THE FORAGING ECOLOGY OF PERUVIAN SEABIRDS

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ABSTRACT.—Most feeding by seabirds in the Peruvian Coastal Current, an upwelling of high productivity off the west coast of South America, takes place in groups. The major prey is an anchovy (*Engraulis ringens*), which occurs in large shoals and is exploited mainly by three species: the Peruvian Booby (*Sula variegata*), Peruvian Brown Pelican (*Pelecanus occidentalis thagus*), and Guanay Cormorant (*Phalacrocorax bougainvillii*). Other foraging situations have different species' compositions, and these appear to be related to the size, depth, and duration of availability of prey. Dominance interactions between species may be important in structuring flocks that are scavenging or feeding on plankton swarms. Interspecific piracy seems unimportant in flocks foraging on fish shoals. Certain species usually arrive first at new feeding situations. These species may be used as guides by other species or merely may be faster and thus reach food sources first. Studies of foraging of seabirds should be a valuable addition to the study of the distribution of birds at sea. *Received 2 April 1982, resubmitted 18 March 1983, accepted 8 July 1983.*

SEABIRDS have some of the largest foraging ranges of any vertebrates: birds with eggs or young may travel 1,000 km from the nest to feed (Fisher and Lockley 1954, Harris 1977, Nelson 1979, Dunnet and Ollason 1982). Despite the fact that they search over such large areas, they forage over very small areas on local concentrations of prey (see Brown 1980 for a review). The study of these patches and their use by birds should improve our understanding of the ecology and distribution of seabirds at sea. For example, Erwin (1977) linked differences in use of patches by three larids to differences in their nesting ecology. Hoffman et al. (1981) showed that the presence of some species may affect the foraging of others; flocks are more than aggregations of noninteracting birds attracted to a common food source.

The structure of seabird flocks has never been investigated in low-altitude upwelling areas. The present paper reports on the numbers and behaviors of seabird species present in different types of feeding flocks in the Humboldt or Peruvian Coastal Current off the west coast of South America. Three general questions were investigated: (1) what percentage of birds forage in flocks over patches of prey, (2) does the species' composition of flocks differ in accordance with the type of feeding situation, and (3) are flocks merely aggregations of independently attracted birds or do the species interact to enhance or inhibit the discovery or exploitation of patches of food (e.g. Hoffman et al. 1981)?

METHODS

The study area.—I gathered most of my observations on Isla Mazorca (11°23'S, 77°45'W), Departamento de Lima, Peru. The island lies approximately 15 km offshore in an area of frequent upwelling (Zuta and Urquizo 1972) and is the site of a large and long-established colony of guano birds, especially Peruvian Booby (*Sula variegata*), Peruvian Brown Pelican (*Pelecanus occidentalis thagus*), and Guanay Cormorant (*Phalacrocorax bougainvillii*) (Murphy 1925; Duffy 1981, 1983a). Other observations were made on 12 boat trips between Isla Mazorca and the port of Huacho (11°07'S, 77°44'W) and from the shore at La Puntilla, Callao Harbor (12°05'S, 77°44'W).

The Peruvian Current is one of the most productive of marine ecosystems (Cushing 1971). It extends from northern Chile to northern Peru and out to the Galapagos Islands, Ecuador (Murphy 1936). The upwelling is confined to a relatively narrow band along the coast (Cushing 1971). The dominant fish species of the upwelling is the Peruvian anchovy or anchoveta (*Engraulis ringens*), which makes up about 90% of pelagic fish stocks in the current, based on relative abundances of eggs and larvae (Santander 1981). The anchoveta is eaten by a wide variety of seabirds, predatory fish, and marine mammals (Coker 1920, Murphy 1936, Jordan and Fuentes 1966, Paulik 1971). A commercial fishmeal industry, which began in 1955, took catches of up to 12 million metric tons of anchoveta, becoming the world's largest single-species fishery before the fish stock and industry collapsed

TABLE 1. Percentage use of different foraging situations by Peruvian seabirds (+ = <0.1).

