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MULTISPECIES SEABIRD FEEDING FLOCKS IN THE GALÁPAGOS ISLANDS[1]

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Abstract. I examined the species composition, frequency, distance offshore, and duration of multispecies seabird feeding flocks in the Galápagos Islands, Ecuador. Flocks were comprised of Galápagos Penguins (*Spheniscus mendiculus*), Flightless Cormorants (*Campsohaelius* [*Nannopterum*] *harrisi*), Brown Pelicans (*Pelecanus occidentalis*), Brown Noddies (*Anous stolidus*), Blue-footed (*Sula nebouxii*) and Masked Boobies (*Sula dactylatra*), Magnificent Frigatebirds (*Fregata magnificens*), and Audubon Shearwaters (*Puffinus lherminieri*). Pursuit-divers, such as Galápagos Penguins and Flightless Cormorants, increase the longevity of flocks. Species such as boobies may tend to dissipate flocks. This study provides field evidence that the presence of pursuit-diving seabirds has a positive effect on the duration of feeding flocks and that the mechanisms that keep prey close to the surface near shore may differ from those in the open ocean.

Key words: foraging behavior, Galápagos Islands, Galápagos Penguins, multispecies feeding flocks, seabirds, Spheniscus mendiculus.

INTRODUCTION

Seabird flocks are temporary associations in which individuals congregate to feed, sometimes in very large numbers. These flocks are particularly prominent in tropical waters (Duffy 1983, Ballance 1993). Because the majority of seabird species that live in the tropics are surface-feeders (Ainley 1977), they often rely on predators such as dolphin or tuna to drive prey to the surface (Ashmole and Ashmole 1967, Pitman and Ballance 1992). Feeding flocks dependent upon dolphin and tuna mainly occur tens to thousands of kilometers from land. For flocks occurring closer to shore, however, the mechanisms that keep prey close to the surface may differ from those in the open ocean. The flocks in the Galápagos are frequent and mainly occur in the inshore waters, sometimes within a few feet of shore. Within these mixed-species flocks, two species of sub-surface seabirds participate, making it feasible that they play a role in helping maintain these inshore feeding flocks.

Species of marine birds that forage by pursuit-diving are restricted to water that has a high abundance of prey, and thus are generally more abundant at high latitudes (Ainley 1977, Diamond 1978). Despite the fact that the Galápagos Islands are within the relatively unproductive waters of the tropics, the confluence of currents and associated high productivity (Houvenaghel 1978, 1984, Feldman 1986) allow this area to support an abundance of marine mammals and seabirds, including pursuit-diving species such as the Flightless Cormorant (*Campsohaelius* [*Nannopterum*] *harrisi*) and the Galápagos Penguin (*Spheniscus mendiculus*). Thus, the waters of the Galápagos Islands provide the opportunity to study inshore seabird feeding flocks in one area of the tropics that contains sub-surface avian foragers.

I investigated multispecies seabird feeding flocks near two islands within the Galápagos Archipelago: the western island, Fernandina, and a centrally located island, Bartolomé. Two general questions were investigated: (1) what is the species composition, frequency, distance offshore, and duration of the feeding flocks and (2) what effect do the sub-surface seabirds of the Galápagos Islands have on the overall duration of the feeding flocks?

METHODS

STUDY AREA AND DATA COLLECTION

This study took place in the Galápagos Archipelago, Ecuador during 1994. I spent 58 days at Cape Douglas, on Fernandina Island, and 21 days on Bartolomé (Fig. 1). Data were gathered between June and August on Fernandina and in September on Bartolomé. Sea-surface-temperature (SST) was taken daily at 07:00 from an exposed section of shore with a mercury thermometer at approximately 50 cm depth. The SST reading that was recorded for the day was the

