langguth, 1983), and the various forms have been variously referred to as members of the "*pearsoni* complex" (e.g., Altuna and Lessa, 1985) or as yet to be described biological species (e.g., Altuna et al., 1999, González, 2001).

The idea that races with fixed chromosomal differences likely are distinct biological species is at the heart of classical ideas about chromosomal speciation, because new rearrangements are assumed to be underdominant and act as a postzygotic reproductive barrier. However, there is no actual record of the consequences of hybridization. Our results are hard to reconcile with a basic requirement of classical chromosomal speciation, namely that different rearrangements found in *C. pearsoni* have been fixed in very small local populations basically by genetic drift. We conclude that there is no reason at this time to recognize different species among the coastal tuco-tucos of Uruguay by virtue of karyotypic differences, since *C. pearsoni* constitutes a morphological and genetic unit. Rather, we think of these coastal tuco-tucos as a single, chromosomally polytypic species, similar to other species in the genus.

On the whole, chromosomal variation has been considered the main factor associated with speciation in *Ctenomys*, based on the widespread notion that chromosomal variation in *Ctenomys* is species-specific and that chromosomal rearrangement are neutral or weakly underdominant. Nevertheless, there is not enough evidence to support this idea (Lessa, 2000). Indeed, some described polymorphisms are unlikely to reduce hybrid fitness (Rieseberg, 2001) and could be neutral and act as transient polymorphisms in the populations (Gava and Freitas, 2003). The role of chromosomal rearrangements as a reproductive barrier in speciation is still controversial. Future research is needed, and we submit that the framework of population genetics should be very useful in further elucidating the mechanisms of speciation in tuco-tucos (Lessa, 2000; Steinberg and Patton, 2000).

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APPENDIX 1.

Original number and corresponding haplotype of 103 individuals analyzed. Haplotypes from H1 to H21 belong to *C. pearsoni*. For *C. torquatus* and *C. rionegrensis* collecting localities are indicated (acronyms CA and EV refer to series in the tissue collection from the Laboratorio de Evolución, Universidad de la República).

Haplotype	Individuals Analysed
H1	CA473, CA475, CA451, CA472, CA454, CA467, CA474, CA453, CA462, CA452
H2	CA371, CA466, CA470
H3	CA497, CA620, CA621, CA623
H4	CA619, CA498, CA624, CA625
H5	CA455
H6	CA364
H7	CA582, CA581, CA583, CA585
H8	CA717
H9	CA558, CA574, CA564, CA563, CA572, CA571, CA 559, CA 568, CA560, CA363, CA570

H10	CA448, CA489
H11	CA362, CA366, CA852, CA841, CA365, CA361
H12	EV954
H13	CA450 EV922, CA351, EV/920
H14	EV910, EV923, 493, EV906, CA552, CA491, EV959, EV924, EV960, CA354, CA359, CA716, CA553, CA446, CA555, EV958
H15	EV1470, CA380, EV1471, EV1472, CA382, EV1473, EV377
H16	CA372, CA374, CA373, CA353, CA375
H17	CA352, CA381
H18	EV1451
H19	CA378
H20	EV1437, EV1439, EV1454, EV1455, EV1456, EV1453, EV1452EV, EV1438, EV1450
H21	CA368, CA486, CA586, CA487, CA482
C. torquatus 1	CA742, CA743 (Balneario Iporá, Tacuarembó)
C. torquatus 2	CA656, CA654 (Estancia ´´El Trillo´´, Río Negro)
C. rionegrensis	EV935 (Estancia ´´Portones de Chaparrei´´, Río Negro)

LITERATURE CITED

Altuna, C. A., G. Francescoli, B. Tassino, and I. Izquierdo
1999 Ecoetología y conservación de mamíferos subterráneos de distribución restringida: El caso de *Ctenomys pearsoni* (Rodentia, Octodontidae) en el Uruguay. Etología 7: 47-54.

Altuna, C. A., I. Izquierdo, and B. Tassino
1992 Estructura de sistemas de cuevas y disponibilidad de forraje en una población de *Ctenomys* (cariomorfo Solís) (Rodentia, Octodontidae). Boletín de la Sociedad Zoologica del Uruguay (2ª época) 7:39-40.

1993 Análisis del comportamiento de excavación en dos poblaciones del complejo *C. pearsoni* (Rodentia, Octodontidae). Boletín de la Sociedad Zoologica del Uruguay (2ª época) 8:275-282.

Altuna, C. A., and E. P. Lessa
1985 Penial mophology in uruguayan species of *Ctenomys* (Rodentia: Octodontidae). Journal of Mammalogy 66:483-488.

Anderson, S., T. L. Yates, and J. A. Cook
1987 Notes on Bolivian mammals. 4. The genus *Ctenomys* (Rodentia, Ctenomyidae) in the eastern lowlands. American Museum Novitates 2891:1-20.

Apfelbaum, L. I., A. I. Massarini, L. E. Daleffe, and O. A. Reig
1991 Genetic variability in the subterranean rodents *Ctenomys australis* and *Ctenomys porteousi* (Rodentia: Octodontidae). Biochemical Systematics and Ecology 19:467-476.

Baker, R. J., and J. W. Bickham
1986 Speciation by monobrachial centric fusions. Proceedings of the National Academy of Sciences (USA) 83:8245-8248.

Beerli, P., and J. Felsenstein
1999 Maximum-likelihood estimation of migration rates and effective population numbers in two populations using a coalescent approach. Genetics 152:763-73.

Berlocher, S. H.
1998 Origins: A brief history of Research on Speciation. Pp. 3-15 in Endless Forms: Species and Speciation (Howard, D. J., and S. H. Berlocher, eds.). Oxford University Press, Oxford, England.

Bidau, C. J., M. D. Jiménez, and J. R. Contreras
1996 Especiación cromosómica y la conservación de la variabilidad genética: El caso del género *Ctenomys* (Rodentia, Caviomorpha, Ctenomyidae). Mendeliana 12:25-37.

Braggio, E., M. D. Giménez, J. R. Contreras, E. Justo, and C. J. Bidau
1999 Karyotypic variation in populations of *Ctenomys* (Rodentia, Ctenomyidae) from La Pampa Province (Argentina). Caryologia 52:131-140.

Cappana, E.
1982 Robertsonian numerical variation in animal speciation: *Mus musculus*, an emblematic model. Pp. 155-174 in Mechanism of Speciation (Barigozzi, C., ed.). Alan R. Liss, New York, New York, USA.

Cavallotto, J. L., R. A. Violante, and G. Parker
1999 Historia evolutiva del Río de la Plata durante el Holoceno. Actas del XIV Congreso geológico argentino (Salta) 1:508-511.

Contreras, J. R., and C. J. Bidau
1999 Líneas generales del panorama evolutivo de los roedores excavadores sudamericanos del género *Ctenomys* (Mammalia, Rodentia, Caviomorpha, Ctenomyidae). Ciencia Siglo XXI, Buenos Aires, No. 1. Fundación Bartolomé Hidalgo, Buenos Aires, Argentina. 22 pp.

Contreras, J. R., and A. Ch. De Contreras
1984 Diagnosis preliminar de una nueva especie de "anguyatutu" (género *Ctenomys*) para la provincia de Corrientes, Argentina (Mammalia, Rodentia). Historia Natural (Corrientes) 4:131-132.

Cook, J. A., S. Anderson, and T. L. Yates
1990 Notes on Bolivian mammals. 6. The genus *Ctenomys* (Rodentia, Ctenomyidae) in the eastern highlands. American Museum Novitates 2980:1-27.

Cook, J. A., E. P. Lessa, and E. A. Hadly
2000 Paleontology, phylogenetic patterns, and macroevolutionary processes in subterranean rodents. Pp. 322-369 in Life Underground: The Biology of Subterranean Rodents (Lacey, E. A., J. L. Patton, and G. N. Cameron, eds.). University of Chicago Press, Chicago, Illinois, USA.

D´Elía, G.
1996 Posición filogenética y dinámica poblacional del roedor subterráneo *Ctenomys rionegrensis*. MSc Thesis. PEDECIBA. Universidad de la República, Uruguay. 160 pp.

D´Elía, G., E. P. Lessa, and J. A. Cook
1998 Geographic structure, gene flow, and maintenance of melanism in *Ctenomys rionegrensis* (Rodentia Octodontidae). Zeitschrift für Säugetierkunde 63:285-296.

1999 Molecular phylogeny of tuco-tucos, genus *Ctenomys* (Rodentia: Octodontidae): evaluation of the *mendocinus* species group and the evolution of asymentric sperm. Journal of Mammalian Evolution 6:19-37.

Felsenstein, J.
1985 Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783-791.

Fitch, W. M.
1971 Toward defining the course of evolution: minimum change for a specific tree topology. Systematic Zoology 20:406-416.

Francescoli, G.
2002 Geographic variation in vocal signals of *Ctenomys pearsoni*. Acta Theriologica 47: 35-44.

Freitas, T. R. O.
1997 Chromosome polymorphism in *Ctenomys minutus* (Rodentia – Octodontidae). Brazilian Journal of Genetics 20:1-17.

2001 Tuco-tucos (Rodentia, Octodontidae) in southern Brazil: *Ctenomys lami* spec. nov. separated from *C. minutus* Nehring 1887. Studies on Neotropical Fauna and Environment 36:1-8.

Freitas T. R. O., and E. P. Lessa

1984 Cytogenetics and morphology of *Ctenomys torquatus* (Rodentia-Octodontidae). Journal of Mammalogy 65:637-642.

Fu, Y. X.

1997 Statistical test of neutrality of mutations against population growth, hitchhiking and background selection. Genetics 147: 915-925.

García, I., M. Ponsa, J. Egozcue, and M. García

2000 Comparative chromosomal analysis and phylogeny in four *Ctenomys* species (Rodentia, Octodontidae). Biological Journal of the Linnean Society of London 69:103-120.

García-Rodríguez, F.

2002 Estudio Paleolimnológico de Lagunas de Rocha, Castillos y Blanca, Sudoeste del Uruguay. PhD Thesis. PEDECIBA. Universidad de la República, Uruguay. 228 pp.

García-Rodríguez, F., and A. Witkowski

2003 Inferring sea level variation from relative percentages of *Pseudopodosira kosugii* in Rocha Lagoon, SE Uruguay. Diatom Research 18:49-59.

Gava, A., and T. R. O. Freitas

2002 Characterization of a hybrid zone between chromosomally divergent populations of *Ctenomys minutus* (Rodentia: Ctenomyidae). Journal of Mammalogy 83:843-851.

2003 Inter and intra-specific hybridization in tuco-tucos (*Ctenomys*) from Brazilian coastal plains (Rodentia, Ctenomyidae). Genetica 119:11-17.

Giménez, M. D., P. M. Mirol, C. J. Bidau, and J. B. Searle

2002 Molecular análisis of populations of *Ctenomys* (Caviomorpha, Rodentia) with high karyotypic variability. Cytogenetics and Genome Research 96:130-136.

González, E. M.

2001 Guía de Campo de los Mamíferos del Uruguay. Introducción al Estudio de los Mamíferos. Vida Silvestre. Montevideo, Uruguay. 339 pp.

Hasegawa, M., H. Kishino, and T. Yano

1985 Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. Journal of Molecular Evolution 22:160-74.

Irwin, D. M., T. D. Kocher, and C. A. Wilson

1991 Evolution of the cytochrome *b* gene of mammals. Journal of Molecular Evolution 32:128-144.

Kiblisky, P., N. Brum-Zorrilla, G. Perez, and F. A. Saez
1977 Variabilidad cromosómica entre diversas poblaciones uruguayas del roedor cavador del género *Ctenomys* (Rodentia-Octodontidae). Mendeliana 2:85-93.

King, M.
1993 Species Evolution: The Role of Chromosomal Change. Cambridge University Press, Cambridge, UK. 336 pp.

Kocher, T. D., W. K. Thomas, A. Meyer, S. V. Edwards, S. Paabo, F. Villablanca, and A. C. Wilson
1989 Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences (USA) 86:6196-200.

Langguth, A., and A. Abella
1970 Especies uruguayas del género *Ctenomys*. Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo 10:1-27.

Lacey, E. A.
2001 Microsatellite variation in solitary and social tuco-tucos: molecular properties and population dynamics. Heredity 86:628-37.

Lacey, E. A., J. E. Maldonado, J. P. Clabaugh, and M. D. Matocq
1999 Interspecific variation in microsatellites isolated from tuco-tucos (Rodentia: Ctenomyidae). Molecular Ecology 8:1754-6.

Lessa, E. P.
2000 The evolution of subterranean rodents: a synthesis. Pp. 389-420 in Life Underground: The Biology of Subterranean Rodents (Lacey, E. A., J. L. Patton, and G. N. Cameron, eds.). University of Chicago Press, Chicago, Illinois, USA.

Lessa, E. P., and J. A. Cook
1998 The molecular phylogenetics of tuco-tucos (Genus *Ctenomys*, Rodentia: Octodontidae) suggests an early burst of speciation. Molecular Biology and Evolution 9:88-99.

Lessa, E. P., and A. Langguth
1983 *Ctenomys pearsoni* n. sp. (Rodentia, Octodontidae) del Uruguay. Resúmenes de Comunicaciones de las Jornadas de Ciencias Naturales, Montevideo 3:86-88.

Mantel, N.
1967 The detection of disease clustering and a generalized regression approach. Cancer Research 27:209-220.

Mascheretti, S., P. M. Mirol, M. D. Giménez, J. R. Contreras, C. J. Bidau, and J. B. Searle
2000 Phylogenetics of the speciose and chromosomally variable rodent genus *Ctenomys*, based on mitochondrial cytochrome *b*. Biological Journal of the Linnean Society 70:361-376.

Massarini, A. I., M. A. Barros, M. O. Ortells, and O. A. Reig
1991 Chromosomal polymorphism and small karyotype differentiation in a group of *Ctenomys* species from Central Argentina (Rodentia: Octodontidae). Genetica 83:131-144.

1995 Variabilidad cromosómica en *Ctenomys talarum* (Rodentia: Octodontidae) de Argentina. Revista Chilena de Historia Natural 68:207-214.

Miller, S. A., D. D. Dikes, and H. H. Polesky
1988 A simple salting procedure for extracting DNA from human nucleated cells. Nucleic Acids Research 16:215.

Navarro, A., and N. H. Barton
2003 Chromosomal speciation and molecular divergence: accelerated evolution in rearranged chromosomes. Science 300:321-4.

Nevo, E.
1979 Adaptive convergence and divergence of subterranean mammals. Annual Review of Ecology and Systematics 10:269-308.

Nielsen, R., and J. Wakeley
2001 Distinguishing migration from isolation: a Markov chain Monte Carlo approach. Genetics 158:885-96.

Novello, A. F., and C. A. Altuna
2002 Cytogenetics and distribution of two new karyomorphs of the *Ctenomys pearsoni* complex (Rodentia, Octodontidae) from southern Uruguay. Zeitschrift für Säugetierkunde 67:188-192.

Novello, A., M. N. Cortinas, M. Suárez, and H. Musto
1996 Cytogenetics and molecular analysis of the satellite DNA of the genus *Ctenomys* (Rodentia, Octodontidae) from Uruguay. Chromosome Research 4:335-339.

Novello, A. F., and E. P. Lessa
1986 G-band homology in two karyomorphs of the *Ctenomys pearsoni* complex (Rodentia: Octodontidae) of Neotropical fossorial rodents. Zeitschrift für Säugetierkunde 51:378-380.

Novello, A., E. Lessa, C. Sambarino, and S. Monzón
1990 Chromosomal variation in two populations of the genus *Ctenomys* (Rodentia, Octodontidae) from Uruguay. Zeitschrift für Säugetierkunde 55:43-48.

Ortells, M. O.
1995 Phylogenetic analysis of G-banded karyotypes among the South American subterranean rodents of the genus *Ctenomys* (Caviomorpha: Octodontidae), with special reference to chromosomal evolution and speciation. Biological Journal of the Linnean Society 54:43-70.

Ortells, M. O., and G. E. Barrantes
1994 A study of genetic distances and variability in several species of the genus *Ctenomys* (Rodentia: Octodontidae) with special reference to a probable causal role of chromosomes in speciation. Biological Journal of the Linnean Society 53:189-208.

Ortells, M. O., J. R. Contreras, and O. A. Reig
1990 New *Ctenomys* karyotypes (Rodentia, Octodontidae) from north-eastern Argentina and from Paraguay confirm the extreme chromosomal multiformity of the genus. Genetica 82:189-201.

Reig, O. A.
1970 Ecological notes on the fossorial octodontid rodent *Spalacopus cyanus* (Molina). Journal of Mammalogy 51:592-600.

Reig, O. A., C. Bosch, J. R. Contreras, and M. O. Ortells
1990 An overview of evolution, systematic, population biology, cytogenetics, and molecular biology in *Ctenomys*. Pp. 71-96 in Evolution of Subterranean Mammals at the Organismal and Molecular Level (Nevo, E., and O. A. Reig, eds.). Progress in Clinical and Biological Research, vol. 335. Wiley-Liss, New York, New York, USA.

Reig, O. A., and P. Kiblisky
1969 Chromosome multiformity in the genus *Ctenomys* (Rodentia, Octodontidae). Chromosoma 28: 211-244.

Rieseberg, L. H.
2001 Chromosomal rearrangements and speciation. Trends in Ecology and Evolution 16:351-358.

Rieseberg, L. H., and K. Livingstone
2003 Chromosomal speciation in primates. Science 300:267-8.

Rossi, M. S., C. A. Redi, G. Viale, A. I. Massarini, and E. Capanna
1995 Chromosomal distribution of the major satellite DNA of South American rodent of the genus *Ctenomys*. Cytogenetics and Cell Genetics 69:179-184.

Schneider, S., D. Roessli, and L. Excoffier
2000 Arlequin (vers. 2.000): a software for population genetic data analysis. Genetics and Biometry Laboratory, University of Geneva, Switzerland.

Schultz, P. H., M. Zarate, W. Hames, C. Camilión, and J. King
1998 A 3.3-Ma impact in Argentina and possible consequences. Science 282:2061-2063.

Slamovits, C. H., J. A. Cook, E. P. Lessa, and M. S. Rossi
2001 Recurrent amplifications and deletions of satellite DNA accompanied chromosomal diversification in South American tuco-tucos (genus *Ctenomys*, Rodentia: Octodontidae): a phylogenetic approach. Molecular Biology and Evolution 18(9):1708-19.

Slatkin, M.
1993 Isolation by distance in equilibrium and non-equilibrium populations. Evolution 47:264-279.

Spirito, F.
1998 The role of chromosomal change in speciation. Pp. 320-329 in Endless Forms: Species and Speciation (Howard, D. J., and S. H. Berlocher eds.). Oxford University Press, Oxford, England.

Steinberg, E. K., and J. L. Patton
2000 Genetic structure and the geography of speciation in subterranean rodents: Opportunities and constraints for evolutionary diversification. Pp. 301-331 in Life Underground: The Biology of Subterranean Rodents (Lacey, E. A., J. L. Patton, and G. N. Cameron, eds.). University of Chicago Press, Chicago, Illinois, USA.

Swofford, D.
2000 PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods), 4.0. Sinauer Associates, Sunderland, Massachusetts, USA.

Tajima, F.
1989 Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585-595.

Thompson, J. D., T. J. Gibson, F. Plewniak, F. Jeanmougin, and D. G. Higgins
1997 The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Research 25:4876-82.

Tomasco, I. H.
2003 Filogeografía del Tucu-tucu *Ctenomys pearson*i: Variación del ADN Mitocondrial y sus Implicancias para la Diferenciación Cromosómica. MSc Thesis. PEDECIBA. Universidad de la República, Uruguay. 90 pp.

Verzi, D. H.

2002 Patrones de evolución morfológica en Ctenomyinae (Rodentia: Octodontidae). Mastozoología Neotropical 9:309-328.

Villar, S.

2000 Caracterización Citogenética y Alozímica de Poblaciones de *Ctenomys* del Uruguay. MSc Thesis. PEDECIBA. Universidad de la República, Uruguay. 99 pp.

Watterson, G. A.

1975 On the number of segregating sites in genetical models without recombination. Theoretical Population Biology 7:256-76.

White, M. J. D.

1968 Models of speciation: new concepts suggest that the classical sympatric and allopatric models are not the only alternatives. Science 159:1065-1070.

1978 Modes of Speciation. W. F. Freeman and Company, San Francisco, California, USA. 455 pp.

Whitlock, M. C., and D. E. McCauley

1999 Indirect measures of gene flow and migration: FST not equal to 1/(4Nm + 1). Heredity 82:117-25.

Wlasiuk, G., J. C. Garza, and E. P. Lessa

2003 Genetic and geographic differentiation in the Río Negro tuco-tuco (*Ctenomys rionegrensis*): inferring the roles of migration and drift from multiple genetic markers. Evolution 57:913-926.

PHYLOGENETIC RELATIONSHIPS OF NEOTOMINE-PEROMYSCINE RODENTS USING DNA SEQUENCES FROM BETA FIBRINOGEN AND CYTOCHROME *B*

RELACIONES FILOGENÉTICAS DE LOS ROEDORES NEOTOMINO-PEROMYSCINOS UTILIZANDO SECUENCIAS DE DOS LOCI MOLECULARES, EL FIBRINÓGENO BETA Y EL CITOCROMO *B*

Serena A. Reeder and Robert D. Bradley

This manuscript is dedicated to Oliver Pearson, particularly in reference to his studies on South American rodents. His influence on South American mammalogy and mammalogists was extraordinary. He will be missed by many.

ABSTRACT

In order to examine phylogenetic relationships in the neotomine-peromyscine rodent complex, DNA sequences from intron 7 of the beta fibrinogen gene were obtained for 21 taxa representing 14 genera of traditional neotomine-peromyscines. Consistently, 5 main clades were recovered. Four of these clades correspond to previously recognized tribes: the Neotomini, Peromyscini, Baiomyini, and Tylomyini. The level of genetic divergence of *Ochrotomys* relative to other traditional peromyscines was higher (12.4%) than the comparison of *Ochrotomys* and the Neotomini (10.3%) and is similar to the comparison of the Baiomyini to the Peromyscini (11.7%). These results indicate that *Ochrotomys* may represent a separate tribe. The Neotomini was sister to *Ochrotomys*, and the Peromyscini and Baiomyini were sister taxa. These 2 groups then formed a sister relationship, and the Tylomyini was basal. In addition, beta fibrinogen sequences were combined with cytochrome *b* sequences from Bradley et al. (2004). The combined data set resulted in a topology that was similar to that generated using beta fibrinogen sequences alone. This result is encouraging toward the goal of generating reliable phylogenetic data from nuclear genes.

Key words: nuclear gene, beta fibrinogen, intron, rodent systematics, Sigmodontinae, neotomine, peromyscine

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El presente manuscrito se dedica a Oliver Pearson, quien fervientemente trabajó en el estudio de los roedores de América del Sur. Su influencia sobre la mastozoología de América del Sur y sobre los mastozoólogos fue realmente extraordinaria. El será extrañado por muchos.

RESUMEN

Con la intención de analizar las relaciones filogenéticas dentro del complejo de roedores neotomino-peromyscino se obtuvieron las secuencias del DNA del séptimo intrón del gen que codifica para el fibrinógeno beta en 21 taxa que representan 14 géneros típicos de los neotomino-peromyscinos. De forma consistente se obtuvieron 5 clados principales, de los cuales 4 correspondieron a tribus previamente reconocidas: la Neotomini, Peromyscini, Baiomyini, y Tylomyini. El grado de divergencia genética de *Ochrotomys* en relación a los otros peromyscinos típicos fue mayor (12.4%) que el que surgió de la comparación entre *Ochrotomys* y los Neotomini (10.3%), pero fue similar al de la comparación de los Baiomyini con los Peromyscini (11.7%). Estos resultados indican que *Ochrotomys* pudiera estar representando una tribu separada. Los Neotomini resultaron ser hermana de los *Ochrotomys*, mientras que los Peromyscini y los Baiomyini fueron taxa hermanas. De esta manera ambos grupos formaron una relación hermana en donde la tribu Tylomyini es la base. Además, las secuencias del fibrinógeno beta fueron combinadas con aquellas obtenidas del citocromo *b* generadas por Bradley et al. (2004). La topología observada para el grupo de datos combinado fue muy similar a la obtenida con las secuencias del fibrinógeno beta solo. Este resultado apoya el uso de genes nucleares para la generación de información filogenética confiable.

Palabras claves: gen nuclear, beta fibrinógeno, intrón, sistemática de roedores, Sigmodontinae, neotominos, peromyscino

INTRODUCTION

The neotomine-peromyscine complex (Muridae: Sigmodontinae) is comprised of 8-18 genera and at least 100 species of some of the most commonly encountered rodents in North America. Historically, these and other North American taxa have been combined with South American taxa into a single group (Cricetinae - now recognized as the Subfamily Sigmodontinae), albeit at different taxonomic levels ranging from the tribe to family rank (Thomas, 1896; Tullberg, 1899; Miller and Gridley, 1918; Ellerman, 1940; Simpson, 1945; Chaline et al., 1977). Rinker (1954) was the first to propose a division between North and South American cricetines and used as examples a *Sigmodon-Oryzomys* complex and a *Neotoma-Peromyscus* complex. Hooper and Musser (1964) furthered this position by arranging taxa into 2 lineages: the North American forms (*Neotoma*, *Peromyscus*, and allies) and the South American forms (*Sigmodon*, *Oryzomys*, and allies). Carleton (1980), based on an extensive morphologic study, recognized 4 tribes within the North American lineage: Neotomini (*Neotoma, Hodomys, Xenomys,* and *Nelsonia*), Peromyscini (*Peromyscus, Reithrodontomys, Neotomodon, Onychomys, Ochrotomys*, and several former subgenera of *Peromyscus* that were elevated to generic status), Baiomyini (*Baiomys* and *Scotinomys*), and Tylomyini (*Tylomys* and *Ototylomys*).

Relationships within the neotomine-peromyscine complex were later addressed by Musser and Carleton (1993) and McKenna and Bell (1997), and both suggested arrangements that differed from those of Carleton's morphologic study (1980). Musser and Carleton (1993) proposed 2 tribes: Peromyscini, including *Baiomys* and *Scotinomys*, and Neotomini. McKenna and Bell (1997) similarly recognized Peromyscini and Neotomini along with a third tribe, the Tylomyini (*Nyctomys, Otonyctomys, Ototylomys*, and *Tylomys*). The difference between the 2 classifications, other than the recognition of the Tylomyini, was the removal of *Baiomys* and *Scotinomys* from the Peromyscini (McKenna and Bell, 1997) and their placement as *incertae sedis* with *Rhagomys*, a taxon whose affinities are uncertain. These classifications were not actual phylogenetic studies, however. Rather, they represent a summation and review of the pertinent literature.

Recently, sequences from the mitochondrial cytochrome *b* gene (Bradley et al., 2004) and the nuclear dentin matrix protein 1 gene (Reeder and Bradley, 2004) were used to elucidate relationships within the North American complex of sigmodontine rodents. Both data sets suggest that the complex is comprised of 4 tribes (Neotomini, Peromyscini, Baiomyini, and Tylomyini), generally following Carleton (1980). Areas that remain problematic include the placement of *Onychomys* and *Ochrotomys*, whether or not *Nyctomys* should be placed in the Tylomyini, and relationships among the tribes. *Onychomys* generally has been aligned with the Peromyscini (Hooper and Musser, 1964; Carleton, 1980; Musser and Carleton, 1993; Sullivan et al., 1995; McKenna and Bell, 1997; Engel et al., 1998; Reeder and Bradley, 2004), however it also has been placed as the basal member within the Neotomini (Bradley et al., 2004). *Ochrotomys* is another problematic genus in that it has been placed both within (Hooper and Musser, 1964; Carleton, 1980; Musser and Carleton, 1993; McKenna and Bell, 1997; Bradley et al., 2004; Reeder and Bradley, 2004) and outside of (Engstrom and Bickham, 1982; Engel et al., 1998) the Peromyscini. Furthermore, some investigators have speculated that it may possibly represent a separate tribe (Carleton, 1989; Bradley et al., 2004; Reeder and Bradley, 2004). *Nyctomys* recently has been placed within the Tylomyini (McKenna and Bell, 1997; Bradley et al., 2004); however, it may be that *Nyctomys* is related distantly to the neotomine-peromyscines or that it is a member of the South American sigmodontine complex (Hershkovitz, 1944, 1962). Alternatively, it may have originated prior to the divergence of the North and South American sigmodontines (Hooper and Musser, 1964; Carleton, 1980). In addition to questions involving these 3 genera, placement of the Baiomyini in relation to the Neotomini and Peromyscini remains unclear. Mitochondrial DNA sequences indicated that the Baiomyini was sister to a clade comprised of the Neotomini and Peromyscini (Bradley et al., 2004), whereas its position was unresolved in relation to the other 2 tribes according to nuclear DNA sequence data (Reeder and Bradley, 2004).

Given the disparity among existing data, an additional independent data set is necessary to elucidate relationships within and among tribes in the North American sigmodontine complex. Mitochondrial genes, although phylogenetically informative, are maternally inherited and found within a single linkage group. Furthermore, lineage sorting potentially can be problematic (Avise, 1994). Nuclear genes, however, are biparentally inherited and are unlinked. Moreover, they have proven effective in resolving questions involving higher-level systematics in rodents (Robinson et al., 1997; Huchon et al., 1999, 2002; Walton et al., 2000; Adkins et al., 2001; DeBry and Sagel, 2001). Recently, intron 7 of the beta fibrinogen (*Fgb*-I7) gene has shown promise in resolving species-level questions in rodents (Carroll and Bradley, 2005), other mammalian taxa (Seddon et al., 2001; Wickliffe et al., 2003), and birds (Prychitko and Moore, 1997, 2000). The objective of this study is to examine phylogenetic relationships within and among tribes of neotomine-peromyscine rodents using sequences from *Fgb*-I7 and to determine its phylogenetic utility at this level. A secondary goal is to combine the *Fgb*-I7 data with cytochrome *b* data from Bradley et al. (2004) in order to further examine relationships within this complex of rodents.

MATERIALS AND METHODS

The sampling strategy for this study was based on Carleton's (1980) morphologic study and attempted to include at least 1 individual per genus. Not included were *Nelsonia* and 4 former subgenera of *Peromyscus* (*Isthmomys*, *Megadontomys*, *Podomys*, and *Habromys*). In cases of genera encompassing several species, such as *Peromyscus* and *Neotoma*, multiple taxa were examined in order to represent the diversity of the genus. Also included was a representative from the genus *Nyctomys*, which was not considered a neotomine-peromyscine in Carleton (1980). Sequences were obtained for 21 taxa representing 14 genera of traditional neotomine-peromyscine rodents, along with 3 South American outgroup taxa (Table 1).

