FEEDING STRATEGIES AND POPULATION SIZE IN TROPICAL SEABIRDS

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Classical theories of avian population dynamics concentrate on the causes of short-term fluctuations of numbers around an average population level that remains relatively constant in the long term. Little attention has been paid to the reasons for the often dramatically different population levels maintained by different species in the same community. There is an implicit assumption, rooted as far back as Malthus and Darwin, that more abundant species have more food available to them than scarcer species, but explicit statements to this effect are rare and dismissive (e.g., Lack 1971, pp. 171–172). Difficulties of making adequate measurements of available food have precluded any more precise statement of this relationship.

Tropical seabirds are convenient subjects for a test of this assumption for two reasons. First, they feed on prey that is either confined to the surface of the ocean or that is made available to them there by predatory fish (Ashmole and Ashmole 1968; Ashmole 1971). There are no deep-diving species feeding tens of meters below the surface, as there are in seabird communities at higher latitudes, perhaps because of a greater abundance of large underwater predators in the tropics. The amount of food available to tropical seabirds is therefore estimated much more accurately by a measure of feeding area alone, than would be the case at higher latitudes. Second, there is in most cases a clear distinction between "pelagic" species (or populations), which obtain most of their food far out to sea, and "inshore" species which feed in shallow water close to land. This distinction is clearest on oceanic islands, where the seafloor usually slopes steeply into deep water within a few miles of the coast. Most species breeding on continental islands feed in water overlying the continental shelf, at least when breeding, and the differences in feeding range are thus less clear-cut. For these reasons, discussion will be restricted for the present to species breeding on tropical oceanic islands.

If it is true that more abundant species have a larger quantity of food available to them and that the amount of food available to a tropical seabird is directly (though not necessarily linearly) related to its feeding area, then it should be true that pelagic feeders are more abundant than inshore feeders. It

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TABLE 1

ABUNDANCE, FEEDING ZONE, AND DISPERSIVE BEHAVIOR OF SEABIRDS BREEDING ON TROPICAL OCEANIC ISLANDS

	BREEDING STATION																										
	1			2			3			4			5			6			7			8			9		
SPECIES	F	D	A	F	D	A	F	D	A	F	D	A	F	D	A	F	D	A	F	D	A	F	D	A	F	D	A
Black-footed albatross (*Diomedea nigripes*)	P	M	6 =	P	M	3		...		P	M	7	P	M	3	P	M	3		...			...			...	
Laysan albatross (*Diomedea immutabilis*)	P	M	6 =	P	M	2	P	?	10	P	M	2	P	M	4	P	M	2		...			...			...	
Red-tailed tropicbird (*Phaethon rubricauda*)	P	(M)	5	P	(M)	8	P	?	8	P	(M)	3	P	M	11	P	M	10	P	M	4 =	P	M	5		...	
White-tailed tropicbird (*Phaethon lepturus*)		...			...			...			...			...			...			...		P	M	3 =	P	M	4
Masked booby (*Sula dactylatra*)	P	R	10	P	R	10	P	R	5	P	R	8	P	R	8	P	R	7	P	R	10		...			...	
Brown booby (*Sula leucogaster*)	I	R	12	I	R	12	I	?	9	I	R	9	I	R	12	I	R	8	I	R	13		...			...	
Red-footed booby (*Sula sula*)	P	R	8	P	R	9		...		P	R	5	P	R	10	P	R	9	P	R	4 =	P	R	2		...	
Great frigatebird (*Fregata minor*)	P	(R)	9	P	(R)	6		...		P	R	6	P	R	9	P	R	6	P	R	2 =	P	R	3		...	
Lesser frigatebird (*Fregata ariel*)		...			...			...			...			...			...		P	R	12	P	R	1		...	
Caspian tern (*Hydroprogne caspia*)		...			...			...			...			...			...			...		I	R	10		...	
Crested tern (*Thelasseus bergii*)		...			...			...			...			...			...		I	R	11	I	R	9		...	
Gray-backed tern (*Sterna lunata*)	I	M	2 =	I	M	5	I	M	3	I	M	10	I	M	5	I	M	5	I	R	8		...			...	
Sooty tern (*Sterna fuscata*)	P	M	1	P	M	1	P	M	4	P	M	1	P	M	1	P	M	1	P	M	1		...			...	
Bridled tern (*Sterna anaethetus*)		...			...			...			...			...			...			...			...		I	R	5
Black-naped tern (*Sterna sumatrana*)		...			...			...			...			...			...			...		I	R	8		...	
Brown noddy (*Anous stolidus*)	P	(R)	2 =	P	(R)	4	P	?	1 =	P	M	4	P	R	2	P	R	4	P	R	7	P	R	6	P	M	3
Black noddy (*Anous tenuirostris*)	I	(M)	4	I	R	7	I	M	6		...		I	R	7	I	R	11	I	M	2 =		...		I	M	1
Blue-gray noddy (*Procelsterna cerulea*)		...			...		I	?	1 =		...		I	?	13		...		I	R	9		...			...	
White or fairy tern (*Gygis alba*)	?	R	11	?	R	11	?	R	7	?	R	11	?	R	12	?	R	12	P	M	6	I	R	7	I	R	2