Species	Number observed	Percentage in foraging situation: Shoal	Scavenging	Sea-lions	Zooplankton	"Other"
Humboldt Penguin (*Spheniscus humboldti*)	18	11	–	–	–	88
Waved Albatross (*Diomedea irrorata*)	52	48	–	–	–	52
Wilson's Storm-Petrel (*Oceanites oceanicus*)	54	94	–	6	–	–
Elliot's Storm-Petrel (*Oceanites gracilis*)	1	–	–	–	–	100
Markham's Storm-Petrel (*Oceanodroma markhami*)	1	–	–	–	–	100
Unidentified storm-petrels	21	5	–	–	–	95
Cape Petrel (*Daption capense*)	2	–	–	–	–	100
Sooty Shearwater (*Puffinus griseus*)	61,234	98	–	+	+	2
Peruvian Diving-Petrel (*Pelecanoides garnoti*)	61	7	–	–	–	93
Magnificent Frigatebird (*Fregata magnificens*)	1	–	–	–	–	100
Neotropical Cormorant (*Phalacrocorax olivaceus*)	11	–	–	–	–	100
Guanay Cormorant (*Ph. bougainvillii*)	115,542	99	–	–	–	1
Red-legged Cormorant (*Ph. gaimardi*)	114	51	–	–	–	49
Blue-footed Booby (*Sula nebouxii*)	2	50	–	–	–	50
Peruvian Booby (*S. variegata*)	402,802	95	–	+	–	5
Peruvian Pelican (*Pelecanus occidentalis thagus*)	3,341	69	+	+	–	30
Red-necked Phalarope (*Phalaropus lobatus*)	1	–	–	–	–	100
Pomarine Jaeger (*Stercorarius pomarinus*)	11	27	–	–	–	72
Jaeger sp. (*Stercorarius* sp.)	7	71	–	–	–	28
Grey Gull (*Larus modestus*)	1,429	41	+	3	43	12
Band-tailed Gull (*L. belcheri*)	554	4	49	3	16	28
Kelp Gull (*L. dominicanus*)	94	3	71	12	14	–
Franklin's Gull (*L. pipixcan*)	743	36	11	1	–	51
Sabine's Gull (*L. sabini*)	86	–	–	–	21	79
"Comic" Tern (*Sterna* sp.)	1,328	1	–	+	44	55
Elegant Tern (*Sterna elegans*)	5	60	–	–	–	40
Sandwich Tern (*S. sandvicensis*)	2	–	–	–	–	100
Peruvian Tern (*S. lorata*)	2	–	–	–	–	100
Inca Tern (*Larosterna inca*)	7,195	26	1	8	30	34
Percentage of total number of birds ($n = 561{,}605$)		94.4	0.1	0.2	0.6	4.7
Number of observations for each foraging type		65	67	49	37	137
Number of species in each foraging type		20	6	10	7	27

in 1972–1973 (Idyll 1973; Duffy 1983b). A pilchard (*Sardinops sagax*) was thought to have replaced the anchoveta during the 1970's (Walsh et al. 1980), but the data are equivocal.

Observations.—I made as many observations of marine birds as possible during the course of other fieldwork between September 1977 and March 1978. I recorded all foraging birds encountered. Species are listed in Table 1.

Most seabirds in the Peruvian Coastal Current are relatively easy to identify. The exceptions are the white "comic" terns (*Sterna* spp.) and the jaegers (*Stercorarius* spp.). Unidentified birds are treated separately but make up only a minuscule proportion of birds observed. I determined numbers in small groups (less than 20–50) by direct counts of individuals. In larger groups, I estimated a subgroup and then counted the number of such subgroups. I defined feeding techniques by following a simplified version of Ashmole's (1971) terminology: piracy, dipping, surface-seizing, plunging, pursuit-plunging, and surface-diving. I added "terrestrial-seizing" for birds feeding on land or in the intertidal zone. For dipping species, I measured duration of contact with water, using a spring-operated stopwatch and subtracting 0.2 s for my reaction time. For diving and plunging species, I measured the duration of submergence from first contact until the bird's head emerged. I measured rates of dipping or surface-seizing by following individual birds until they completed 10 attempts or ceased feeding. I recorded interspecific interactions that included association with marine mammals, aggressive displacement from potential sources of food, kleptoparasitism, and order of arrival at food sources. Not all of these data could be collected simultaneously, so, in the results, the sample sizes may differ between different measurements.

I assumed that the foraging behaviors and situations I encountered were proportional to their true abundances. I attempted to observe as wide a variety of foraging situations as possible by watching from both ships and land; by attempting observations at

TABLE 2. Species' occurrences over dense shoals of fish (+ = < 0.1).