Genomic DNA was isolated from frozen liver tissue using the DNeasy tissue kit (Qiagen, Valencia, CA). Polymerase chain reaction (PCR) amplifications were performed in 35 μl reactions that contained 1 μl DNA template, 3.5 μl of 10X buffer, 2 μl $MgCl_2$, 2 μl of 2.5 mM dNTPs, 2 μl of each 2 μM primer, and 1.5 units of *Taq* polymerase. Primers (Table 2) *Fgb*-I7U-*Rattus* and *Fgb*-I7L-*Rattus* (Wickliffe et al., 2003) were used to amplify *Fgb*-I7, and additional primers (Carroll, 2002) were used for sequencing. Thermal profile conditions included 1 cycle of initial denaturation at 93°C for 1 min; 35 cycles of 93°C denaturation for 1 min, 55°C annealing for 1 min, and 72°C extension for 2 min 45 sec; and a final extension of 72°C for 2 min. Double stranded amplicons were purified using the QIAquick PCR purification kit (Qiagen®, Valencia, California) and sequenced in both directions using Big-Dye chain terminators and an ABI Prism 310 genetic analyzer (PE Applied Biosystems, Inc., Foster City, California). All sequences generated in this study were deposited in GenBank (accession numbers are listed in Table 1).

Table 1 (facing page). Specimens examined, listed alphabetically within tribes. Abbreviations for museum identification numbers are as follows: Museum of Texas Tech University (TK), Royal Ontario Museum (FN), Tarleton State University Natural History Collection (P), and The Museum of Southwestern Biology (NK). Cytochrome *b* sequences were obtained from GenBank.

*Sequences for the cytochrome *b* gene were generated from the same individuals as the beta fibrinogen sequences except for *Osgoodomys banderanus* and *Nyctomys sumichrasti*.

**No cytochrome *b* sequences were available for *Scotinomys teguina* so a sequence from *S. xeramplinus* was substituted.

***Only partial cytochrome *b* sequences were available for *Holochilus sciureus* and *Oryzomys palustris*.

Species	Museum ID #	*Fgb*-I7 GenBank #	Cyt *b* GenBank #
Tribe Neotomini			
Hodomys alleni	TK45042	AY274197	AF186801
Neotoma leucodon	TK51948	AY274198	AF186828
Neotoma cinerea	NK36287	AY274199	AF186799
Neotoma mexicana	TK78350	AY274200	AF294345
Xenomys nelsoni	TK19559	AY274201	AF307838
Tribe Peromyscini			
Neotomodon alstoni	TK45302	AY274202	AY195796
Ochrotomys nuttalli	TK31929	AY274203	AY195798
Onychomys arenicola	TK46462	AY274204	AY195793
Onychomys leucogaster	TK31705	AY274205	AY195794
Osgoodomys banderanus	TK45401	AY274206	AF155383*
Peromyscus attwateri	TK23396	AY274207	AF155384
Peromyscus boylii	TK48636	AY274208	AF155388
Peromyscus difficilis	TK93120	AY274209	AY376416
Peromyscus mexicanus	TK93314	AY274210	AY376425
Reithrodontomys fulvescens	TK23469	AY274211	AF176257
Reithrodontomys sumichrasti	TK20994	AY274212	AF176256
Tribe Baiomyini			
Baiomys taylori	TK32211	AY274213	AF548469
Scotinomys teguina	P.048	AY274214	AF108706**
Tribe Tylomyini			
Nyctomys sumichrasti	TK72922	AY274215	AY195801*
Ototylomys phyllotis	FN32557	AY274216	AY009788
Tylomys nudicaudus	TK41551	AY274217	AF307839
Outgroup taxa			
Sigmodon hispidus	TK84530	AY459371	AF425200
Holochilus sciureus	TK17914	AY274218	AF108697***
Oryzomys palustris	TK28621	AY274219	AY041185***

Table 2. Primers used in amplification and cycle sequencing of *Fgb*-I7.

Primer name	Sequence 5′-3′	Study described
Fgb-I7U-*Rattus*	GGGGAGAACAGAACCATGACCATCCAC	Wickliffe et al. (2003)
Fgb-I7L-*Rattus*	ACCCCAGTAFTATCTGCCATTCGGATT	Wickliffe et al. (2003)
bFIB-I7U	GACAATTCACAATGGCATGTACTTCAG	Carroll (2002)
bFIB-I7L	GTATCTGCCATTAGGGTTGGCTGCATG	Carroll (2002)

Sequencher 3.0 software (Gene Codes, Ann Arbor, MI) was used to align contiguous fragments and to proof nucleotide sequences, and chromatograms were examined to be sure that all heterozygous sites or base changes in a single taxon were valid. CLUSTAL X (Thompson et al., 1997) was used for a multiple sequence alignment of nucleotides, which was then adjusted by eye.

Data analysis was performed using PAUP*4.0b10 (Swofford, 2002). Maximum parsimony (branch and bound search option) was conducted using equal weighting. Variable nucleotide characters were treated as unordered and discrete, and heterozygous sites were identified by the designated IUB polymorphic symbol. Sequences were analyzed treating gaps as a fifth character state. All uninformative characters were removed from parsimony analyses. Robustness of topologies was assessed via bootstrapping (Felsenstein, 1985) with 1,000 iterations and Bremer support indices (Bremer, 1994) calculated with the software program Autodecay (Eriksson, 1997).

MODELTEST (Posada and Crandall, 1998) analyzed 56 models of evolution to determine the most appropriate model for the data set. The Kimura 2-parameter (1980) model was selected and subsequently used for maximum likelihood and neighbor joining analyses. Pairwise genetic distances were generated using the Kimura 2-parameter model (1980) as well. To obtain values for comparisons within and among tribes, the mean of the pairwise comparisons was calculated, along with its standard deviation. MrBayes (Huelsenbeck and Ronquist, 2001) was used for Bayesian analysis using the GTR+I+G model to provide a more complex model than that used in the maximum likelihood analysis. Four Markov chains were run for 2 million generations and were sampled every 100th generation. After a visual inspection of likelihood scores, trees generated before stabilization of the likelihood values were discarded. A consensus tree (50% majority rule) was constructed from the remaining trees.

Tree topologies were constrained to conform to the hypotheses of Carleton (1980), Bradley et al. (2004), and Reeder and Bradley (2004). The Shimodaira-Hasegawa (Shimodaira and Hasegawa, 1999) test was used to determine if constrained topologies were significantly worse than the unconstrained topology.

Finally, *Fgb*-I7 sequences were combined with the cytochrome *b* sequences (1143 bp) from Bradley et al. (2004) or taken from GenBank under the conditional data combination approach (Bull et al., 1993; de Queiroz, 1993; Huelsenbeck et al., 1994; Drovetski, 2002). Sequences from each of the data sets were truncated so that only taxa shared between studies were analyzed. Sequences for the cytochrome *b* gene were generated from the same individuals as the *Fgb*-I7 sequences except for *Osgoodomys* *banderanus*, *Nyctomys sumichrasti*, *Oryzomys palustris* (partial sequence – 726 bp), and *Holochilus sciureus* (partial sequence – 801 bp). In the case of *O. banderanus* and *N. sumichrasti*, sequence from another individual of the same species was substituted. Cytochrome *b* sequences were not available for *Scotinomys teguina*, so a sequence from *S. xeramplinus* was substituted in order to represent the genus. This resulted again in the examination of 21 species representing 14 genera of neotomine-peromyscine rodents, along with 3 South American sigmodontines as outgroups (Table 1). The partition homogeneity test, also called the incongruence-length-difference (ILD) test, was used to examine heterogeneity among data partitions (Mickevich and Farris, 1981; Farris et al., 1994). MrBayes (Huelsenbeck and Ronquist, 2001) was used for Bayesian analysis using the GTR+I+G model and the parameters described above for the *Fgb*-I7 analysis.

RESULTS

Sequences obtained for *Fgb*-I7 were aligned with published sequences from Seddon et al. (2001) to ensure that the appropriate fragment was amplified, and all possessed the highly conserved splice sites found in vertebrate taxa (5′-GTnYnAG-3′). The length of the intron varied among taxa (from 566 bp in *N. cinerea* and *N. leucodon* to 625 bp in *Sigmodon hispidus*) due to insertion and deletion events and resulted in 668 aligned sites. Overall nucleotide frequencies were: A = 30.6%, C = 22.5%, G = 16.9% and T = 30.0%, and the transition to transversion ratio was approximately 3:1. Heterozygosity values ranged from zero (9 taxa) to 7 (*Peromyscus mexicanus*) polymorphic sites, with a mean of 1.83 per taxon. Insertion and deletion events were present in the data, varied in length, and appeared to be conserved at different taxonomic levels. For example, a 12 bp deletion was present in all members of traditionally recognized neotomine rodents, a 4 bp deletion was present in members of the Tylomyini, a 24 bp deletion defined the neotomine-peromyscine-baiomyine clade, and members of the genus *Neotoma* shared a 21 bp deletion.

Under a parsimony framework, 491 uninformative characters were excluded with 177 characters remaining. A strict consensus tree (Fig. 1) was constructed from the 8 equally parsimonious trees (Length = 371 steps, CI = 0.633, RI = 0.761, RC = 0.482, HI = 0.367) with 5 clades apparent. Clade I consisted of 5 taxa representing 3 genera (*Neotoma, Hodomys,* and *Xenomys*), clade II consisted of 1 taxon representing 1 genus (*Ochrotomys*), clade III consisted of 10 taxa representing 5 genera (*Peromyscus, Neotomodon, Osgoodomys, Onychomys,* and *Reithrodontomys*), clade IV consisted of 2 taxa representing 2 genera (*Scotinomys* and *Baiomys*), and clade V comprised 3 taxa representing 3 genera (*Ototylomys, Tylomys,* and *Nyctomys*). Clades I and II formed a sister relationship, as did clades III and IV. These 2 larger clades were sister to each other, with clade V being basal. Bootstrap support was strong for clades I, III, and IV (100%, 100%, and 96%, respectively), as well as for a clade consisting of I, II, III, and IV (99%) and another consisting of all 5 clades (100%). Bootstrap values were high for genera in which multiple representatives were included, suggesting all genera were monophyletic with the exception of *Peromyscus*, which was represented by an unresolved polytomy of *Peromyscus, Neotomodon,* and *Osgoodomys*.

The topology produced by maximum likelihood analysis (not shown) was similar to the topology generated in parsimony in that both contained 5 clades comprised of

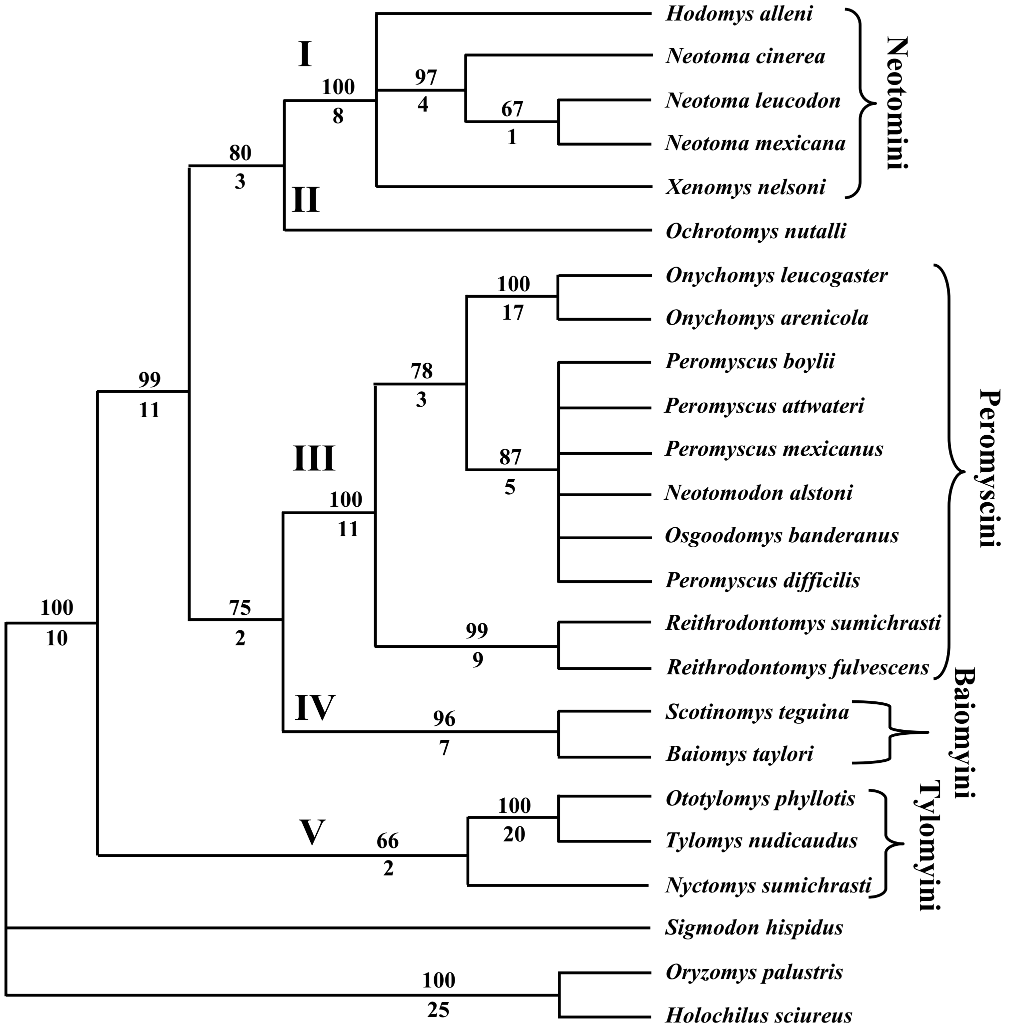

Figure 1. Strict consensus tree obtained from maximum parsimony (equal weighting) of *Fgb*-I7 nucleotide sequences. Numbers above branches are bootstrap values, and numbers below are Bremer support indices.

the same genera. Again, clades I and II were sister as were clades III and IV. These 2 clades then formed a sister relationship, and clade V was basal. As opposed to the parsimony tree, *Peromyscus* did form a monophyletic group that was sister to a clade containing *Neotomodon* and *Osgoodomys*. *Reithrodontomys* was placed basally within clade III in both likelihood and parsimony analyses.

Bayesian analysis resulted in a tree (Fig. 2) similar to both parsimony and likelihood analyses. *Hodomys* and *Xenomys* formed a sister relationship within clade I, as opposed to parsimony (unresolved) and likelihood (joining in a stepwise fashion). As in the parsimony analysis, *Peromyscus* did not form a monophyletic group. Instead,

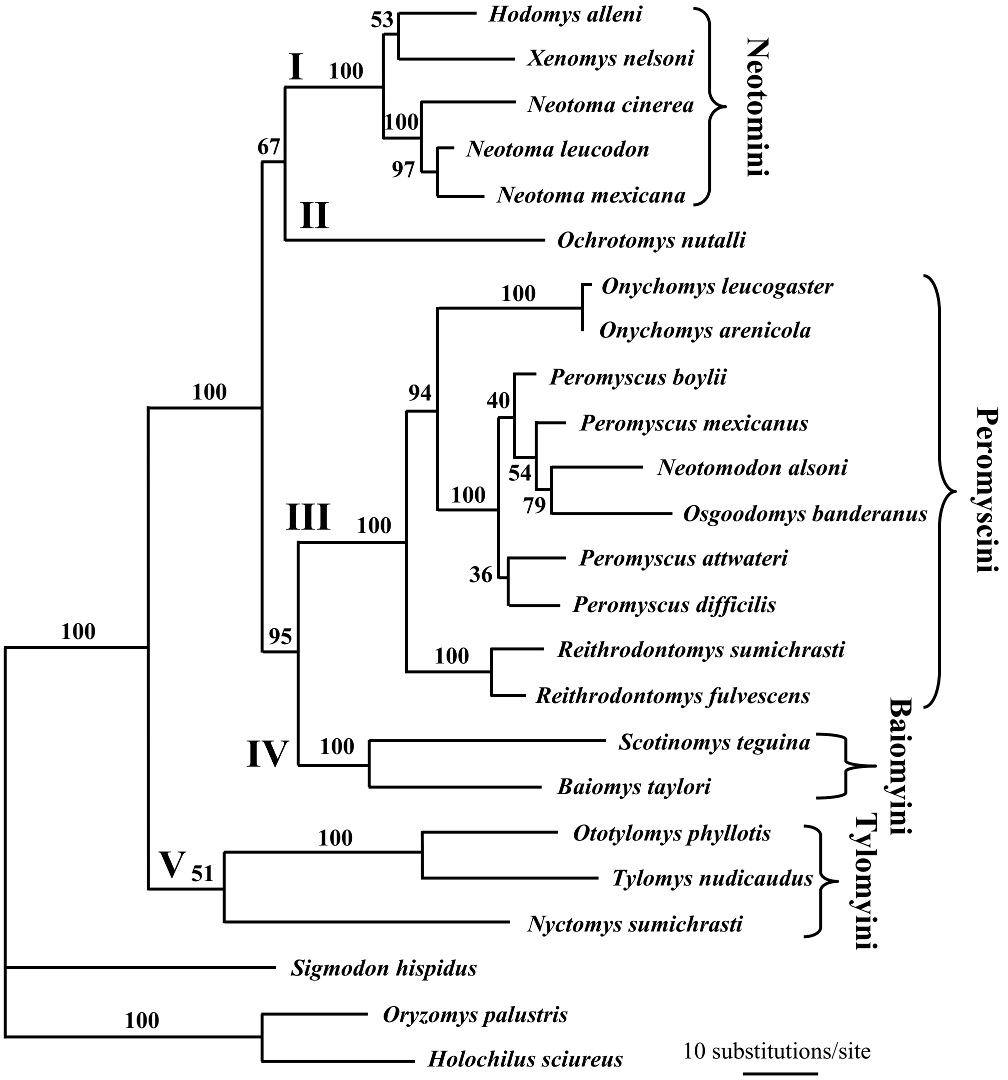

Figure 2. Tree obtained from Bayesian analysis of *Fgb*-I7 with posterior probability values (≥95 = support) above or below branches.

Neotomodon and *Osgoodomys* were more closely related to some forms of *Peromyscus* than other forms of *Peromyscus* were to each other. *Reithrodontomys* was the basal member of clade III. All other relationships were identical to the previous topologies. The monophyly of all genera in which multiple species were examined was supported (posterior probabilities ≥ 95) with the exception of *Peromyscus*. Support was present for clades I, III, and IV in addition to a sister relationship of clades III and IV, a larger clade containing clades I-IV, and finally a clade including I-V.

The topology generated by neighbor joining analysis (not shown) contained 5 clades that were similar to those obtained from the analyses described above. Specifically,

Table 3. Average sequence divergence within and among tribes using the Kimura 2-parameter model (1980) of evolution. Standard deviations (±) are listed in parentheses.

Comparison	Percent sequence difference (%)
Tylomyini vs. *Ochrotomys*	18.8 (1.1)
Tylomyini vs. Peromyscini	17.1 (0.9)
Tylomyini vs. Baiomyini	16.9 (1.8)
Tylomyini vs. Neotomini	16.1 (1.0)
Baiomyini vs. *Ochrotomys*	13.0 (0.5)
Peromyscini vs. *Ochrotomys*	12.4 (1.0)
Baiomyini vs. Peromyscini	11.7 (1.0)
Baiomyini vs. Neotomini	11.1 (0.6)
Peromyscini vs. Neotomini	11.0 (1.1)
Neotomini vs. *Ochrotomys*	10.3 (1.0)
Within Tylomyini	14.1 (5.6)
Within Baiomyini	10.0 (n/a)
Within Peromyscini	5.1 (1.9)
Within Neotomini	4.2 (1.3)

P. mexicanus formed a sister relationship to *Neotomodon*, and *Osgoodomys* joined in a stepwise fashion. This clade was sister to a clade containing *P. boylii, P. attwateri,* and *P. difficilis*. All other relationships were identical to those obtained from the Bayesian analysis.

Constraining *Onychomys* into the Neotomini, as hypothesized by Bradley et al. (2004), resulted in a significantly worse topology ($p = 0.001$) when examined with the Shimodaira-Hasegawa test (Shimodaira and Hasegawa, 1999). All other constraints produced topologies that were not significantly worse than the unconstrained topology: *Peromyscus* (sensu stricto) as sister to *Reithrodontomys* (Carleton, 1980) resulted in a value of $p = 0.054$, and *Ochrotomys* within the Peromyscini (Hooper and Musser, 1964; Carleton, 1980; Musser and Carleton, 1993; McKenna and Bell, 1997; Bradley et al., 2004; Reeder and Bradley, 2004) resulted in a value of $p = 0.575$. Furthermore, constraining *Ochrotomys* outside of a clade consisting of traditional neotomine-peromyscine rodents resulted in a value of $p = 0.444$, not significantly worse than the unconstrained topology.

Pairwise comparisons of Kimura 2-parameter genetic distances (Table 3) produced percent sequence divergence values among tribes that ranged from 10.3% (Neotomini vs. *Ochrotomys*) to 18.8% (Tylomyini vs. *Ochrotomys*). Within tribal levels ranged from 4.2% (within Neotomini) to 14.1% (within Tylomyini).

The partition homogeneity test indicated that the *Fgb*-I7 and cytochrome *b* data were not heterogeneous and therefore could be combined ($p = 0.218$). The combined

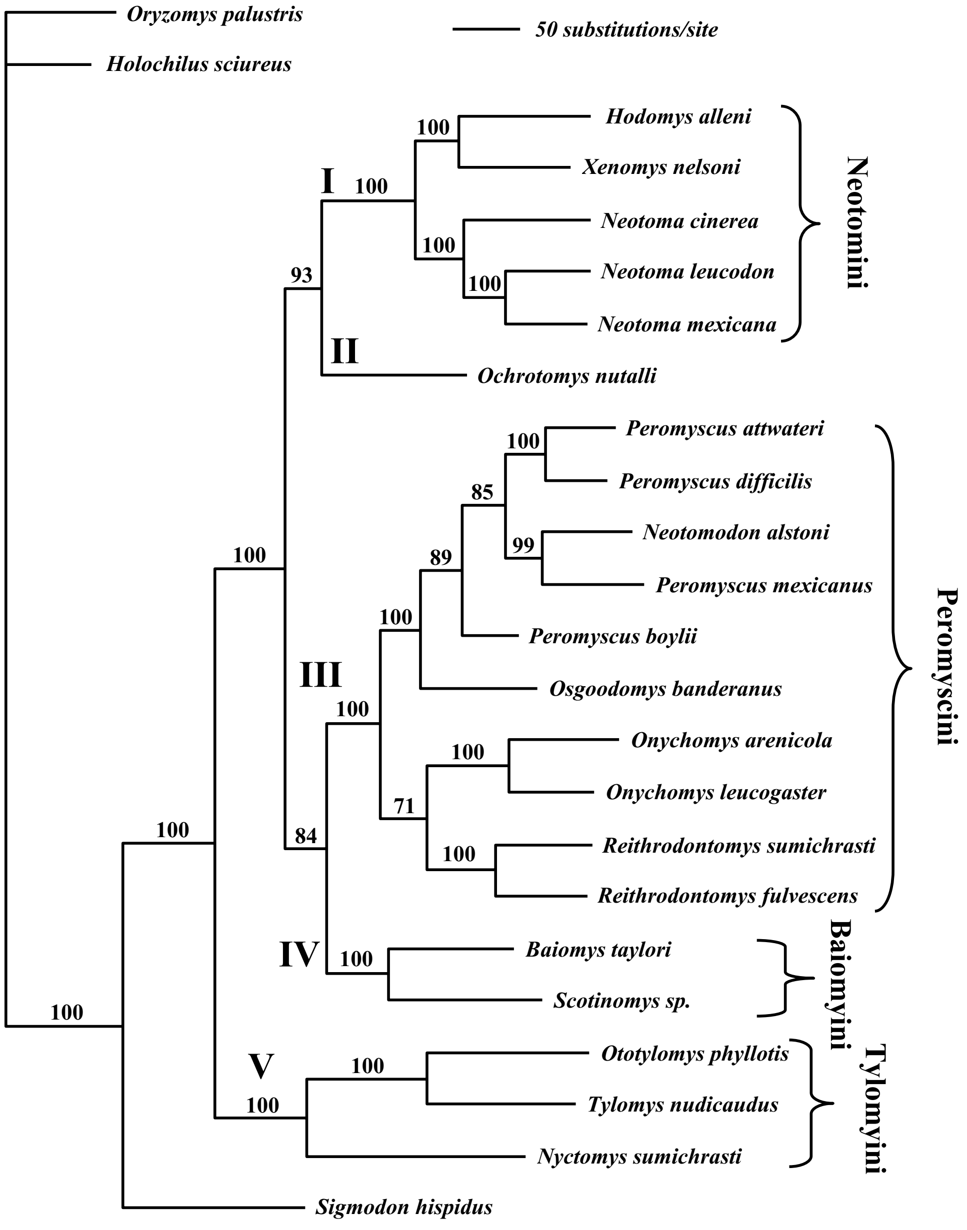

Fig. 3. Tree obtained from Bayesian analysis of combined *Fgb*-I7 and cytochrome *b* sequences with posterior probability values (≥95 = support) above or below branches.

data set produced a topology (Fig. 3) similar to that produced in the *Fgb*-I7 only tree. Minor differences existed internally (i.e. relationships between some of the *Peromyscus* taxa); however, the 5 main clades were retained. In addition, clade probability values were increased at all nodes except the 1 joining the Peromyscini and Baiomyini.

DISCUSSION

DNA sequences obtained from the *Fbg*-I7 gene appear to be phylogenetically informative at the tribal level in sigmodontine rodents. Although insertion and deletion events were present, they were not overly problematic for sequence alignment. In addition, heterozygosity was low (44 of 16,032 aligned sites) and did not affect phylogenetic analyses. As previous studies (Prychitko and Moore, 1997, 2000; Giannasi et al., 2001; Wickliffe et al., 2003) have demonstrated, *Fgb*-I7 shows a high A-T content (60.6% in this study), characteristic of noncoding regions (Li and Graur, 1991). The transition to transversion ratio was approximately 3:1, higher than previous studies have shown. Prychitko and Moore (1997) reported a ratio of 1.24:1, and Carroll and Bradley (2005) calculated a value of 1.46:1. The higher value potentially can be explained in that the taxa examined in this study are more divergent and of a higher taxonomic rank than those in previous studies.

Five main clades consistently were identified in all analyses of *Fgb*-I7. Four of these clades have been recognized as tribes in previous studies (Carleton, 1980; McKenna and Bell, 1997; Bradley et al., 2004; Reeder and Bradley, 2004). Herein, the Neotomini is comprised of *Neotoma, Hodomys,* and *Xenomys*, the Peromyscini includes *Peromyscus, Osgoodomys, Neotomodon, Onychomys* and *Reithrodontomys*, the Baiomyini consists of *Baiomys* and *Scotinomys*, and the Tylomyini consists of *Tylomys, Ototylomys,* and *Nyctomys*. It appears that *Ochrotomys* also may represent a separate tribe. The level of genetic divergence of *Ochrotomys* relative to other traditional peromyscines was higher (12.4%) than the comparison of *Ochrotomys* and the Neotomini (10.3%) and is similar to the comparison of the Baiomyini to the Peromyscini (11.7%). The position of *Ochrotomys* was not significantly worse when constrained within the Peromyscini or outside of a clade consisting of the Neotomini and Peromyscini. An alternative view is that *Ochrotomys* may be a member of the Neotomini. Examining the number of synapomorphies may help to explain this phenomenon. Although a high number of synapomorphies are found basally and at the mid-levels, there is a paucity of synapomorphies (3) supporting *Ochrotomys* as sister to the Neotomini. Within the genus *Sigmodon*, Carroll and Bradley (2005) found a similar lack of synapomorphies between clades when using *Fgb*-I7. It probably is prudent to refrain from designating a formal taxonomic position for this genus until further data become available.

The sister relationship between the Peromyscini and the Baiomyini is not surprising as *Baiomys* and *Scotinomys* previously were classified as peromyscine rodents (Hooper and Musser, 1964; Musser and Carleton, 1993). In addition, the relationship of the Tylomyini as the basal member to a clade of rapidly radiating neotomine-peromyscine-baiomyine rodents has been suggested previously (Carleton, 1980; Bradley et al., 2004; Reeder and Bradley, 2004).

Although *Nyctomys* is relatively divergent from a clade of *Ototylomys* and *Tylomys*, it has support for being included as a North American sigmodontine rodent. The high level of divergence within the Tylomyini and low level of support for *Nyctomys* within the tribe is probably due to missing data (final 83 bp) at the 3′ end of the *Nyctomys* sequence, thus artificially elevating the amount of sequence divergence between it and the other 2 taxa. McKenna and Bell (1997) and Bradley et al. (2004) also recognized *Nyctomys* as a tylomyine rodent.

The relationships of *Peromyscus*, *Neotomodon*, and *Osgoodomys* remain unclear; however, examining these associations in detail is beyond the scope of this study. Both *Reithrodontomys* and *Onychomys* were well supported within the Peromyscini, but support for *Reithrodontomys* as the basal genus within the tribe was rather low. In order to resolve questions that remain within this group of rodents, a combined analysis of multiple data sets should be examined in the future.

The combined analysis using 2 data sets (*Fgb*-I7 and cytochrome *b*) supported the topology and phylogenetic relationships obtained from the *Fgb*-I7 only data set. Although the combined data set was more heavily weighted by the larger number of characters supplied by the cytochrome *b* data set, it appears that *Fgb*-I7 was informative and produced similar results to the cytochrome *b* data. This result is encouraging toward the goal of generating reliable phylogenetic data from nuclear genes.

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LITERATURE CITED

Adkins, R. M., E. L. Gelke, D. Rowe, and R. L. Honeycutt
2001 Molecular phylogeny and divergence time estimates for major rodent groups: evidence from multiple genes. Molecular Biology and Evolution 18:777-791.

Avise, J. C.
1994 Molecular Markers, Natural History, and Evolution. Chapman and Hall, New York, New York, USA. 511 pp.

Bradley, R. D., C. W. Edwards, D. S. Carroll, and C. W. Kilpatrick
2004 Phylogenetic relationships of neotomine-peromyscine rodents: based on DNA sequences from the mitochondrial cytochrome *b* gene. Journal of Mammalogy 85:389-395.

Bremer, K.
1994 Branch support and tree stability. Cladistics 10:295-304.