SOURCES.—Authorities for breeding censuses: (1) Lisianski Island (Clapp and Wirtz 1975); (2) Laysan Island (Ely and Clapp 1973); (3) Gardner Pinnacles) (Clapp 1972); (4) Kure Atoll (Woodward 1972); (5) French Frigate Shoals (Amerson 1971); (6) Pearl and Hermes Reef (Amerson, Clapp, and Wirtz 1974); (7) Christmas Island, Pacific Ocean (Schreiber and Ashmole 1970); (8) Aldabra Atoll (Diamond 1971, 1975*a*); (9) Cousin Island, Seychelles (Diamond 1975*b*).

NOTE.—F = feeding zone; D = dispersive behavior; A = abundance rank; P = pelagic; I = inshore; R = resident; M = migrant.

should also be true that migrant species are more abundant than resident species, because movement to an alternative feeding area outside the breeding area is equivalent to increasing the feeding area used during the year. These two predictions were tested as follows.

Information on population sizes was taken from censuses of breeding seabirds on nine tropical oceanic islands, two in the Indian Ocean and seven in the Pacific. Because different islands may differ in the productivity of the surrounding ocean, which would be expected to influence the population levels of all the species breeding there, the absolute numbers at each station were not used; instead, the species were ranked according to their abundance at each station, the most abundant being ranked 1 and so on. Burrow-nesting species were excluded because they are notoriously difficult to count. Information on feeding range was obtained from the general literature (Nelson 1970; Ashmole 1971 and references therein; Brown 1975) and my own field experience with 15 of the 19 species involved. Pelagic feeders are those which feed usually out of sight of land, incubate the egg in shifts of several days, and feed the chick once a day or even less frequently; inshore feeders usually feed within sight of land, incubate in shifts of one day or less, and feed the chick several times a day. Most species are consistently either inshore or pelagic feeders throughout their range, so if the requisite information was not available for a particular species, at a particular station, it was classified according to its behavior elsewhere. Only *Gygis alba* is known to be inconsistent in this respect, and its feeding range was scored only when positively recorded for that particular station. Migratory behavior is more variable and was scored only where definitely known for that station.

Thus for each breeding station, each nesting species was ranked according to its abundance relative to other species in that community and placed in one of four categories representing increasing order of feeding area: inshore resident, pelagic resident, inshore migrant, pelagic migrant (table 1). The number of species of each rank that fall into each category was then set out, and the median rank calculated for each category (table 2).