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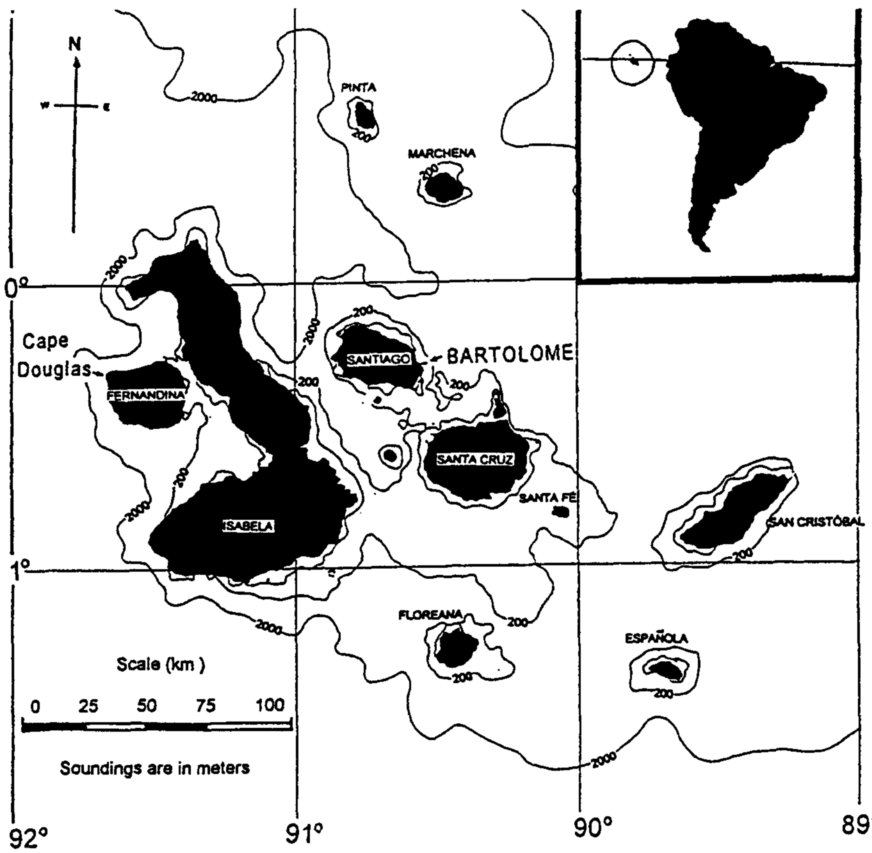

FIGURE 1. Bathymetric map of the Galápagos Archipelago.

average of three separate readings taken consecutively.

A total of 588 hours on Fernandina and 192 hours on Bartolomé were spent collecting data on feeding flocks. Continuous observations were carried out daily from a fixed station on shore between 07:00 and 18:00. For each feeding flock observed, the species composition, distance offshore, and duration of the flock were recorded. On an average day, it was possible to see flocks that were up to 1 km offshore, although few flocks occurred at that distance. The distance offshore of the feeding flock was estimated to the nearest 100 m based upon several landmarks of known distance. The duration of the flock was estimated to the nearest minute by recording with a stopwatch the approximate time the flock formed and the approximate time that the birds terminated feeding and dispersed.

Three fish samples from feeding flocks were collected with a fish net and were preserved in alcohol for subsequent identification. Two of the samples were taken from feeding flocks near Fernandina, and one was collected on a beach on Bartolomé. In addition, in my daily swims I was able to approach the feeding seabirds within a flock and observe specific behaviors of the different species.

DATA ANALYSIS

I define a feeding flock as one that contains 10 or more actively feeding seabirds that are within 3 m from each other. Often, Storm-Petrels (*Oceanodroma* spp.) participated in feeding flocks at both study sites, although it was difficult to identify species. Furthermore, because Storm-Petrels are small and did not congregate in large numbers at feeding flocks, they were often difficult to spot and count accurately. For these reasons, I excluded them from the analyses.

Data were checked for normality and log-transformed when necessary. Results are reported as

TABLE 1. Species that participated in feeding flocks on Fernandina and Bartolomé from June to September 1994. Participation frequency refers to the number of times in which each species formed part of a flock. Total number of flocks = 277 for Fernandina and 39 for Bartolomé. Values are means ± SD.

Common name	Total number individuals		Mean no. individual/flock		Participation frequency	
	Fernandina	Bartolomé	Fernandina	Bartolomé	Fernandina	Bartolomé
Audubon Shearwater	22,782	160	133 ± 185	80 ± 99	62	5
Blue-footed Booby	9,244	190	73 ± 99	10 ± 10	46	49
Masked Booby	0	5	0	2 ± 1	0	8
Brown Noddy	1,721	188	20 ± 18	15 ± 15	31	33
Brown Pelican	1,064	82	11 ± 12	5 ± 3	37	44
Galápagos Penguin	364	108	5 ± 4	7 ± 4	26	39
Magnificent Frigatebird	51	28	5 ± 5	6 ± 5	4	13
Flightless Cormorant	13	0	1 ± 0.5	0	4	0
Galápagos Sea Lion	14	10	4 ± 3	3 ± 5	1	8
Bottlenose Dolphin	65	0	11 ± 7	0	2	0