Species	Number present	Number/ occurrence	All birds at shoals (%)	Frequency at shoals (%)
Peruvian Booby	381,957	6,160	68	95
Guanay Cormorant	114,380	2,288	20	77
Sooty Shearwater	60,036	7,504	11	12
Peruvian Pelican	2,320	122	0.4	29
Inca Tern	1,888	118	0.3	25
Grey Gull	584	117	0.1	8
Franklin's Gull	270	39	+	11
Red-legged Cormorant	58	12	+	8
Wilson's Storm-Petrel	51	25	+	3
Waved Albatross	25	4	+	9
Band-tailed Gull	23	7	+	5
"Comic" tern	8	3	+	5
Jaeger sp.	5	1.3	+	5
Peruvian Diving-Petrel	4	0.6	+	5
Pomarine Jaeger	3	1.0	+	5
Elegant Tern	3	3	+	1.5
Kelp Gull	3	3	+	1.5
Humboldt Penguin	2	1	+	3
Blue-footed Booby	1	1	+	1.5
Storm-petrel sp.	1	1	+	1.5

night, using a full moon or bioluminescence; and by combining observations from before (September–October) and during (November–March) the breeding season. The 7-month period should also have been long enough to sample any seasonal variations in foraging.

RESULTS

This study was conducted after the collapse of the anchoveta stock (Idyll 1973). This collapse has affected the populations of guano birds (Duffy 1983b), but food did not appear to be in short supply around Isla Mazorca during my study. Foraging trips by Guanay Cormorants and Peruvian Boobies took less than 3 h (Duffy 1983a). Vogt (1942) considered trips over 6 h to indicate food shortages. I frequently observed shoals of fish, and birds feeding upon them, around the islands. After October, anchovetas were frequent in regurgitations or stomach casts of the cormorant, booby, and pelican. I assume that the foraging behaviors I observed were similar to those used before the collapse of the anchoveta stock.

FORAGING SITUATIONS

A total of 561,605 individuals of at least 28 species occurred in 355 observations of birds foraging (Table 1). Only 48 of all individuals seen were feeding alone. After fieldwork, I found that the records could be divided into five arbitrary but recognizable foraging situations: shoal-foraging, scavenging, foraging over sealions, feeding on zooplankton swarms, and miscellaneous other situations. These are referred to as shoal, scavenging, sealion, zooplankton, and "other" foraging groups throughout this paper.

Foraging over shoals of fish.—Shoals of anchoveta and other fish were frequently fed upon by seabirds in the waters around Mazorca. Bird flocks were characteristically very dense. I assumed other such dense bird flocks were also feeding on fish shoals, even when I could not see the fish. Of all individuals, 94% foraged over shoals of fish. Twenty species participated (Table 1), but 98% of the individuals over shoals were of three species: Peruvian Booby, Guanay Cormorant, and Sooty Shearwater (Table 2). Inca Terns and Brown Pelicans were less numerous than shearwaters but more consistently present. Other species comprised 0.1% or less of the flocks. The mean flock size over shoals was 8,363.5 birds (SD = 12,629.3; $n = 65$).

Many large groups foraging over shoals persisted for 2–3 h or more. In other cases, instead of large groups, the birds formed a mosaic of smaller aggregations, which persisted for only about 15 min. Peruvian Boobies initiated 9 of 10 such ephemeral groups.

TABLE 3. Species' occurrences over sealions.

Species	Number present	Number/occurrence	All birds with sealions (%)	Frequency with sealions (%)
Inca Tern	567	13.8	80.6	84
Grey Gull	43	4.3	6.1	20
Sooty Shearwater	42	6.0	6.0	17
Band-tailed Gull	16	1.4	2.2	22
Kelp Gull	11	1.1	1.6	20
Peruvian Booby	11	2.2	1.6	10
Franklin's Gull	5	1.0	0.7	10
"Comic" tern	4	2.0	0.6	4
Wilson's Storm-Petrel	3	3.0	0.4	2
Peruvian Pelican	1	1.0	0.1	2

TABLE 4. Species' occurrence at zooplankton swarms.

Species	Number present	Number/occurrence	All birds at zooplankton (%)	Frequency at zooplankton (%)
Inca Tern	2,191	66.4	62	89
Grey Gull	621	28.2	17.5	59
"Comic" tern	580	30.5	16.4	51
Band-tailed Gull	87	10.9	2.4	22
Sooty Shearwater	27	5.4	0.8	13.5
Sabine's Gull	18	9.0	0.5	5
Kelp Gull	13	2.6	0.4	13.5

Foraging over sealions.—The southern sealion [*Otaria byronia* (*flavescens*)] provided food for the birds, either by chasing fish to the surface or by thrashing large fish and cephalopods to pieces. Birds usually fed only in a very small area immediately surrounding the sealion. Ten species, but only 0.1% of all individuals, foraged over sealions (Table 1). The major beneficiary of sealion activity was the Inca Tern: 80% of the birds over sealions belonged to this species (Table 3). The other nine species occurred irregularly and in small numbers. Average flock size over sealions was 14.3 birds (SD = 45.7; $n = 49$).

