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### OBSERVATIONS OF MULTISPECIES SEABIRD FLOCKS AROUND SOUTH GEORGIA

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ABSTRACT.—We observed 195 multispecies feeding flocks of birds near Bird Island, South Georgia, between 4 February and 5 March in 1986. Up to 19 seabird species plus Antarctic fur seals (*Arctocephalus gazella*) were involved. Black-browed Albatross (*Diomedea melanophris*), Macaroni Penguins (*Eudyptes chrysolophus*), and prions (*Pachyptila* spp.) were the most abundant species. Most flocks were in the vicinity of a large inshore patch of Antarctic krill (*Euphausia superba*), and most observed feeding was by Black-browed Albatross, which appeared to initiate and dominate the flocks. Short feeding bouts by surface-feeding species appeared to be coupled with the surfacing of penguins and seals. We conclude that foraging penguins and seals caused prey to approach the surface where near-surface foraging species could feed. *Received 2 July 1990, accepted 2 March 1991*.

BIRDS, mammals, and fish commonly form multispecies feeding assemblages at sea (Murphy 1936, Bailey 1966, Ashmole and Ashmole 1967, Duffy 1983). Some assemblages result from the independent attraction of several species to a prey concentration with little interaction among the various predators (Ryder 1957, Evans 1982). However, most authors argue that many species benefit from feeding in groups (Sealy 1973, Brown 1980, Enticott 1986, Pierotti 1988b), because others locate or concentrate prey. Assemblages may comprise species that play particular roles in the initiation, maintenance, and disruption of the group (Hoffman et al. 1981, Porter and Sealy 1982).

Species that use different foraging methods (e.g. aerial vs. diving predators) differ in their prey-finding capabilities. Black-legged Kittiwakes (*Rissa tridactyla*) are catalysts to flock formation in Alaskan waters (Hoffmann et al. 1981), where they find concentrations of prey and alert other birds to its location by their conspicuous feeding behavior. Diving predators are able to find subsurface prey and may influence the distribution of prey at the surface (Brown 1980, Grover and Olla 1983). Marine mammals and penguins have been observed driving fish to the surface while feeding (Jehl 1974, Boswall and MacIver 1975). Surface-feeding seabirds may be attracted by the presence of other predators as much as by the prey itself.

Feeding assemblages appear to occur when resources are clumped. The degree to which predators are interactive may represent an adaptive response to a high degree of resource patchiness (Hoffman et al. 1981, Duffy 1983). Antarctic krill (Euphausia superba) is one of the most highly aggregated prey of birds and mammals in Antarctica (Hamner et al. 1983), and krill is an important component in the diet of most predators and an essential resource for many seabird species (Croxall and Prince 1987). Although vastly abundant, the tendency of krill to form dense subsurface swarms may make it difficult for many seabird species to locate and track over time. Feeding in multispecies flocks may be a beneficial behavior for seabirds, particularly surface-feeding species, in Antarctica.

Although krill is a major component in the diets of seabirds breeding on South Georgia (Croxall and Prince 1980, 1987), little is known of the means by which seabirds capture krill. Observations of Antarctic birds feeding at sea are few and are biased towards the scavenging behavior of some petrels and albatross near ships (Griffiths 1982, Weimerskirch et al. 1986, Harp-

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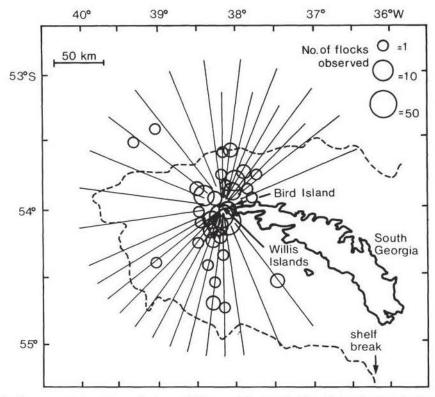


Fig. 1. Survey area showing main transect lines and the distribution of multispecies feeding flocks.

er 1987). Some of the flying species are thought to feed extensively at night (Croxall and Prince 1980, Prince and Francis 1984, Harper 1987), which appears plausible given that krill conduct diel vertical migrations and are closest to the surface at night (Croxall et al. 1985). Although multispecies assemblages have not previously been recorded around South Georgia, they might be another way that seabirds find krill concentrations near the surface.