Bull, J. J., J. P. Huelsenbeck, C. W. Cunningham, D. L. Swofford, and P. J. Waddell
1993 Partitioning and combining data in phylogenetic analysis. Systematic Biology 42:384-397.

Carleton, M. D.
1980 Phylogenetic relationships in neotomine-peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. Miscellaneous Publications, Museum of Zoology, University of Michigan 157:1-146.

1989 Systematics and evolution. Pp. 7-142 in Advances in the Study of *Peromyscus* (Kirkland, G. L., Jr., and J. N. Layne, eds.). Texas Tech University Press, Lubbock, Texas, USA.

Carroll, D. S.
2002 Molecular evolution in the *Sigmodon hispidus* complex using DNA sequences from intron 7 of the beta fibrinogen gene. Molecular phylogenetics of the genus *Sigmodon* based on nuclear and mitochondrial DNA sequences. Ph.D. Dissertation, Texas Tech University, Lubbock, Texas, USA. 83 pp.

Carroll, D. S., and R. D. Bradley
2005 Systematics of the genus *Sigmodon*: DNA sequences from beta fibrinogen and cytochrome *b*. Southwestern Naturalist 50: 342-349.

Chaline, J., P. Mein, and F. Petter
1977 Les grandes lignes d'une classification evolutive des Muroidea. Mammalia 41:245-252.

de Queiroz, A.
1993 For consensus (sometimes). Systematic Biology 42:368-372.

DeBry, R. W., and R. M. Sagel
2001 Phylogeny of Rodentia (Mammalia) inferred from the nuclear encoded gene IRBP. Molecular Phylogenetics and Evolution 19:290-301.

Drovetski, S. V.
2002 Molecular phylogeny of grouse: individual and combined performance of W-linked, autosomal, and mitochondrial loci. Systematic Biology 51:930-945.

Ellerman, J. R.
1940 The Families and Genera of Living Rodents. Vol. 1. Rodents other than Muridae. British Museum of Natural History, London, UK.

Engel, S. R., K. M. Hogan, J. F. Taylor, and S. K. Davis
1998 Molecular systematics and paleobiogeography of the South American sigmodontine rodents. Molecular Biology and Evolution 15:35-49.

Engstrom, M. D., and J. W. Bickham
1982 Chromosome banding and phylogenetics of the golden mouse, *Ochrotomys nuttalli*. Genetica 59:119-126.

Eriksson, T.
1997 Autodecay, version 3.03. Botaniska Institution, Stockholm University, Stockholm, Sweden.

Farris, J. S., M. Kallersjo, A. G. Kluge, and C. Bult
1994 Testing significance of incongruence. Cladistics 10:315-319.

Felsenstein, J.
1985 Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783-791.

Giannasi, N., A. Malhotra, and R. S. Thorpe
2001 Nuclear and mtDNA phylogenies of the *Trimeresurus* complex: implications for the gene versus species tree debate. Molecular Phylogenetics and Evolution 19:57-66.

Hershkovitz, P.
1944 Systematic review of the Neotropical water rats of the genus *Nectomys* (Cricetinae). Miscellaneous Publications, Museum of Zoology, University of Michigan 58:1-101.

1962 Evolution of Neotropical cricetines rodents (Muridae) with special reference to the phyllotine group. Fieldiana: Zoology, 46:1-524.

Hooper, E. T., and G. G. Musser
1964 The glans penis in Neotropical cricetines (family Muridae), with comments on classification of muroid rodents. Miscellaneous Publications, Museum of Zoology, University of Michigan 123:1-57.

Huchon, D., F. M. Catzeflis, and E. J. P. Douzery
1999 Molecular evolution of the nuclear von willebrand factor gene in mammals and the phylogeny of rodents. Molecular Biology and Evolution 16:577-589.

Huchon, D., O. Madsen, M. J. J. B. Sibbald, K. Ament, M. J. Stanhope, F. Catzeflis, W. W. de Jong, and E. J. P. Douzery

2002 Rodent phylogeny and a timescale for the evolution of Glires: evidence from an extensive taxon sampling using three nuclear genes. Molecular Biology and Evolution 19:1053-1065.

Huelsenbeck, J. P., D. L. Swofford, C. W. Cunningham, J. J. Bull, and P. J. Waddell

1994 Is character weighting a panacea for the problem of data heterogeneity in phylogenetic analysis? Systematic Biology 43:288-291.

Huelsenbeck, J. P., and F. Ronquist

2001 MrBayes: Bayesian inference for phylogeny. Biometrics 17:754-756.

Kimura, M.

1980 A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16:111-120.

Li, W. H., and D. Graur

1991 Fundamentals of Molecular Evolution. Sinauer Associates, Sunderland, Massachusetts, USA. 487 pp.

McKenna, M. C., and S. K. Bell

1997 Classification of Mammals above the Species Level. Columbia University Press, New York, USA. xii + 631 pp.

Mickevich, M. F., and J. S. Farris

1981 The implications of congruence in *Menidia*. Systematic Zoology 30:351-370.

Miller, G. S., and J. W. Gridley

1918 Synopsis of the supergeneric groups of rodents. Journal of the Washington Academy of Science 8:431-448.

Musser, G. M., and M. D. Carleton

1993 Family Muridae. Pp. 501-756 in Mammal Species of the World: A Taxonomic and Geographic Reference. Second ed. (Wilson, D. E., and D. M. Reeder, eds.). Smithsonian Institution, Washington, D.C., USA.

Posada, D., and K. A. Crandall

1998 MODELTEST: Testing the model of DNA substitution. Bioinformatics 14:817-818.

Prychitko, T. M., and W. S. Moore

1997 The utility of DNA sequences of an intron from the beta-fibrinogen gene in phylogenetic analysis of woodpeckers (Aves: Picidae). Molecular Phylogenetics and Evolution 8:193-204.

2000 Comparative evolution of the mitochondrial cytochrome *b* gene and nuclear β-fibrinogen intron 7 in woodpeckers. Molecular Biology and Evolution 17:1101-1111.

Reeder, S. A., and R. D. Bradley
2004 Molecular systematics of neotomine-peromyscine rodents based on the dentin matrix protein 1 gene. Journal of Mammalogy 85:1194-1200.

Rinker, G. C.
1954 The comparative mycology of the mammalian genera *Sigmodon*, *Oryzomys*, *Neotoma*, and *Peromyscus* (Cricetinae), with remarks on their intergeneric relationships. Miscellaneous Publications, Museum of Zoology, University of Michigan 83:1-124.

Robinson, M., F. Catzeflis, J. Briolay, and D. Mouchiroud
1997 Molecular phylogeny of rodents, with special emphasis on murids: evidence from nuclear gene LCAT. Molecular Phylogenetics and Evolution 8:423-434.

Seddon, J. M., F. Santucci, N. J. Reeve, and G. M. Hewitt
2001 DNA footprints of European hedgehogs, *Erinaceus europaeus* and *E. concolor*: Pleistocene refugia, postglacial expansion and colonization routes. Molecular Ecology 10:2187-2198.

Shimodaira, H., and M. Hasegawa
1999 Multiple comparisons of log-likelihoods with applications to phylogenetic inference. Molecular Biology and Evolution 16:1114-1116.

Simpson, G. G.
1945 The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History 85:1-350.

Sullivan, J., K. E. Holsinger, and C. Simon
1995 Among-site rate variation and phylogenetic analysis of 12S rRNA in sigmodontine rodents. Molecular Biology and Evolution 12:988-1001.

Swofford, D. L.
2002 PAUP*: phylogenetic analysis using parsimony (*and other methods) version 4.0b10. Sinauer Associates, Sunderland, Massachusetts, USA.

Thomas, O.
1896 On the genera of rodents: an attempt to bring up to date the current arrangement of the order. Proceedings of the Zoological Society of London 1896:1012-1028.

Thompson, J. D., T. J. Gibson, F. Plewniak, F. Jeanmougin, and D. G. Higgins
1997 The CLUSTAL X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Research 24:4876-4482.

Tullberg, T.
1899 Ueber das System der Nagethiere, eine phylogenetische Studie. Acta Societatis Medicorum Upsaliensis 3:1-514.

Walton, A. H., M. A. Nedbal, and R. L. Honeycutt
2000 Evidence from intron 1 of the nuclear transthyretin (prealbumin) gene for the phylogeny of African mole-rats (Bathyergidae). Molecular Phylogenetics and Evolution 16:467-474.

Wickliffe, J. K., F. G. Hoffmann, D. S. Carroll, Y. V. Dunina-Barkovskaya, R. D. Bradley, and R. J. Baker
2003 Intron 7 (*Fgb*-I7) of the fibrinogen, B beta polypeptide (*Fgb*): a nuclear DNA phylogenetic marker for mammals. Occasional Papers, The Museum, Texas Tech University 219:i+1-6.

NUCLEOLAR ACTIVITY AND DISTRIBUTION OF RIBOSOMAL GENES IN *PHYLLOTIS* RODENT SPECIES AND THEIR LABORATORY HYBRIDS

ACTIVIDAD NUCLEOLAR Y DISTRIBUCIÓN DE GENES RIBOSOMALES EN ESPECIES DE ROEDORES DEL GÉNERO *PHYLLOTIS* Y EN SUS HÍBRIDOS DE LABORATORIO

Laura I. Walker and Sergio V. Flores

This work is dedicated to the memory of the late Professor Dr. Oliver Pearson, who was a leader in the areas of zoology and evolutionary biology. Dr. Pearson made significant contributions to the knowledge of South American mammals. He died in March 2003.

ABSTRACT

The expression of nucleolar organizer regions (NORs), distinguished through silver staining procedures, and the distribution of ribosomal genes, detected by fluorescent *in situ* hybridization with a ribosomal DNA probe, were studied in 3 *Phyllotis* rodent species and their laboratory generated hybrids. In the hybrids between the more genetically distant species, the NORs of one parental genome were preferentially expressed. This result differs from the codominant rDNA expression previously detected in hybrids between the 2 more genetically similar of the 3 species, and suggests that nucleolar dominance is related to the compatibility of parental genomes. The mean area of each fluorescent signal was significantly larger in *P. magister*, which has 3 nucleolar chromosome pairs, than in *P. darwini* and *P. xanthopygus*, which have 4 nucleolar chromosome pairs each. Nevertheless, the total area of rDNA signals per cell was similar in the karyotypes of all 3 species, strongly suggesting that rDNA genes have been redistributed in these genomes rather than gained or lost during evolutionary divergence.

Key words: nucleolar dominance, interspecific hybrids, NOR activity, FISH signal areas

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RESUMEN

La expresión de las regiones organizadoras del nucléolo (NORes), revelada mediante procedimientos de tinción con plata, y la localización cromosómica de los genes ribosomales, detectada por hibridación *in situ* con una sonda para ADNr, se estudió en 3 especies de roedores del género *Phyllotis* y en sus híbridos de laboratorio. Los híbridos entre las 2 especies genéticamente más distantes expresaron preferentemente los NORes de uno de los genomas parentales. Este resultado difiere de la expresión codominante del ADNr previamente encontrada en los híbridos derivados del par de especies genéticamente más cercanas y sugiere que la dominancia nucleolar está relacionada con la compatibilidad de los genomas parentales. El área promedio de cada señal fluorescente fue significativamente mayor en *P. magister*, con 3 pares de cromosomas nucleolares, que en *P. darwini* y *P. xanthopygus*, cuyos cariotipos tienen 4 pares de cromosomas nucleolares cada uno. Sin embargo, el área total de señales de ADNr por célula fue similar en los cariotipos de las 3 especies, sugiriendo fuertemente que durante la divergencia evolutiva de estas formas, los genes ribosomales se redistribuyeron entre los genomas, no produciéndose ni ganancias ni pérdidas significativas de los mismos.

Palabras claves: dominancia nucleolar, híbridos interespecíficos, actividad NOR, áreas de señal FISH

INTRODUCTION

The chromosomal distribution and position of nucleolar organizer regions (NORs) generally are detected by silver staining procedures (Goodpasture and Bloom, 1975; Sánchez-Rufas et al., 1982). Positive Ag reaction of chromosomal NORs (AgNORs) is believed to reflect the transcriptional activity of ribosomal genes during the preceding interphase of the cell cycle (Howell, 1977; Hubbel, 1985; Jiménez et al., 1988), while *in situ* hybridization with rDNA probes makes it possible to detect all the chromosomal regions containing ribosomal genes in a karyotype. Thus, the use of both procedures is required to distinguish between active and inactive rRNA gene clusters in a particular genome (Shubert and Künzel, 1990; Pendás et al., 1993; Mellink et al., 1994).

Interchromosomal, intercellular, and inter-individual variability in the number and size of AgNOR bands and *in situ* hybridization signals have been reported in most species that have been analyzed (Sánchez et al., 1989; Zurita et al., 1997, 1998, 1999). It is generally accepted that, while variability among AgNOR bands mainly depends on specific metabolic cell demands (Sánchez et al., 1989; Berríos et al., 1992), differences among *in situ* hybridization signals reflect variations in the number of ribosomal genes present in each particular NOR (Wachtler et al., 1986; Suzuki et al., 1990; Leitch and Heslop-Harrison, 1992; Mellink et al., 1994). Moreover, in some mammal species a direct relationship has been established between the number of ribosomal genes in a particular NOR and its level of expression (Zurita et al., 1998, 1999).

Interspecific hybrids have often shown the existence of nucleolar dominance, that is, the preferential expression of ribosomal genes from one of the 2 parental species (Honjo and Reeder, 1973). First described in plants (Navashin, 1928, 1934), nucleolar dominance is now known in insects, amphibians, and mammals (Reeder, 1985; Pikaard and Chen, 1998). The mechanisms that, in the cells of the hybrids, discriminate between parental sets of rRNA genes and initially establish nucleolar dominance remain obscure. Nevertheless, the subsequent enforcement of dominance through successive mitoses is an epigenetic phenomenon, under the influence of both DNA methylation and histone deacetylation (Chen and Pikaard, 1997).

We have previously obtained laboratory hybrids between 3 species of the Andean rodent genus *Phyllotis* (Rodentia, Muridae): *P. darwini*, *P. xanthopygus*, and *P. magister* (Walker et al., 1984, 1999). Each of these species has small and multiple AgNORs, located in the telomeric regions of 3 or 4 chromosomal pairs (Walker et al., 1998, 1999; Spotorno et al., 2001). We have also previously shown that in the cells of the hybrids between the sister species *P. darwini* and *P. magister*, both parental NOR sets are expressed with similar frequencies (Walker et al., 1999).

In the present paper we will demonstrate that, to the contrary, nucleolar dominance occurs in the cells of the hybrids between the phylogenetically more distant species *P. darwini* and *P. xanthopygus*. This and previous results suggest that in phyllotine hybrids, nucleolar dominance or codominance would be established at a genomic level, according to the distance and compatibility between the progenitor genomes. The use of a procedure to directly measure every fluorescent rDNA *in situ* hybridization signal area, has allowed us to assess the amount and evolution of ribosomal genes in the genomes of these 3 species.

MATERIALS AND METHODS

Specimens. Specimens of the 3 *Phyllotis* species were trapped alive in Chilean territory or were the direct laboratory descendants of wild-caught individuals. Skulls and skins of all the animals studied were prepared as voucher specimens and were deposited in the collection of the Laboratorio de Citogenética, Facultad de Medicina, Universidad de Chile (LCM).

Taxa, original localities, number and sex of the animals examined (with collection numbers between brackets) were as follows: *P. darwini* (4 males and 2 females): IV Región: Las Tacas, 1 female (LCM 667); Aucó, 1 male (LCM 755); Talinay, 1 male (LCM 1008); Pichidangui, 1 male (LCM 1850) and 1 female (LCM 1848); Fray Jorge, 1 male (LCM 1955). *P. magister*: II Región: Ojo Opache, mouth of the Loa River, 4 males (LCM 1693, 1728, 1795, 2034) and 3 females (LCM 1691, 1741, 2054). *P. xanthopygus* (2 males and 3 females): II Región: San Pedro de Atacama, 1 female (LCM 996); IV Región: El Indio, Río Elqui, 1 male (LCM 1696); Región Metropolitana: Baños Morales, 1 female (LCM 587); Farellones, 1 male (LCM 1798) and 1 female (LCM 1913).

Interspecific hybrids were obtained from laboratory crosses between the parental species. The crosses, that always included the reciprocal ones, the parental species (male x female), the number and sex of the examined hybrids (with collection numbers between brackets) were: *darwini* x *xanthopygus*, 2 males (LCM 624, 937) and 2 females (LCM 764, 998); *xanthopygus* x *darwini*, 1 male (LCM 758); *darwini* x *magister*, 1 female (LCM 1964); *magister* x *darwini*, 1 male (LCM 1740).

Cytogenetic Analyses. Chromosome preparations were made from bone marrow cells using the conventional *in vivo* colchicine, hypotonic method, preceded by yeast injection to improve the mitotic index (Lee and Elder, 1980). Active NORs were detected by the silver staining procedure described by Sánchez-Rufas et al. (1982). To unambiguously identify the chromosomes carrying NORs, we used a sequential AgNOR G-banding technique (NOR-G banding), developed in our laboratory. The number and chromosomal distribution of active NORs were then recorded in the cells of each parental species and compared with those found in the cells of the hybrids.

Fluorescent *in situ* hybridization (FISH) was performed using a chicken rDNA probe formed by the terminal 3′ sequences of the 18S gene. The probe was labeled with biotin by nick translation, using the Bionick Labelling System (Gibco BRL) and according to the instructions of the manufacturer. FISH and detection of the hybridization signals were performed following the protocols previously described by Iturra et al. (1998, 2001). Metaphases were counterstained with propidium iodide-antifade solution (Oncor). Chromosome signals were detected using a Nikon fluorescence microscope equipped with the appropriate filter and photographed with Kodak Ektachrome 400 color film. Images from FISH were then scanned and the probe signal areas were measured in pixels, using a commercial software package (IPLab, v2.420, Scanalytics). Chromosomes having fluorescent signals in each karyotype were identified according to their previously described sizes and morphologies (Walker et al., 1979, 1984). The mean values obtained for the total FISH signal areas in each of the 3 karyotypes were compared using the Student *t*-test for independent variables.

RESULTS

Phyllotis darwini showed 4 chromosomal pairs carrying active NORs (Nos. 3, 7, 9, 12; Fig. 1A) and *P. magister* had a maximum of 3 chromosomal pairs bearing NORs (Nos. 3, 9, 12). These observations on the number and chromosomal distribution of telomeric AgNOR bands confirmed those previously described for both species (Walker et al., 1999). In the cells of *P. magister* x *P. darwini* hybrids, both parental NOR sets exhibited similar frequencies of activity, as it was previously reported (Walker et al., 1999), indicating that ribosomal genes of the 2 species were codominantly expressed.

Also according to previous descriptions (Spotorno et al., 2001), *P. xanthopygus* showed telomeric NORs located in 4 chromosomal pairs (Nos. 3, 6, 12, 16; Fig. 1B). The abundant pericentromeric heterochromatin present in all the *P. xanthopygus* chromosomes (Walker et al., 1984, 1991) was also stained with silver nitrate, producing Ag^+ centromeric bands (Fig. 1B); these bands were absent in *P. darwini* chromosomes (Fig. 1A), where there are smaller quantities of heterochromatin (Walker et al., 1984, 1991).

In the NOR-banded metaphases of *P. darwini* x *P. xanthopygus* hybrids, a minimum of 2 and a maximum of 6 chromosomes carrying active NORs were detected. As expected, the Ag-banded karyotype of the hybrids displayed 2 distinct kinds of chromosomes: half of them had pericentromeric Ag^+ bands, as in *P. xanthopygus*, whereas in the other half, such Ag^+ bands were lacking, as in *P. darwini* (Fig. 1C–E), making it possible to distinguish the parental origin of NOR chromosomes. One of the 2 metaphases of the same hybrid female appearing in Fig. 1 showed 4 active NORs, half of them being located in *P. darwini* chromosomes (Fig. 1C, E), and the other, had 5 active NORs, 3 of which were located in *P. darwini* chromosomes (Fig. 1D).

NOR expression variability, previously registered in *P. darwini* and *P. magister* (Walker et al., 1999), was also detected in *P. xanthopygus*. The average number and

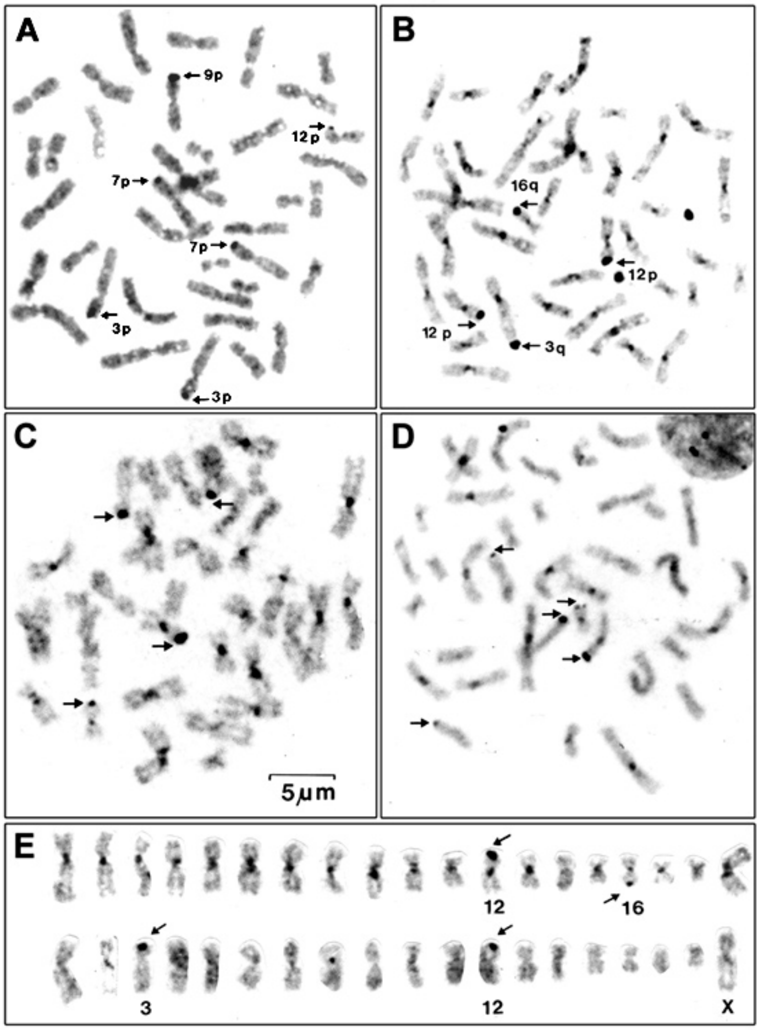

Figure 1. Multiple telomeric AgNORs (arrows) in NOR-G banded metaphases of *Phyllotis darwini*, *P. xanthopygus*, and their hybrids. (A) *P. darwini* male. (B) *P. xanthopygus* female (note also the Ag+ pericentromeric bands in all the chromosomes; see text). The NORs of chromosome 6 were not Ag positively stained in this metaphase. (C and D) *P. darwini* x *P. xanthopygus* hybrid female. (E) Same as (C), but parental chromosomal sets were ordered by size and NOR-G bands, and separated according to the presence or absence of centromeric Ag+ bands (upper row, *P. xanthopygus* origin; lower row, *P. darwini* origin).

standard deviation of active NORs per cell recorded in *P. darwini*, *P. magister* and *P. xanthopygus* were 3.58 ± 0.77 (N = 81), 3.02 ± 0.77 (N = 57), and 3.46 ± 1.58 (N = 51), respectively.

Three distinct patterns of NOR activity, each with characteristic but different

Table 1. Number of cells having both (+/+), only one (+/-) or no (-/-) active NORs in each of the nucleolar chromosome pairs of *P. darwini* (A) and *P. xanthopygus* (B).

Specimens LCM number* (sex)	Number of cells	Nucleolar chromosomal pairs											
		chr 3			chr 7			chr 9			chr 12		
(A) *P. darwini*		+/+	**+/-**	-/-	+/+	**+/-**	-/-	+/+	+/-	**-/-**	+/+	**+/-**	-/-
1850 (m)	17	9	8	0	1	16	0	0	5	12	1	11	5
755 (m)	13	3	9	1	2	9	2	1	6	6	1	9	3
667 (f)	12	4	8	0	4	8	0	2	6	4	0	9	3
Total	42	16	**25**	1	7	**33**	2	3	17	**22**	2	**29**	11
		chr 3			chr 6			chr 12			chr 16		
(B) *P. xanthopygus*		+/+	**+/-**	-/-	+/+	**+/-**	-/-	+/+	+/-	**-/-**	+/+	**+/-**	-/-
1798 (m)	14	1	9	4	0	4	10	0	5	9	1	7	6
587 (f)	14	2	11	1	3	8	3	2	3	9	2	11	1
1913 (f)	17	4	10	3	10	7	0	7	7	3	2	10	5
Total	45	7	**30**	8	13	**19**	13	9	15	**21**	5	**28**	12

*The specimen numbers are those of the mammal laboratory collection (LCM); m = male, f = female. Bold characters indicate the most frequent pattern of NOR activity (+/+, +/- or -/-) detected for each chromosomal pair.

frequencies, were detected for each of the 4 *P. darwini* and *P. xanthopygus* nucleolar chromosomes (Table 1): active NORs were present in both homologous chromosomes (+/+), in only one of them (+/–) or in none of them (–/–). In these 2 species, as in *P. magister* (Walker et al., 1999), the most frequent condition was that in which only one member of each nucleolar chromosome pair was active (+/–, Table 1). The exceptions were one pair of NOR chromosomes in each species karyotype, which showed absence of activity in both homologous members as the most frequent condition (*P. darwini* No. 9 and *P. xanthopygus* No. 12, Table 1), and thus revealing the low expression level of the ribosomal genes located herein.

The analysis of 51 metaphases from 4 *P. darwini* x *P. xanthopygus* hybrids (male *P. darwini* x female *P. xanthopygus*, LCM 764, 937, 998, and male *P. xanthopygus* x female *P. darwini*, LCM 758, Table 2) indicated that the 4 *P. darwini* NOR chromosomes showed, in general, a higher frequency of expression than the *P. xanthopygus* NOR chromosomes (Table 2), independently of the *P. darwini* progenitor sex. The small *P. xanthopyygus* nucleolar chromosome No.16 was the only exception to this rule, since its ribosomal genes were expressed in a relatively high proportion of the examined cells (51%, Table 2). On the other hand, a total of 161 active NORs were detected in the cells of these hybrids, 104 in *P. darwini* chromosomes and only 57 in *P. xanthopygus* ones (Table 2).

Representative results obtained after *in situ* hybridization with the rDNA probe are shown in Fig. 2. Four to 6 telomeric fluorescent signals were recorded in the parental species and hybrid metaphases (Fig. 2A–E). The *P. darwini* x *P. xanthopygus* hybrids showed rDNA-FISH signals on the nucleolar chromosomes of both parental sets. Since constitutive heterochromatin fluoresces strongly with the propidium iodide counterstain and the karyotypes of the parental species differ substantially in the amount of pericentromeric heterochromatin (Walker et al., 1984), we could

Table 2. Number and frequency of cells showing active NORs in each of the parental nucleolar chromosomes of the *P. darwini* x *P. xanthopygus* hybrids.

Hybrid specimens LCM number* (sex)	Number of cells	Nucleolar active chromosomes of the two parental genomes							
		P. darwini				*P. xanthopygus*			
		chr 3	chr 7	chr 9	chr 12	chr 3	chr 6	chr 12	chr 16
764 (f)	8	8	2	1	1	4	1	1	5
937 (m)	13	10	4	5	4	0	2	3	4
998 (f)	17	16	8	8	8	1	7	4	10
758 (m)	13	7	9	9	4	3	3	2	7
Total	51	41	23	23	17	8	13	10	26
%	100.0	80.4	45.1	45.1	33.3	15.7	25.5	19.6	51.0

*The specimen numbers are those of the mammal laboratory collection (LCM); m = male, f = female.

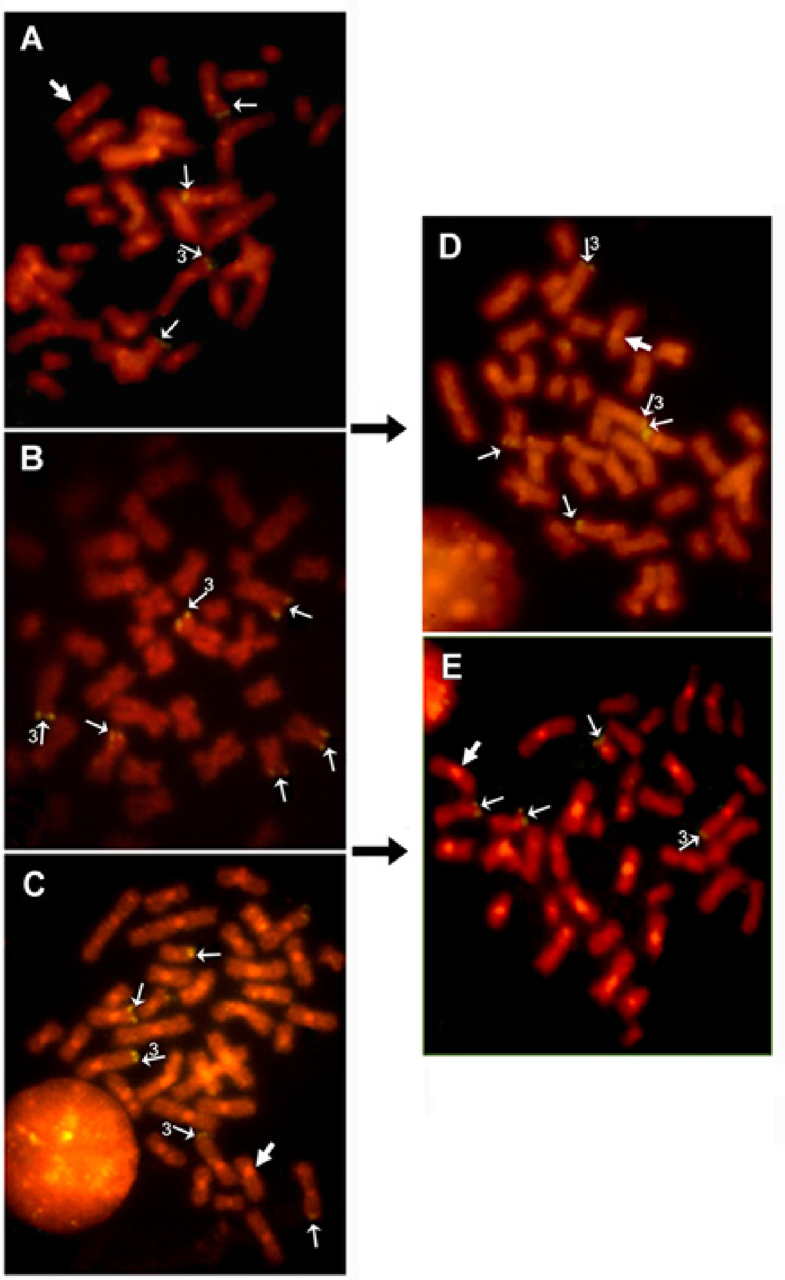

Figure 2. Fluorescence *in situ* hybridization of a18S rDNA biotinilated probe in metaphases of the 3 parental species and the 2 types of hybrids: (A) *P. magister*, (B) *P. darwini*, (C) *P. xanthopygus*, (D) *P. darwini* x *P. magister* hybrid, and (E) *P. darwini* x *P. xanthopygus* hybrid. Thin arrows indicate the location of hybridization signals (A – E) and thick arrows show the pericentromeric heterochromatin, fluorescing brilliantly with the propidium iodide counterstain (A, C, D, E).

distinguish the parental origin of the NOR-bearing chromosomes in the metaphases of the hybrids. Thus, some signals were located in *P. xanthopygus* chromosomes, with propidium iodide fluorescent centromeres, and others in *P. darwini* chromosomes, with non-fluorescent centromeres (Fig. 2E).