Foraging on zooplankton swarms.—Dipping or surface-seizing of zooplankton involved seven species and 0.6% of all individuals (Table 1). Only three species were common: Inca Terns, "comic" (mainly Arctic) terns, and Grey Gulls made up 96% of all neuston-feeders (Table 4). Sooty Shearwaters and Kelp, Band-tailed, and Sabine's gulls were rare and irregular.

The prey I observed were 1-cm, reddish crustacea swarming in densities of up to 1,000/m^2 at or just below the surface. Some patches persisted for hours, but most were short-lived, lasting no more than 5 min. Most of the neuston-feeding took place in the austral spring, before anchoveta became common in stomach pellets of cormorants.

"Comic" and Inca terns hovered in "cones" of birds over zooplankton patches: a few birds would be close to the surface, and a much greater number would be above and outside. Hovering was punctuated by irregular bouts of dipping. Sabine's Gulls landed briefly on the water to peck at prey, whereas the three other gull species sat on the water while feeding. The species occupied characteristic positions around the cone of hovering birds. Grey Gulls (with Kelp and Band-tailed gulls if present) sat on the surface below the cone, Inca Terns were at the center of the hovering birds, and "comic" terns were at the periphery.

Grey Gulls had the highest feeding rates, followed by Inca and then "comic" terns (Table 5). The higher rate of the Grey Gull was not due entirely to the difference in foraging methods (surface-seizing vs. hovering + dipping): Band-tailed and Sabine's gulls had lower rates than the terns, even though Band-tailed Gulls foraged in the same manner as Grey Gulls and Sabine's Gulls used a foraging method intermediate between dipping and surface-seizing.

During one observation period when several species were foraging over short-lived patches of zooplankton, Inca Terns arrived before Grey Gulls at surface patches 7 of 7 times (binomial, $P = 0.008$). The mean group size during all zooplankton feeding was 95.9 (SD = 83.2; $n = 37$).

Scavenging.—At sea, birds scavenged fish offal, sealion corpses, and nestlings that had fallen from the guano islands. On land, they scavenged bird corpses, pellets regurgitated by cormorants, and regurgitations from nestlings. Seven species, but only 0.1% of all individuals in this study, scavenged (Table 1). Band-tailed Gulls were the most numerous, both in numbers and in frequency of occurrence (Table 6). Kelp Gulls were frequent, but rarely more than two birds were present. Inca Terns occurred infrequently but in large numbers.

Kelp Gulls specialized on corpses (43 of 67; 67%), whereas only 57 of 272 (21%) Band-tailed Gulls were necrophagous. The difference is significant (2×2 contingency table, corrected for

TABLE 5. Feeding rates (dips or pecks per second).

Species	$\bar{x}$	SD	n	Number of birds
Grey Gull	0.584	0.466	477	50
Inca Tern	0.355	0.181	452	53
Arctic Tern	0.166	0.062	147	18
Band-tailed Gull	0.153	0.146	71	11
Sabine's Gull	0.120	—	7	1

TABLE 6. Species' occurrences in scavenging situations.

Species	Number present	Number/occurrence	All birds scavenging (%)	Frequency scavenging (%)
Band-tailed Gull	272	5.7	51	70
Inca Tern	97	13.9	18	10
Franklin's Gull	86	17.2	16	7.5
Kelp Gull	67	2.4	12.6	42
Grey Gull	7	1.4	1.3	7.4
Peruvian Pelican	3	1.5	0.6	3.0

continuity; $\chi^2 = 19.1$; $P < 0.001$). The most important sources of food for Band-tailed Gulls while scavenging were regurgitated pellets of cormorants (101 of 272; 37%). Inca Terns and Franklin's and Grey gulls fed on small particulate offal in the water.

This gradient in food size paralleled the apparent dominance hierarchy. Kelp Gulls invariably displaced Band-tailed and Grey gulls. Band-tailed Gulls displaced Franklin's Gulls and Inca Terns, and Franklin's Gulls displaced Inca Terns. Reversals were not observed.

Mean group size was 8.1 birds (SD = 19.8; $n = 67$).