We observed multispecies feeding flocks near Bird Island, where acoustic surveys indicated krill concentrations (Everson pers. comm.). We describe the species composition of those flocks, the feeding behavior we observed, and the coincidence of surface- and subsurface-feeding species.

#### MATERIALS AND METHODS

Our observations were made between 4 February and 5 March, 1986, from the R.R.S. 'John Biscoe' around Bird Island (54°00'S, 38°03'W) as part of an integrated survey of Antarctic krill, fur seals, and birds (Hunt et al. 1986). We conducted a continuous survey of seabirds and seals from the ship along 38 radial transects (Fig. 1), counting all animals in a 90° arc from the bow to the beam of the ship, to a distance of 300 m from the observer. We entered data on the numbers, species, and behaviors observed directly into a microcomputer (Updegraff and Hunt 1985). We detected krill with an echosounder (Simrad EK400) mounted 5 m below the surface on the ship's hull. Details of the methods for the acoustic study, a description of the sampling design, and the results of the overall survey are reported elsewhere (Hunt et al. 1986).

During 25 and 26 February we observed 33 multispecies flocks while the ship drifted within 200 m of them. We used a hand-held tape recorder to document the details of feeding activity and videotaped 14 of the 33 flocks. From the videotapes we documented dive times (using the timer on the videotape), foraging methods, and other behavioral details. Because of the narrow camera angle, the large sea swell, and the inability always to maintain the ship at an appropriate distance, we were able to view the full extent and duration of only 8 flocks on videotape.

From the field studies and videotapes, we defined a "typical" flock and used this definition to extract flocks from the data set gathered on the general survey. We defined a *flock* as 5 or more individuals of 3 or more species, sitting on the water or feeding. By specifying 3 species, we excluded the large number

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Species	Frequency	Abundance (range)
Surface feeding		
Black-browed Albatross (Diomedea melanophris)	87.7	19.4 (0-136)
Gray-headed Albatross (D. chrysostoma)	64.6	3.9 (0-30)
Prions (Pachyptila spp.)	58.9	55.2 (0-600)
Giant-petrels (Macronectes spp.)	42.1	5.7 (0-30)
Cape Petrel (Daption capense)	32.8	7.1 (0-33)
White-chinned Petrel (Procellaria aeguinoctialis)	31.8	4.6 (0-125)
Wilson's Storm-Petrel (Oceanites oceanicus)	24.6	3.8 (0-20)
Wandering Albatross (D. exulans)	12.8	1.5 (0-5)
Black-bellied Storm-Petrel (Fregetta tropica)	1.5	1.3 (0-2)
Southern Black-backed Gull (Larus dominicanus)	1.5	1.0 ()
Greater Shearwater (Puffinus gravis)	1.0	1.0(-)
Sooty Shearwater (P. griseus)	0.5	1.0 ()
Southern Skua (Catharacta lonnbergi)	0.5	1.0 ()
Subsurface feeding		
Macaroni Penguin (Eudyptes chrysolophus)	33.3	20.5 (0-64)
Antarctic fur seal (Arctocephalus gazella)	23.1	5.1 (0-20)
Gentoo Penguin (Pygoscelis papua)	12.8	3.8 (0-25)
Diving petrels (Pelecanoides spp.)	2.6	7.6 (0-26)
Macaroni, Gentoo and unidentified penguins	39.0	22.8 (0-125)
Penguins and seals	49.2	/

TABLE 1. Relative frequency (% of flocks with species present) and mean abundance (number per flock) of seabirds and seals in 195 multispecies flocks.

of single-species flocks and those involving 2 closely related species. This excluded prion flocks and diving petrel flocks, which did not function in a manner similar to multispecies flocks and were not the subject of this study. We focused on flocks of birds that were

TABLE 2. Observed totals during survey (T), percentage of the sum of the totals  $(\frac{T}{\Sigma T} \times 100)$ , totals observed in flocks (TF), and percentage of totals observed during survey occurring in flocks × 100). (For abundant species in 195 multispecies flocks.)