Significant differences exist between the mean area of fluorescent signal for *P. magister* (141.67 ± 76.61 px, $N = 69$) and those of the other 2 species, *P. darwini* (119.94 ± 62.56 px, $N = 189$, $t = 2.32$, *d.f.* = 256, $p = 0.021$) and *P. xanthopygus* (116.20 ± 52.33 px, $N = 276$, $t = 3.26$, *d.f.* = 343, $p = 0.001$). Nevertheless, the total area of rDNA signal per cell was very similar in the 3 karyotypes: 545.6 ± 96.9 px; 520.1 ± 130.2 px, and 492.4 ± 102.2 px, in *P. darwini, P. magister* and *P. xanthopygus*, respectively. The small variations of these values were not significantly different ($t_{darwini\,-\,magister} = 0.111$, *d.f.* = 17, $p = 0.913$; $t_{magister\,-\,xanthopygus} = 1.778$, *d.f.* = 34, $p = 0.084$), despite the distinct number of nucleolar chromosomes present in each species.

DISCUSSION

The number of structural NORs per karyotype and their chromosomal distribution are thought to be species-specific cellular characters. However, NOR transcriptional activity is quite variable and, for many mammalian species, is often considered an individual characteristic (Mikelsaar et al., 1977; Mayr et al., 1987; Suzuki et al., 1990; Zurita et al., 1997) dependent mainly on specific metabolic cell demands (Sánchez et al., 1989; Berríos et al., 1992).

In the *Phyllotis* species studied here, the ribosomal genes were more dispersed in *P. darwini* and *P. xanthopygus* genomes, with 4 chromosomal pairs carrying NORs (Fig. 1), than in *P. magister* genome, with 3 NOR chromosomal pairs (Walker et al., 1999). Each species showed the expected interchromosomal, intercellular, and inter-individual NOR activity variation (Table 1; Walker et al., 1999), although all 3 species had very similar levels of total NOR activity. Thus, the indices of NOR activity, calculated as the ratio between the number of active and structural NORs per cell (Walker et al., 1999), were nearly equal for *P. darwini, P. magister* and *P. xanthopygus* (0.448, 0.503, and 0.495, respectively).

Because the most frequent NOR activity pattern found in the 3 species was that in which only one member of each nucleolar chromosome pair was active (Table 1; Walker et al., 1999), specific regulation of rDNA transcription, by either suppression or activation, likely occurs. As in other mammal species, rDNA cytosine methylation and histone deacetylation could be operating over the genomic compartment containing the ribosomal genes, thus favoring the expression of only one member of each NOR chromosomal pair in the parental species or only one parental genome in the hybrids (Flavell et al., 1988; Chen and Pikaard, 1997; Houchins et al., 1997; Pikaard, 1999).

Previously, we found that in the hybrids of the sister species *P. darwini* and *P. magister,* the ribosomal genes of both parental species were active and functioned in a codominant form. Moreover, from a reproductive point of view, these hybrids conformed to Haldane's rule, since females were fertile and males were infertile (Walker et al., 1999). Thus, codominant NOR expression, meiotic normality and gametic differentiation of, at least, female hybrids, indicate that *P. darwini* and *P. magister* genomes can function in relative harmony and compatibility when they are placed together in the nuclei of their laboratory generated hybrids.

Contrary to this observation of codominance, there appears to be nucleolar dominance for ribosomal genes in hybrids between *P. darwini* x *P. xanthopygus*, with the parental genome of *P. darwini* expressed far more frequently than that of the *P. xanthopygus* (Table 2). Moreover, if we assume *a priori* that both parental NOR sets have the same probability to be expressed in the cells of hybrids, half of the 161 active NORs (80-81) recorded in the 4 hybrid individuals studied (Table 2), should be located in *P. darwini* chromosomes and the other half in those of *P. xanthopygus*. However, 104 active NORs were found to be in *P. darwini* chromosomes and only 57 were registered in those of *P. xanthopygus* (Table 2), indicating clearly and significantly that the expression of *darwini* nucleolar organizer regions dominate over those of *P. xanthopygus* ones ($\chi^2 = 7.924$, *d.f.* = 3, $p < 0.05$).

Previous results (Walker et al., 1984) showed that both male and female *P. darwini* x *P. xanthopygus* hybrids are completely sterile, with the meiotic process arrested in their gonads. We suspect that sterility is caused by chromosomal differences and incompatibility between the parental species genomes. The nucleolar dominance in rDNA gene expression detected here would be another manifestation of the difficulty for those two genomes to function together in the nuclei of the hybrid individuals.

Taken as a whole, our data suggest that in the *Phyllotis* species analyzed here, the level of nucleolar dominance is positively correlated with the phylogenetic divergence. These results are in accordance with previous cytogenetic data, showing that there are larger differences between *P. darwini* and *P. xanthopygus* karyotypes than between those of *P. darwini* and *P. magister*, which have only small dissimilarities (Walker et al., 1979, 1984, 1991). The results also agree with data obtained from molecular analyses performed in these 3 species, since in the phylogenetic trees based on protein electrophoretic data or cytochrome *b* gene sequences, *P. xanthopygus* is always placed in a clade separate from that which groups *P. darwini* and *P. magister* (Steppan, 1998; Spotorno et al., 2001; Kuch et al., 2002).

Differences in the number and size of the hybridization signals between homologous and among non-homologous chromosomes were detected in the parental species and their hybrids (Fig. 2). Because the *in situ* hybridization procedure directly detects ribosomal DNA, these differences would be evidence of polymorphism for the number of ribosomal genes present at the different NOR sites (Wachtler et al., 1986; Pendás et al., 1993; Mellink et al., 1994; Zurita et al., 1998).

The rDNA fluorescent signal areas per chromosome were significantly different in the 3 species karyotypes, though the total fluorescent areas of the three species genomes were similar ($p < 0.05$). Thus, each relatively large fluorescent NOR site of *P. magister* (141.67 ± 76.61 px), with only 3 NOR chromosomes, apparently contains significantly larger numbers of ribosomal genes than the smaller fluorescent NOR sites of *P. darwini* (119.94 ± 62.56 px) and *P. xanthopygus* (116.20 ± 52.33 px), each with 4 NOR chromosomes. Nevertheless, the total number of ribosomal genes in each species is similar. These findings imply that the differences in the number of ribosomal genes located in the NORs of the 3 species can be explained through genomic redistribution of rDNA genes, rather than either gain or loss during evolution.

Since chromosomal evolution in *Phyllotis* has proceeded mainly through multiple and independent centric fusions from an ancestral telocentric karyotype (Pearson and Patton, 1976; Walker et al., 1979, 1984; Spotorno et al., 2001), the proposed karyotypic redistribution of rDNA genes can be confirmed comparing the G-banding patterns of NOR chromosomal arms in the 3 species metacentric karyotypes. The ribosomal genes of the sister species *P. magister* and *P. darwini* appeared located in homologous chromosomal arms, those with the same G-banding patterns. On the contrary, none of the 4 NOR chromosomes of the more distantly related species, *P. xanthopygus*, showed G-banding homology with any of the *P. magister* or *P. darwini* NOR chromosomes or chromosomal arms (Spotorno et al., 2001), thus confirming that ribosomal genes have undergone a complete redistribution in these genomes.

According to morphological and cytogenetic analyses, *P. darwini* is the most primitive of these 3 species, and *P. xanthopygus* is the more derived taxon (Simonetti and Spotorno, 1981; Walker et al., 1991). Since 4 NOR chromosomes were detected in *P. darwini* and *P. xanthopygus*, and only 3 in *P. magister*, reduction in NOR number seems to have occurred during the divergence of *P. magister* genome. On the other hand, in the phyllotine genus *Loxodontomys,* which chromosomally evolved mainly by the occurrence of tandem fusions (Walker and Spotorno, 1992), there has also been a reduction from 4 to 3 NOR-bearing chromosomes (Walker and Spotorno, 1992; Spotorno et al., 2001).

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LITERATURE CITED

Berríos, S., J. Koifman, and R. Fernández-Donoso
1992 Tissue and sex differences in the expression of nucleoli in mouse somatic cells. European Journal of Morphology 30:297-303.

Chen, Z. J., and C. S. Pikaard
1997 Epigenetic silencing of RNA polymerase I transcription: a role for DNA methylation and histone modification in nucleolar dominance. Genes and Development 11:2124-2136.

Flavell, R. B., M. O'Delland, and W. F. Thompson
1988 Regulation of cytosine methylation in ribosomal DNA and nucleolus organizer expression in wheat. Journal of Molecular Biology 204:523-534.

Goodpasture, C., and S. E. Bloom
1975 Visualization of nucleolar organizer regions in mammalian chromosomes using silver stain. Chromosoma 53:37-50.

Honjo, T., and R. H. Reeder
1973 Preferential transcription of *Xenopus laevis* ribosomal RNA in interspecies hybrids between *Xenopus laevis* and *Xenopus mulleri*. Journal of Molecular Biology 80:217-228.

Houchins, K., M. O'Dell, R. B. Flavell, and J. P. Gustafson
1997 Cytosine methylation and nucleolar dominance in cereal hybrids. Molecular and General Genetics 255:294-301.

Howell, W. M.
1977 Visualization of ribosomal gene activity: silver stains proteins associated with rRNA transcribed from oocyte chromosomes. Chromosoma 62:361-367.

Hubbel, H. R.
1985 Silver staining as an indicator of active ribosomal genes. Stain Technology 60:285-294.

Iturra, P., N. Lam, M. De la Fuente, N. Vergara, and J. F. Medrano
2001 Characterization of sex chromosomes in rainbow trout and coho salmon using fluorescence *in situ* hybridization (FISH). Genetica 111:125-131.

Iturra, P., J. F. Medrano, N. Lam, N. Vergara, and J. C. Marín
1998 Identification of sex chromosome molecular markers using RAPDs and fluorescent *in situ* hybridization in rainbow trout. Genetica 101:209-213.

Jiménez, R., M. Burgos, and R. Díaz de la Cuadra
1988 A study of the Ag-staining significance in mitotic NOR`s. Heredity 60:125-127.

Kuch, M., N. Rohland, J. L. Betancourt, C. Latorre, S. Steppan, and H. N. Poinar
2002 Molecular analysis of a 11,700-year-old rodent midden from the Atacama Desert, Chile. Molecular Ecology 11:913-924.

Lee, M. R., and F. F. B. Elder
1980 Yeast stimulation of bone marrow mitoses for cytogenetic investigations. Cytogenetics and Cell Genetics 26:36-40.

Leitch, I. J., and J. S. Heslop-Harrison
1992 Physical mapping of the 18S - 5.8S - 26S rRNA genes in barley by *in situ* hybridization. Genome 35:1013-1018.

Mayr, B., W. Schleger, and H. Auer
1987 Frequency of Ag-stained nucleolus organizer regions in the chromosomes of cattle. Journal of Heredity 78:206-207.

Mellink, C. H. M., A. A. Bosma, and N. A. De Haan
1994 Variation in size of Ag-NORs and fluorescent rDNA *in situ* hybridization signals in six breeds of domestic pig. Hereditas 120:141-149.

Mikelsaar, A. V., M. Schmid, H. Krone, G. Schwarzacher, and W. Schenedl
1977 Frequency of Ag-stained nucleolus organizer regions in the acrocentric chromosomes of man. Human Genetics 37:73-77.

Navashin, M.
1928 Amphiplastie, eine neue karyologische Erscheinung. Proceedings of the International Conference of Genetics 5:1148-1152.

1934 Chromosomal alterations caused by hybridization and their bearing upon certain general genetic problems. Cytologia 5:169-203.

Pearson, O. P., and J. L. Patton
1976 Relationships among South American phyllotine rodents based on chromosome analysis. Journal of Mammalogy 57:339-350.

Pendás, A. M., P. Morán, and E. García-Vázquez
1993 Multi-chromosomal location of ribosomal RNA genes and heterochromatin association in brown trout. Chromosome Research 1:63-67.

Pikaard, C. S.
1999 Nucleolar dominance and silencing of transcription. Trends in Plant Science 4:478-483.

Pikaard, C. S., and Z. J. Chen
1998 Nucleolar dominance. Pp. 275-293 in RNA Polymerase I: Transcription of Eukaryotic Ribosomal RNA (Paule, M. R., ed.). R. G. Landes, Austin, Texas, USA.

Reeder, R. H.
1985 Mechanisms of nucleolar dominance in animals and plants. Journal of Cell Biology 101:2013-2016.

Sánchez, A., M. Burgos, R. Jiménez, and R. Díaz de la Guardia
1989 Quantitative analysis of silver staining of the nucleolar organizer regions in *Eliomys quercinus*. Genome 32:978-982.

Sánchez-Rufas, J. S., P. Iturra, W. De Souza, and P. Esponda
1982 Simple silver staining procedures for the localization of nucleolus and nucleolar organizers under light and electron microscopy. Archives Biologie Bruxelles 93:267-274.

Schubert, I., and G. Künzel
1990 Position-dependent NOR activity in barley. Chromosoma 99:352-359.

Simonetti, J., and A. E. Spotorno
1981 Divergencia adaptativa en la radiación filotina. Medio Ambiente 51:88-95.

Spotorno, A. E., L. I. Walker, S. V. Flores, M. Yévenes, J. C. Marín, and C. Zuleta
2001 Evolución de los filotinos (Rodentia, Muridae) en los Andes del Sur. Revista Chilena de Historia Natural 74:151-166.

Steppan, S.
1998 Phylogenetic relationships and species limits within *Phyllotis* (Rodentia: Sigmodontinae): concordance between mtDNA sequence and morphology. Journal of Mammalogy 79:573-593.

Suzuki, H., Y. Kurihara, T. Kanehisa, and K. Moriwaki
1990 Variation in the distribution of the silver staining nucleolar organizer regions on the chromosomes of the wild mouse, *Mus musculus*. Molecular Biology and Evolution 7:271-282.

Walker, L. I., S. V. Flores, and A. E. Spotorno
1998 Nucleolar dominance in phyllotine rodent hybrids. Cytogenetics and Cell Genetics 81:134. Abstracts of 13th International Chromosome Conference, Ancona, Italy.

Walker, L. I., M. Rojas, S. Flores, A. Spotorno, and G. Manríquez
1999 Genomic compatibility between two phyllotine rodent species evaluated through their hybrids. Hereditas 131:227-238.

Walker, L. I., and A. E. Spotorno
1992 Tandem and centric fusions in the chromosomal evolution of the South American phyllotines of the genus *Auliscomys* (Rodentia, Cricetidae). Cytogenetics and Cell Genetics 61:135-140.

Walker, L. I., A. E. Spotorno, and J. Arrau
1984 Cytogenetic and reproductive studies of two nominal subspecies of *Phyllotis darwini* and their experimental hybrids. Journal of Mammalogy 65:220-230.

Walker, L. I., A. E. Spotorno, and R. Fernández-Donoso
1979 Conservation of whole arms during chromosomal divergence of phyllotine rodents. Cytogenetics and Cell Genetics 24:209-216.

Walker, L. I., A. E. Spotorno, and J. Sans
1991 Genome size variation and its phenotypic consequences in *Phyllotis* rodents. Hereditas 115:99-107.

Watchler, F., A. H. N. Hopman, J. Wiegant, and H. G. Schwarzacher
1986 On the position of nucleolus organizer regions NORs in interphase nuclei. Studies with a new non-autoradiographic *in situ* hybridization method. Experimental Cell Research 167:227-240.

Zurita, F., R. Jiménez, M. Burgos, and R. Díaz de la Guardia
1998 Sequential silver staining and *in situ* hybridization reveal a direct association between rDNA levels and the expression of homologous nucleolar organizing regions: a hypothesis for NOR structure and function. Journal of Cell Science 111:1433-1439.

Zurita, F., R. Jiménez, R. Díaz de la Guardia, and M. Burgos
1999 The relative rDNA content of a NOR determines its level of expression and its probability of becoming active. A sequential silver staining and *in situ* hybridization study. Chromosome Research 7:563-570.

Zurita, F., A. Sánchez, M. Burgos, R. Jiménez, and R. Díaz de la Guardia
1997 Interchromosomal, intercellular and interindividual variability of NORs studied with silver staining and *in situ* hybridization. Heredity 78:229-234.

ECOLOGICAL AND PHYLOGENETIC SIGNIFICANCE OF AFLP DNA DIVERSITY IN 4 SPECIES OF BLIND SUBTERRANEAN MOLE RATS (*SPALAX*) IN ISRAEL

EL SIGNIFICADO ECOLÓGICO Y FILOGENÉTICO DE DIVERSIDAD DE AFLP EN EL ADN DE 4 ESPECIES DE *SPALAX* EN ISRAEL

Andrei V. Polyakov, Alex Beharav, Tamar Krugman, Aaron Avivi, and Eviatar Nevo[1]

ABSTRACT

We examined 426 loci of Amplified Fragment Length Polymorphisms (AFLP) in Israeli *Spalax*, across coding and noncoding regions of genomes, along a gradient of increasing aridity. We compared and contrasted AFLP diversity with previous phylogenetic and ecological conclusions, based on other protein and DNA molecular markers in 114 subterranean blind mole rats representing 4 species of the *Spalax ehrenbergi* superspecies in Israel: *S. galili* ($2n$=52), *S. golani* ($2n$=54), *S. carmeli* ($2n$=58), and *S. judaei* ($2n$=60). The following results were indicated: (i) Of the 426 AFLP loci scored, 354 loci (=83.1%) proved polymorphic and 72 loci (=16.9%) were monomorphic in all 12 tested populations. (ii) A total of 321 (=90.7%) of 354 polymorphic loci varied significantly ($p < 0.05$) among populations, and 306 loci (86.4%) varied significantly ($p < 0.05$) between species, indicating highly significant *interpopulation* and *interspecies* differences in allele frequencies. (iii) Average polymorphism, P, was 29.3% (range, 19.7 – 41.1%) for populations and 50.8% for species, indicating highly significant differences between populations and species. (iv) The average value of genic diversity, He, was = 0.111 (range, 0.073 - 0.155) for populations and 0.170 for species, and was significantly different between populations. (v) Genetic differentiation between populations averaged Gst = 0.506 over all loci, indicating strong interpopulation divergence. (vi) Genetic distance between populations averaged D = 0.144 (range 0.018 – 0.257). (vii) A cluster analysis divided species into northern (*S. galili* and *S. golani*) and southern (*S. carmeli* and *S. judaei*) pairs. (viii) Discriminant analysis correctly classified 100% of the 114 animals to their species domains by diversity of 4 loci. (ix) AFLP diversity indices (P and He) are significantly correlated with biotic variables: *positively* correlated with plant cover and population density, but *negatively* correlated with territory size. (x) AFLP genetic distances are highly correlated with other molecular markers (allozyme, RAPD, mtDNA, and SSR). We conclude that AFLP diversity, spreading across *coding* and *noncoding* genomic regions, is subject to natural selection like other molecular

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markers and displays molecular ecological adaptive radiation caused by interacting biotic and abiotic environmental stresses.

Key words: Adaptive radiation, AFLP, ecological genetics, genetic diversity, mole rats, molecular adaptation, natural selection, *Spalax ehrenbergi*, speciation

RESUMEN

Examinamos 426 loci de AFLP (*Amplified Fragment Length Polymorphisms*) en regiones codificantes y no codificantes de los genomas, a lo largo de un gradiente de aridez creciente. Los patrones descubiertos con estos marcadores se comparan y contrastar con conclusiones filogenéticas y ecológicas previamente establecidas en base a otros marcadores moleculares proteicos y del ADN en 114 ratas topo ciegas que representan a cuatro especies de la superespecies *Spalax ehrenbergi* en Israel: *S. galili* (2n=52), *S. golani* (2n=54), *S. carmeli* (2n=58), y *S. judaei* (2n=60). Los resultados fueron los siguientes: (i) De los 426 loci examinados, 345 (83.1%) resultaron polimórficos y 72 loci (16.9%) fueron monomórficos en las 112 poblaciones examinadas. (ii) un total de 321 (90.7%) de los 354 loci polimórficos variarion significativamente ($p < 0.05$) entre poblaciones, y 306 loci (86.4%) variaron significativamente ($p < 0.05$) entre especies, indicando diferencias altamente significativas en frecuencias alélicas entre poblaciones y entre especies. (iii) El polimorfismo medio, *P*, fue 29.3% (rango, 19.7-41.1%) para las poblaciones y 50.8% para las especies, indicando diferencias altamente significativas entre poblaciones y especies. (iv) El valor medio de la diversidad génica, *He*, fue 0.111 (rango, 0.073 - 0.155) para las poblaciones y 0.170 para las especies, y fue significativamente diferente entre las poblaciones. (v) La diferenciación genética entre poblaciones promedió Gst = 0.506 entre todos los loci, indicando una importante divergencia interpoblacional. (vi) La distancia genética entre poblaciones fue en promedio *D* = 0.144 (rango 0.018 - 0.257). (vii) Un análisis de agrupamientos dividió las especies en un par en el norte (*S. galili* y *S. golani*) y uno en el sur (*S. carmeli* y *S. judaei*). (viii). Un análisis discriminante clasificó correctamente al 100% de los 114 individuos a sus dominios de especie basados en la diversidad de los cuatro loci. (ix) Los índices de diversidad de AFLP (*P* y *He*) están correlacionados significativamente con variables bióticas: positivamente con la cobertura vegetal y la densidad poblacional, pero negativamente con el tamaño del territorio. (x) Las distancias genéticas basadas en AFLP están altamente correlacionadas con las basadas en otros marcadores moleculares (alozimas, RAPD, ADNmit, y SSR). Concluimos que la diversidad en AFLP, tanto en regiones codificantes como no codificantes, está sujeta a la selección natural como otros marcadores moleculares y muestra una radiación adaptativa ecológica a nivel molecular causada por estrés interactivo de origen biótico y abiótico.

Palabras claves: Adaptación molecular, AFLP, diversidad genética, especiación, genética ecológica, radiación adaptativa, rata topo, selección natural, *Spalax ehrenbergi*

INTRODUCTION

The blind subterranean mole rat of the *Spalax ehrenbergi* superspecies (Rodentia, Spalacidae) ranges throughout the East Mediterranean region from southern Turkey to northern Egypt (Nevo, 1999; Nevo et al., 2001). It is one of the most extensively studied mammals in the wild in terms of its ecology, genetics, morphology, physiology, behavior, and evolution (see Nevo, 1991, 1999, and Nevo et al., 2001 and references therein). In this superspecies at least 12 allospecies have been described in the Near East including Israel (Nevo et al., 2001), Jordan (Nevo et al., 2000), and Turkey (Nevo et al., 1994a, 1994b, 1995). In Israel this species complex consists of 4 species, with diploid numbers $2n$=52, $2n$=54, $2n$=58, and $2n$=60 distributed parapatrically in 4 climatic regimes across minor southward and minor eastward transects of increasing aridity (Nevo, 1991; Nevo et al., 2001; Fig. 1). Based on molecular, genetic, cytological, behavioral, and ecological studies (see Nevo, 1991 and complete list of *Spalax* publications at http://evolution.haifa.ac.il), Nevo et al. (2001) assigned provisional species names to the 4 species in Israel: (1) *Spalax galili*, $2n$=52, distributed predominantly in the cool, humid Upper Galilee Mountains; (2) *Spalax golani*, $2n$=54, distributed in the cool, semi-dry Golan Heights; (3) *Spalax carmeli*, $2n$=58, ranging in the humid, warm Lower Galilee Mountains and central coastal plain; and (4) *Spalax judaei*, $2n$=60, ranging in warm-dry Samaria, Judea, and the warm, dry, southern coastal plain and northern Negev Desert (Fig. 1). Thus, the 4 chromosomal species are distributed across a major transect of increasing aridity southward from the Mediterranean to the Negev Desert; and a minor transect of increasing aridity from the Mediterranean Sea to the Golan Heights (Fig. 1). These species are young Pleistocene (Catzeflis et al., 1989), closely related allospecies at different stages of evolutionary divergence, occupying different climatic regimes; thus, they provide an excellent evolutionary model for the study of allopatric or peripatric speciation and climatic adaptive radiation (Nevo, 1999; Nevo et al., 2001).

Population genetic studies (Suzuki et al., 1987; Nevo et al., 1993, 1994a, 1999, 2001; Nevo et al., 1999, Reyes et al., 2003) indicated that the species complex in Israel consists of 2 major clades, the northern and older one consisting of the species pair *S. galili* ($2n$=52) and *S. golani* ($2n$=54), and the younger central and southern species pair *S. carmeli* ($2n$=58) and *S. judaei* ($2n$=60). These studies also indicated that there is little or no gene flow between *S. galili* and *S. golani*, whereas between these 2 northern species and *S. carmeli* and *S. judaei* there is evidence of some ongoing gene flow based on natural hybridization (Nevo & Bar El, l976; Nevo, 1985). DNA-DNA hybridization (Catzeflis et al., 1989) suggests that *S. golani* is the oldest species, originating 1.6 ± 0.30 million years ago (mya). The split between *S. golani* and *S. galili* occurred first, followed by the split between *S. carmeli* and *S. judaei*. The most recent speciation event in this species complex is that of the *S. judei* from *S. carmeli,* which was 0.2 ± 0.04 mya. Thus, the mole rat superspecies in Israel consists of 2 different species pairs, a northern and a southern, each representing a different stage of evolutionary divergence. The northern pair (*S. golani* and *S. galili*) is the older species pair (Lower Pleistocene), whereas the southern pair (*S. carmeli* and *S. judaei*) is younger (Upper Pleistocene).

Results from recent genetic studies on subterranean mammals (Nevo et al., 1994a,b, 1996, 1999; Ben-Shlomo et al., 1996; Reyes et al., 2003) as well as on wild cereals (Li et al., 2000, 2002b; Turpeinen et al., 2001; Fahima et al., 2002; Gupta et al., 2002; Sharma et al., 2003) show that systems tend to support the environmental adaptive theory of

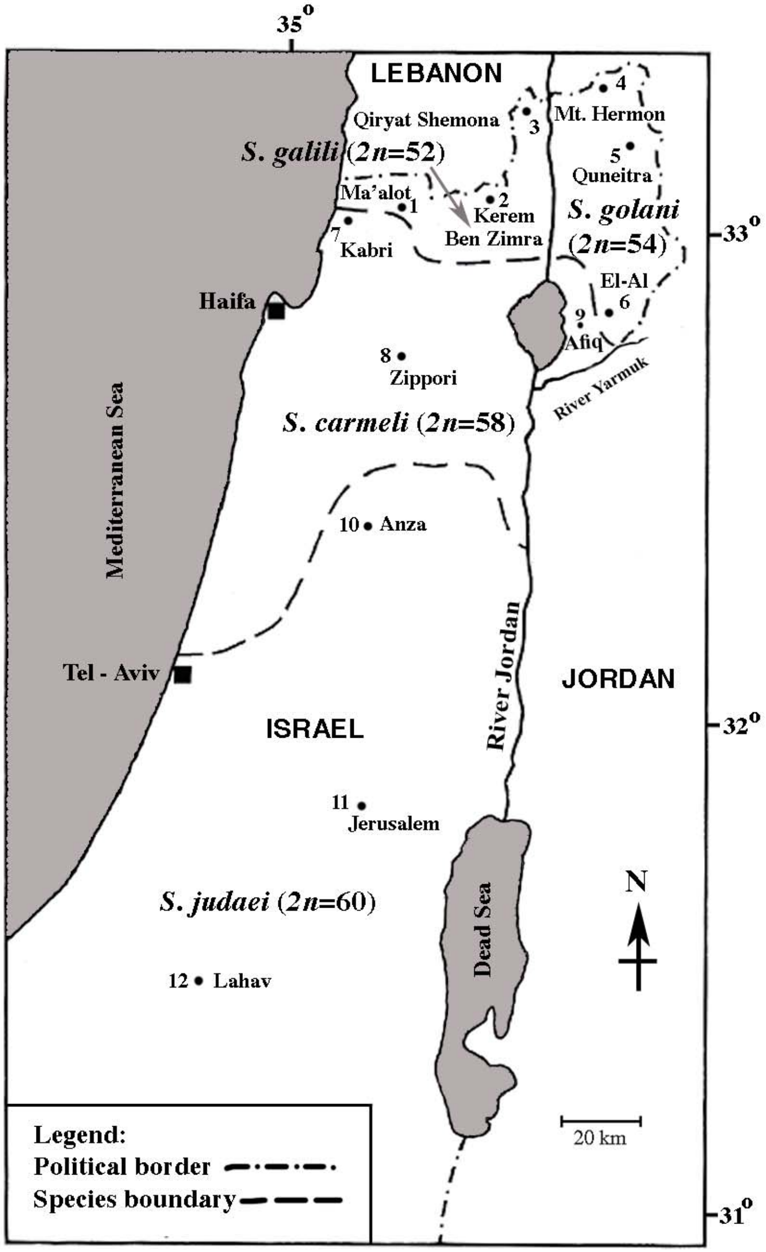

Figure 1. Geographic distribution of 12 populations of 4 species of blind mole rats of the *S. ehrenbergi* superspecies, in Israel, were analyzed in this study. Also shown are the ranges of the 4 species (dashed lines), *S. galili* (2n=52), *S. golani* (2n=54), *S. carmeli* (2n=58), and *S. judaei* (2n=60), across a gradient of increasing aridity towards the south. Numbers indicate sampling localities that also appear in Table 1.

genetic diversity, which hypothesizes that genetic diversity in nature is nonrandom and oriented by combinatorial abiotic and biotic environmental stresses (Nevo, 1988, 1998, 1999, 2001). A genetic diversity survey of *S. ehrenbergi*, analyzed by allozymes (Nevo et al., 1994a) revealed low-level polymorphism. Analysis of restriction fragment length polymorphisms (RFLP) revealed a higher level of polymorphism (Nevo, 1991; Ben-Shlomo and Nevo, 1993; Ben-Shlomo et al., 1996), and analysis of DNA fingerprinting (Nevo et al., 1996) and diversity evaluated by random amplified polymorphic DNA (RAPD) showed an even higher level of polymorphisms (Ben-Shlomo et al., 1996). The highest level of polymorphisms was obtained recently by analysis of microsatellite (SSR) markers (Karanth et al., 2004). Here, we analyzed the novel method of AFLP (Vos et al., 1995) in an attempt to compare and contrast genomic AFLP diversity with all previously studied protein and DNA markers. Our major question was: does AFLP diversity reflect similar or different environmental correlates as compared to all other protein and DNA markers? Likewise, while molecular markers are generally considered neutral, we indirectly explored their adaptive nature using environmental correlates. For the rationale of using this method see Nevo (1998).

