

COMPETITION FOR NESTING SPACE AMONG PERUVIAN GUANO BIRDS

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ABSTRACT.—In the mid-1940's, Peruvian managers greatly increased the nesting space available to the three principal surface-nesting species of the Peruvian Coastal Current: the Guanay Cormorant (*Phalacrocorax bougainvillii*), the Peruvian Booby (*Sula variegata*), and the Peruvian Brown Pelican (*Pelecanus occidentalis thagus*). The combined populations of these three species increased from 8 to 20 million birds. The annual rate of increase of the population rose from 8 to 18%. The three species appear to have evolved in the face of a shortage of nesting space. They have not diverged in their respective breeding seasons. Each species has habitat preferences for nesting, but the overlap is great. The booby and cormorant compete through a "scramble" to occupy space before it is settled by the other species. Neither can displace the other from nest sites. The pelican is dominant over the other two in aggressive interactions and frequently usurps their nests. Pelicans are apparently confined to nesting in level areas, whereas the other two species can nest on a greater range of gradients.

Despite the facts that nesting space is limited and that its scarcity has a demonstrated effect upon the combined populations, interspecific competition for nesting space was difficult to document. Interspecific aggressive interactions were few and involved only a small percentage of the three populations. The individuals most affected by competition, those denied nesting space, were displaced from the area of competition and were thus less accessible for study. Received 7 June 1982, accepted 14 January 1983.

FOR several millennia, seabirds have nested on islands off the coast of Peru (Hutchinson 1950). The Guanay Cormorant (*Phalacrocorax bougainvillii*), Peruvian Booby (*Sula variegata*), and Peruvian Brown Pelican (*Pelecanus occidentalis thagus*) are the principal nesting species. Ten other species also nest (Murphy 1925, 1936; Galarza 1968) but tend to occupy burrows, caves, or other habitats not used by the three major species.

There are fewer than 40 guano islands along the Peruvian coast; many are small, and only a portion of the surfaces of the remainder appears suitable for nesting because of human disturbance, heat, or ectoparasites (LaValle 1918, Vogt 1942, Duffy 1983a). Where the birds do nest, densities are very high, generally 2–3 nests per m² (Vogt 1942; Table 1).

Murphy (1925), Vogt (1942), and Nelson (1978) have suggested that space suitable for nesting was limited compared with the numbers of birds that could be supported by the high productivity of the Humboldt or Peruvian Coastal Current. Opinions differ as to how space was partitioned. Murphy (1925) suggested that competition with pelicans had forced boobies

to nest on cliffs during the 19th century but that boobies outcompeted pelicans when humans visited the islands. Hutchinson (1950) concluded that, before exploitation by humans, Guanay Cormorants lost out in competition with boobies and pelicans, but, with the disturbance caused by human exploitation of guano deposits, Guanays were competitively superior. Vogt (1942) appeared to believe that differences in tolerances to high temperatures and human disturbance, as well as the use of cliffs by boobies, led to habitat partitioning with minimal interspecific interactions. Nelson (1978) believed that, although boobies could displace cormorants and pelicans were dominant over both cormorants and boobies, few birds came into direct interspecific contact and competition. He suggested (p. 589) that "... meaningful competition, if it occurs, takes the form of 'swamping out'—one species, once established and undisturbed by man, more or less continuously occupying traditional areas and merely by its presence excluding others." This, however, does not explain how dominant species were excluded from nesting in areas occupied by subordinate species.

In this paper I examine the assumption that space was limited and investigate how the three major species partition available nesting space with reference to interspecific interactions and behavioral and morphological limitations.

METHODS

If a resource limits a population, then an increase in the resource should produce an increase in the population. Birds and other mobile organisms are not usually conducive to testing this hypothesis, but Peruvian management practices allow us to examine such an increase in nesting space.

Jordan and Fuentes (1966) estimated the combined populations of the three species between 1909 and 1964 based on guano harvests. In the 1940's, following a sharp decrease in the population during a series of El Niño events, when upwelling stops and food becomes scarce (Vogt 1940), Peruvian authorities began fencing off coastal headlands in the hopes of providing more nesting space, a larger population, and a greater production of guano. Here, I compare population levels and the percentage of annual increases before and after the creation of the new sites.