	$\frac{T}{\Sigma T}$ ×			$\frac{TF}{T} \times$	
	Т	100	TF	100	
Black-browed Alba-					
tross	18,991	6.1	2,357	12.4	
Gray-headed Alba-					
tross	4,762	1.5	383	8.0	
Prions	220,058	70.4	4,823	2.2	
Giant-petrels	1,475	0.5	135	9.2	
Cape Petrel	1,327	0.4	371	28.0	
White-chinned Petrel	8,028	2.6	330	4.1	
Wilson's Storm-Petrel	22,388	7.2	150	0.7	
Wandering Albatross	684	0.2	12	1.8	
Macaroni Penguin	16,468	5.3	870	5.3	
Gentoo Penguin	918	0.3	21	2.3	
Antarctic fur seal	17,289	5.5	140	0.8	
Total	312,388				

feeding or sitting on the water. Birds were regarded as attempting to feed when seen surface seizing, diving, plunging, etc. (as defined by Harper et al. 1985). Intervals of active feeding were termed feeding frenzies. Our data contained 195 flocks that met our criteria, and these were used to describe flock size and species composition.

We could extract different kinds of information from the flocks seen in passing on the survey from those watched at length. In our results we refer to the following sets of flocks: survey total (195 flocks), studied flocks (n = 33), videotaped flocks (n = 14), and feeding events (frenzies) observed from initial formation through dispersion (n = 8). Note that each small sample is a subset of the larger sample that precedes it. When presenting data on feeding attempts, the 33 studied flocks were considered separately from the survey total data.

We collected 17 birds from the flocks: 6 Antarctic Prions (Pachyptila desolata), 6 Macaroni Penguins (Eudyptes chrysolophus), 3 Northern Giant-Petrels (Macronectes halli) and 2 White-chinned Petrels (Procellaria aequinoctialis). The stomachs and crops of these birds were removed and preserved in 80% ethanol, and their contents were examined.

#### RESULTS

Species composition.-We identified 19 species in the 195 flocks observed (Table 1). Blackbrowed Albatross (Diomedea melanophris), Macaroni Penguins, and prions (Pachyptila spp.) were

Species	Frequen- cy (%)	Mean abun- dance (range)		
Black-browed Albatross	100.0	28.7 (2-70)		
Gray-headed Albatross	81.8	3.7 (1-10)		
Prions	100.0	29.1 (4-80)		
Giant-petrels	100.0	10.1 (1-30)		
Cape Petrel	69.7	3.8 (1-17)		
White-chinned Petrel	24.4	1.7 (1-6)		
Wilson's Storm-Petrel	57.6	1.6 (1-5)		
Wandering Albatross	42.4	1.7 (1-5)		
Black-bellied Storm-Petrel	3.0	1.0 —		
Greater Shearwater	3.0	1.0 -		
Southern Skua	3.0	1.0 -		
Diving petrels	6.0	13.0 (1-26)		
Antarctic Fur Seal	66.7	4.1 (1-17)		
Macaroni," Gentoo," and		and the second second		
unidentified penguins	84.8	26.7 (3-125)		
All penguins and seals	97.0			

TABLE 3. Relative frequency and abundance of seabirds and seals in 33 multispecies flocks observed during 25-26 February 1986.

 Macaroni Penguins were positively identified in 75.8% of the flocks (mean abundance = 18.6, range: 1-45) and Gentoo Penguins were positively identified in 42.4% of the flocks (mean abundance = 5.1, range: 1-25).

the most abundant. Black-browed Albatross were the most frequent participants and the most active of the surface-feeding species. Grayheaded Albatross (*D. chrysostoma*) and giant petrels (*Macronectes* spp.) were frequent flock participants but were always seen in low numbers.