Recent advances in molecular marker techniques have demonstrated that amplified fragment length polymorphism (AFLP) can generate large numbers of molecular markers without any previous knowledge of the genetic constitution of the genotypes under investigation (Vos et al., 1995). This method combines universal applicability with high powers of discrimination and reproducibility (Janssen et al., 1996; Savelkoul et al., 1999). The AFLP technique is a method by which a selection of restriction fragments of a total genomic digest is detected by amplification using PCR. It is a versatile method, able to detect the presence of restriction fragments in almost any DNA, regardless of its complexity. The technique allows efficient identification of DNA polymorphisms because large numbers of restriction fragments may be detected simultaneously. The fact that this method does not discriminate between coding and noncoding regions allows random sampling of the entire genome, which is also true for microsatellites. Compared with other DNA-based marker techniques, the AFLP has proven to be very powerful and efficient for generating high polymorphism, and it is used for genetic mapping, medical diagnostics, phylogenetic studies, and microbial typing in bacteria (Janssen et al., 1996), plants (Pakniyat et al., 1997; Thoquet et al., 2002; Peng et al., 2003), and animals (Ajmone-Marsan et al., 2002). We recently used it successfully in a microscale analysis of blind subterranean mole rats of the northern species *Spalax galili* (Polyakov et al., 2004).

The AFLP has several advantages compared to various other molecular typing methods including discriminatory power, flexibility, reproducibility, and production of clear banding patterns suitable for computerized analysis (Johannes et al., 1998). Previously, in most AFLP studies, radioactive AFLP was used for polymorphism detection. The use of radioactive compounds is laborious, expensive, and needs special laboratory equipment and protection. We improved the method by using fluorescently labeled primers detected by an automated sequence apparatus as an excellent alternative to radioactive AFLP (Satish et al., 2001). Here, we describe AFLP diversity and divergence in the 4 species of the *S. ehrenbergi* superspecies in an attempt to examine the phylogeny and ecological correlates of the superspecies in Israel. We demonstrate that phylogenetic trees created by AFLP polymorphism are consistent with our previous phylogenetic trees created by other protein, nuclear, and mitochondrial DNA markers. Moreover, our results, using AFLP, which represent both coding and

Table 1. Geographic and climatic data for 12 populations and 4 species of the *S. ehrenbergi* superspecies in Israel. Abbreviations as follows: Geographical: Ln = longitude (decimals), Lt = latitude (decimals), Al = Altitude (m); Climatic: Tm = mean annual temperature, Rn = mean annual rainfall (mm); Edaphic: So = soil type (1 = terra rossa, 2 = rendzina, 3 = basalt, 4 = loess); Biotic: Cv = Plant cover (%), Pl = climatic plant community (mole rats live only in open spaces or secondary habitats; 1 = tragacantic batha, 2 = marginal batha, 3 = live oak maquis of *Quercus calliprinos – Pistacia palaestina*, 4 = *Quercus ithaburensis – Styrax officinalis* park forest, 5 = *Ceratonia siliqua – Pistacia lentiscus* park forest); Dn = mole rat population density (animals per 10000 m^2); Te = territory size (m^2) (From Nevo et al., 1994a).

No.[a]	Species and Population	Type*	Ln	Lt	Al	Tm	Rn	So	Cv	Pl	Dn	Te
S. galili (2*n*=52)												
1	Maalot	NHZ	35.27	33	500	16.8	785	1	85	3	31	59
2	Kerem-Ben-Zimra	C	35.47	33.03	700	16.5	650	2	88	3	40	52
3	Qiryat-Shemona	M	35.57	33.22	187	19	655	1	90	5	23	52
S. golani (2*n*=54)												
4	Mt. Hermon	M	35.73	33.3	1300	12.4	1450	1	80	1	32	56
5	Quneitra	C	35.83	33.12	950	14.9	857	3	40	3	22	54
6	El-Al	NHZ	35.75	32.8	370	18.7	464	3	100	4	39	49
S. carmeli (2*n*=58)												
7	Kabri	NHZ	35.15	33.02	100	20	600	2	75	5	30	54
8	Zippori	C	35.28	32.74	250	18.5	500	2	75	4	26	44
9	Afiq	NHZ, M	35.70	32.77	325	18.8	460	3	70	4	17	47
S. judaei (2*n*=60)												
10	Anza	NHZ	35.22	32.35	400	18	630	2	65	3	22	74
11	Jerusalem	M	35.23	31.78	700	17.5	500	1	45	3	24	91
12	Lahav	C	34.87	31.38	400	18.8	303	4	20	2	15	92

[a] Population numbers as shown in Fig. 1- Map of Israel

* Type of population: C = central, M = marginal, NHZ = near hybrid zone.

noncoding genomic regions, show that blind mole rats of the *S. ehrenbergi* superspecies in Israel are subjected to natural selection, primarily climatic selection, eliminating alternative explanations, as we showed previously by using other molecular systems displaying molecular-ecological adaptive radiation.

MATERIALS AND METHODS

Species and Populations Tested

We examined AFLP diversity in 114 subterranean blind mole rats, 9-10 individuals from each of 12 populations of the *S. ehrenbergi* superspecies, comprising 4 species from Israel: *S. galili* ($2n$=52), *S. golani* ($2n$=54), *S. carmeli* ($2n$=58), and *S. judaei* ($2n$=60). The species sampled (i.e., populations and their ecogeographical backgrounds) appear in Table 1 and Fig. 1. Climatic data are from Amiran et al. (1970) and publications of the meteorological service of Israel. Full climate data were presented in Table 1 of Nevo et al., 1994a.

AFLP Procedure

Genomic DNA was extracted from each of the 114 individuals as described in Nevo et al. (1996). AFLP analysis was carried out in accordance with Vos et al. (1995) with modifications for an automated sequencer ALFexpress® (Pharmacia, Sweden) as described by Satish et al. (2001). Briefly, 500ng DNA was digested by *Eco*RI and *Mse*I and then ligated to *Eco*RI and *Mse*I double-stranded adapters. The digested and ligated DNA was then amplified by PCR (30 cycles) (Perkin-Elmer thermal cycler, PE-9700) using nonselective primers (Eco+A/Mse+C) in a volume of 20μl. The product was diluted 20-fold and only 5μl was used in subsequent selective PCR. The selective PCR was performed using Eco primers labeled at the 5′ end by Cy-5 (Genosys, Sigma). The optimal ratio between the primers was 1:2 (250nM of the labeled and 500nM non-labeled primers) in a 20μl PCR reaction. Primer combinations were chosen according to the resolution of the PCR product on a sequencing gel. The following 9 primer combinations were used for AFLP analysis: EcoACA/MseCGA; EcoACT/MseCCG;CGT;CTC;CGA EcoAGT/MseCCG;CGT;CTC;CGA, using sequencing gels on an ALFexpress automated sequencer at 1800V, 50mA, and 50W at 50°C for 5 hours. Product sizes were calculated by the ALFwin™ Fragment Analysis software using an ALF sizer (50-500kb) as an external marker.

Data Scoring and Statistical Analysis

AFLP bands were regarded as loci with alleles present (1) or absent (0). We scored reproducible bands in different samples across the gel and in multiple gels. The identification of 426 distinct and scorable bands (=loci) led to the construction of a 114 individuals x 426 loci data matrix, which was analyzed for diversity within and between populations or species. Results were analyzed using the program POPGENE version 1.31 (Yeh et al., 1999, http://www.ualberta.ca/~fyeh) as a dominant mode of inheritance in a diploid organism, assuming Hardy-Weinberg equilibrium. If there are some deviations from Hardy-Weinberg assumptions, the comparison between populations or species is still expected to be valid. Allele frequencies, polymorphism (*P*) at 5%, gene diversity (*He*), the degree of genetic differentiation among the subdivided populations relative to the total diversity (G_{ST}), and genetic distance coefficients (*D*) were calculated according to Nei (1973, 1978). A typical cluster scheme of the 12 populations and 4 species based on the calculated *D* values was constructed with *STATISTICA* (StatSoft, inc., version 6, 2001, http://www.statsoft.com), based on the unweighted pair group method with arithmetic averages (UPGMA), with bootstrapping 1000 times using the Tools for Population Genetic Analysis (TFPGA) program version 1.3 (Miller, 1997).

Discriminant analysis and Spearman rank correlation were conducted with SAS software (SAS Institute 1996). Discriminant analysis procedures were carried out as follows: 1. SAS procedure PROC STEPDISC, using STEPWISE option, was used to choose loci which were the best differentiating factors among the 12 populations and among the 4 species; 2. SAS procedure PROC NEIGHBOR, which is suitable for classification when the classes have radically non-normal distribution, was used for correct classification of animals into their respective populations or species, based on the loci chosen by PROC STEPDISC.

RESULTS

Pattern of Variation of AFLP Loci

Of the 426 AFLP loci scored, 354 loci (83.1%) showed polymorphism among the 114 *S. ehrenbergi* animals collected from 12 different geographic locations in Israel, while 72 loci (16.9%) were monomorphic in all 12 tested populations. χ^2-test for homogeneity of the allele frequencies (representing the proportion of individuals in a population or species that displayed the band in question) showed that a total of 321 (90.7%) loci and 306 loci (86.4%) out of the 354 polymorphic loci varied significantly ($p < 0.05$) among the 12 populations and among the 4 species, respectively (Table 2). These total proportions of significant loci far exceed the 5% level expected by chance (binomial test, $p < 0.0001$), indicating high significant interpopulation and interspecies differences in allele frequencies.

Only 6 alleles (1.7%) out of the 354 polymorphic loci were unique to 1 species, 2 for each of the 3 species: *S. galili*, *S. carmeli,* and *S. judaei*. The proportions of alleles that were divided into 6 categories based on their frequencies (Table 3) varied significantly between the species ($\chi^2 = 71.9$, *d.f.* = 15, $p < 0.001$). The proportion of monomorphic alleles was highest in *S. judaei*. The number of loci with allele frequencies between 0.75 - < 1 increased easterly from *S. galili* to *S. golani*, and from *S. carmeli* southward toward *S. judaei* in the Negev Desert, displaying twice the increase in frequency towards the drier region.

AFLP Genetic Diversity

A summary of the genetic diversity of the AFLP data is given in Table 4. For each population and species we calculated the percentage of polymorphic loci (*P*) and gene diversity (*He*) (Nei, 1973). The average value of *P* was 29.3% (range, 19.7-41.1%) for populations and 50.8% (range, 38.7-59.4%) for species. The level of polymorphism appeared to be marked and very significantly different among populations ($\chi^2 = 98.8$,

Table 2. Summary of single-locus χ^2 tests for homogeneity of allele frequencies of 354 polymorphic AFLP loci in 12 populations belonging to 4 species of *S. ehrenbergi* from Israel.

	Number of Loci	
Significance	Between Populations	Between Species
$P < 0.001$	274	211
$0.001 < P < 0.01$	33	59
$0.01 < P < 0.05$	14	36
Total $P < 0.05$	321	306
Total $P > 0.05$	33	33
Total Polymorphic Loci	354	354

Table 3. Number of AFLP alleles, across 354 polymorphic loci (= present alleles), in 4 species of *S. ehrenbergi* superspecies from Israel. Six categories are distinguished based on their frequencies.

	Frequency (*f*)					
Species	0[a]	>0-0.25	0.25-0.5	0.5-0.75	0.75-<1	1[a]
S. galili	36	70	32	83	47	86
S. golani	28	66	37	63	49	111
S. carmeli	17	81	54	79	39	84
S. judaei	45	55	34	35	41	144

[a] Frequency 0 or 1 indicates number of alleles that were monomorphic within a species.

Table 4. Summary of genetic diversity based on 426 AFLP loci, of 12 populations belonging to 4 species of the *S. ehrenbergi* superspecies in Israel.

No.[a]	Superspecies and Population	Sample Size (*N*)	Polymorphism (*P*_5%)[b]	Gene diversity (*He*)[c]
S. galili (2n=52)				
1	Maalot	10	27.5	0.104^{cde}
2	Kerem-Ben-Zimra	9	41.1	0.155^{a}
3	Qiryat-Shemona	9	31.0	0.123^{bc}
	Mean		33.2	0.127
	Overall	28	54.5	0.180^{b}
S. golani (2n=54)				
4	Mt. Hermon	10	27.2	0.107^{cd}
5	Quneitra	10	23.0	0.086^{ef}
6	El-Al	9	35.5	0.136^{ab}
	Mean		28.5	0.110
	Overall	29	50.5	0.168^{b}
S. carmeli (2n=58)				
7	Kabri	9	25.8	0.098^{de}
8	Zippori	10	39.0	0.136^{ab}
9	Afiq	9	32.9	0.132^{b}
	Mean		32.6	0.122
	Overall	28	59.4	0.207^{a}
S. judaei (2n=60)				
10	Anza	10	24.2	0.091^{def}
11	Jerusalem	10	25.1	0.091^{def}
12	Lahav	9	19.7	0.073^{f}
	Mean		23.0	0.085
	Overall	29	38.7	0.125^{c}

[a] = Population numbers as shown in Fig. 1 (Map of Israel)
[b] = Percentage of polymorphic loci 5%
[c] = Gene diversity, equivalent to the expected heterozygosity under panmixia (Nei 1973). Statistical differences (between populations and species) presented by different letters using the Waller-Duncan's k-ratio t test over all loci (SAS Institute, 1996) at $p < 0.05$.

d.f. = 11, $p < 0.0001$) and species ($\chi^2 = 39.7$, *d.f.* = 3, $p < 0.0001$). The average value of *He* was 0.111 (range, 0.073-0.155) for populations and 0.170 (range, 0.125-0.207) for species (Table 4). As noted above, a very significant interpopulation (analysis of variance over all loci: $F = 9.68$, *d.f.* = 11, 4675, $p < 0.0001$) and interspecies ($F = 18.1$, *d.f.* = 3, 1059, $p < 0.0001$) differences were recorded.

A relatively low value of diversity was obtained for all populations belonging to the southern species *S. judaei* ($2n$=60) and for the Quneitra population belonging to the northern species *S. golani* ($2n$=54) compared to that of populations belonging to the northern species *S. galili* ($2n$=52) and also to that of populations belonging to the central species *S. carmeli* ($2n$=58), the latter generally displayed a relatively high value of diversity (Table 4). The lowest values of diversity were obtained for the southern Lahav population (*S. judaei*), P = 19.7%, *He* = 0.073, while the highest values were obtained for the northern Kerem-Ben-Zimra population (*S. galili*), P = 41.1%, *He* = 0.155. The comparison from all data of the 4 species shows that diversity was significantly lowest in *S. judaei* (P = 38.7%, *He* = 0.125), increasing in the order *S. golani* (P = 50.5%, *He* = 0.168) < *S. galili* (P = 54.5%, *He* = 0.180) < *S. carmeli* (P = 59.4%, *He* = 0.207).

Genetic Differentiation Within and Among Subpopulations

The total gene diversity (H_T) of the subdivided populations was partitioned into the mean gene diversity within the populations (H_S) and the average gene diversity among populations ($D_{ST} = H_T - H_S$). Gene diversity between populations was expressed relative to total diversity as $G_{ST} = D_{ST} / H_T$ (Nei, 1987). We have used $G_{ST,}$ which is more appropriate for molecular data (Crow, 2004) rather than the near-equivalent F_{ST} (Wright, 1951), to emphasize that this method is intended for molecular data. The standard assumption is that G_{ST} measures the degree of subdivision independent of allele frequencies. Crow (2004) showed that this is indeed true, provided there is no selection or mutation and that migration, splitting, and fusion are independent of allele frequencies.

G_{ST} of the 354 polymorphic loci, resulting from such partitioning of the 12 populations, varied from 0.014 to 1.0 at a single locus with an average of 0.506 for all loci. According to Wright (1978), the range of 0.05-0.15 for G_{ST} may indicate moderate differentiation, while a 0.15-0.25 range may indicate great differentiation, and above 0.25 may indicate very great differentiation. Therefore, the present data showed low differentiation at only 1 locus, moderate differentiation at 27 loci, great differentiation at 25 loci, and very great differentiation at 301 loci. To test the significance of these results, we applied a permutation test by producing 1,000 randomized data sets using random permutations of the individual animal data in the various populations. The G_{ST} obtained from the randomized data sets of the permutation test averaged 0.146, ranging from 0.124–0.205. Thus, G_{ST} was lower for all 1,000 randomized data sets ($p < 0.001$) when compared to the mean of the real data. In other words, the partition of AFLP genetic diversity in the present study showed very great divergence among the 12 populations.

The G_{ST} of 354 polymorphic loci, resulting from such partitioning of the 4 species, varied from 0.002 to 1.0 at a single locus with an average of 0.302. The present data showed low differentiation at 35 loci, moderate differentiation at 116 loci, great differentiation at 76 loci, and very great differentiation at 127 loci. The G_{ST} obtained from 1,000 randomized data sets of the permutation test averaged 0.043, ranging from 0.033–0.084. Thus, G_{ST} was lower for all 1,000 randomized data sets ($p < 0.001$) when

Table 5. Coefficients of unbiased genetic distance (*D*, Nei, 1978) based on 426 AFLP loci, between 12 populations, belonging to 4 species of *S. ehrenbergi* in Israel.

a) Between populations

Species		*S. galili*			*S. golani*			*S. carmeli*			*S. judaei*		
	Population	1	2	3	4	5	6	7	8	9	10	11	12
S. galili 2n=52	1. Maalot	****											
	2. Kerem-Ben-Zimra	0.052	****										
	3. Qiryat-Shemona	0.036	0.043	****									
S. golani 2n=54	4. Mt. Hermon	0.142	0.110	0.137	****								
	5. Quneitra	0.166	0.132	0.160	0.018	****							
	6. El-Al	0.130	0.099	0.125	0.096	0.106	****						
S. carmeli 2n=58	7. Kabri	0.239	0.179	0.226	0.168	0.172	0.215	****					
	8. Zippori	0.208	0.144	0.203	0.144	0.154	0.185	0.073	****				
	9. Afiq	0.177	0.144	0.167	0.061	0.060	0.118	0.131	0.121	****			
S. judaei 2n=60	10. Anza	0.257	0.186	0.249	0.171	0.177	0.217	0.083	0.032	0.141	****		
	11. Jerusalem	0.240	0.176	0.235	0.159	0.169	0.205	0.081	0.039	0.132	0.027	****	
	12. Lahav	0.253	0.198	0.255	0.187	0.193	0.220	0.099	0.068	0.144	0.059	0.034	****

D: Mean = 0.144, Range = 0.018-0.257

Table 5 (continued).

(b) Between and within species (means from (a))

Species	*S. galili*	*S. golani*	*S. carmeli*	*S. judaei*
S. galili	0.044			
S. golani	0.133	0.073		
S. carmeli	0.187	0.142	0.108	
S. judaei	0.228	0.189	0.091	0.040

(c) Between species (pooled data)

Species	*S. galili*	*S. golani*	*S. carmeli*
S. galili	****		
S. golani	0.099	****	
S. carmeli	0.141	0.088	****
S. judaei	0.198	0.157	0.051

D: Mean = 0.122, Range = 0.051-0.198

compared to the mean of the real data. To conclude, we demonstrated that the partition of AFLP genetic diversity showed very great divergence among the 4 species as well as among the 12 populations. We will later show that this pattern is nonrandom and correlated with biotic environmental stress variation.

The total gene diversity (H_T) can easily be further extended to subdivisions of a population and is further subdivided into a number of subpopulations. In this case, H_S may be decomposed into gene diversities within and between subpopulations (H_C and D_{CS}, respectively). Therefore, $H_T = H_C + D_{CS} + D_{ST}$. The relative degree of gene differentiation attributable to subpopulations within populations can be measured by $G_{CS(T)} = D_{CS}/H_S$. (Nei, 1987, p.190). By analyzing our data as a 3-level hierarchical data set (species, populations, and individuals), the amounts of G_{ST} and $G_{CS(T)}$ were 0.320 and 0.273, respectively; i.e., the between-species, between populations within species, and between individuals within populations variance component accounted for 32.0, 27.3, and 40.7%, respectively, from the total variance.

Genetic Distance and Cluster Analysis

Coefficients of unbiased genetic distance (*D*; Nei, 1978) were calculated for paired comparisons of the 12 populations and the 4 species. The mean value of *D* derived from all populations paired was 0.144 (range, 0.018-0.257; Table 5a). The intraspecies comparisons between populations generally showed lower distance values than interspecies comparison (Table 5a, b). An exception was the intraspecies comparisons between populations belonging to *Spalax carmeli, 2n*=58, which displayed a higher mean distance (0.108) than interspecies comparison between populations belonging to the species *S. carmeli* and *S. judaei* (mean 0.091, Table 5b), possibly because of the relative isolation of the Afiq population. The highest mean genetic distance (*D* = 0.228)

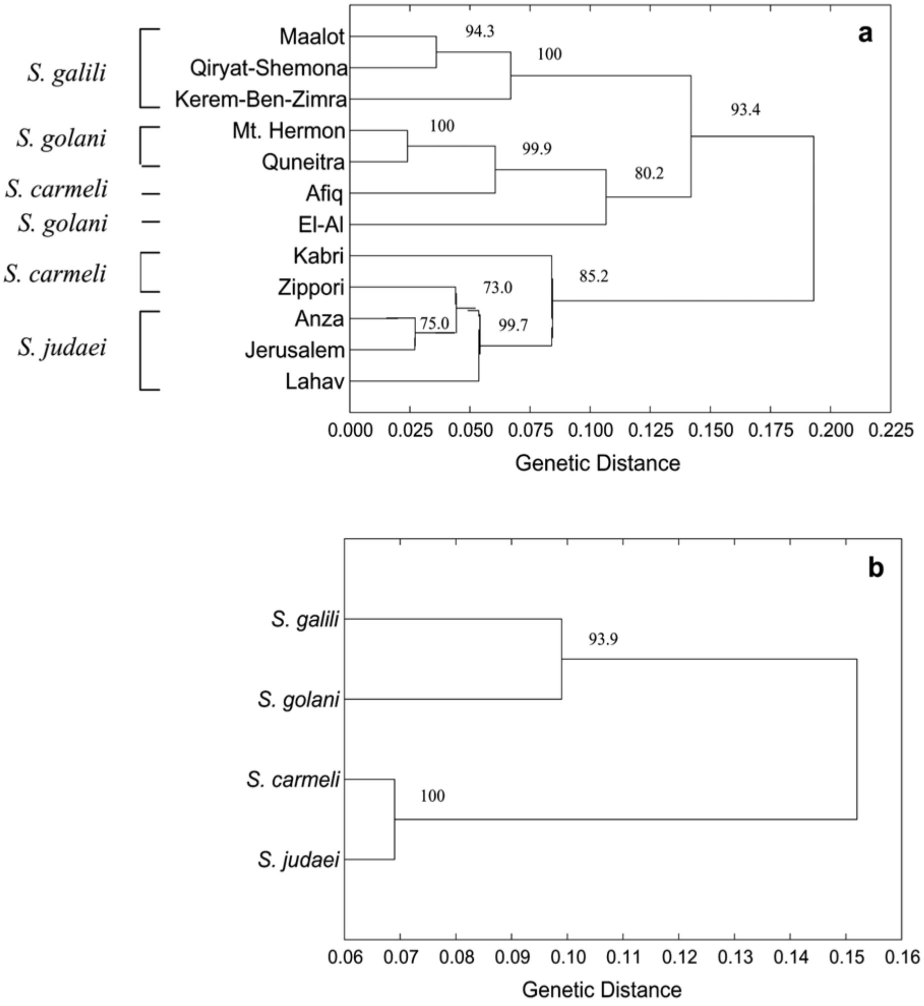

Figure 2. Dendrogram of the genetic relationships among 12 *S. ehrenbergi* populations (a) and among their 4 species (b) from Israel based on Nei's (1978) calculated, unbiased genetic distance obtained from 426 AFLP loci, using the UPGMA method. The numbers on the branches are percentage values from bootstrap analysis with 1,000 replications.

from the interspecies comparison was obtained between populations belonging to the species *S. galili* and *S. judaei,* descending in the order *S. golani* and *S. judaei* (average *D* = 0.189) > *S. galili* - *S. carmeli* (average *D* = 0.187) > *S. golani* - *S. carmeli* (average *D* = 0.142) > *S. galili* - *S. golani* (average *D* = 0.133) > *S. carmeli* - *S. judaei* (average *D* = 0.091).

To represent the relationship between populations, we applied cluster analysis (UPGMA) to generate a dendrogram based on *D* values. Two main clusters were evident (Fig. 2a). The first cluster (Fig. 2a) included all populations belonging to the northern species pair *S. galili* and *S. golani* (2*n*=52 and 2*n*=54), but also the Afiq population, which belongs to *S. carmeli* ($2n$=58). This cluster is divided into the *S. galili* and *S. golani* subclusters. Noteworthy, the Afiq population was clustered with *S. golani*. Afiq always proved to be genetically unique and separated from the other western populations of the species (see Nevo et al. 2001). The second cluster included all populations belonging to the species *S. carmeli* (2n=58) and *S. judaei* (2n=60), except the Afiq population, as was true in clusters based on RAPD markers (Ben-Shlomo et al., 1996, dendrogram not published) and SSR markers (Karanth et al., 2004). In conclusion, most populations were clustered as expected given their species ID, but Afiq may represent an incipiently speciating population (see Discussion).

The comparison of the 4 species derived from the overall data shows similar results. The highest genetic distance (0.198) was obtained between the species *S. galili* and *S. judaei* (Table 5c), descending in the order *S. golani* - *S. judaei* (D = 0.157) > *S. galili* - *S. carmeli* (D = 0.141) > *S. galili* - *S. golani* (D = 0.099) > *S. golani* - *S. carmeli* (D = 0.088) > *S. carmeli* - *S. judaei* (D = 0.051). Cluster analysis divided the species into 2 clusters (Fig 2b). The first cluster included the northern species pair, *S. galili* - *S. golani,* whereas the second cluster included the southern species pair, *S. carmeli* and *S. judaei*, as was obtained by all other molecular markers (see Discussion).

Discriminant Analysis

Discriminant analysis, which generally provides a means of statistically distinguishing among several populations with a large sample of genetic data, but a small sample of genotypes in each population (Beharav and Nevo, 2003), was performed. The STEPDISC procedure selected those loci that best differentiated the 12 populations and for the 4 species. The levels of correct classification of individual animals into their respective populations by 3, 5, 7, and 9 best differentiating loci were 35.8, 48.7, 56.2, and 74.7%, respectively (classification expected by chance, without variable selection: 100/12 = 8.33%). The levels of correct classification of individual animals into their respective species by 2, 3, and 4 best differentiating loci were 70.6, 94.8, and 100%, respectively (Percent correct classification, expected by chance: 100/4 = 25%). In other words, AFLP diversity is an excellent method for population and species classification.

Association with Ecogeographical Variables

Is AFLP diversity associated with the environment or is it distributed randomly?

Table 6. Spearman rank correlation coefficient between genetic indices based on 426 AFLP loci and 3 biotic variables (for symbols, see Table 1) in 12 populations of *S. ehrenbergi* from Israel.

Biotic Variable	Polymorphism	Gene Diversity
Plant cover (Cv)	0.771**	0.802**
Population density (Dn)	0.613*	0.648*
Territory size (Te)	-0.811**	-0.804**

*, **, statistically significant at $p < 0.05$ and $p < 0.01$, respectively

Analysis of Spearman rank correlation coefficients among genetic diversity based on 426 AFLP loci and 23 ecogeographical variables (part of the data in Table 1, full data in Table 1 of Nevo et al., 1994a) was conducted for the 12 populations of *S. ehrenbergi*. No significant correlation was obtained with any of the geographical, climatic, and water availability variables. However, significant correlations of both polymorphism (*P*) and gene diversity (*He*, mean overall loci) were obtained with the biotic variables (Table 6): positive correlation with plant cover (*Cv*) and with mole rat population density (*Dn*), but negative correlation with territory size (*Te*).

Association among Alleles

We estimated Spearman correlation coefficients for the allele frequencies of each of the 354 polymorphic loci among the different populations with the 23 ecogeographical variables: 760 (9.33%) out of the total matrix of 8,142 (= 354 x 23) correlations were

Table 7. Spearman rank correlation coefficient (r_s) among 5 molecular markers for gene diversity (a), mean number of alleles (b), and genetic distance values (c), in 12 populations of *S. ehrenbergi* superspecies from Israel.

a. Gene diversity (*N*[1] = 12)

	AFLP	Allozymes	RAPDs	mtDNA
Allozyme	-0.298			
RAPD	-0.504@	0.609*		
mtDNA	0.073	-0.355	0.209	
SSR	-0.368	0.782**	0.777**	-0.073

b. Mean number of alleles (*N* = 12)

	AFLP	Allozymes	RAPDs	mtDNA
Allozyme	-0.053			
RAPD	-0.443	0.191		
mtDNA	-0.028	-0.438	0.170	----
SSR	-0.182	0.442	0.557@	0.133

c. Genetic distance (*N* = 66)

	AFLP	Allozymes	RAPDs	mtDNA
Allozyme	0.488***			
RAPDs	0.606***	0.319**		
mtDNA	0.664***	0.622***	0.655***	
SSR	0.720***	0.483***	0.665***	0.460***

[1] Number of observations

Level of significance: @ = $p < 0.10$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

significant at $p < 0.05$. The total proportion of significant correlations (9.33%) exceeds the 5% level expected by chance (binomial test, $p < 0.0001$). In addition, to test the significance of these results, a Monte Carlo permutation test was applied by producing 1,000 randomized data sets by random permutations between the allele frequencies and the ecogeographical data. The total number of significant correlations obtained (by random permutations) ranged from 102–1,031, the median was 322, and the total number of significant correlations of 95% from the 1,000 randomized data sets was 637, i.e., significantly lower compared to that obtained from the real data (760).