mean ± SD or SE. The software packages SYSTAT (ver. 5.0) and STATISTICA (ver. 5.0) were used to perform statistical tests, and a critical value of $P \leq 0.05$ was accepted as significant. Student's *t*-tests and both univariate (ANOVA) and multivariate analysis of variance (MANOVA) were used to test for differences between groups. Canonical correlation analyses were used to determine whether feeding flocks were correlated with environmental factors (SST), and linear regressions and Pearson correlation analyses were used to test for significant associations between variables. In tests where multiple comparisons were made, I used a Bonferroni-adjusted significance level of 0.007, based upon the comparison of the eight seabird species.

RESULTS

SPECIES COMPOSITION

Eight species of seabirds participated in the feeding flocks at both sites. However, no flock comprised more than five species in the area near Fernandina or more than three near Bartolomé; the mean number of participant species was 2 for each site (Fernandina: 2.1 ± 1.3, n = 277, Bartolomé: 2.1 ± 1.1, n = 39). Six out of eight species were common participants in flocks at both islands; the Masked Booby (*Sula dactylatra*) only participated in flocks near Bartolomé, and the Flightless Cormorant only participated in flocks near Fernandina. The most common participants in feeding flocks were Audubon Shearwaters (*Puffinus lherminieri*) and Blue-footed Boobies (*Sula nebouxii*) near Fernandina, and Brown Pelicans (*Pelecanus occidentalis*), Galápagos Penguins, and Blue-footed Boobies near Bartolomé (Table 1). Even though Audubon Shearwaters are fairly widespread throughout the Archipelago, they participated in only 5% of the feeding flocks in the waters near Bartolomé. In contrast, off the coast of Fernandina, they were recorded in 62% of the flocks.

FREQUENCY OF FLOCKS AND SST

A total of 277 feeding flocks was recorded near Fernandina, and 39 off Bartolomé Island. Flocks occurred more frequently near Fernandina (5.2 ± 6.8 flocks day^{-1}, n = 51 flocks), with 0.9 flocks hr^{-1}, than near Bartolomé (2.8 ± 2.1 flocks day^{-1}, n = 17), with 0.4 flocks hr^{-1}.

The mean SST of the water near Fernandina was significantly colder than the water off Bartolomé (18.9 ± 1.0°C , n = 54, and 21.6 ± 1.3°C, n = 21, respectively; $t_{75} = 8.14$, $P < 0.001$). Near the Fernandina site, both the number of flocks and the total number of birds in flocks were negatively correlated with SST ($r = -0.6$, $P < 0.001$ and $r = -0.7$, $P < 0.001$, respectively). The relationship between SST and the abundances of the individual species that participated in foraging flocks was negative for all species at the Fernandina site, except Flightless Cormorants and Magnificent Frigatebirds (*Fregata magnificens*), most likely because of the small sample sizes for these two species. Near Bartolomé, there were no significant relationships between SST and the number of flocks ($r = -0.29$, $P = 0.34$), or the number of birds in flocks ($r = -0.31$, $P = 0.35$).

DISTANCE FROM SHORE

Flocks occurred most often close to shore and decreased in frequency with distance from shore (Fig. 2). Near Bartolomé, 71% of the flocks oc-

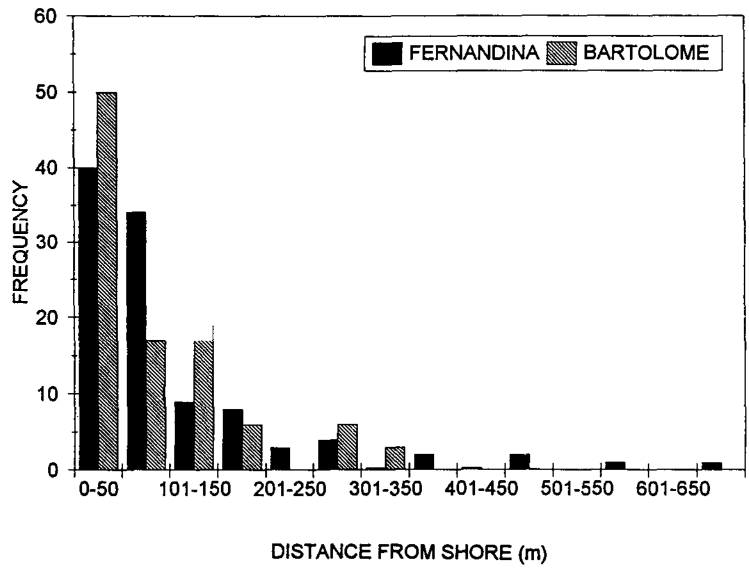

FIGURE 2. Frequency distribution of the distance offshore of feeding flocks near Fernandina and Bartolomé Islands.