"Other" foraging.—This group includes those records that did not fall into the preceding categories. Twenty-seven species and 4.7% of all individuals were involved in foraging situations lumped into this category (Table 1). Among the different situations were the few inshore records from sandy bottoms, very dispersed feeding on what were probably small anchoveta shoals (most of the Peruvian Booby, Sooty Shearwater, and Guanay Cormorant records), solitary foraging, and loose aggregations of apparently solitary species (Humboldt Penguin and Red-legged Cormorant). The most common species were the Peruvian Booby (73.6%) and Inca Tern (Table 7). The 25 other species comprised less than 18% of the individuals in this category. No species occurred in all "Other" foraging situations. Even the most common by number, the Peruvian Booby, occurred only 36% of the time. Fourteen of the species occurred in less than 5% of the observations. Group size was not calculated because of the artificial nature of this category.

FORAGING BEHAVIOR

Seven foraging techniques were used by the species observed in this study (Table 8). Seven species used only a single technique [piracy, 2; plunge, 1; pursuit-plunge, 1; surface-dive, 3 (or 4 if a single piracy record for Guanay Cormorant is excluded)]. Two species used 2 techniques, 4 species used 3, and 4 species used 4. When foraging methods are ranked according to their most common usage (Table 8), surface-seizing proves to be the dominant foraging method of 6 species, surface-diving of 4 species, dipping of 3 species, piracy of 2 species, pursuit-plunging of 1 species, and plunging of 1 species. Species that primarily used surface-diving had the narrowest range of foraging methods, only 1.25 per species. Species that primarily used terrestrial seizing (four gulls) had the widest range, averaging four techniques each. Surface-seizing species averaged 3.6 methods; dipping species, 3.5; pirating species, 2.8; plunging species, 2.4; and pursuit-plunging species, 2.0.

The species varied greatly in the amount of time spent on individual feeding attempts, based on duration of contact with water (Table 5, Fig. 1). Dipping by Inca Terns took only 0.25 s (SD = 0.325; $n = 68$) while Humboldt Penguins were submerged a mean time of 75.0 s (SD = 44.9; $n = 14$). Only three species had submergence durations of over 20 s (Fig. 1): solitary Guanay Cormorants, Red-legged Cormorants, and Humboldt Penguins.

Dives by Guanay Cormorants foraging at anchoveta shoals were much shorter (9.55 s; SD = 4.45; $n = 144$) than dives by Guanays elsewhere (32.85 s; SD = 22.15; $n = 16$; $P < 0.001$, $t = 11.04$; $F = 24.77$; correction for unequal variances). On the other hand, Peruvian Boobies plunging at shoals showed no significant differences in durations of submergence (shoal = 3.12 s; SD = 1.29; $n = 234$; all other situations = 2.99 s; SD = 1.17; $n = 254$; $P > 0.05$).

The final component of foraging behavior measured was intraspecific group size in dif-

TABLE 7. Species' occurrences at "Other" foraging situations (+ = < 0.1).

Species	Number present	Number/ occurrence	All birds at "Other" (%)	Frequency at "Other" (%)
Peruvian Booby	20,834	425	73.6	36
Inca Tern	2,452	84	8.7	21
Guanay Cormorant	1,162	193	4.1	4
Sooty Shearwater	1,129	188	4.0	4
Peruvian Pelican	1,017	39	3.6	19
"Comic" tern	736	52	2.6	10
Franklin's Gull	382	32	1.3	9
Grey Gull	173	16	0.6	8
Band-tailed Gull	156	10	0.5	12
Sabine's Gull	68	11	0.2	4
Peruvian Diving-Petrel	57	3.8	0.2	11
Humboldt Penguin	56	2.5	0.2	16
Waved Albatross	27	2.7	0.1	7
Storm-petrel sp.	20	6.7	0.1	2
Red-legged Cormorant	16	2.0	+	6
Neotropical Cormorant	11	3.7	+	2
Pomarine Jaeger	8	2.0	+	3
Jaeger sp.	2	1.0	+	1
Cape Petrel	2	1.0	+	1
Peruvian Tern	2	2.0	+	0.5
Sandwich Tern	2	2.0	+	0.5
Elegant Tern	2	1.0	+	1
Blue-footed Booby	1	1.0	+	0.5
Northern Phalarope	1	1.0	+	0.5
Elliot's Storm-Petrel	1	1.0	+	0.5

ferent foraging situations. Variances were very large, group sizes ranging over four orders of magnitude. Of 18 species with sufficient records (Fig. 2), 10 species had mean group sizes of less than 10/occurrence, and 5 had means of 10–100/occurrence. No species had mean group sizes of 100–1,000/occurrence, but the three most common species (Guanay Cormorant, Peruvian Booby, and Sooty Shearwater) had group sizes of 1,000–10,000/occurrence.