Study sites.—Most fieldwork was conducted on Isla Mazorca (11.6 ha; 11°23'S, 77°45'W) between September 1977 and March 1978. Other observations were made on Isla Guañape Norte (25 ha; 08°32'S, 78°58'W), Isla Macabi (8 ha; 07°47'S, 79°30'W), and Islas Ballestas (32 ha; 13°44'S, 76°24'W) in February and March 1979. All of these islands are protected by guards and remain essentially undisturbed during the breeding season.

Nest characteristics.—Nest shape and materials can determine such things as density, permissible slopes of underlying substrates, and the number of young that can be reared in the nest. On Mazorca, I measured nest diameter, outside height, and distance to nearest neighbor for the three species. After the breeding season, using an inclinometer attached to a 16-cm straightedge, I measured the maximum slope under nests. Using a 2-m straightedge and inclinometer, I determined the slope of ground adjacent to nests, using the mean of three measurements. Density was computed by counting all complete nests within 2 × 2-m squares for 38 cormorant, 49 booby, and 2 pelican samples.

Exposure to wind and nest temperature are believed to be important in partitioning nesting space (Vogt 1942). To investigate this, I measured the temperatures of guano crusts on the rims of occupied nests on Isla Macabi on 20 February 1979 over 2 h. The sky was partially overcast, and there were southerly winds of 20 kph and a shaded ambient air temperature of between 24 and 26°C. These conditions are typical of breeding-season conditions (e.g. Vogt 1942; pers. obs.), so that resulting temperatures were

likely to have been representative. Atypical wind conditions are associated with El Niño phenomena (Vogt 1942), which usually produce mass desertions of nests (Vogt 1940).

Species' interactions.—I originally planned to watch interspecific interactions over set periods of time, but interactions were so rare that I made most observations on an opportunistic basis during the 7 months of fieldwork. I noted the species and whether antagonists were defending nest sites or were nonbreeders. A bird was considered to have won if it displaced the other from the scene of the conflict.

Although the three species have elaborate repertoires of agonistic behavior (Vogt 1942, Nelson 1978; pers. obs.), I used interspecific jabbing—with or without contact—as the only behavioral criterion for an interaction, as more subtle aggressive or territorial displays do not necessarily constitute communication between species.

Settlement patterns.—On Mazorca, I observed where each species first established nest sites in relation to wind, slope, substrate, and "cliff" edges (where "cliff" was any edge with a vertical drop of over 1 m).

I monitored four booby nesting areas containing both cliff and interior nest sites to see at which type of nest site eggs were laid first. West Platform had a maximum of 42 sites (26 edge); Lee Platform, 43 (14); East Platform, 58 (12); and Barranca, 79 (12). I waited for turnovers or shifts in positions to determine nest contents. No birds flushed from their nests during these observations, so I believe I had minimal deleterious effects.

To determine whether nesting success was greater in cliff-edge or interior nests, I compared the number of 4-10-week-old booby young in nests in the two habitats on Mazorca, Macabi, Guañape Norte, and the Ballestas islands. Only nests with young were sampled. This would have produced a bias if nests in either habitat were more likely to suffer complete nesting failure. This did not appear to be the case.

Overlap between species.—Guards resident on the islands map birds and their state of breeding fortnightly. I chose the islands of Mazorca and Macabi Grande, because I was most familiar with their topography; both are small (11.6 ha and 5.4 ha, respectively) and relatively flat.

I partitioned the maps from Macabi into 450 quadrats, each representing approximately 121 m² (11 × 11 m), and did the same for Mazorca, dividing it into 530 quadrats of approximately 225 m² (15 × 15 m). For each year of available records (Mazorca: 30 nesting seasons; Macabi: 31 seasons), I chose the census showing the greatest area of nests with eggs in order to plot the quadrats used by each species, because competitive pressure should be most severe then. From these, I obtained maps of frequency of use for each island. Three decades of records reduce the mapping errors that occur during any one year. I also