The abundance of prions in the flocks in part reflects their high densities at sea. They were the most numerous species in the flocks, and they were also 10 times more abundant than any other species on the overall survey, yet only 2.2% of the total number of prions occurred in the multispecies flocks (Table 2). Similarly, only a small proportion (0.7%) of storm-petrels occurred in the flocks. Conversely, although we saw low numbers of giant petrels in the flocks, these represented a higher proportion (9.2%) of their numbers in the survey. Spearman's rank correlation showed a significant mismatch between the species ordered by total numbers (T) at sea, and ordered by numbers occurring in flocks (TF) (Table 2; n = 11, rho = 0.673,  $P \leq$ 0.05). The numbers of birds in the flocks are not a simple reflection of their abundance at sea.

The penguins and seals were present in the flocks probably more often than abundance (Table 1) would imply, because when active underwater they are difficult to see from a passing ship. During more detailed behavioral observations from an almost stationary ship, pen-

TABLE 4. Totals (for surface-feeding species) observed feeding during survey (FT), percentage of the sum of the totals observed ( $\frac{FT}{\Sigma FT} \times 100$ ), totals observed feeding in 195 multispecies flocks (FF), and percentage of total feeding occurring in flocks ( $\frac{FF}{FT} \times 100$ ).

	$\frac{FT}{\Sigma FT}$ ×			$\frac{FF}{FT}$ ×	
	FT	100	FF	100	
Black-browed Alba-					
tross	361	1.0	277	76.7	
Gray-headed Albatross	64	0.1	43	67.2	
Prions	25,694	71.9	1,256	4.2	
Giant-petrels	32	0.1	19	59.4	
Cape Petrel	54	0.2	14	25.9	
White-chinned Petrel	47	0.1	24	51.1	
Wilson's Storm-Petrel	9,493	26.5	58	0.6	
Wandering Albatross	5	0.1	0	0	
Total	35,750				

guins or seals were present in 32 of 33 flocks studied (Table 3). Penguins were often difficult to identify, and the entry in Table 3 for "Macaroni, Gentoo, and unidentified penguins" is the most representative of actual numbers present.

We saw giant-petrels and Cape Petrels (*Daption capense*) more frequently in the 33 flocks we watched during the behavioral study than in the survey overall (Table 3). Giant-petrels were in all 33 flocks studied, whereas they occurred in fewer than half of the total 195 flocks. Cape Petrels occurred in 23 of the behavioral study flocks, yet they were present in less than a third of the flocks seen during the overall survey. The participation of these two species in the flocks appeared to vary temporally or spatially.

Feeding activities and diet.—Our most frequent observations of feeding birds throughout the survey involved prions and Wilson's Storm-Petrels (*Oceanites oceanicus*) (Table 4). Prions were frequently seen feeding in single-species flocks, the size ranging from 5 to 2,500 individuals (mean = 39.2 for 5,033 flocks total). While prions were seen feeding most frequently in the multispecies flocks, this accounted for a small proportion of their total observed feeding (4.2%); similarly, only 0.6% of the total observed feeding by Wilson's Storm-Petrels was in multispecies flocks.

Apart from the prions and Wilson's Storm-

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	% krill			Surface		Deep	
		plunge	seize	dive	dipping	pattering	diving
Black-browed Albatross	39	~	~	~			
Gray-headed Albatross	16	~	~	1			
Dove Prion	53				~		
Giant-petrels	12-15 <sup>a</sup>	~	~	~			
Cape Petrel	85*		~	~	~		
White-chinned Petrel	52		~				
Wilson's Storm-Petrel	36 <sup>b</sup>					1	
Wandering Albatross	0						
Macaroni Penguin	93						~
Gentoo Penguin	73						V
Antarctic fur seal	100						~

TABLE 5. The percentage of krill by weight in the diets of seabirds and fur seals at Bird Island, and their foraging methods in multispecies flocks during February 1986.