curred within 60 m of shore (range 2–350 m). The flocks near Bartolomé occurred on average closer to shore than those in the waters off Fernandina (81.1 ± 93.1 m , n = 31 and 119.5 ± 139.2 m, n = 267, respectively; r = 0.15, $F_{1,298}$ = 7.0, $P < 0.01$).

Near Fernandina, there was a significant negative correlation between the number of species in flocks and the distance offshore ($r = -0.26$, $P < 0.01$, n = 185 flocks), but a significant positive correlation between the total number of birds in the flock and the distance offshore (r = 0.21, P = 0.001, n = 185). Thus, there was a reduction in species diversity with an increase in the distance offshore of the flocks, even though flocks increased in size with distance from shore. Near Bartolomé the trend was similar, although not significant for the number of species or number of birds.

The different species within the flocks foraged nonrandomly with respect to the distance from shore. Flocks of birds where Galápagos Penguins, Brown Pelicans, and Brown Noddies (*Anous stolidus*) were present were significantly closer to shore than when these species were absent (Table 2). At Bartolomé, the trends were similar to those on Fernandina, although not significant. Blue-footed Boobies and Audubon Shearwaters foraged the farthest offshore at Fernandina, whereas Masked Boobies foraged the farthest offshore at Bartolomé.

DURATION OF FLOCKS

The mean duration of the flocks near Fernandina was 51.3 ± 102.1 min, significantly greater (t_{206} = 2.1, $P < 0.05$) than the mean duration of the flocks near Bartolomé (20.2 ± 21.4 min). In the waters near Fernandina, about half of the feed-

TABLE 2. Mean distance offshore for flocks where Galápagos Penguins, Brown Pelicans, and Brown Noddies were present and absent at the Fernandina site. Total number of flocks = 259.

	Distance offshore (m)		
	Present	Absent	t
Galápagos Penguin	8.5 ± 75.4	138.5 ± 156.9	3.3**
Brown Pelican	73.5 ± 82.4	152.0 ± 160.5	5.3**
Brown Noddy	94.6 ± 106.2	135.9 ± 154.2	2.8*

* $P < 0.01$.
** $P < 0.001$.

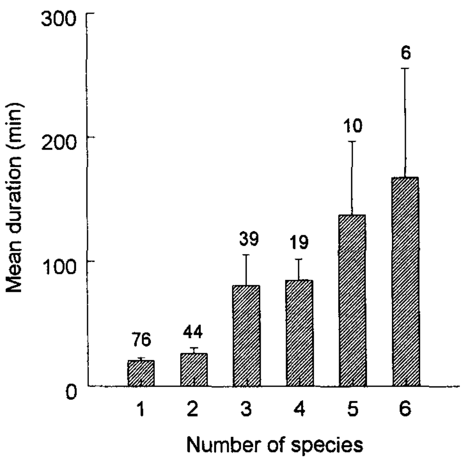

FIGURE 3. Mean (± SE) duration of feeding flocks composed of one to six species near Fernandina Island.

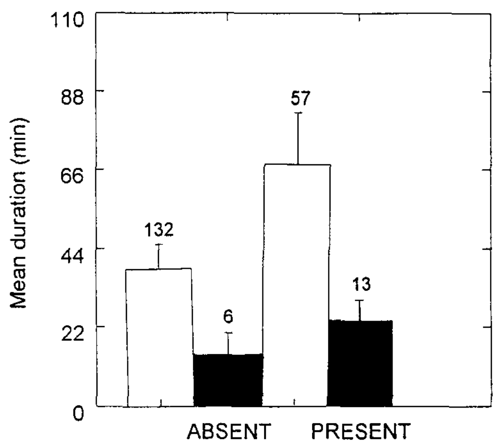

FIGURE 4. Duration of feeding flocks (± SE) with Galápagos Penguins and Flightless Cormorants present and absent near Fernandina and Bartolomé Islands. Solid bars represent Bartolomé and the open bars represent Fernandina.

ing flocks (53%) lasted 20 min or less. However, 16% of the feeding flocks observed had a duration greater than 1 hr, and several lasted most of a day. The maximum duration of all the flocks recorded was 11 hr and occurred at the Fernandina site on July 11.