Group size varied between foraging situations (Tables 2–4, 6–7), the largest intraspecific groups tending to occur in shoal-foraging, followed by "Other," zooplankton, scavenging, and sealions.

DISCUSSION

FORAGING IN GROUPS

Over 99% of all birds foraged in groups. Solitary foraging was rare: only Humboldt Penguins (13.5% of 39 observations), Red-legged Cormorant (12% of 73), and Peruvian Diving Petrels (100% of 3; see also Murphy 1936) foraged alone with any frequency. These data suggest that, even in the highly productive Peruvian Coastal Current, most food for seabirds occurs in patches. Similar patterns of aggregation have been observed in other oceanographic zones listed by Ashmole (1971): the tropical Pacific (Gould 1974, King 1974), boreal Pacific (Porter and Sealey 1981, Schneider 1982), and Benguela Current (Duffy pers. obs.).

Because anchoveta were the main food taken by birds during the study period and because anchoveta typically occur in shoals (Vogt 1942), most shoals exploited by the birds were probably comprised of anchoveta. Anchoveta have very patchy distributions. In one survey, 55% of the total biomass was confined to 13% of the survey area, while, in another, 36% of the biomass was concentrated in only 3.4% of the area (Johannesson and Vilchez 1980). Similar concentrations have been reported for the northern anchovy (*Engraulis mordax*) off California (Mais 1974). Densities within patches may range up to 2120 metric tons/km^2 in Peru (Johannesson and Vilchez 1980). Anchoveta are therefore both patchy enough and sufficiently abundant to explain the large aggregations typical of birds in the Peruvian coastal upwelling area.

TABLE 8. Percentage use of foraging techniques by Peruvian seabirds (* = dominant method for each species).

Species	Piracy	Dipping	Terrestrial-seizing	Surface-seizing	Plunging	Pursuit-plunging	Surface dive	Sample size
Humboldt Penguin	—	—	—	—	—	—	—	37
Waved Albatross	100*	—	—	—	—	—	100*	17
Sooty Shearwater	4	—	—	59*	—	36	—	22
Diving-Petrel	—	—	—	—	—	100*	—	3
Peruvian Pelican	18	—	—	63*	19	—	—	498
Peruvian Booby	2	—	—	7	91*	—	—	786
Guanay Cormorant	1	—	—	—	—	—	99*	152
Neotropical Cormorant	—	—	—	—	—	—	100*	36
Red-legged Cormorant	—	—	—	—	—	—	100*	73
Pomarine and unidentified Jaeger	100*	—	—	—	—	—	—	15
Grey Gull	1	3	3	94*	—	—	—	508
Band-tailed Gull	11	1	39	49*	—	—	—	349
Kelp Gull	7	1	16	75*	—	—	—	73
Franklin's Gull	15	77*	1	4	—	—	—	26
Sabine's Gull	—	—	—	100*	—	—	—	24
Arctic Tern	—	85*	—	—	15	—	—	426
Inca Tern	1	93*	—	—	5	—	—	483
Number of species for which each technique is the dominant	2	3	0	6	1	1	4	

PREY CHARACTERISTICS AND FORAGING SITUATIONS

There were considerable differences in the species' compositions among foraging situations (Tables 2-4, 6-7) and in the use of different types of patches by each species (Table 1). Are these reflections of differences in prey composition and behavior or of limitations in the foraging behaviors of the bird species?

First, I consider the anchoveta. Most shoals occur within 40 m of the surface and many are found at the surface during the day, but most occur between 10 and 20 m depth (Jordan 1976, Johannesson and Vilchez 1980). Surface-feeding species, such as gulls and terns, occurred at fish shoals, so some anchoveta must occur at the surface. Other shallowly foraging birds, such as Waved Albatross, jaegers, and the pelican, stole fish from seabird species that foraged at depths where anchoveta were most abundant (Duffy 1980).

The most abundant birds at shoals were three species that can plunge, pursuit-plunge, or surface-dive after deeper prey if necessary: the Peruvian Booby, Guanay Cormorant, and Sooty Shearwater (Table 8). The tendency for these species to forage and feed in large numbers would also facilitate finding shoals (Olson 1964). Two other deeply foraging species, the Humboldt Penguin and Red-legged Cormorant, should also have been able to reach depths where anchoveta are abundant, but neither species was common at shoals. The penguin formerly fed at shoals (Paessler 1922, Murphy 1936). Its present rarity may reflect a recent serious population decline because of incidental mortality in fishing nets and from poaching and because of the collapse of the anchoveta stocks (Duffy et al. in press). Red-legged Cormorants appeared to specialize in foraging in inshore waters with rocky substrates (Coker 1920, Murphy 1936, Brown et al. 1975, pers. obs.).