\* Croxall and Prince 1987.

<sup>b</sup> Croxall et al. 1988.

Petrels, Black-browed Albatross were seen to feed most frequently (Table 4) and the majority of this feeding was in the multispecies flocks (76.7% of the 361 total observations). Few other species were seen to feed frequently. Although a high percentage of feeding attempts by Grayheaded Albatross, White-chinned Petrels, and Cape Petrels were in the flocks, the total number of observed feeding attempts for these species was low.

Dietary information from the South Georgia colonies showed the importance of krill for most of the breeding species (Table 5), and the small collection of birds taken from the multispecies flocks confirmed that the birds were capturing krill. All of the Macaroni Penguins (n = 6), Northern Giant-Petrels (n = 3), and Whitechinned Petrels (n = 2) collected had eaten large amounts of Antarctic krill. Of the 6 Antarctic Prions collected, 2 had eaten Antarctic krill, together with other small zooplankton (Thysanoessa, copepods). The remaining 4 prions had not eaten krill. The stomachs of 2 were empty, and 2 had eaten copepods. We collected no Blackbrowed Albatross, but contemporary data from the colonies shows that 39% of their diet was krill (Croxall and Prince pers. comm.).

Foraging methods used by the species observed feeding in the 33 flocks studied varied (Table 5). We have no observations of feeding for some of the less frequent participants. Blackbrowed Albatross made repeated surface dives; sometimes many individuals divided simultaneously. The duration of 80 dives by Blackbrowed Albatross ranged from 0.5 to 5.8 s, with a mean ( $\pm$ SD) of 2.9  $\pm$  1.3 s. Before dives they would often open their wings partially (Fig. 2), and they emerged from most dives in a similar posture. Of all 431 observed feeding attempts by Black-browed Albatross, 62% were surfaceseizing, 32% surface-diving, and 6% surfaceplunging. Only 2 dives were timed for giantpetrels: 0.8 and 3.5 seconds. Of the 51 feeding attempts by giant-petrels, 79% were surfaceseizing, 15% surface-diving, and 6% surfaceplunging. We saw relatively few feeding attempts by Gray-headed Albatross. Two surface dives were timed at 1.9 and 4.6 seconds.

Most species other than Black-browed Albatross fed within a few seconds of the emergence of penguins, seals, or both, a pattern seen also in giant-petrels (Fig. 3). In the minute before a penguin or seal surfaced, Black-browed Albatross made more feeding attempts than any other species.

The emergence of penguins or seals was followed by frenetic movement and feeding by the surface-feeding birds. The 14 flocks videotaped provided good views of 28 feeding frenzies. In 10 cases birds converged on seals, and in 13 cases on penguins; in 5 cases neither seals nor penguins were visible. On 6 additional occasions, surface-feeding birds converged on a site where penguins (5 times) or seals (1 time) emerged, but they did not feed.

Prions and storm-petrels were difficult to track. They flew continuously, and their numbers generally increased during feeding events and decreased as the albatross stopped feeding and drifted on the water. After the first burst of activity, prions and storm-petrels continued to glean food from the sea surface long after other birds had stopped.

On the videotapes, the events in 8 feeding



Fig. 2. Flock involving Antarctic fur seals, Black-browed Albatross, giant-petrels, Cape Petrels and a Grayheaded Albatross. To the upper right is a Black-browed Albatross with its wings open, the posture often seen before a dive. Also on the right a Black-browed Albatross is chasing a giant-petrel. The spatial arrangement evident here is typical, with the fur seals at the front, followed by the Black-browed Albatross, and with the giant-petrels at the rear. Note also the "gawky look" or puffed cheeks on the Black-browed Albatross. (Photograph: G. C. Cripps.)

frenzies were seen clearly, which enabled us to document fully the birds' behavior. These frenzies varied in duration (10–176 s;  $\bar{x} \pm SD = 43.8 \pm 55.3$ ). The most common bird to arrive first at a new feeding site was the Black-browed Albatross (73.6% of 224 birds total). Giant-petrels (22.9%) and Gray-headed Albatross (3.6%) were the other active species. Of 148 observations of feeding attempts, 83.8% were by Black-browed Albatross, 8.8% by giant-petrels, and 7.4% by Gray-headed Albatross.