Near Fernandina, the number of species in a flock and the total number of birds in a flock both increased with the duration of flocks (number of species: $r = 0.49$, $P < 0.001$, $n = 185$ flocks; and number of birds: $r = 0.36$, $P < 0.001$, $n = 185$ flocks). Near Bartolomé, there also was a positive correlation between the number of birds that formed a flock and the duration of the flock ($r = 0.50$, $P < 0.05$, $n = 16$), although there was no relationship between the number of species and the duration of the flock. Feeding flocks that contained multiple species were of greater duration than single species flocks ($t_{192} = 5.0$, $P < 0.01$, Fig. 3).

Flocks that included diving birds (penguins and/or Flightless Cormorants at Fernandina and only penguins at Bartolomé) were of greater duration than those that did not contain these species ($t_{187} = 3.4$, $P < 0.01$, Fig. 4), although the results for Bartolomé were not significant. There was a significant negative relationship between the abundance of Blue-footed Boobies and the duration of flocks near Fernandina ($r = -0.15$, $P < 0.05$, $n = 90$), suggesting that large numbers of Blue-footed Boobies tend to disrupt flocks.

SPECIES ASSOCIATIONS

Certain species of seabirds in the Galápagos often were found together. Near Fernandina, Brown Noddies were positively associated with penguins ($r = 0.31$, $P < 0.001$, $n = 268$ flocks) as well as with pelicans ($r = 0.59$, $P < 0.001$, $n = 268$ flocks). Brown Pelicans were positively associated with Galápagos Penguins both at Fernandina and Bartolomé (Fernandina: $r = 0.28$, $P < 0.001$, $n = 268$; Bartolomé: $r = 0.34$, $P < 0.001$, $n = 28$). In addition, penguins were positively associated with Flightless Cormorants at Fernandina ($r = 0.27$, $P < 0.001$, $n = 54$). Audubon Shearwaters and Blue-footed Boobies rarely occurred together, despite the fact that these two species were the most numerous in feeding flocks. These two species co-occurred in only 17% of the flocks that I recorded. Indeed, there was a significant negative correlation between the presence of these two species ($r = -0.43$, $P < 0.01$, $n = 268$).

Flocks were significantly larger at Fernandina when Blue-footed Boobies or Audubon Shearwaters were present (boobies: $t_{266} = 4.43$, $P < 0.001$; shearwaters: $t_{266} = 4.42$, $P < 0.001$).

PREY AND SEABIRD BEHAVIOR

Collected fish samples from Fernandina were identified by P. Smith as Pacific Sardines (*Sardinops sagax*), and the fish collected at Bartolomé was identified by A. Kitaysky as possibly a sandlance (*Ammodytes* spp.).

Within individual flocks, penguins tended to dive under the school and feed on the way up to the surface, or picked off fish that were at the bottom sides of the school (Mills, unpubl. data). Flightless Cormorants approached the fish from the sides, preying on fish in the periphery of the school. The behavior of these two species appeared to keep the fish school close to the surface and clumped, where surface or near-surface feeding birds such as Audubon's Shearwaters, Brown Pelicans, and Brown Noddies could access the fish more easily. Blue-footed Boobies, on the other hand, generally dive in the center of the flock (Mills 1996), and presumably in the center of the fish school. In large feeding flocks, Blue-footed Boobies coordinate their diving, so that they dive simultaneously. This coordinated activity may stun and confuse the fish momentarily, allowing the boobies to feed on them.

DISCUSSION

SST AND FEEDING FLOCKS

A greater number, frequency, and duration of flocks were observed off Fernandina, the island with the lower average SST; the number of flocks and abundances of the individual species was greater at lower SST at both sites. Seabird flocks occur mostly when SST is below 23°C, because low SST is associated with higher productivity and a more abundant food supply (Boersma 1974, 1978). In the Galápagos, there is spatial as well as temporal variation in SST and productivity, either of which, or both, may have influenced the species composition, frequency, distance offshore, and duration of the flocks recorded in this study.