Clearly, both predictions are upheld; pelagic feeders outnumber inshore feeders, and migrants outnumber residents. Two categories, pelagic migrants and inshore migrants, are not significantly different; the other two categories differ significantly both from each other and from each of the other two (table 3). Migrants outnumber residents to a greater extent ($P < .001$) than pelagic feeders outnumber inshore feeders ($P < .02$); this suggests that migration to a different feeding area outside the breeding area has a more potent effect on abundance than does the extension of the feeding range during the breeding season. This suggests that the mortality that limits population size—the "key factor" in K-factor terminology—takes place outside the breeding season. Lack (1966) considered that regulatory mortality in tropical seabirds also occurs outside the breeding season, when food is putatively less abundant, whereas Ashmole (1963) suggested that regulation is most likely to occur when the birds are breeding. Although both workers discussed population regulation rather

TABLE 2

RANK ORDER OF ABUNDANCE IN RELATION TO FEEDING ZONE AND DISPERSIVE BEHAVIOR

Rank Order of Abundance	Inshore Residents	Pelagic Residents	Inshore Migrants	Pelagic Migrants	All Inshore	All Pelagic	All Residents	All Migrants
1	0	1	1	6	2	8	1	7
2	1	4	2	3	3	7	5	5
3	0	1	1	6	1	7	1	7
4	0	3	1	5	1	8	3	6
5	1	2	3	2	4	4	3	5
6	0	4	1	2	1	6	5	3
7	3	2	0	1	3	3	6	1
8	3	3	1	1	4	5	6	2
9	3	4	0	0	4	4	7	0
10	1	4	1	1	2	6	5	2
11	2	0	0	1	2	1	5	1
12	3	0	0	0	3	0	4	0
13	1	0	0	0	2	0	1	0
Total	18	28	11	28	32	57	52	39
Median Rank	8.3	5.8	4.2	2.8	7.3	3.8	7.3	3.1

TABLE 3

PROBABILITY LEVELS OF DIFFERENCE IN ABUNDANCE RANK BETWEEN SEABIRDS*

	All Residents	All Pelagic	All Inshore
All Migrants	< .001	> .2	< .001
All Residents		< .001	> .7
All Pelagic			< .02

	Inshore Residents	Pelagic Residents	Inshore Migrants
Pelagic Residents	< .02		
Inshore Migrants	< .01	< .05	
Pelagic Migrants	< .001	< .01	> .5

* Using different combinations of feeding zone and dispersive behavior, using the median test (Siegel 1956).

than limitation, they did not always distinguish clearly between the two. They disagreed about the season at which the greatest mortality would occur as much as about that at which density-dependent mortality might take place. My results, suggesting that most mortality takes place outside the breeding season, may therefore shed some light on this controversy.

This effect has considerable evolutionary significance, because the probability of extinction of a population is inversely related to its size. There should be a selective advantage in extending the feeding range if this results in a larger population; these results suggest that this is best achieved by moving to a different feeding area outside the breeding season.

Closer examination of the effects of different feeding areas on seabirds reveals a number of complications that would be expected to confuse the simple relationship on which these predictions were based. Food density is presumably not the same in shallow water as in deep, nor is it necessarily the same in deep water at all distances from land. The productivity of coral reefs far exceeds that of the open ocean, and the population of food available to seabirds presumably follows a similar pattern. If food density inshore = D_I, food density in deep water = D_P, the respective feeding areas of an inshore species = I and a pelagic feeder = P, and the numbers N_I and N_P of each species are directly proportional to the amount of food available in each area (i.e., $D_I \cdot I$ and $D_P \cdot P$, respectively); then there are three possible situations: (1) If $D_I/D_P >$

P/I, then $N_I > N_P$; (2) if $D_I/D_P = P/I$, then $N_I = N_P$; (3) if $D_I/D_P < P/I$, then $N_I < N_P$.