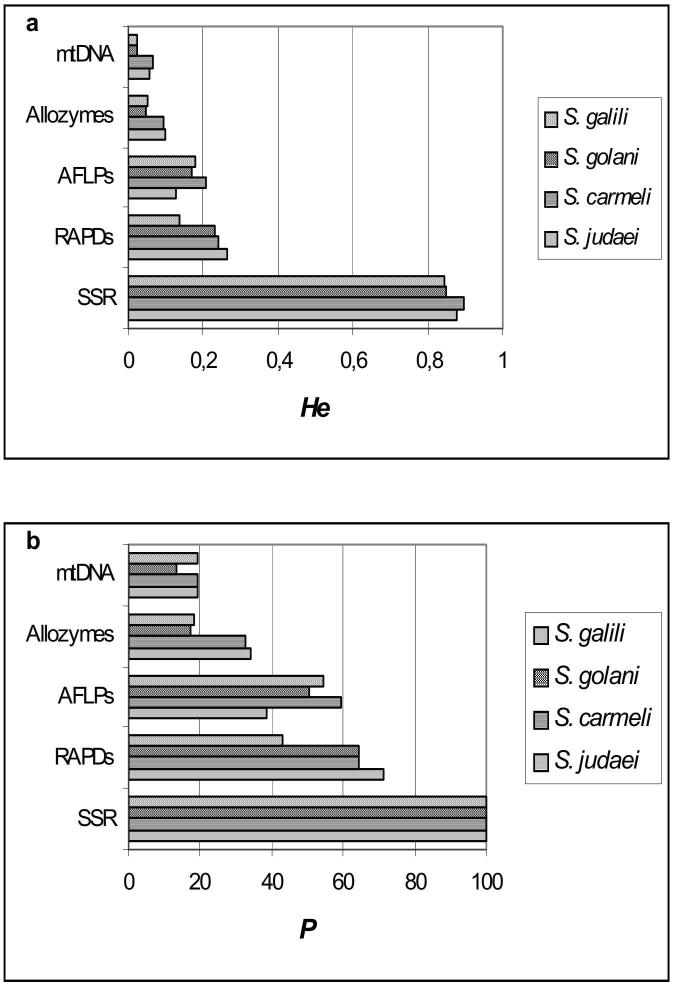

Figure 3. Nei's gene diversity (*He*) (a) and polymorphism (*P*) values (b) obtained by 5 molecular markers, in 4 species of the *S. ehrenbergi* superspecies in Israel.

Consequently, we suggest that allele frequencies are not randomly distributed among the different populations. By contrast, selection may be working on allele associations, suggesting linkage disequilibria.

Comparisons of Gene-Diversity Profile Revealed by AFLP and Other Molecular Markers

The genetic diversity profiles of the 12 populations of *S. ehrenbergi* superspecies obtained in this study with AFLP markers were compared to those obtained previously with allozyme markers (Nevo et al., 1994a), RAPD markers (Ben-Shlomo et al., 1996), mtDNA markers (Nevo et al., 1993), and also to those obtained recently with 19 SSR markers (Karanth et al., 2004). The results, presented in Table 7a, showed negative Spearman rank correlations between AFLPs with allozyme gene diversity (*He*) value (r_s = -0.298; not significant) as well as between AFLP with RAPD *He* values (r_s = -0.504; $p < 0.1$) and between AFLP with SSR *He* values (r_s = -0.378; not significant). The same trend was obtained with the mean number of allele (*A*) values (Table 7b). We preferred to compare *A*, but not polymorphism (*P*), since all the 19 SSR loci were found to be polymorphic (100% polymorphism) among all 12 populations as well as in the 4 species.

Note the relatively high *He* values obtained in the species *S. carmeli* and *S. judaei* compared with those of *S. galili* and *S. golani* by all the following markers: SSR, mtDNA, allozymes, and RAPDs (Fig. 3). Parallel genetic patterns of increasing diversities southward with increasing aridity toward the Negev Desert have been also shown for DNA fingerprints as well as for chiasmata frequency (Nevo et al., 1996). *S. carmeli* revealed the highest *He* value also for AFLP markers, but the lowest values for AFLP diversity were obtained for *S. judaei* (Fig. 3a, b). A lower *He* value was obtained also for *S. judaei* compared to that of *S. carmeli* for the mtDNA and SSR markers, but not for *P*.

Notably, a significant positive Spearman correlation was obtained between the genetic distance (*D*) values of the 12 populations by each pair of methods (Table 7c). The highest correlation was obtained between AFLP with SSR *D* values (r_s = 0.720; $p < 0.001$).

DISCUSSION

Relation between Genetic Diversity and Environment

Generally, the genetic diversity of fungi, plants, and animals is nonrandomly distributed in nature (Nevo, 1988, 1998, 2001). We show here that the distribution of genetic diversity among the 12 populations of the *Spalax ehrenbergi* superspecies in Israel, revealed by 354 AFLP polymorphic loci, which are spread across the genome at both coding and noncoding genomic regions, supports the environmental adaptive theory of genetic diversity, i.e., it is driven by natural selection. A total of 321 (90.7%) AFLP loci and 306 loci (86.4%) out of the 354 AFLP polymorphic loci varied significantly between the various populations and between the various species, respectively, significantly associated with biotic factors. By analyzing our data as a 3-level hierarchical data set, the between-species and between-populations-within-species variance components accounted for high values, 32.0 and 27.3%, respectively, from the total variance.

Importantly, the AFLP diversity is nonrandom both at the microscale analysis of blind mole rats (Polyakov et al., 2004) as well as at the macroscale analysis presented here. The microscale test of selection is a more powerful test, and its conclusion is also valid for the macroscale.

The general pattern of increase in genetic diversity with aridity and climatic unpredictability seen in previous studies (Nevo et al., 1994a, 1996; Ben-Shlomo et al., 1996) is only partly displayed here with AFLP diversity, increasing towards *S. carmeli* but declining in *S. judaei*. Notably, the number of loci with allele frequencies between 0.75 - < 1 increased eastward from *S. galili* to *S. golani*, and southward from *S. carmeli* toward *S. judaei* in the Negev Desert, displaying a double trend of increase in frequency towards the southern and eastern xeric regimes. A similar increase was demonstrated earlier in allozyme and DNA markers across Israel, both across macro- and microsites (Nevo et al., 2001).

Relatively high values of diversity were obtained for the populations of Zippori and Afiq belonging to the central species *S. carmeli*. However, relatively low values of diversity were obtained for the 3 populations belonging to the southern species *S. judaei* and also for the Kabri population belonging to *S. carmeli*. The reasoning for the lower levels was discussed at length in Huang et al. (2002). Apparently, under extreme ecological stresses, the level of partly regulatory systems declines, as shown in several systems such as barnacles (Nevo et al., 1978), wild barley (Huang et al., 2002), and others.

Here, we demonstrated that in *Spalax*, which is an outcrossing organism, AFLP, extending over both coding and noncoding genomic DNA, is subjected to natural climatic selection and represents, at least partly, adaptive structures. No overall linkage or hitchhiking explanations are relevant to outcrossers because of common recombination. Likewise, we can eliminate restriction of gene flow as the cause of genetic divergence because populations are continuously distributed in the main range of the species (Nevo et al., 1982). The notion of "junk DNA" for diverse molecular protein and DNA markers has been continuously challenged since the early l990s. The uniquely huge noncoding genome appears increasingly more associated with regulating genome dynamics (e.g., Lev-Maor et al., 2003; review in Li et al., 2002a, 2004).

Our results suggest that AFLP markers associated with biotic environmental factors, spreading across the coding and noncoding genome, are nonrandom and are correlated with genetic distances of other protein (allozymes) and DNA (RAPDs, SSRs fingerprints) molecular markers. The major result is that AFLP markers appear to represent adaptive structures largely subjected to natural selection.

Comparison with Other Markers

The results described here indicate that the AFLP show moderate levels of genetic diversity among the blind mole rats of Israel compared with other kinds of markers (Fig. 3a). Likewise, there is a parallel genetic pattern of higher genetic diversity in *S. carmeli* and *S. judaei* than in *S. galili* and *S. golani* as measured by SSR, mtDNA, allozymes, RAPDs (Fig 3b), DNA fingerprints, and chiasmata frequency (Nevo et al., 1996). The general trend of increase in genetic diversity from the wetter north to the drier south is less clearly observed in the present case of AFLPs (Fig. 3a), mainly due to the relatively low values of diversity that were obtained for populations belonging to the southern species *S. judaei.* Nevertheless, a weak trend does exist for *S. galili* to *S. carmeli* (Table 4), and genetic distances among populations are similarly correlated by all molecular markers, including AFLP (Table 7c).

Phylogenetic Relationships

The UPGMA tree derived from the AFLP data splits the blind mole rat populations into 2 major clusters (Fig. 2a). The first cluster represents populations belonging to the northern species pair, *S. galili* and *S. golani,* except for population no. 9 from Afiq, which belongs to *S. carmeli*, and the second cluster represents populations belonging to the southern species pair, *S. carmeli* and *S. judaei*. Previous studies with a range of markers such as allozymes (Nevo et al., 1994a), mtDNA (Nevo et al., 1993), SSR markers (Karanth et al., 2004), and DNA hybridization (Catzeflis et al., 1989) also identified the old pair of species, *S. galili* and *S. golani*, as distinct from the younger species pair, *S. carmeli* and *S. judaei* (see Beiles et al., 1984; Nevo et al., 2001).

Afiq: Active Incipient Speciation?

The present results suggest that there is very little active gene flow between the older and newer species pairs. The major exception is the Afiq population of *S. carmeli*. The AFLP data place this population with the populations at Mt. Hermon and Quneitra, which belong to *S. golani* (Fig. 2a). A number of other nuclear markers have also shown that the Afiq population is genetically more similar to *S. golani* than to *S. carmeli* (Nevo, 1991; Ben-Shlomo & Nevo, 1993; Ben-Shlomo et al., 1996). It should be noted that the Afiq population is bound by the Jordan River to the west and the Yarmuk River to the south (Fig. 1). These rivers might serve as natural barriers limiting gene flow between the Afiq population and the rest of *S. carmeli* in Israel west of the Jordan River. The existence of gene flow barriers between the Afiq population and other populations of the species *S. carmeli* is a possible explanation for the genetic difference among these populations (Ben-Shlomo et al., 1996). To the north there is no natural barrier that separates the Afiq population from *S. golani*. Afiq is south of the hybrid zone separating it from the southern El-Al populations of *S. golani*. The unique genetic structure of the Afiq population might be due to hybridization of *S. carmeli* with *S. golani*, in conjunction with reduced gene flow between the Afiq population and the rest of the *S. carmeli* species west of the Jordan River. A more plausible explanation, based on multiple studies summarized in Nevo et al. (2001), is that Afiq, which resides in the southern, warm, dry Golan Heights, shared by Afiq (2n=58) and El-Al (2n=54), is currently undergoing active incipient speciation, splitting from *S. carmeli* as a unique fifth "embryonic species" in the *Spalax ehrenbergi* superspecies and adaptively radiating in the unique warmer and drier climatic regime of the southern Golan. This hypothesis calls for further in-depth investigation, including critical mate-choice experiments, to assess the potential evolution of premating isolating mechanisms between *S. golani* to the north and *S. carmeli* to the south of the Golan Plateau.

Regional and Local Adaptive Radiation in the *Spalax ehrenbergi* Superspecies

In Israel climatic environmental variables co-vary: both rainfall and drought gradually decrease southwards. Concomitantly, temperature and evaporation increase southwards along a gradient of increased aridity from >1,000 mm annual rainfall in the north to 91 mm at the southern margin of *Spalax* distribution near Sede Boquer in the northern Negev Desert.

The sensitivity of AFLP polymorphism was dramatically indicated in the *S. galili* edaphic populations in the eastern Upper Galilee. We examined genomic diversity of anonymous regions across the genome, most probably including coding and noncoding amplified fragment length polymorphisms, at a microscale in the Upper Galilee Mountains in 20 individuals of the blind mole rat, *Spalax galili* (Polyakov et al., 2004). We compared 10 individuals from each of 2 nearby populations in Upper Galilee, separated by only a few dozen to hundreds of meters and living in 2 sharply contrasting ecologies: white chalk and rendzina soil with *Sarcopterium spinosum* and *Majorana syriaca*, versus black volcanic basalt soil with *Carlina hispanica-Psorelea bitominosa* and *Alhagi graecorum* plant formations. The microsite tested ranged in an area of less than 10,000 m^2. Of 729 AFLP loci, 433 (59.4%) were polymorphic, with 211 soil-unique alleles. Genetic polymorphism was significantly higher on the ecologically more xeric and stressful chalky rendzina soil than on the neighboring mesic basalt soil. This is a remarkable pattern for a mammal that is capable of dispersing between tens and hundreds of meters each generation (Nevo, 1999). These results cannot be explained by migration (which would exclude sharp genomic soil divergence). Natural selection is the only evolutionary adaptive force that can cause genetic divergence across the genome matching the sharp microscale ecological contrast. These results clearly suggest the sensitivity of AFLP polymorphism to environmental stresses (e.g., aridity) and mirrors, at a local scale, the pattern discussed in this paper at the regional scale across Israel between and within species. Similar dramatic genetic divergence due to sharp interslope ecological divergence was found in diverse model organisms across life in the "Evolution Canyon" models (Nevo, 2001).

In conclusion, natural selection appears to play an important role in maintaining adaptive genetic diversity at various coding and noncoding AFLP loci among mole rats, at both macro- and microgeographical scales, suggesting, together with other markers, that the nuclear and mitochondrial genomes alike are subject to natural selection in accordance with ecological stress. Additionally, this study demonstrated that AFLP might be used to determine the phylogenetic relationship between closely related species, as was previously shown by allozyme and DNA (both nuclear and mitochondrial) markers (Nevo et al., 2001).

ACKNOWLEDGMENTS

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LITERATURE CITED

Ajmone-Marsan, P., R. Negrini, E. Milanesi, R. Bozzi, I. J. Nijman, J. B. Buntjer, A. Valentini, and J. A. Lenstra
2002 Genetic distances within and across cattle breeds as indicated by biallelic AFLP markers. Animal Genetics 33:280-6.

Amiran D. H. K., J. Elster, M. Gilead, N. Rosenan, N. Kadmon, and U. Paran (eds.)
1970 Atlas of Israel. Second ed. Surveys of Israel Ministry of Labor. Elsevier, Jerusalem and Amsterdam. 298 pp.

Beharav, A. and E. Nevo
2003 Validation of discriminant analysis for genetic data. Genetica 119:259-267.

Beiles, A., G. Heth, and E. Nevo
1984 Origin and evolution of assortative mating in actively speciating mole rats. Theoretical Population Biology 26:265-270.

Ben-Shlomo, R., T. Fahima, and E. Nevo
1996 Random amplified polymorphic DNA of the *Spalax ehrenbergi* superspecies in Israel. Israel Journal of Zoology 42:317-326.

Ben-Shlomo, R., and E. Nevo
1993 Myosin heavy chain DNA polymorphisms of subterranean mole rats of the *Spalax ehrenbergi* superspecies in Israel. Genetics Selection Evolution 25:211-227.

Catzeflis, F. M., E. Nevo, J. E. Ahlquist, and C. G. Sibley
1989 Relationships of the chromosomal species in the Eurasian mole rats of the *Spalax ehrenbergi* group as determined by DNA-DNA hybridization, and an estimate of the spalacid-murid divergence time. Journal of Molecular Evolution 29:223-232.

Crow, J.F.
2004 Assessing population subdivisions. Pp. 35-42 in Evolutionary Theory and Processes: Modern Horizons. Papers in Honour of Eviatar Nevo (Wasser, S. P., ed.), Kluwer Academic Publishers, Dordrecht, The Netherlands.

Fahima, T., M. S. Roder, K. Wendehake, V. M. Kirzhner, and E. Nevo
2002 Microsatellite polymorphism in natural populations of wild emmer wheat, *Triticum dicoccoides,* in Israel. Theoretical and Applied Genetics 104:17-29.

Gupta, P. K., P. K. Sharma, H. S. Balyan, J. K. Roy, S. Sharma, A. Beharav, and E. Nevo
2002 Polymorphism at rDNA loci in barley and its relation with climatic variables. Theoretical and Applied Genetics 104:473-481.

Huang, Q., A. Beharav, Y. Li, V. Kirzhner, and E. Nevo
2002 Mosaic microecological differential stress causes adaptive microsatellite divergence in wild barley, *Hordeum spontaneum*, at Neve Yaar, Israel. Genome 45:1216-1229.

Janssen, P., G. Coopman, R. Huys, J. Swings, M. Bleeker, P. Vos, M. Zabeau, and K. Kersters
1996 Evaluation of the DNA fingerprinting method AFLP as a new tool in bacterial taxonomy. Microbiology 142:1881-1893.

Johannes, G. M., J. S. Koeleman, J. B. Dennis, H. M. S. Paul, and C. M. J. E. Vandenbroucke-Graul
1998 Comparison of amplified ribosomal DNA restriction analysis, random amplified polymorphic DNA analysis, and amplified fragment length polymorphism fingerprinting for identification of *Acinetobacter* genomic species and typing of *Acinetobacter baumannii*. Journal of Clinical Microbiology 9:2522-2529.

Karanth, P. K., A. Avivi, A. Beharav, and E. Nevo
2004 Microsatellite diversity in subterranean mole rats of the *Spalax ehrenbergi* superspecies populations in Israel: speciation and adaptation. Biological Journal of the Linnean Society 83:229-241.

Li, Y., T. Fahima, A. B. Korol, J. Peng, M. S. Roder, V. Kirzhner, A. Beiles, and E. Nevo
2000 Microsatellite diversity correlated with ecological-edaphic and genetic factors in three microsites of wild emmer wheat in North Israel. Molecular Biology and Evolution 17:851-862.

Li, Y. C., A. B. Korol, T. Fahima, A. Beiles, and E. Nevo
2002a Microsatellites: genomic distribution, putative functions and mutational mechanisms: a review. Molecular Ecology 12:2453-2465.

Li, Y. C., A. B. Korol, T. Fahima, and E. Nevo
2004 Microsatellites within genes: Structure, function, evolution. Molecular Biology and Evolution 21:991-1007.

Li, Y. C., M. S. Roder, T. Fahima, V. M. Kirzhner, A. Beiles, A. B. Korol, and E. Nevo
2002b Climatic effects on microsatellite diversity in wild emmer wheat (*Triticum dicoccoides*) at the Yehudiyya microsite, Israel. Heredity 89:127-132.

Miller, M. P.
1997 Tools for Population Genetic Analysis (TFPGA) version 1.3. A Windows program for the analysis of allozyme and molecular population genetic data. Northern Arizona University (http://herb.bio.nau.edu/~miller).

Nei, M.
1973 Analysis of gene diversity in subdivided populations. Proceedings of the National Academy of Sciences (U.S.A.) 70:3321-3323.

1978 Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583-590.

1987 Molecular Evolutionary Genetics. Columbia University Press, New York, New York, USA. 512 pp.

Nevo, E.

1985 Speciation in action and adaptation in subterranean mole rats: Patterns and theory. Bollettino di Zoologia 52:65-95.

1988 Genetic diversity in nature: patterns and theory. Evolutionary Biology 23:217-247.

1991 Evolutionary theory and processes of active speciation and adaptive radiation in subterranean mole rats, *Spalax ehrenbergi* superspecies in Israel. Evolutionary Biology 25:1-125.

1998 Molecular evolution and ecological stress at global, regional and local scales: The Israeli perspective. Journal of Experimental Zoology 282:95-119.

1999 Mosaic Evolution of Subterranean Mammals. Regression, Progression, and Global Convergence. Oxford University Press, New York, New York, USA. 413 pp.

2001 Evolution of genome-phenome diversity under environmental stress. Proceedings of the National Academy of Sciences (U.S.A.) 98:6233-6240.

Nevo, E., and H. Bar-El

1976 Hybridization and speciation in fossorial mole rats. Evolution 30:831-840.

Nevo, E., A. Beiles, and T. Spradling

1999 Molecular evolution of cytochrome b of subterranean mole rat, *Spalax ehrenbergi* superspecies, in Israel. Journal of Molecular Evolution 49:215-226.

Nevo, E., R. Ben-Shlomo, A. Beiles, Y. Ronin, S. Blum, and J. Hillel

1996 Genomic adaptive strategies: DNA fingerprinting reveal ecogenetic parallelism to allozymes, RAPDs, mitochondrial DNA, and chiasma frequency in the actively speciating mole rats in Israel. Pp. 55-70 in Gene Families: Structure, Function, Genetics and Evolution (Holmes, R. S., and H. A. Lim, eds.). World Scientific, Singapore.

Nevo, E., M. G. Filippucci, and A. Beiles

1994a Genetic polymorphisms in subterranean mammals *(Spalax ehrenbergi)* superspecies in the Near East revisited: Patterns and theory. Heredity 72:465-487.

Nevo, E, M. G. Filippucci, C. Redi, A. Korol, and A. Beiles
1994b Chromosomal speciation and adaptive radiation of mole rats in Asia Minor correlated with increased ecological stress. Proceedings of the National Academy of Sciences (U.S.A.) 91:8160-8164.

Nevo, E., M. G. Filippucci, C. Redi, S. Simson, G. Heth, and A. Beiles
1995 Karyotype and genetic evolution in speciation of subterranean mole rats of the genus *Spalax* in Turkey. Biological Journal of the Linnean Society 54:203-229.

Nevo, E., G. Heth, and A. Beiles
1982 Population structure and evolution in subterranean mole rats. Evolution 36:1283-1289.

Nevo, E., R. L. Honeycutt, H. Yonekawa, K. Nelson, and N. Hanzawa
1993 Mitochondrial DNA polymorphism in subterranean mole-rats of the *Spalax ehrenbergi* superspecies in Israel, and its peripheral isolates. Molecular Biology and Evolution 10:590-604.

Nevo, E., E. Ivanitskaya, and A. Beiles
2001 Adaptive Radiation of Blind Subterranean Mole Rats: Naming and Revisiting the Four Sibling Species of the *Spalax ehrenbergi superspecies* in Israel: *Spalax galili* (2n=52), *S. golani* (2n=54), *S. carmeli* (2n=58) and *S. judaei* (2n=60). Bachkhuys Publishers, Leiden, The Netherlands. 204 pp.

Nevo, E., E. Ivanitskaya, M. G. Filippucci, and A. Beiles
2000 Speciation and adaptive radiation of subterranean mole rats, *Spalax ehrenbergi* superspecies, in Jordan. Biological Journal of the Linnean Society 69:263-281.

Nevo, E., T. Shimony, and M. Libni
1978 Pollution selection of allozyme polymorphisms in barnacles. Experientia 34:1562-1564.

Pakniyat, H., W. Powell, E. Baird, L.L. Handley, D. Robinson, C. M. Sorimgeour, and E. Nevo
1997 AFLP variation in wild barley (*Hordeum spontaneum* C. Koch) with reference to salt tolerance and associated ecogeography. Genome 40:332-341

Peng, J. H., Y. I. Ronin, T. Fahima, M. S. Roder, Y. C. Li, E. Nevo and A. B. Korol
2003 Domestication quantitative trait loci in Triticum dicoccoides, the progenitor of wheat. Proceedings of the National Academy of Sciences (USA) 100:2489-2494

Polyakov, A., A. Beharav, A. Avivi, and E. Nevo
2004 Mammalian microevolution in action: aadaptive edaphic genomic divergence in blind subterranean mole rats. Proceedings of the Royal Society of London B (Supplement) 271:S156-S159, and online at (http://www.pubs.royalsoc.ac.uk/bio_let_homepage.shtml).

Reyes, A., E. Nevo, and C. Saccone
2003 DNA sequence variation in the mitochondrial control region of subterranean mole rats, *Spalax ehrenbergi* superspecies in Israel. Molecular Biology and Evolution 20:622-632.

SAS Institute Inc.
1996 SAS User Guide: Statistics. Version 6.09 SAS Institute Inc. Cary, North Carolina, USA.

Satish, N., T. Krugman, O. N. Vinogradova, E. Nevo, and Y. Kashi
2001 Genome evolution of the cyanobacterium *Nostoc linckia* under sharp microclimatic divergence at "Evolution Canyon," Israel. Microbial Ecology 42:306-316

Savelkoul, P. H. M., H. Aarts, J. M. de Haas, J. Dijkshoorn, L. B. Duim, M. Otsen, J. L. M. Rademaker, L. Schouls, and J. A. Lenstra
1999 Amplified-fragment length polymorphism analysis: the state of an art. Journal of Clinical Microbiology 37:3083-3091

Sharma, S., A. Beharav, H. S. Balyan, E. Nevo, and P. K. Gupta
2004 Ribosomal DNA polymorphism and its association with geographical and climatic variables in 27 wild barley populations from Jordan. Plant Science 166:467-477.

Suzuki, H., K. Moriwaki, and E. Nevo
1987 Ribosomal DNA (rDNA) spacer polymorphism in mole rats. Molecular Biology and Evolution 4:602-610.

Thoquet, P., M. Ghérardi, E. P. Journet, A. Kereszt, J. M. Ané, J. M. Prosperi, and T. Huguet
2002 The molecular genetic linkage map of the model legume *Medicago truncatula*: an essential tool for comparative legume genomics and the isolation of agronomically important genes. BMC Plant Biol. 2 (1) (online at http://www.biomedcentral.com/1471-2229/2/1).

Turpeinen, T., T. Tenhola, O. Manninen, E. Nevo, and E. Nissila
2001 Microsatellite diversity associated with ecological factors in *Hordeum spontaneum* populations in Israel. Molecular Ecology 10:1577-1591.

Vos, P., R. Hogers, M. Bleeker, M. Reijans, T. van de Lee, M. Hornes, A. Frijters, J. Pot, J. Peleman, M. Kuiper and M. Zabeau
1995 AFLP: a new technique for DNA fingerprinting. Nucleic Acids Research 23:4407-4414.

Wright, S.
1951 The genetical structure of populations. Annals of Eugenics 15: 323-354.

1978 Evolution and the Genetics of Populations. Vol. 4, Variability Within and Among Natural Populations. University of Chicago Press, Chicago, Illinois, USA. 580 pp.

Yeh F.C., R.-C. Yang, and T. Boyle
1999 POPGENE version 1.31. Microsoft Windows-based Freeware for Population Genetic Analysis. Quick user guide. University of Alberta, Edmonton, Alberta, Canada.

INTERSPECIFIC SCALING AND ONTOGENETIC GROWTH PATTERNS OF THE SKULL IN LIVING AND FOSSIL CTENOMYID AND OCTODONTID RODENTS (CAVIOMORPHA: OCTODONTOIDEA)

EFECTO DEL TAMAÑO ENTRE ESPECIES Y PATRÓN DE CRECIMIENTO ONTOGENÉTICO DEL CRÁNEO EN ROEDORES CTENÓMIDOS Y OCTODÓNTIDOS (CAVIOMORPHA: OCTODONTOIDEA)

Aldo I. Vassallo and Matías S. Mora

DEDICATION

This work is dedicated to the memory of Oliver Payne Pearson for his great contributions to increase our knowledge of North and South American mammals and his efforts to help the careers of his colleagues, especially young South American biologists.

ABSTRACT

We assessed the effect of size on skull attributes of ctenomyid and octodontid rodent species using an allometric approach. We focus on traits which have long been considered of relevance for tooth digging, such as the development of the mandibular angle and masseteric crest, and the robustness of incisors. Interspecific comparisons of adult specimens revealed important shape differences between *Ctenomys*, on one hand, and octodontid genera (except *Spalacopus* and, partly, *Aconaemys*) plus the early ctenomyid *Actenomys*, on the other. In addition, we found that larger *Ctenomys* species possess both proportionally broader lower jaws and more robust incisors. For these traits, the ontogenetic trajectories of the skull in the small *Ctenomys talarum* and large *C. australis* do not differ in either slope (allometric coefficient) or intercept. In this sense, our study clearly shows that evolutionary ontogenetic scaling was associated with skull shape variation within the limits of a single genus, *Ctenomys.* On the other hand, *C. australis* and the extinct *Actenomys*, which differ sharply in skull morphology and possibly in fossorial habits and ecological niche, differ significantly in the slope and/or intercept of their ontogenetic trajectories. This fact indicates the complexity of changes in development responsible for the departure from ontogenetic scaling in ancient and extant ctenomyines, in association with morphological diversification of the skull above the species level.

Key words: allometry, *Ctenomys,* ontogeny, Rodentia, skull

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RESUMEN

Se utilizó una aproximación alométrica para analizar el efecto del tamaño sobre caracteres craneanos en roedores octodóntidos y ctenómidos. Se enfatizó en aquellos caracteres considerados como adaptaciones a la excavación con los incisivos, tales como el desarrollo del ángulo mandibular, la cresta masetérica y la robustez de los incisivos. Las comparaciones interespecíficas, realizadas en base a especímenes adultos, revelaron importantes diferencias en la forma craneana entre *Ctenomys*, por un lado, y géneros octodóntidos (excepto *Spalacopus* y, parcialmente, *Aconaemys*) más el ctenomino extinto *Actenomys*, por el otro. Además, las especies de *Ctenomys* de mayor tamaño mostraron mandíbulas proporcionalmente más anchas e incisivos más robustos en sección transversal. Para estos caracteres, las trayectorias ontogenéticas del cráneo en la especie de pequeño tamaño *Ctenomys talarum* y en la de mayor tamaño *C. australis* no difirieron ni en la pendiente (coeficiente de alometría) ni en la intersección. En este sentido, el presente análisis muestra claramente que un crecimiento ontogenético evolutivo se asocia con la variación en la forma del cráneo dentro de los límites de un género, *Ctenomys*. En forma contrastante, *C. australis* y el extinto *Actenomys*, que difieren marcadamente en la morfología del cráneo y, posiblemente, en sus hábitos excavadores y nicho ecológico, difieren significativamente en la pendiente y/o en la intersección, de sus trayectorias ontogenéticas. Este hecho indica que, al comparar ctenominos primitivos y actuales, cambios complejos en el desarrollo produjeron un apartamiento del simple crecimiento ontogenético, en asociación con una diversificación morfológica del cráneo por sobre el nivel de especie.