At both sites there was a general decrease in SST as the cold season progressed. However, the overall SST was colder on Fernandina, and it was coupled with an increase in seabird activity, including an increase in the number and frequency of flocks, migration of penguins into the area, and the onset or increase in the reproduction of penguins and Flightless Cormorants (Mills 1994). In contrast, no increase in activity was observed on Bartolomé during my stay, although the time that I was on Bartolomé was less than my stay at Fernandina.

The spatial variation in sea-surface temperatures and productivity in the Galápagos Islands is the result of the Cromwell Current, which travels from west to east, and is forced to the surface around the two westernmost islands of Fernandina and western Isabela. This phenomenon results in the influx of nutrients into the upper water layers, lowering the temperature of the surface waters and increasing its productivity (Houvenaghel 1978, 1984, Feldman 1986).

The spatial variability in oceanographic conditions within the archipelago may result in a possible difference in the type or quantity of prey that is available at the two islands in the present study, which may explain the differences observed in the flocks. There is little information on pelagic fish communities within the archipelago and the information gathered from the present study is not sufficient to answer this question. However, I never observed large schools of sardines on Bartolomé as I did on Fernandina. Another possible explanation of the differences recorded in the feeding flocks may be the different times within the cold season in which the data were collected, and based upon this, one may predict flocks with different species compositions. Except for the fact that Flightless Cormorants were absent from the central island of Bartolomé, and Masked Boobies were absent from the Fernandina flocks, the remainder of the species were found at both sites and breed in the vicinity of both areas (Harris 1982). Even though the species that were recorded in the flocks at both islands were similar, the participation frequency within the flocks differed between islands. The most striking difference was the participation of Audubon Shearwaters. This species participated in almost every flock at Fernandina, but only participated in two at Bartolomé. It is unclear why this was the case, although my observations of foraging Audubon's Shearwaters coincide with the more productive areas of the archipelago. Based upon the lower SST, the increase in seabird activity, and the greater number and frequency of feeding flocks near Fernandina, it seems fair to conclude that prey were more abundant at this site than in the area around Bartolomé, at least at the times that I was collecting data.

THE EFFECT OF DIVERS ON FLOCK DURATION

When penguins or cormorants were present, the flocks lasted longer near Fernandina. In the Bartolomé area, flocks lasted longer when penguins were present, although the results were not significant. The Galápagos Penguin population near Bartolomé is relatively low compared to the Fernandina population (Mills 1993, Soria et al. 1994, Vargas 1995). On five occasions, feeding flocks that were driven by fish such as tuna (unidentified species) were observed near Bartolomé. It is possible that because of the smaller number of sub-surface avian foragers found in this area, flocks more often are driven and maintained by sub-surface predators such as tuna, which would be similar to the driving force of flocks in the open ocean and away from shore. I also observed feeding flocks around southern Isabela and Fernandina islands that were initiated by Sierra mackerel (*Scomberomus sierra*). These mackerel-based flocks were seen while I was traveling between islands, and the flocks were farther offshore than those flocks recorded in the present study.

Diving animals play important roles in maintaining multispecies feeding flocks in many oceans of the world. In the eastern tropical Pacific, a high percentage of seabird feeding flocks are initiated and maintained by sub-surface predators, specifically dolphin (*Stenella attenuata* and *S. longirostris*) and yellowfin tuna (*Thunnus albacares*), which drive smaller fish to the surface (Au and Pitman 1986, Ballance 1993). Pitman and Ballance (1992) found that 76% of the Parkinson's Petrels (*Procellaria parkinsoni*) that they observed were associated with feeding dolphins. In addition, Sooty Terns (*Sterna fuscata*), because they are unable to feed deeper than a few centimeters below the surface of the water, also depend upon prey made available to them by sub-surface predators (Au and Pitman 1986). In the Bering Sea, in 67% of the incidences where feeding gray whales (*Eschrichtius robustus*) created mud plumes, seabirds foraged in the plumes (Obst and Hunt 1990). Several diving seabirds, such as species of Antarctic and Sub-Antarctic penguins (Harrison et al. 1991), Magellanic Penguins *Spheniscus magellanicus* (Jehl 1974, Boswall and MacIver 1975), Murres *Uria* spp. (Chilton and Sealy 1987, Hunt et al. 1988), and Marbled Murrelets *Brachyramphus marmoratus* (Mahon et al. 1992) have been noted to actually make prey available to other species (usually surface-feeding seabirds) by driving prey to the surface, keeping prey close to the surface, or by inadvertently injuring or killing prey that can be fed upon by birds at the surface.