The results given above suggest that the third of these alternatives is the usual situation. If a bird is to benefit from pelagic feeding, it must feed far enough from land so that N_P/P is large enough to compensate for any greater density of food in shallow as compared to deep water. This may explain the otherwise puzzling observation, made by Ashmole and Ashmole (1967) in the Pacific and by myself in the Indian Ocean, of sooty terns (perhaps the most pelagic and migratory of all tropical seabirds) flying past flocks of brown noddies feeding, within sight of land, on the same prey species that sooty terns also take. The pelagic habit, to be effective, must take the bird far beyond the range of potential competitors that feed inshore.

A further complication is introduced by the factors governing the distance it pays the bird to travel, in relation to the energy expended in making the journey. Even if the density of prey remains constant with increasing distance from land, its usefulness to the bird decreases because more energy is needed to exploit it. Two situations are possible. First, pelagic feeders might not simply quarter all the available ocean, but travel to specific areas of high food density, such as fronts and upwellings; Ashmole and Ashmole (1967) and Ashmole (1971) have emphasized the importance of such oceanic centers of high productivity for pelagic seabirds. In this case, the significant feature of both the migrant and pelagic habits may be in allowing birds to locate areas of maximum prey abundance and so avoid periods of scarcity at particular locations, rather than simply to roam over larger areas. Second, the energy expended in foraging at a distance may be compensated adequately by the reduced competition that must occur as the bird moves away from the land; because the birds are concentrated at the breeding station, the density of birds decreases away from land (roughly in proportion to the square of the distance from land), whereas the density of prey presumably does not. Opposing the advantage to be gained from reduced competition may be that favoring proximity to other birds if, as Ward and Zahavi (1973) have suggested, flock-feeding birds benefit from information supplied by other individuals on the location of food sources. This is likely to be important only where food sources are localized, either spatially (e.g., upwellings, convergences) or temporally (prey brought to the surface by predatory fish). Which of these effects—access to distant sources of high prey density, information gathering, and reduced competition far from land—is more important remains unknown. All may operate, and a species' feeding range is likely to be a compromise adjusted to the balance between these conflicting pressures.

Differences in body size affect the amount of food a bird can carry, but not its flying range, which depends solely on the lift:drag ratio. There is thus no general relationship between body size and feeding range or migratory behavior in tropical seabirds.

Lack (1967) discussed interrelationships of adaptations in marine birds and related a number of features of breeding behavior to the colonial habit. In particular he noted that pelagic feeders tend to nest in large colonies, inshore feeders in smaller, less dense colonies. The view put forward here is that pelagic feeders are more numerous than inshore feeders and so, if nest sites are limited (as they often are for seabirds), must inevitably breed in larger colonies than the scarcer inshore-feeding species; adaptations for colonial nesting are thus seen as a consequence of the pelagic or migratory habit.

With so many factors complicating the apparently straightforward difference between inshore and pelagic feeders, it is perhaps surprising that the simplistic prediction of relative abundances of species adopting these strategies should be as successful as it is. The effect must be a powerful one indeed to override so many confounding influences. The pelagic habit has previously been regarded as one requiring a battery of special adaptations: single-egg clutch, slow growth and resistance to starvation of chicks, and deferred maturity and high survival of adults. This study reveals the other side of the coin; real and necessary as these adaptations are, they are abundantly rewarded by greater population size with its attendant diminution of the risk of extinction.

SUMMARY

The available prey of seabirds nesting on tropical oceanic islands can be considered to be distributed in two dimensions; their feeding area thus gives an estimate of the volume of available prey. This is greater in pelagic feeders and in migrants than in inshore-feeding and resident species. If prey abundance determines population size of a predator, pelagic feeders should be more abundant than inshore feeders and migrants more numerous than resident species. Analysis of the seabird communities of nine tropical oceanic islands confirms both these predictions. Migration is a more effective booster of population size than the pelagic habit, suggesting that limiting mortality occurs outside the breeding season. The pelagic habit has long been viewed as requiring numerous adaptations to cope with its inherent drawbacks; here, the evolutionary advantage of the larger population sizes made possible is emphasized.

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