The zooplankton that I observed being taken as prey and in the water at zooplankton foraging situations were small (approximately 1 cm), locally very abundant, and present near the surface for only short periods of at most 5 min. The most common birds at zooplankton situations were small gulls and terns, which foraged by dipping and surface-seizing. Larger species may have found it energetically inefficient to eat such small prey and to make frequent moves from one short-lived patch to another. Species that forage in groups would

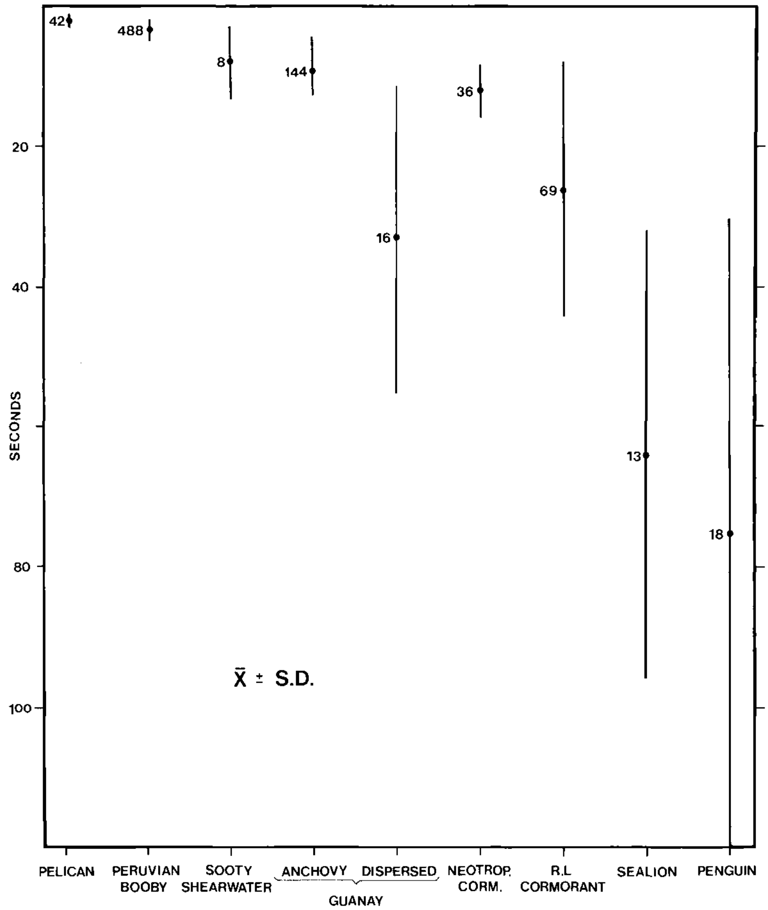

Fig. 1. Durations of submergence of some more common Peruvian seabirds (means and standard deviations; numbers = sample sizes).

also have found the patches too small: individuals would have done better to forage alone or in smaller groups.

Scavenging and feeding opportunities provided by sealions were also short-lived and small, which would favor small numbers of small birds. The exception would be scavenging at corpses that were rich and relatively persistent food sources. In this case, dominance in interspecific interactions rather than agility would be the most useful attribute. The largest of the gulls, the Kelp Gull, was the corpse-specialist, displacing the other species.

The common species in both scavenging and sealion situations fed by surface-seizing or dipping. Deeper foraging would have been of little use in obtaining fish offal, corpses, or bits of fish thrashed to pieces by a sealion on the surface. Deeper foraging methods might also have made birds more vulnerable to predation by sealions.

Species' Interactions and Foraging Groups

Are the species in a foraging group present because each has responded independently to a common stimulus or does the presence of one species affect either the discovery or exploitation of prey by other species?