Palabras clave: alometría, *Ctenomys,* ontogenia, Rodentia, cráneo

INTRODUCTION

Morphological adaptation usually produces changes in the relative proportions of body parts, resulting in enhanced functional performance relative to particular locomotor or feeding habits. The allometric approach, which deals with variation in particular body parts associated with variation of the overall size of organisms, has been a useful way to study adaptation in living and fossil lineages (Emerson and Bramble, 1993; Silva, 1998). Allometric relationships generally are interpreted as reflecting changes in physiological and structural requirements associated with changes in body size (Schmidt-Nielsen, 1991). It has been proposed that particular functional requirements associated, for example, with particular locomotor habits or behaviors exert selective pressures changing the "normal" proportions among body parts (Fairbairn, 1992). For example, a study of interspecific allometry of limb proportions in digging ctenomyid rodents (Casinos et al., 1993) showed that a particular locomotor activity can exert selective pressure on long bone design; by analyzing the diameter/length relationship, they showed that for a given diameter the corresponding length was relatively low. The position of fossil taxa in relation to the regression line calculated from living species allowed the authors to suggest a "morphocline," the plesiomorphic state of which would be represented by the fossil taxon, with long bone design similar to that of generalized, surface dwelling rodents (Figs. 1-4 in Casinos et al., 1993).

Rodent skulls exhibit some of the most specialized sets of traits associated with processing hard vegetal foods (Hanken and Hall, 1993; Satoh, 1997; Feldhamer et al., 1999). This includes extremely variable occlusal patterns of the cheek teeth, highly developed masseteric and pterygoid musculature (which acts within an advantageous mechanical context), and ever-growing upper and lower incisors, shared with the lagomorphs and some unrelated fossil taxa (example *Paedotherium*, Notoungulata) (Maynard-Smith and Savage, 1959; Woods, 1972; Butler, 1985; Wake, 1993; Koenigswald et al., 1994; Neveu and Gasc, 1999). Rodent incisors may represent exaptations for a broad array of non-feeding functions and behaviors, such as dam construction in beavers, colony defense in bathyergids, and tunnel excavation in several rodent groups. Besides the well-known positive allometry between rostral length and basicranium length for mammals in general (Radinsky, 1985), Vassallo (2000) recently showed a nearly isometric relationship between out-lever and in-lever arms of the masseteric musculature in caviomorph rodents, and hence the maintenance of a given mechanical relationship, in spite of substantial variation in size.

The sister taxa Ctenomyidae and Octodontidae (Rodentia: Caviomorpha) includes 8 living genera which have evolved a number of morphological, physiological, and behavioral adaptation to fossorial and subterranean habits (Pearson, 1959; Mares and Ojeda, 1982; Reig, 1986; Kohler et al., 2000; Gallardo and Kirsch, 2001; Olivares et al., 2004). Seven of these genera are grouped within the family Octodontidae, representing a diverse array of specializations to fossorial habits, from surface dwelling forms such as *Octodontomys gliroides*, to fully subterranean species such as *Spalacopus cyanus* (Reig, 1970; Pearson, 1984; Begall and Gallardo, 2000). In contrast, the remaining genus (*Ctenomys*, family Ctenomyidae) includes about 60 extant fully subterranean species (Reig, 1986; Reig et al., 1990; Lessa and Cook, 1998; Lacey et al., 2000). In addition, various ctenomyid fossil taxa add to the morphological diversity of the family (Reig and Quintana, 1992; Fernández et al., 2000; Verzi, 2002).

The lateral expansion of the angular process and masseteric crest of the mandible, which are indicators of masseter development, and a greater cross sectional area of the incisors are two traits considered to be key adaptations for tooth digging in subterranean ctenomyids (Verzi, 1994, 2002; Fernandez et al., 2000; Mora et al., 2003). A strong masseteric musculature produces great in-forces which, in turn, result in out-forces at the tip of incisors sufficient for breaking hard soils (Hildebrand, 1985; Lessa, 1990; Vassallo, 1998; Stein, 2000). On the other hand, the cross sectional area of the incisors is correlated with resistance to shearing and bending stress, which is of importance in particular feeding habits and digging behaviors (Biknevicius et al, 1996; Bacigalupe et al, 2002; Mora et al; 2003). Interspecific morphological analysis and allometric studies on adult specimens (Verzi, 1994, 2002; Fernández et al., 2000; Mora 2001; Olivares, 2001; Mora et al., 2003) has demonstrated considerable variation in skull shape among living and early ctenomyids. However, no studies have integrated neontological variation in skull shape among taxa to evolutionary changes in the ontogeny. The integration of these 2 data sets is crucial to our understanding of morphological evolution within the highly diverse Octodontidae and Ctenomyidae. Here, we analyze interspecific scaling, and postnatal intraspecific growth pattern of skull traits having important functional and ecological correlates, such as the angular process of the mandible and the cross sectional area of the incisors, to assess possible ontogenetic changes underlying the shape differences present among living and fossil taxa. Specifically, we investigate the evolution of ontogenetic trajectories at 2 different hierarchical levels: interspecific variation among extant species within the genus *Ctenomys*, and inter-generic variation between this genus and the ancestral ctenomyine *Actenomys*.

MATERIAL AND METHODS

Interspecific Scaling Relations

The analysis presented here was based on skulls of 164 adult specimens of 21 species of *Ctenomys* (*C. argentinus, C. australis, C. azarae, C. boliviensis, C. bonettoi, C. dorbignyi, C. haigi, C. latro, C. leucodon, C. magellanicus, C. mendocinus, C. occultus, C. opimus, C. perrensi, C. porteousi, C. pundti, C. rionegrensis, C. roigi, C. talarum, C. tuconax, C. tucumanus*); 15 adult specimens of *Octodon* (7 *O. bridgesi* and 8 *O. degus*); 7 adult specimens of *Spalacopus cyanus*; 2 adult specimens of *Aconaemys sagei*; and 6 adult specimens of *Octodontomys gliroides*. Five well-preserved adult specimens of the Pliocene genus *Actenomys* were also included. The following linear measurements were taken using a digital caliper (to the nearest 0.01 mm): upper incisor width and thickness; mandibular width across the masseteric crests; basicranium axis length (see Fig. 1 in Mora et al., 2003). Incisor cross section, as a measure of resistance to shearing and bending stress, was calculated according to Biknevicius et al. (1996). The basicranium axis length (length of basioccipital plus basisphenoid) was used as a conservative measure of size that changes little when other skull characters do change markedly (Radinsky, 1985). A detailed list of specimens and localities is provided in the appendix.

Ontogenetic Sequences of *Ctenomys*

The analysis of ontogenetic growth pattern was based on skulls of 16 adults and 38 juvenile and subadult specimens (*Ctenomys australis*) and 22 adults and 49 juvenile and subadult specimens (*Ctenomys talarum*) (see "Specimens Examined"). Individuals were collected at Necochea, Buenos Aires Province, Argentina, during ecological censuses, mainly in 1987-1988. We recorded the upper incisor width and thickness, mandibular width across the masseteric crests, condylo-incisor length (i.e., the distance between the jaw condyle and the tip of the lower incisor, as a measure of out-lever arm of jaw adductor muscles), mandibular height at the level of m1, and basicranium axis length using a digital caliper (to the nearest 0.01 mm). In spite of significant sexual body size dimorphism (Malizia et al., 1991) no significant differences were detected between the growth curves of males and females (neither the allometric coefficient nor the y-intercept) when these skull traits were "standardized" against size (basicranium length); consequently, we pooled sexes in subsequent analysis.

Ontogenetic Sequences of *Actenomys*

Analyses were based on 21 lower jaws ranging from small, presumably newborn individuals, to adult specimens. Individuals came from the collection of Museo de Ciencias Naturales "Lorenzo Scaglia", Mar del Plata, Argentina (see appendix). The following measurements were taken using a digital caliper (to the nearest 0.01 mm): condylo-incisor length, lower incisor width and thickness, mandibular width across the masseteric crests. In most cases, mandibles were the only fragment present or the skull was partially or totally destroyed. Hence, we used mandibular height at the level of m1 as a measure of size increase during ontogeny (instead of basicranium length); this should serve as a good proxy for size, as basicranium length and mandibular height in *Ctenomys australis* are significantly correlated ($r = 0.81$, $t = 6.70$, $p < 0.001$).

Allometric Analyses

For the purpose of both interspecific and ontogenetic analyses, linear cranial measurements were $\log_{10}$ transformed. Bivariate equations were calculated as reduced major axis Model II regressions because neither variable is considered independent (i.e., there was error associated with the measurements of both x and y) and it is the structural relationship between the 2 variables that is required. The slope, the intercept, and their respective confidence intervals were calculated according to the computation method provided by Legendre and Legendre (1998; see also Sokal and Rohlf, 1981). Because of the high correlation between the skull variables analyzed and basicranium axis length, similar results were obtained with Model I (least squares) regression. We tested slopes and elevation with analysis of covariance (ANCOVA; Zar, 1984).

For our analysis of interspecific scaling relations the traditional allometric approach fails to account for non-independence of taxa (Harvey and Pagel, 1991), so we also analyzed the skull measurements using phylogenetically independent contrasts (Felsenstein, 1985). Log_{10} data were converted to phylogenetically independent standardized contrasts using the PDTREE module of the phylogenetic diversity program (PDAP) version 5.0 (Garland et al., 1993). Standardization tests in PDTREE indicated that Grafen's branch length transformation (Grafen, 1992) was the appropriate method for assigning arbitrary branch lengths (Garland et al., 1992). This method assumes a gradual Brownian motion model of evolution, and the height of each node is proportional to the number of species derived from it. Slopes, confidence intervals, and other regression statistics were obtained from PDTREE. No complete phylogeny of *Ctenomys* species exists, so we combined partial phylogenies of Cook and Lessa (1998), Lessa and Cook (1998), and Ortells and Barrantes (1994), all based on molecular evidence, to obtain the phylogenetic tree used in PDTREE.

RESULTS

Interspecific Scaling

Across 21 species of *Ctenomys*, the fossil ctenomyid *Actenomys*, and 5 species of octodontid rodents, both mandibular width and incisor cross section were significantly and positively associated with basicranium length (Fig. 1). In *Ctenomys*, the mandibular width across the masseteric crest, as a measure of masseter development, increases with positive allometry (allometric coefficient = 1.28 [95% C.I.: 1.22-1.36]) with respect to basicranium length (Table 1; Fig. 1A). Larger *Ctenomys* species thus possess proportionally broader lower jaws. Results obtained by the method of phylogenetically independent contrasts for continuous variables did not differ from those obtained by traditional reduced major axis regression (allometric coefficient = 1.30 [95% C.I.: 1.04-1.56], $N = 20$ contrasts; Fig. 2A), although the 95% confidence interval was broader for independent contrasts. The analysis of the effect of size on skull allometry was precluded in the Octodontidae because the genera within this taxa show limited

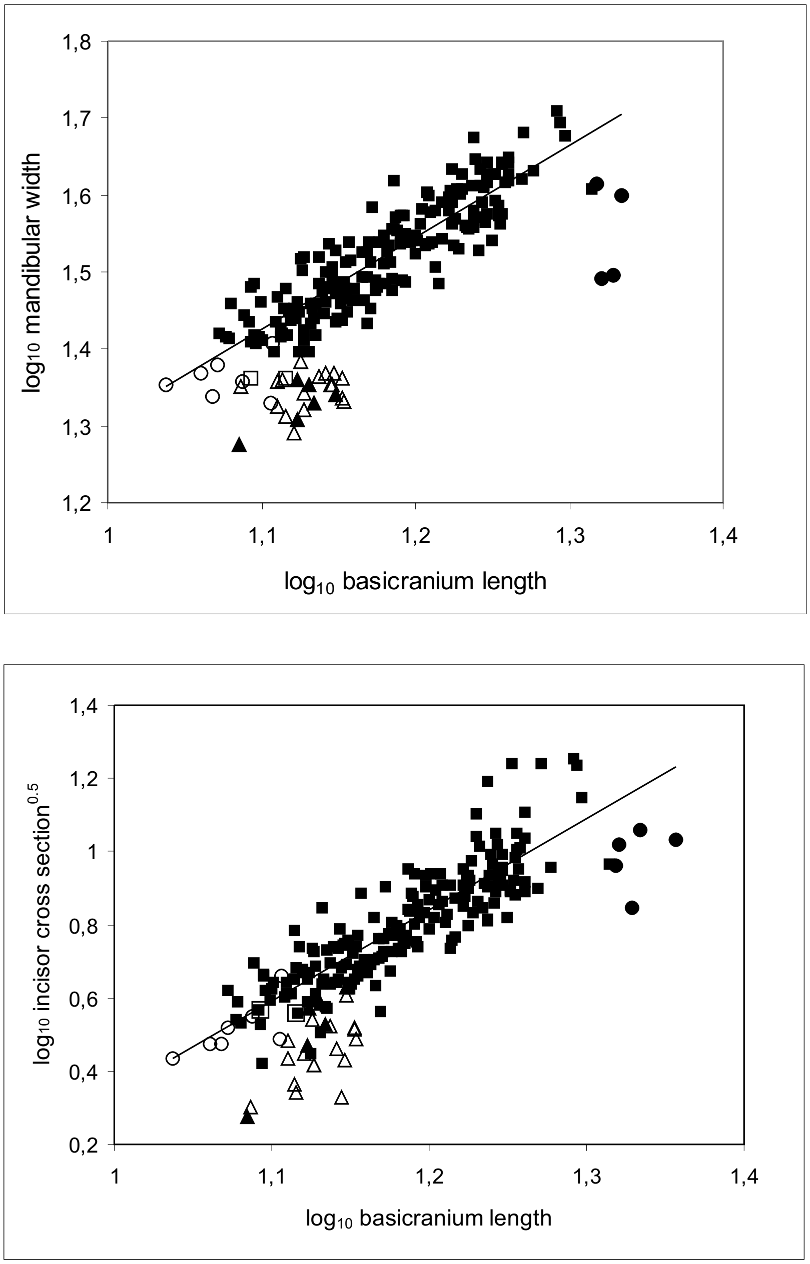

Figure 1. Graph of logarithmic coordinates of skull measurements in octodontoid rodents. Solid squares, *Ctenomys*; open squares, *Aconaemys sagei*; solid triangles, *Octodontomys gliroides*; open triangles, genus *Octodon*; open circles, *Spalacopus* cyanus; solid circles, Pliocene fossile ctenomyine *Actenomys*. A: mandibular width vs. basicranium length; B: incisor cross section vs. basicranium length. Regression line fitted only for *Ctenomys*.

Table 1.- Allometric equations ($y=axb$; Model II regression) of skull variables calculated for adult specimens of 21 *Ctenomys* species differing in body size (see Methods and "Specimens Examined"), and ontogenies of *C. australis*, *C. talarum*, and the early Pliocene ctenomyine *Actenomys*. Abbreviations: BAS=basicranium axis length; HMC=height of the mandibular corpus at the level of m1. All variables are $\log_{10}$ transformed.

	Regression Equation	*r*	95% Confidence intervals	
			b	*a*
Ctenomys adults				
BAS/mandibular width	y= 0.18x1.28	0.88	1.22 – 1.36	0.07 – 0.30
BAS/incisor cross section$^{0.5}$	y= -1.55x1.26	0.83	1.17 – 1.36	-1.41– -1.69
C. australis ontogeny				
BAS/mandibular width	y= -0.37x1.74	0.88	1.61 –1.88	-0.66 – -0.09
BAS/incisor cross section$^{0.5}$	y= -0.97x1.32	0.95	1.25 – 1.39	-1.10 – -0.83
C. talarum ontogeny				
BAS/mandibular width	y= -0.41x1.61	0.97	1.55 – 1.66	-0.52 – -0.31
BAS/incisor cross section$^{0.5}$	y= -0.85x1.20	0.98	1.16 – 1.23	-0.92 – -0.80
Actenomys ontogeny				
HMC/mandibular width	y= 0.37x1.20	0.87	0.99 – 1.45	0.06 – 0.69
HMC/incisor cross section$^{0.5}$	y= -0.71x0.99	0.93	0.87 – 1.14	-0.91– -0.52
HMC/condyle-incisor length	y= 0.59x1.03	0.96	0.88 – 1.09	0.44 – 0.75
C. australis ontogeny				
HMC/mandibular width	y= 0.38x1.15	0.98	1.00 – 1.25	0.29 – 0.47
HMC/incisor cross section$^{0.5}$	y= -1.29x1.58	0.98	1.49 – 1.68	-1.42 – -1.17
HMC/condyle-incisor length	y= 0.29x1.17	0.97	1.09 – 1.26	0.19 – 0.40

variation in overall size. However, it is clear that, with the exception of the subterranean *Spalacopus*, octodontine species fall below the trend for *Ctenomys* species (Fig. 1A). This is also the case for the Pliocene genus *Actenomys*.

Under the hypothesis of geometric similarity (Schmidt-Nielsen, 1991), the $\log_{10}$ square root of incisor cross section must scale to $\log_{10}$ basicranium axis length with an exponent of 1 (i.e., isometry). We found a positive allometric pattern for this relationship (allometric coefficient = 1.26 [95% C.I.: 1.17-1.36]), suggesting that larger *Ctenomys* species have proportionally more robust incisors (Table 1; Fig 1B; Fig. 3). Results obtained by the method of phylogenetically independent contrasts for continuous variables yielded a similar allometric pattern, although the allometric coefficient was

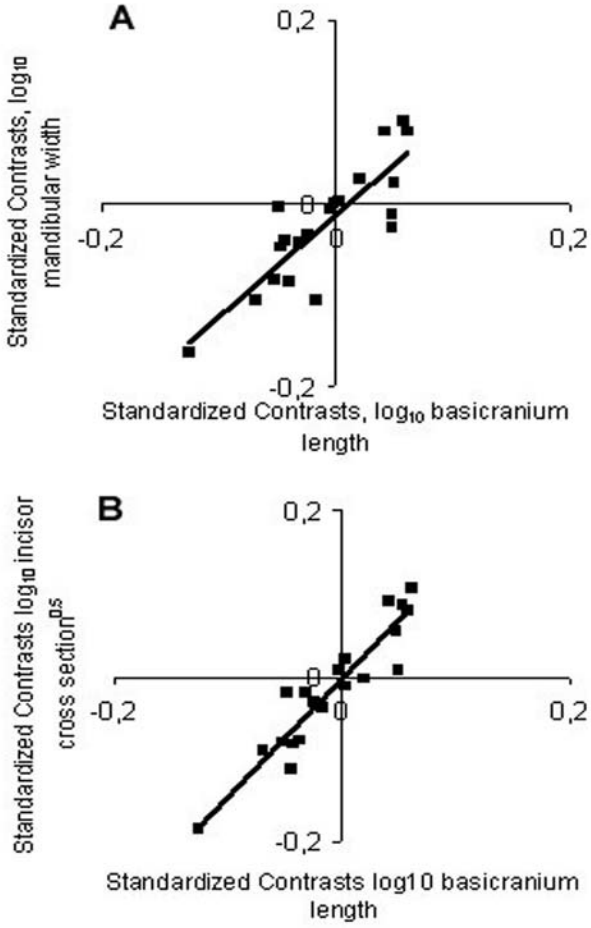

Figure 2. Relationships of the standardized contrasts of mandibular width (A) and incisor cross section (B) vs. basicranium length in species of *Ctenomys* differing in body size.

greater than that obtained by reduced major axis regression (allometric coefficient = 1.37 [95% C.I.: 1.18-1.57]) , number of contrasts = 20; Fig. 2B). Once again, octodontine taxa (except *Spalacopus* and *Aconaemys*) and *Actenomys* fall below the regression line for *Ctenomys* (Fig. 1B).

Ontogenetic Scaling

Across the ontogenetic sequences of *Ctenomys talarum* and *C. australis*, both mandibular width and incisor cross section were significantly and positively associated with basicranium axis length. For both species, mandibular width grows allometrically (Table 1; Fig. 4A; Fig. 5) reflecting the development, and strengthening, of the jaw and masseteric musculature during ontogeny. The cross sectional area of incisors also

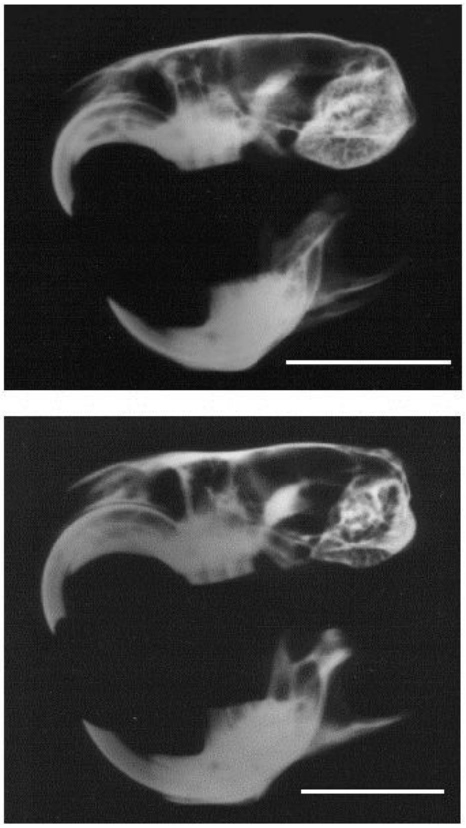

Figure 3. X-ray lateral view of the skull of *Ctenomys bonettoi* (above body weight 100 g) and *C. tucumanus* (below; body weight 240 g) showing interspecific differences in incisor robustness due to positive allometry of incisor cross section vs. skull size. Scale bar = 2 cm.

grows allometrically in both species (Table 1; Fig. 4B), also reflecting the strengthening of incisors to manage bending and shearing stresses. For these 2 traits, the allometric coefficients were slightly greater in the larger *C. australis*. Nonetheless, the confidence intervals for both the slope and y-intercept overlap broadly between the species. An ANCOVA revealed no significant differences between the slopes ($F = 2.17$, *d.f.* = 121, $p > 0.1$; $F = 1.08$, *d.f.* = 121, $p > 0.25$; incisor cross section and mandibular width, respectively) or elevations ($F = 0.26$, *d.f.* =122, $p > 0.25$; $F = 1.14$, *d.f.* = 122, $p > 0.25$; incisor cross section and mandibular width, respectively) of *C. talarum* and *C. australis* growth curves.

For the skull traits we studied, the ontogenetic pattern of growth of the extant *Ctenomys australis* and the Pliocene ctenomyine *Actenomys* (estimated mass 1300 g.; Fernández et al., 2000) differs largely, reflecting evolutionary changes in their ontogenetic trajectories (Fig. 6). The height of the mandibular corpus at the level of m1 was used as an indicator of overall size increase because the basicranium was

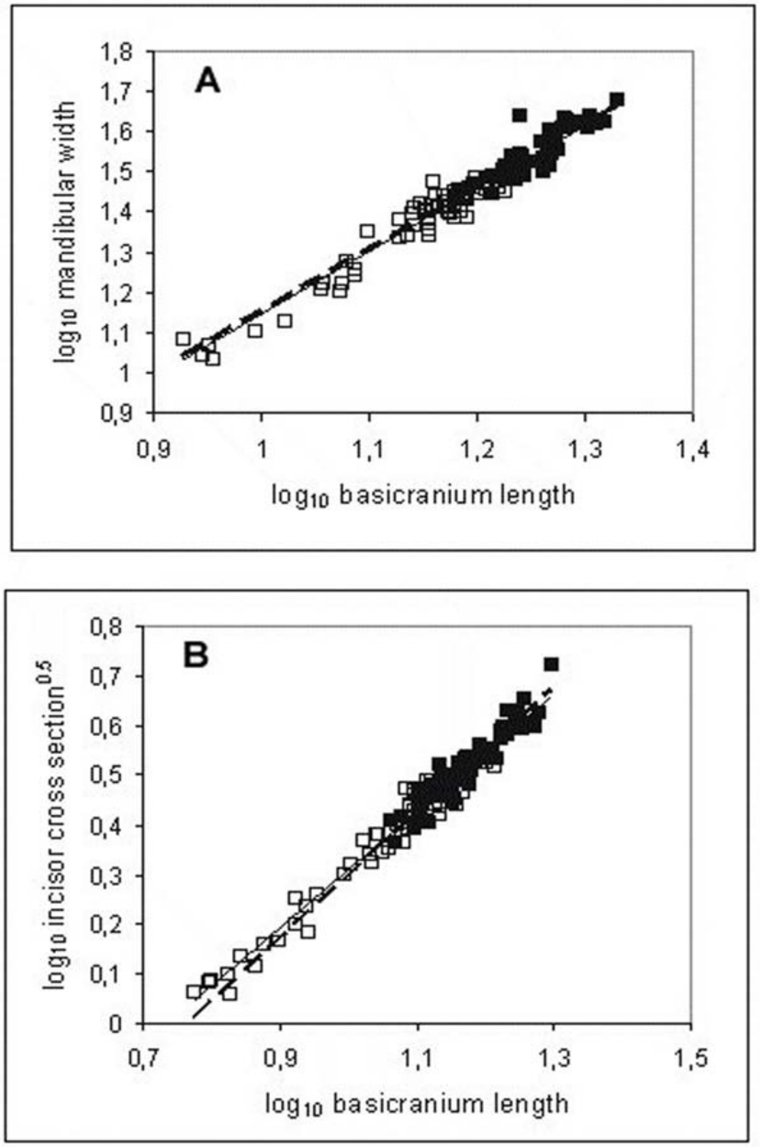

Figure 4. Graph of logarithmic coordinates of skull measurements in ontogenies of 2 *Ctenomys* species differing in body size. Open squares, solid line: *Ctenomys talarum*; adult body weight 150 g; solid squares, broken line: *C. australis*; adult body weight 400 g. A: mandibular width vs. basicranium length; B: incisor cross section vs. basicranium length.

absent or partly destroyed in most fossil specimens. For the skull trait mandibular width across the masseteric crest, the allometric coefficient calculated for *Actenomys* was slightly greater than that of *Ctenomys* (Table 1). The values of *Actenomys* fall below those measured in the living species (Fig. 6A). While the ANCOVA revealed

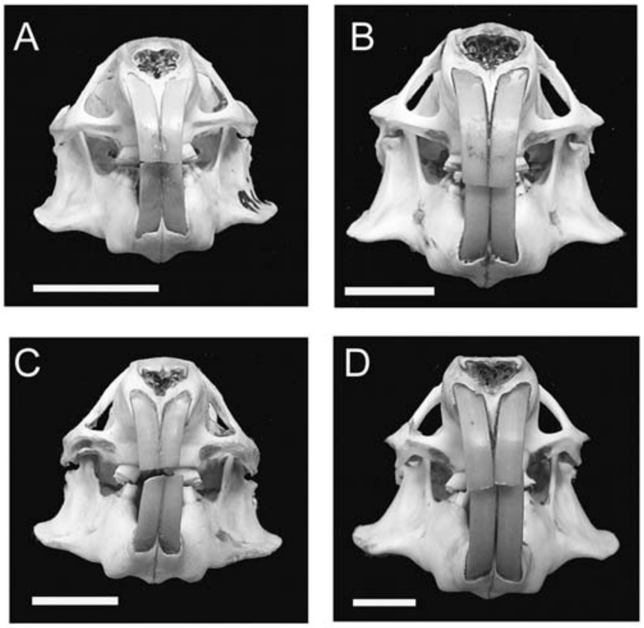

Figure 5. Anterior view of the skull of juvenile (A; C) and adult (B; D) males of *Ctenomys talarum* (above) and *C. australis* (below) showing differences in mandibular width due to allometric growth during ontogeny. Note differences in the development of the mandibular angle and masseteric crest between juvenile and adult specimens. Scale bar = 1 cm.

no significant differences between the slopes ($F = 0.46$, *d.f.* = 50, $p > 0.25$), there were significant differences between the elevations ($F = 15.38$, *d.f.* = 51, $p < 0.001$) of the growth curves for *C. australis* and *Actenomys*. The condylo-incisor length is a measure of the out-lever arm for the adductor jaw muscles. Contrary to the pattern observed for the mandibular width, the values for *C. australis* here fall below those measured in *Actenomys*, denoting an overall shortening of the jaw in the living ctenomyine (Fig. 6B; Fig. 7), which is also indicated by the non overlapping confidence intervals of the y-intercept (Table 1), and significant differences between elevations ($F = 17.50$, *d.f.* = 51, $p < 0.001$; ANCOVA) of their growth curves.

Inter-generic differences in incisor robustness between the extant *Ctenomys australis* and the Pliocene *Actenomys* were the outcome of a postnatal change in the direction of the ontogenetic trajectory. We found a significant difference in the allometric coefficient (Table 1) and slopes ($F = 31.3$, *d.f.* = 50, $p < 0.001$, ANCOVA) when comparing the growth curves relating the cross sectional area of the lower incisors vs. the height of the mandibular corpus in *C. australis* and the fossil ctenomyine (Fig. 6C).

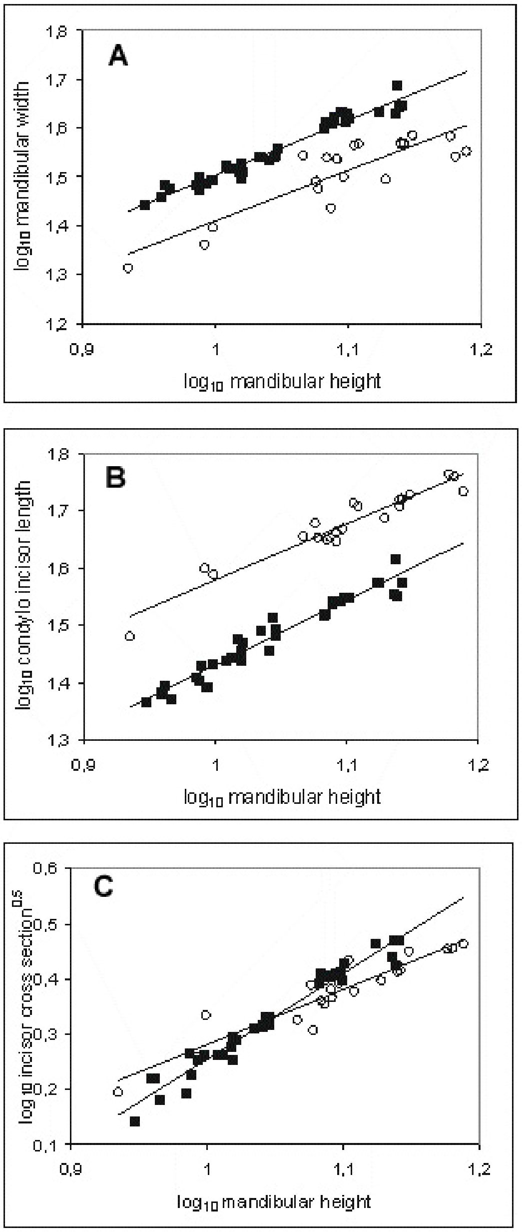

Figure 6. Graph of logarithmic coordinates of skull measurements in ontogenies of the extant *Ctenomys australis* (solid squares) and the fossil ctenomyine *Actenomys* (open circles). A: mandibular width vs. mandibular height; B: condylo-incisor length vs. mandibular height; C: incisor cross section vs. mandibular height.