Behavioral sequence of flocks.—The surfacefeeding species were responsive to the penguins and seals. Feeding frenzies were typically initiated by Black-browed Albatross that left an old feeding site and flew towards a nearby area where penguins or fur seals, or both, were diving. Sometimes the albatross would move into an empty area and start feeding, but almost inevitably penguins and seals would emerge shortly afterwards. Occasionally albatross would converge on penguins and seals, and no feeding would follow. Usually on arrival at a new feeding focus, Black-browed Albatross would start feeding immediately with shallow surface diving, plunging, and seizing. Often dozens of Black-browed Albatross would converge within a few seconds of the first arrival.

The other species appeared to respond to the initial actions of the Black-browed Albatross. Occasionally, Gray-headed Albatross and giantpetrels were involved in forming a new focus, but they always arrived after the first Blackbrowed Albatross and never played a central role. Usually these 2 species stayed on the periphery of the flock (Fig. 2). Black-browed Albatross were seen to peck and adopt aggressive postures towards them when they were encountered within a frenzy. Many of the behaviors we observed within the flocks are the same as those associated with territorial behavior on the breeding colonies (Tickell 1984). Albatross were seen "surface stabbing," and frequently they puffed out their cheek feathering, which exposed their colored gape-stripe, a posture Tickell termed "the gawky look" (Fig. 2).

Black-browed Albatross made many more feeding attempts than did any other surfacefeeding species. Other participants, such as White-chinned Petrels, followed Black-browed Albatross and arrived at the feeding flocks later. They invariably stayed on the outer edges of

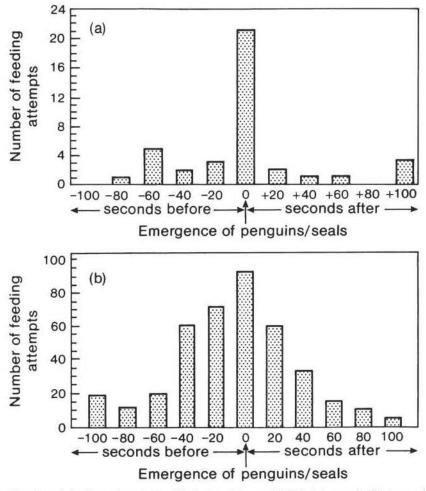


Fig. 3. Number of feeding attempts by (a) giant-petrels and (b) Black-browed Albatross relative to the emergence of penguins/seals.

the frenzies and were not seen to feed. Prions and storm-petrels were always around the frenzies, usually at the edge of the flock, and always arrived after the Black-browed Albatross.

#### DISCUSSION

Function of flocks.—The species that participated in the flocks were converging to feed and very likely captured krill. The Macaroni Penguins, Northern Giant-Petrels, and Whitechinned Petrels that we collected all had full stomachs. Dietary information from the nearest colonies also indicated that krill was an important prey for these birds. Fur seals and Macaroni Penguins are major krill predators around South Georgia, where Macaroni Penguins take 68% of all krill consumed by seabirds (Croxall et al. 1984, Croxall et al. 1985). Several species that fed on krill in the multispecies flocks were not krill specialists according to colony studies. Giant-petrels have a diverse diet that usually includes only 12–15% krill, but crops of birds collected from the flock were distended by *E. superba*, which implies that this may be one of the circumstances in which they capture krill.

The association of the surface-feeding species and subsurface-foraging penguins and seals appears to be critical to flock formation. Subsurface-feeding species can locate prey at depth. Penguins and seals may also influence the movement of krill by driving prey to the surface, as observed for Magellanic Penguins (Spheniscus magellanicus) (Jehl 1974, Boswall and MacIver 1975). This may help surface-feeding birds to track prey patches. Tuna and dolphins force prey to the surface in tropical waters (Ashmole and Ashmole 1967, Au and Pitman 1986). Surface-feeding seabirds often feed with whales (Evans 1982, Pierotti 1988a) and diving birds such as penguins (Jehl 1974) and auks (Hunt et al. 1988, Grover and Olla 1983).