Peruvian Boobies tended to be the first to forage at anchoveta shoals, and Inca Terns were first at zooplankton swarms. They may have found the patches of prey and then attracted other species, or the booby and tern may merely have responded to new patches already apparent to other species. Cormorants and other

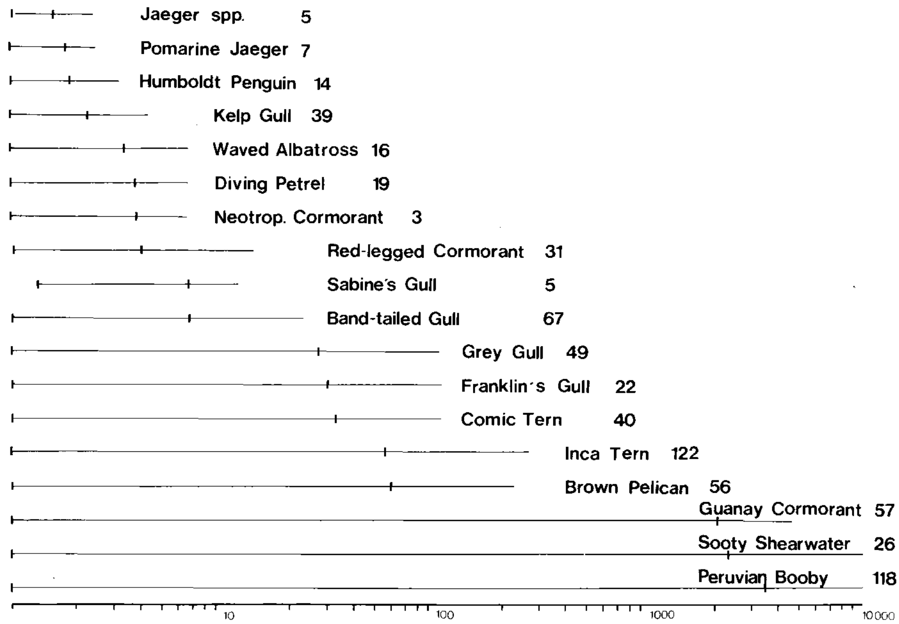

Fig. 2. Intraspecific group sizes combined from all feeding situations (mean and standard deviation; numbers = sample sizes; x-axis = log-scale).

species frequently ignored plunging by a single booby. Like species in the boreal Pacific using Black-legged Kittiwakes (*Rissa tridactyla*) to locate patches (Hoffman et al. 1981), however, Peruvian seabirds may respond only to repeated plunging or dipping by "nuclear" (Sealy 1973) or "catalyst" species (Hoffman et al. 1981). Feeding at a patch may be enhanced in a number of ways by the presence of other species (e.g. Hoffman et al. 1981). If successful foraging requires disruption of a shoal and its antipredator defenses, mass plunging or surface-diving would probably send fish fleeing from one bird to another, destroy the fish-to-fish orientation necessary for coordinated evasive action (Shaw 1978), or perhaps cause overuse of anaerobic muscle tissue so that fish could no longer use bursts of speed to escape (Blaxter 1969). Such anaerobic stress could conceivably even lead to death (Parker and Black 1959). All of these would appear to be more effective with increases in the size of the bird flock relative to the size of the shoal being attacked. There must be, however, some upper limit at which the food per bird decreases with further increases in flock size.

Among the potential negative effects of the presence of other species in foraging groups, kleptoparasitism is the most visible. The average number of pirates (pelicans, jaegers, and albatrosses) was so low at shoal and "Other" foraging situations (Tables 2 and 7), relative to the numbers of potential hosts, that piracy does not appear to be a decisive factor in flock foraging. Displacement from prey, particularly carrion, may be much more important in determining which species are present at scavenging situations. Big species, such as the Kelp Gull, monopolize large carrion, while small scraps and offal go to smaller, more agile birds such as the Inca Tern. Size may also play a part in groups feeding on zooplankton. The larger, surface-seizing gulls settle over the densest part of zooplankton swarms and have the highest foraging rates, while the smaller species dip their prey around the periphery, where prey are presumably less abundant. The smaller, faster species have an advantage at new patches, which they can exploit before the larger birds arrive.

Although one or two species are characteristic of certain foraging situations, a much larger number of species are minor, occasional participants. It is difficult to imagine how these species could coevolve with others to take advantage of the foraging situations studied here.

These peripheral species may themselves be major participants in other foraging situations than those studied here. For example, Neotropical Cormorants, Peruvian Brown Pelicans, Peruvian Boobies, Franklin's Gulls, and Black Skimmers (*Rynchops niger*) seem to be the main participants in foraging groups in estuaries and bays (pers. obs.). Brown (1981) identified a group of surface-feeding storm-petrels (Hydrobatidae) as characteristic of warmer, offshore waters. Foraging over dolphins (Delphinidae) seems to be more important in northern waters (Brown 1981, pers. obs.) but was never seen farther south during this study.

Feeding seabirds are much rarer than birds flying or sitting on the water, so distributional studies have concentrated on nonfeeding birds. Closer study of feeding groups may serve as a valuable adjunct to distributional studies, because it is while feeding that seabirds have their closest links to the marine environment.

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