If the presence of diving species increases the overall duration of flocks, then this suggests that divers actually help in making prey available to other species of birds that are unable to dive for their prey. Sub-surface foragers accomplish this by diving at the periphery of the flock and approaching prey from the bottom or edges of the school, as my observations of penguins and cormorants suggest (Mills, unpubl. data). In near-shore waters, flocks may form as a result of the concentration of prey due to physical effects such as fronts, internal waves, and tidal currents in combination with shallow water, or by biological factors such as sub-surface animals driving prey to the surface. In certain areas of the Galápagos, these near-shore flocks, once formed, are maintained by pursuit-diving species. Away from shore, where diving seabirds are rare or absent, surface or near-surface foraging seabirds rely on other methods of keeping prey close to the surface.

SPECIES INTERACTIONS

Flocks form where there is an abundance of food available to predators (Sealy 1973, Haney and McGillivary 1985). Once one or several birds begin actively feeding, other birds that are in the vicinity approach that area and begin feeding as well, which in turn attracts other birds from farther away (Sealy 1973, Hoffman et al. 1981, Haney et al. 1992). Seabirds continue to feed until they deplete the food resource, become satiated, or until the prey are able to escape. Visual recruitment is an important factor in flock formation. This importance is clearly revealed in the positive relationship found in the present study between the number of species, the number of individuals, and the duration of the flock. Thus, flocks that last longer than others have a better chance of attracting a greater number of species and a greater number of birds. Hoffman et al. (1981) used the name of "catalysts" to describe those species whose active foraging is very conspicuous and is used by other birds as indicators of areas with a high abundance of prey, therefore allowing a rapid development of a flock. I found that Audubon Shearwaters and Blue-footed Boobies were the catalysts for the Fernandina flocks, and Brown Pelicans and penguins were the catalysts of flocks in the vicinity of Bartolomé. Shearwaters and Boobies are very conspicuous when they are feeding on a prey patch. However, foraging penguins are not highly visible and it may seem odd that they would act as catalysts. This may be explained by the fact that penguins are highly associated with pelicans, whose feeding is highly visible. In my study, it was almost always the case that flocks that contained penguins also contained pelicans.

"Suppressors" are those species that disrupt the spatial structure of a flock because of their feeding habits (Hoffman et al. 1981). In the Galápagos, Blue-footed Boobies, which are plunge-divers, may act as suppressors, given their tendency to dive in the center of a fish school. This type of feeding method may cause prey to disperse and therefore shorten the longevity of the flock. Likewise, Bayer (1983) hypothesized that the feeding flocks that he observed in Alaska were of short duration because the feeding activity of the plunging Black-legged Kittiwakes (*Larus tridactyla*) dispersed the prey. Hoffman et al. (1981) also found that both the Short-tailed (*Puffinus tenuirostris*) and Sooty Shearwaters (*P. griseus*), which pursuit-plunge, dispersed prey.

Species are attracted to a common resource and therefore, as Veit (1995) notes, positive associations between different species are expected. However, the nature of the interactions among species may be useful in predicting which species are most often found together in flocks and which are not (in the case of a negative relationship). Where feeding niches overlap, certain species may actually avoid each other (but see Veit 1995). Ashmole (1968) found that around Christmas Island, *Anous stolidus* fed closer to land than *Sterna fuscata,* which flew over flocks of *A. stolidus* to forage further offshore, even though they feed on similar-sized prey. The only negative relationship encountered in the present study was between Blue-footed Boobies and Audubon Shearwaters. This suggests that these two species actively avoid each other, although the reason for this is unclear. Perhaps Audubon Shearwaters tend to avoid areas where Blue-footed Boobies are feeding because of their prey-dispersing tendencies. Another possible explanation is that they may be feeding on different prey. Boersma (1974) and Harris (1977) both report that Audubon Shearwaters in the Galápagos feed on zooplankton and Blue-footed Boobies feed on medium-sized fish (Harris 1977). However, on several occasions on Fernandina I observed shearwaters feeding on sardines as did other species in the feeding flocks, including Blue-footed Boobies. Perhaps on those occasions when shearwaters were not found foraging with boobies, they were feeding on zooplankton, although this has not been determined.

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