Although the subsurface predators may have been driving prey to the surface, they may also have created sufficient debris in the process of feeding to enable birds at the surface to scavenge on damaged, dead, or fragmented prey (Hunt et al. 1988, Obst and Hunt 1990). The sequence of events we observed suggested that birds at the surface ate live prey most of the time. The feeding activity of the bird indicated prey was available at the surface for only a short time; long periods of inactivity were broken by short bouts of feeding. In contrast, birds scavenging on prey are typically seen pecking at the surface for long periods of time (Obst and Hunt 1990). The prions and storm-petrels appeared to pick particles from the surface minutes after other species had stopped feeding, and they may have been scavenging. We did not see these small birds sitting on the water, and perhaps their frequent occurrence in the stomach contents of giant petrels (Hunter 1983) explains their feeding on the periphery of the flocks.

Role of species in flocks.—The feeding flocks resulted from the actions of only penguins, seals, and Black-browed Albatross. Prey appeared to be made available to procellariids by foraging penguins and seals. Black-browed Albatross were central to the formation of flocks at the surface while other species followed their lead. Black-browed Albatross responded to each other, while a few individuals seemed to track the movements of penguins and seals.

Feeding flocks in the north Pacific were typically initiated by individual gulls or kittiwakes (Hoffman et al. 1981). Different species using different foraging techniques act as initiators in different systems. Examples are plunging boobies and terns in the Humboldt Current (Duffy 1983), surface-diving cormorants in the Benguela Current (Duffy 1989), alcids in British Columbia (Chilton and Sealy 1987), pursuitplunging shearwaters in Alaska (Hoffman et al. 1981), and surface-seizing gulls in the north Pacific and Atlantic (Hoffman et al. 1981, Sealy 1973, Grover and Olla 1983, Chilton and Sealy 1987, Pierotti 1988b). Around Bird Island surface-seizing Black-browed Albatross initiated the flocks at the surface.

In each system a different group of species responds to the prey patches discovered by the initiators. In the northern Pacific, flocks were dominated by gulls and diving species such as alcids and cormorants (Sealy 1973, Baltz and Morejohn 1977, Hoffman et al. 1981, Chilton and Sealy 1987, Hunt et al. 1988). In Peru and South Africa, flocks were dominated by plunging boobies and terns, diving cormorants, and surface-feeding gulls and procellariids (Duffy 1983, 1989). Most of the species that occur at sea near South Georgia were seen in the multispecies flocks. These were mainly surface-foraging procellariids; diving or plunging species were virtually absent.

Hoffman et al. (1981) argued that the duration of a flock is determined by the balance between the actions of the subsurface predators that drive prey to the surface, and the actions of the nearsurface predators that drive down, disperse, or deplete prey. They found that the most disruptive species in the flocks were surface-plunging shearwaters, which made prey unavailable to the other birds. In the case of the flocks around South Georgia, Black-browed Albatross initiated flocks, and then became the most disruptive species active in them. Their shallow diving, which started up to 40 s before any other species attempted to feed, may permit them to dominate a prey patch and may also disperse or deplete the prey before it becomes available to many other near-surface feeding species.

Feeding flocks may be an important means by which seabirds capture krill. The interactions between the birds in these flocks are likely to have wide-ranging effects on the distribution and behavior of some species, especially if dominant Black-browed Albatross exclude others from prey patches. Presumably prey is not so highly localized at night (Everson 1982), and many of the seabird species that remain at the periphery of the flocks are regarded as primarily nocturnal (Harper 1987). However, we believe that at least some of these species feed more diurnally than was thought previously, and we suggest that species interactions are a mechanism by which prey may be aquired during daylight.

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