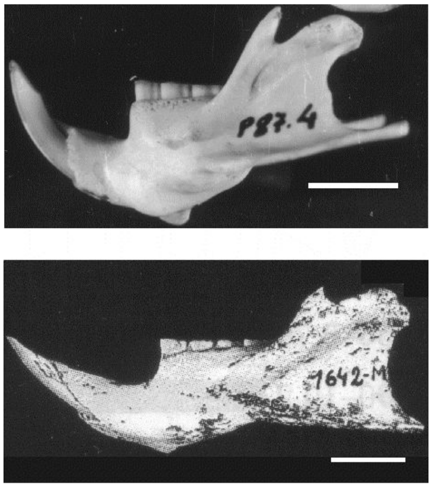

Figure 7. Lateral view of the lower jaw of the extant *Ctenomys australis* (above) and the Pliocene ctenomyine *Actenomys* (below). Note the overall shortening, particularly the condylo-incisor distance, and strengthening of the jaw of *C. australis*. Differences in incisor thickness can also be noted. Scale bar = 1 cm.

DISCUSSION

The intensification of the hystricognath condition – lateral expansion of the mandibular angle and masseteric crest (Woods, 1985) – clearly differentiates representatives of *Ctenomys* from genera within Octodontidae, except *Spalacopus* and *Aconaemys* (Fig. 1A; see also Vassallo and Verzi, 2001). The enlargement of the mandibular angle is related with the hypertrophy of the masseteric adductor muscles, a conjecture supported by the fact that muscle growth has a heritable epigenetic impact on bone development (Herring and Lakars, 1981). This derived condition also produces a clear difference between *Ctenomys* and early, fossil ctenomyids such as *Actenomys*, with the notable exception of *Eucelophorus* (see Reig and Quintana, 1992; Verzi, 2002). In conjunction with other traits, the morphological evolution of the masticatory apparatus accompanied the adaptive diversification of the families Ctenomyidae and Octodontidae, producing an array of fossil and living taxa, from surface-dwelling to very specialized, scratch and chisel-tooth digging subterranean forms. The hypertrophy of adductor muscles, mandibular angle, and the masseteric crest has been functionally related to the development of greater out-forces at the tip of the incisors, forces that are required to effectively break the soil and cut fibrous roots during digging activities and tunnel construction (Vassallo, 1998; Olivares et al., 2004). A plesiomorphic character state – characterized by a poorly developed mandibular angle and masseteric crest – independently changed to the aforementioned derived condition several times during the diversification of ctenomyid and octodontid rodents. Thus, unrelated taxa such as *Ctenomys*, *Eucelophorus*, and *Spalacopus* converged to a similar condition, in association with the recurrent emergence of fully subterranean habits (Lessa et al., 2004).

Ctenomys show considerable variation in body size: the various species range from 90 g (*C. pundti*) to 700-900 g (*C. tuconax*, *C. conoveri*). Previous analysis showed that larger *Ctenomys* species have proportionally larger masseteric muscles, as indicated by both myological (Vassallo, 1998) and osteological data (Mora et al., 2003). The mean multivariate allometric coefficient for mandibular width with respect to a series of skull measurements used in a recent morphometric analysis was 1.13 (Mora et al., 2003). In that study we proposed that allometry could be partly responsible for altering skull proportions of extant *Ctenomys* species through scaling (Alberch et al., 1979; Lessa and Patton, 1989; Klingenberg, 1998). The present comparative analysis of the ontogenetic growth pattern of 2 species markedly differing in body size, *C. australis* and *C. talarum*, allowed us to draw some conclusions about this issue. The expected strong positive allometry of mandibular width vs. basicranium axis length is indicative of normal bone and muscle development, and correlated shape change during the ontogeny of *Ctenomys* (Fig. 4 and 5; for another example, see Abdala et al., 2001). Accordingly, the masseteric musculature represents 0.035 % ($N = 5$) of the body mass of young specimens of *C. australis,* while this figure is approximately 0.073 % ($N = 8$) in adult specimens (Vassallo, unpublished data). For mandibular width vs. basicranium axis length we did not find substantial differences in either the slope or the y-intercept between the ontogenies of *C. talarum* and *C. australis* (Table 1; Fig. 4A). The allometric coefficient for incisor cross section vs. basicranium length was only marginally greater in *C. australis*; there was no significant difference in the y-intercept between these species (Table 1; Fig. 4B). Hence, we conclude that maintenance of a given ontogenetic trajectory through the range of sizes of extant *Ctenomys* species (i.e., ontogenetic scaling) is sufficient to explain the observed shape differences between small and large species.

Although some studies have associated ontogenetic scaling with heterochronic changes (progenesis and hypermorphosis), other changes in growth dynamics can produce the same allometric pattern; thus, inferring heterochrony from allometric data should be taken with caution (Klingenberg, 1998, and references therein). A similar pattern was observed in the North American subterranean species *Thomomys townsendii* (Rodentia, Geomyidae), whose increased incisor procumbency, a condition considered an adaptation for tooth digging, is solely the outcome of increased overall skull size, i.e. ontogenetic scaling (Lessa and Patton, 1989).

Actenomys was an early Pliocene ctenomyid whose paleo-caves protrude on shore cliffs in southern Mar del Plata, Argentina. We chose this genus because, for several traits usually considered to be adaptations for digging in the family Ctenomyidae, it shows a plesiomorphic condition, in particular regarding the width of the jaw across the masseteric crest and the robustness of the incisors (Fig. 1; see also Verzi, 1994, 2002). In *Actenomys*, the long bones of both fore- and hind limbs are rather elongated, showing a slight departure from the condition seen in *Octodon*, indicating that aboveground locomotion was both common and agile in the fossil ctenomyid. However, *Actenomys* possess an incipient development of the teres major process, which could be reasonably interpreted as an indicator of daily digging activities associated with a semi-subterranean mode of life (Fernández et al. 2000; see also Schleich and Vassallo, 2003). When studying mandibular width, we found no substantial difference between the slopes of the growth curves of *Actenomys* and the extant subterranean species *C. australis* (Table 1). The values of *Actenomys* fall below those measured in the living species throughout the ontogenetic sequence; i.e., growth-independent shape differences exists (Fig. 6A). This parallel shift of the entire ontogenetic trajectory, termed lateral transposition (*sensu* Klinberger, 1998) indicates that alterations in development have occurred in early, prenatal stages. As noted above, a wider mandible results from the lateral expansion of the mandibular angle and masseteric crest and thus this trait may be used to assess muscle development in living and fossil octodontid taxa (Verzi, 1994, 2002; Vassallo and Verzi, 2001; Olivares et al., 2004). It is clear that muscle growth during the postnatal period, as reflected by the allometric relationship between mandibular width and height of the mandibular corpus for both *Actenomys* and *Ctenomys* (Table 1; Fig. 6A), results from an increase in individual muscle fiber size, or hypertrophy; the number of myofibrils within the enlarged muscle fiber can increase more than 10-fold during development (Wolpert, 1998). Thus, early embryonic, prenatal differences in the number of muscle precursor cells, myoblasts (Carlson, 1988; Langeland and Kimmel, 1997), is compatible with the lateral transposition observed between the ontogenetic trajectories of *Actenomys* and *Ctenomys australis* (Fig 6A).

The overall shortening of the condylo-incisor distance during the entire postnatal ontogeny of living *Ctenomys*, as compared with *Actenomys* (Figs. 6B, 7), may lead to greater out-forces at the tip of the incisors due to the reduction of the out-lever arm of the masseters (Hildebrand, 1988; Lessa, 1990). The differences between the growth curves of these 2 taxa (i.e., lateral transposition; Fig. 6B) might be caused by prenatal differences in the overall shape of the mesenchymal condensation of neural-crest-derived cells from which later originate the mandibular ramus and processes (Atchley and Hall, 1991; Wolpert, 1998).

Differences in incisor robustness between extant *Ctenomys* species and *Actenomys* (Fig. 1B) resulted from a change in slope of the ontogenetic trajectory (Table 1; Fig. 6C). This evolutionary change in the direction of the ontogenetic trajectory suggests a possible dissociation of growth dynamics between incisor cross section and mandibular height during the postnatal sequence of *C. australis* and *Actenomys*. Rodent incisors are regenerative tissues that grow continuously throughout life. Several genetic and epigenetic factors affect mammalian tooth morphogenesis, in particular rodent incisor development (Gilbert, 1997; Harada et al., 2002). A change in the amount and/or rate of dentin deposition, possibly associated with developmental units affecting the initial odontoblast cell population (Atchley and Hall, 1991), may be a likely factor producing the observed differences in the postnatal growth curves of fossil and extant ctenomyines.

CONCLUSIONS

All extant *Ctenomys* species are very similar in their general adaptations to life underground, particularly morphological digging adaptations of the skull and forelimbs. It seems apparent that the most variable attribute in this genus is overall body size, although all living species have similar strict subterranean habits and high digging capabilities. We found that larger *Ctenomys* species possess both proportionally broader lower jaws and more robust incisors. Nonetheless, for these traits, the ontogenetic trajectories of the skull in the small *Ctenomys talarum* and large *C. australis* do not differ in either slope (allometric coefficient) or intercept, in association with the conservation of the *bauplan*, or basic structure, of the skull. In this sense, our study strongly supports an association between evolutionary ontogenetic scaling and skull shape variation within the limits of a single genus, *Ctenomys*. On the other hand, *C. australis* and the extinct *Actenomys*, which sharply differ in skull morphology (Verzi, 2002; Fig. 1) and, possibly, in fossorial habits and ecological niche (Fernández et al., 2000) significantly differ in the slope and/or intercept of their ontogenetic trajectories, as demonstrated by our present analysis. This fact indicates the complexity of evolutionary changes in development responsible for the departure from ontogenetic scaling in ancient and extant ctenomyines, in association with morphological diversification of the skull above the species level.

Differences between fossil and living ctenomyids, with strong adaptive implications regarding the evolution of fossorial habits, such as the strengthening of the masticatory apparatus, surely have a developmental basis, as suggested by the postnatal growth patterns presented here. It would be informative to study ontogenetic series, including prenatal stages, of some living octodontid species, such as *Octodon degus*, which share with the fossil *Actenomys* some plesiomorphic character states, like the relatively poorly developed masseteric muscles, mandibular angle, and incisor cross section.

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APPENDIX 1. SPECIMENS EXAMINED

Octodontid specimens in this study are deposited in the collections of the Museo Municipal de Historia Natural "Lorenzo Scaglia", Mar del Plata, Argentina (MMMP); Museo de La Plata, La Plata, Argentina (MLP), Museo de Historia Natural, Santiago, Chile (MHNC), and Laboratorio de Ecofisiología, Universidad Nacional de Mar del Plata, Argentina (LEMP). The respective museum-catalog numbers are given. Specimens separated by commas.

Ctenomys australis Argentina, Necochea, Parque Lillo LEMP P: 1; 4; 8; 9; 10; 12; 14; 16; 17; 18; 23; 31; 33; 35; 38; 39; 41; 42; 46. CA: 2; 4; 5; 6. MMMP: 3236; 82.240.

Ctenomys argentinus Argentina, Chaco, Colonia Benítez MMMP: 2450; 2451; 2452; 2453.

Ctenomys azarae Argentina, La Pampa MMMP 2287; 1515; 1595; 1596; 1597. La Pampa, Villarino MMMP: 82-101; 82-164; 82-225.

Ctenomys boliviensis LEMP: 129; 137.

Ctenomys bonettoi Argentina, Chaco, Colonia Elisa MMMP 0673.

Ctenomys dorbignyi Argentina, Corrientes, San Miguel MMMP 3459. Curuzú Laurel MMMP 3432. Berón de Astrada, Mbariguí MMMP 3456; 3452; 3424; 3425; 3426; 3427; 3428; 3455; 3457.

Ctenomys haigi Argentina, Chubut, Puerto Madryn MMMP 1925.

Ctenomys latro Argentina, Tucumán, Ticucho MMMP 1-87; 2426. Tapia MMMP 2427; 2428; 2500; 2501; 2502; 2807; 2808; 3187; 3188; 3189; 3190.

Ctenomys leucodon Bolivia, Depto. La Paz, Comanche LEMP 4999; 5793.

Ctenomys magellanicus Argentina, Tierra del Fuego, Colonia Herke MMMP 2500; 2501; 2502; 2808. Ruta 3 km2908 MMMP 2807. Tierra del Fuego MMMP D4M.

Ctenomys mendocinus MMMP 2276; 2655; 2711.

Ctenomys occultus Argentina, Tucumán, Monteagudo MMMP 3184; 3185; 3186; 3187.

Ctenomys opimus Argentina, Jujuy, Tres Cruces MMMP 2202; 3101; 3102; 3103; 3104; 3105. Bolivia, Potosí, Laguna Colorada, Campamento ENDE LEMP 929.

Ctenomys porteousi Argentina, Buenos Aires, Bonifacio MMMP 1337; 1338 ; 1340; 1343; 1347; 1348; 1350; 1351; 2288; 2289; 2290; 2291; 2292; 2293; 2296; 2297.

Ctenomys perrensi Argentina, Corrientes, Yatayti MMMP 2437; 2438. Goya MMMP 2440; 2474; 3136; 3417; 3418; 3419; 3420; 3422; 3423; 3453. Salados MMMP 2447.

Ctenomys pundti Argentina, Córdoba MMMP I1658; I1659; I1660; I1661; K1; K33; K38; K43; K48; K51; K52; K62; K68.

Ctenomys rionegrensis Argentina, Entre Ríos, Concordia MMMP1961; 1962.

Ctenomys roigi Argentina, Corrientes, Costa Manción` MMMP 2410; 2411; 2412; 2442; 2461.

Ctenomys talarum Argentina, Necochea, Parque Lillo LEMP CT 4; CT5; CT5D7; CT(14)19; CT(20)13; CT(15)1; CT16(8); CT19; CT7D(9); CT107.88.

Ctenomys tuconax Argentina, Tucumán, El Infiernillo MMMP 2429; 2430; 2661; 2960; 2962; 2963; 3182; 3303; 3304; 3305; 3310; 3311; 3342; 3346; 3695.

Ctenomys tucumanus Argentina, Tucumán, El Cardillar MMMP 2298; 2300. Ticucho MMMP 3181.

Octodon bridgesi Argentina, Neuquen, Parque Nacional Lanin, MLP: 12.VII.88.1; 12.VII.88.2; 12.VII.88.3; 12.VII.88.4; 12.VII.88.5; 12.VII.88.6; 12.VII.88.7.

Octodon degus
Chile, Santiago, Los Dominicos, MHNC 913; 914; 915; 921; 951; 955; 956; 957.

Spalacopus cyanus Chile, El Chisco Norte MMMP 3807. Aconcagua Norte, Papudo MMMP 3583; 3585; 3590; 3591. Santiago, Lagunillas MHNC 702; 704.

Aconaemys sagei Argentina, Neuquen, Pampa de Hui Hui MLP 17.II. 92.8; 17.II.92.10.

Octodontomys gliroides Jujuy, Tilcara, MMMP 755; 2200; 2532; 3057; 3557; MLP 12VII88.10.

Actenomys priscus MMMP 411-M; 497-M; 1567-M; 208-S; 586-S.

Ontogenetic sequence of *Ctenomys talarum*

Argentina, Necochea, Parque Lillo, LEMP P: 2; 3; 5; 7; 17; 20; 21; 27; 34; 40; 44; 103; 107; 118; 121; V: 53; 54; 56; 57; 59; I: 74; 77; 79; 80; 93; 94; FA: 2; 4; 5; 7; 8; 9; 11. CT: 1; 4; 5; 17; 19; 21; 5D7; 6D2; 7D9; 17.13.3; 7(55)(4); 14(19); 15(1); 16(8); 20(13); C: 1; 2; 3; J: 1; 2; 4; 5; 6; 7; 136; 147; 141.177; 143.179; 144.180; 145.181; 146.182; 147.183; 152.188; 156.193; 159.195; 162.198; 163.199; 218.

Ontogenetic sequence of *Ctenomys australis*

Argentina, Necochea, Parque Lillo, LEMP P 1; 4; 8; 9; 10; 12; 14; 16; 18; 19; 22; 23; 24; 28; 29; 32; 33; 35; 36; 37; 38; 39; 41; 42; 43; 45; 46; 48; 50; 51; 55; 62; CA: 18; 19; 20; 20.3.92; 21; 22; 23; 25; 26; 26.6; 28; 81. JUV: 32; 36; 43; 44; 45; 46; 48; 50; 51; 62.

Ontogenetic sequence of *Actenomys priscus*

MMMP M: 517; 564; 793; 804; 896; 1231; 1550; 1559; 1560; 1562; 1644; 1645; 2024; 2041; 2073; 2120; 2404. S: 385; 718; 720; 766.

LITERATURE CITED

Abdala, F., D. A. Flores, and N. P. Giannini
2001 Postweaning ontogeny of the skull of *Didelphis albiventris*. Journal of Mammalogy 82:190-200.

Alberch, P., S. J. Gould, G. F. Oster, and D. B. Wake
1979 Size and shape in ontogeny and phylogeny. Paleobiology 5:296-317.

Atchley, W. R., and B. K. Hall
1991 A model for development and evolution of complex morphological structures. Biological Review 66:101-157.

Bacigalupe, L. D., J. Iriarte-Díaz, and F. Bozinovic
2002 Functional morphology and geographic variation in the digging apparatus of cururos (Octodontidae: *Spalacopus cyanus*). Journal of Mammalogy 83:145-152.

Begall, S., and M. H. Gallardo
2000 *Spalacopus cyanus* (Rodentia: Octodontidae): an extremist in tunnel constructing and food storing among subterranean mammals. Journal of Zoology (London) 251:53-60.

Biknevicius, A. R., B. Van Valkenburgh, and J. Walker
1996 Incisor size and shape: implications for feeding behaviours in saber-toothed "cats." Journal of Vertebrate Paleontology 16:510-521.

Butler, P. M.
1985 Homologies of molar cusps and crests, and their bearing on assessments of rodent phylogeny. Pp. 381-401 in Evolutionary Relationships Among Rodents: A Multidisciplinary Analysis (Luckett, W. P., and J. L. Hartenberger, eds). Plenum Press, New York, New York, USA.

Carlson, B. M.
1988 Patten's Fundations of Embriology. Interamericana, McGraw-Hill, Mexico, DF. 644 pp.

Casinos, A., C. Quintana, and C. Viladiu
1993 Allometry and adaptation in the long bones of a digging group of rodents (Ctenomyinae). Zoological Journal of the Linnean Society 107:107-115.

Cook, J. A., and E. P. Lessa
1998 Are rates of diversification in subterranean South American tuco tucos (genus *Ctenomys*, Rodentia: Octodontidae) unusually high? Evolution 52:1521-1527.

Emerson, S. B., and D. M. Bramble
1993 Scaling, allometry and skull design. Pp. 384-421 in The Skull: Functional and Evolutionary Mechanisms (Hanken, J., and B. K. Hall, Eds.). The University of Chicago Press, Chicago, Illinois, USA.

Fairbairn, D. J.
1992 The origin of allometry: size and shape polymorphism in the common waterstrider, *Gerris remigis* Say (Heteroptera, Gerridae). Biological Journal of the Linnean Society 45:167-186.

Feldhamer, G. A., L. C. Drickamer, S. H. Vessey, and J. F. Merritt
1999 Mammalogy: Adaptation, Diversity and Ecology. McGraw-Hill, Boston, Massachusetts, USA. 563 pp.

Felsenstein, J.
1985 Phylogenies and the comparative method. American Naturalist 125:1-15.

Fernández, M. E., A. I. Vassallo, and M. Zárate
2000 Functional morphology and paleobiology of the Pliocene rodent *Actenomys* (Caviomorpha: Octodontidae): The evolution to a subterranean mode of life. Biological Journal of the Linnean Society 71:71-90.

Gallardo, M. H., and J. A. W. Kirsch
2001 Molecular relationships among Octodontidae (Mammalia: Rodentia: Caviomorpha). Journal of Mammalian Evolution 8:73-89.

Garland, T., Jr., A. W. Dickerman, and C. M. Janis
1993 Phylogenetic analysis of covariance by computer simulation. Systematic Biology 42:265-292.

Garland, T., Jr., P. H. Harvey, and A. R. Ives
1992 Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology 41:18-32.

Gilbert, S.
1997 Developmental Biology. Fifth ed. Sinauer Associates, Sunderland, Massachusetts, USA. 918 pp.

Grafen, A.

1992 The uniqueness of phylogenetic regression. Journal of Theoretical Biology 156:405-423.

Hanken, J., and B. K. Hall

1993 The Skull. The University of Chicago Press, Chicago, Illinois, USA. 460 pp.

Harada, H., T. Toyono, K. Toyoshima, M. Yamasaki, N. Itoh, S. Kato, K. Sekine, and H. Ohuchi

2002 FGF10 maintains stem cell compartment in developing mouse incisors. Development 129:1533 -1541.

Harvey, P. H. and M. D. Pagel

1991 The Comparative Method in Evolutionary Biology. Oxford University Press, New York, USA. 239 pp.

Herring, S. W., and T. C. Lakars

1981 Craniofacial development in the absence of muscle contraction. Journal of Craniofacial Genetics and Developmental Biology 1:341-357.

Hildebrand, M.

1985 Digging of quadrupeds. Pp. 89-109 in Functional Vertebrate Morphology (Hildebrand M., D. M. Bramble, K. F. Liem, and D. B. Wake, eds.). The Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.

1988 Analysis of Vertebrate Structure. Third ed. John Wiley and Sons, Inc, New York, USA. 701 pp.

Klingenberg, C. P.

1998 Heterochrony and allometry: the analysis of evolutionary change in ontogeny. Biological Review 73:79-123.

Koenigswald, W. V., P. M. Sander, M. B. Leite, T. Mörs, and W. Santel

1994 Functional symmetries in the schmelzmuster and morphology of rootless rodent molars. Zoological Journal of the Linnean Society 110:141-179.

Köhler, N., M. H. Gallardo, L. C. Contreras, and J. C. Torres-Mura

2000 Allozymic variation and systematic relationships of the Octodontidae and allied taxa (Mammalia, Rodentia). Journal of Zoology (London) 252:243-250.

Lacey, E. A., J. L. Patton, and G. N. Cameron

2000 Life Underground: The Biology of Subterranean Mammals. The University of Chicago Press, Chicago, Illinois, USA. 449 pp.

Langeland, J. A., and C. B. Kimmel
1997 Fishes. Pp. 383-409 in Embryology (Gilbert, S.F., and A.M. Raunio, eds.). Sinauer Associates, Sunderland, Massachusetts, USA.

Legendre, P., and L. Legendre
1998 Numerical Ecology. Elsevier, Amsterdam. 853 pp.

Lessa, E. P.
1990 Morphological evolution of subterranean mammals: integrating structural, functional, and ecological perspectives. Pp. 211-230 in Evolution of Subterranean Mammals at the Organismal and Molecular Levels (Nevo, E., and O. A. Reig, eds.). Allan Liss, New York, New York, USA.

Lessa, E. P., and J. A. Cook
1998 The molecular phylogenetics of tuco-tucos (genus *Ctenomys*, Rodentia: Octodontidae) suggests an early burst of speciation. Molecular Phylogenetics and Evolution 9:88-99.

Lessa, E.P., and J. L. Patton
1989 Structural constraints, recurrent shapes, and allometry in pocket gophers (genus *Thomomys*). Biological Journal of the Linnean Society 36:349-363.

Lessa, E.P., A. I. Vassallo, and D. H. Verzi
2004 Adaptations for digging in living and fossil Octodontidae (Rodentia: Caviomorpha). Abstracts 7 International Congress of Vertebrate Morphology, p. 307.

Mares, M. A., and R. A. Ojeda
1982 Patterns of diversity and adaptation in South American histricognath rodents. Pp. 393-432 in Mammalian Biology in South America (Mares, M. A., and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, Special Publication Series, 6. University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

Maynard-Smith, J., and J. G. Savage
1959 The mechanics of mammalian jaws. School Science Review 40:289-301.

Mora, M.
2001 Análisis alométrico, morfológico y functional en el cráneo del género *Ctenomys* en relación al aparato masticatorio excavatorio (Rodentia, Octodontidae, Ctenomyinae). Tesis de Licenciatura. Universidad Nacional de Mar del Plata. 200 pp.

Mora, M., A. I. Olivares, and A. I. Vassallo

2003 Size, shape and structural versatility of the skull of the subterranean rodent *Ctenomys* (Rodentia, Caviomorpha): functional and morphological analysis. Biological Journal of the Linnean Society 78:85-96.

Neveu, P., and J. P. Gasc

1999 A cinefluorographical study of incisor sharpening in *Spalax giganteus* Nehring, 1898 (Rodentia, Mammalia). Mammalia 63:505-518.

Olivares, A. I.

2001 Morfología del aparato masticatorio en roedores octodóntidos: significado funcional y adaptativo (Rodentia, Caviomorpha, Octodontidae). Tesis de Licenciatura. Universidad Nacional de Mar del Plata. 220 pp.

Olivares, A. I., D. H. Verzi, and A. I. Vassallo

2004 Masticatory morphological diversity and chewing modes in octodontid rodents (Rodentia, Octodontidae). Journal of Zoology 263:167-177.

Ortells, M. O. and G. E. Barrantes

1994 A study of genetic distances and variability in several species of the genus *Ctenomys* (Rodentia: Octodontidae) with special reference to a probable causal role of chromosomes in speciation. Biological Journal of the Linnean Society 53:189-208.

Pearson, O. P.

1959 Biology of the subterranean rodents, *Ctenomys*, in Perú. Memorias del Museo de Historia Natural "Javier Prado" 9:1-56.

1984 Taxonomy and natural history of some fossorial rodents of Patagonia, southern Argentina. Journal of Zoology 202:225-237.

Radinsky, L. B.

1985 Approaches in evolutionary morphology: a search for patterns. Annual Review of Ecology and Systematic 16:1-14.

Reig, O. A.

1970 Ecological notes on the fossorial octodont rodent *Spalacopus cyanus* (Molina). Journal of Mammalogy 51:592-601.

1986 Diversity pattern and differentiation of high Andean rodents. Pp 404-439 in High Altitude Tropical Biogeography (Vuilleumier, F., and M. Monasterio, eds.). Oxford University Press, Oxford, UK.

Reig, O. A., C. Busch, J. R. Contreras, and M. O. Ortells

1990 An overview of evolution, systematics, population biology, cytogenetics, molecular biology, and speciation in *Ctenomys*. Pp. 71-96 in Evolution of Subterranean Mammals at the Organismal and Molecular Levels (Nevo, E., and O. A. Reig, eds.). Allan Liss, New York, New York, USA.

Reig, O. A., and C. A. Quintana

1992 Fossil ctenomyine rodents of the genus *Eucelophorus* (Caviomorpha: Octodontidae) from the Pliocene and Early Pleistocene of Argentina. Ameghiniana 29:363-380.

Satoh, K.

1997 Comparative functional morphology of mandibular forward movement during mastication of two murid rodents, *Apodemus speciosus* (Murinae) and *Clethrionomys rufocanus* (Arvicolinae). Journal of Morphology 231:131-142.

Schleich, C. E., and A. I. Vassallo

2003 Bullar volume in subterranean and surface dwelling caviomorph rodents. Journal of Mammalogy 84:185-189.

Schmidt-Nielsen, K.

1991 Scaling: Why is Animal Size so Important? Cambridge University Press, Cambridge, Massachusetts, USA.

Silva, M.

1998 Allometric scaling of body length: elastic or geometric similarity in mammalian design. Journal of Mammalogy 79:20-32.

Sokal, R. R., and F. J. Rohlf

1981 Biometry. 2nd Edition. W.H. Freeman and Co, New York, New York, USA. 859 pp.

Stein, B. R.

2000 Morphology of subterranean rodents. Pp. 19-61 in Life underground: The Biology of Subterranean Mammals (Lacey, E. A., J. L. Patton, and G. N. Cameron, eds.). The University of Chicago Press, Chicago, Illinois, USA.

Vassallo, A.I.

1998 Functional morphology, comparative behaviour, and adaptation in two sympatric subterranean rodents genus *Ctenomys* (Caviomorpha: Octodontidae). Journal of Zoology 244:415-427.

2000 Alometría e isometría en varias especies de roedores caviomorfos, con comentarios sobre la estructura del aparato masticatorio del Orden Rodentia. Mastozoología Neotropical 7:37-46.

Vassallo, A. I., and D. H. Verzi

2001 Patrones morfológicos craneanos y modalidades de masticación en roedores caviomorfos. Boletín de la Sociedad de Biología de Concepción 72:139-145.

Verzi, D. H.
1994 Origen y evolución de los Ctenomyinae (Rodentia, Octodontidae): un análisis de anatomía cráneo-dentaria. Tésis Doctoral. Universidad Nacional de La Plata, La Plata, Argentina.

2002 Patrones de evolución morfológica en Ctenomyinae (Rodentia, Octodontidae). Mastozoología Neotropical 9:309-328.

Wake, M. H.
1993 The skull as a locomotor organ. Pp. 197-240 in The Skull: Functional and Evolutionary Mechanisms (Hanken, J., and B. K. Hall, eds.). The University of Chicago Press, Chicago, Illinois, USA.

Wolpert, L.
1998 Principles of Development. Oxford University Press, Oxford, UK. 484 pp.

Wood, A. E.
1974 The evolution of the Old World and New World hystricomorphs. Pp. 21-60 in The Biology of Hystricomorph Rodents (Rowlands, I. W., and B. J. Weir, eds.). Academic Press, London, UK.

Woods, C. A.
1972 Comparative myology of jaw, hyoid, and pectoral appendicular regions of new and old world hystricomorph rodents. Bulletin of the American Museum of Natural History 147:115-198.

Woods, C. A., and J. W. Hermanson
1985 Mycology of hystricognath rodents: an analysis of form, function and phylogeny. Pp. 515-548 in Evolutionary Relationships among Rodents (Luckett, W. P., and J. L. Hartenberger, eds.). Plenum Press, New York, New York, USA.

Zar, J. H.
1984 Biostatistical Analysis. 2nd edition. Prentice Hall, Englewood Cliffs, New Jersey, USA. 718 pp.

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