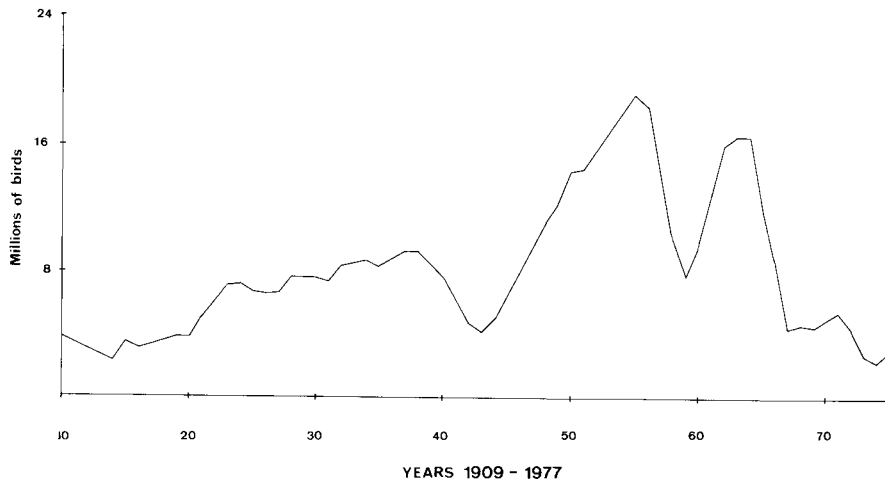


Fig. 1. Three-year running means of guano bird numbers based on guano harvests (after Duffy 1980).

calculated the percentage of area used by one species that was never used by a second species and the percentage of quadrats used by two or more species over the years.

RESULTS

Did nest space limit the population?—Between 1909 and 1940, the combined populations of the three species increased as more islands came under the protection of Peruvian authorities (Jordan and Fuentes 1966). The population then leveled off at about 8 million birds (Fig. 1). The mean increase per year was 8% (SE mean = 4.2; $n = 23$; years of El Niño excluded). After 1946, with the creation of breeding sites free of terrestrial predators on the mainland, the population of the three species rose as high as 20 million and the percentage annual increase more than doubled to 18% (SE mean = 4.5; $n = 18$; excluding El Niño years).

More recently, because of overfishing, the bird populations have fallen sharply (Nelson 1978, Tovar 1978, Valdivia 1978, Duffy 1980), but the two islands studied here were both covered with nesting or roosting birds during at least part of my study, so conditions were presumably similar to those in effect when space was in short supply throughout the islands.

Nest characteristics.—Nest structure and location differed among the three species (Table 1). Cormorants made substantial nests of guano, feathers, and debris. Their nests were twice as high on the downhill side as were nests of boo-

bies, which had only low rims of guano and pebbles. Pelicans scraped depressions into mats of feathers and guano, which they gathered from outside their colonies. Pelicans also usurped booby and cormorant nests but rapidly reduced them to shallow depressions.

Pelicans tended to nest on flat surfaces; boobies and cormorants used areas with considerable slopes (Table 1), and boobies even nested on the ledges of perpendicular cliffs. Boobies and cormorants showed no difference in the overall angles of nesting slopes (excluding cliffs), but slopes of nest sites were twice as steep for cormorants. Cormorants and pelicans nested at densities of around three nests/m², whereas booby nests were only two-thirds as dense (Table 1).

The three species appeared to differ in their temperature tolerances (Table 2). Cormorants preferred the coolest sites and pelicans the warmest. The differences were significant (extension of the median test, $\chi^2 = 8.758$, $df = 2$; $P < 0.01$; Siegel 1956) and agreed with earlier work of Vogt (1942).

Species' interactions.—During the 6 months of fieldwork on Mazorca and 3 weeks on other islands, I saw only 193 interspecific aggressive interactions on land. There were tens or hundreds of thousands of nesting birds on the islands, but they nested in monospecific subcolonies, and very few pairs came into interspecific contact (Nelson 1978). Watches at contiguous subcolonies showed that aggressive interactions were primarily directed at conspe-

TABLE 1. Nest and nest-site characteristics of the three major nesting species on Isla Mazorca.

	Guanay Cormorant		Peruvian Booby		Brown Pelican	
	$\bar{x} \pm \text{SD}$	<i>n</i>	$\bar{x} \pm \text{SD}$	<i>n</i>	$\bar{x} \pm \text{SD}$	<i>n</i>
Overall slope	21° ± 7°	100	21° ± 13°	105	2° ± 2°	20
Microsite slope	12° ± 12°	400	6° ± 6°	420	2° ± 2°	26
Density (<i>n</i> /m ²)	3.0 ± 0.5	38	1.9 ± 0.6	49	2.75-3.0	2
Height of downhill side of nest	17 ± 4 cm	100	9 ± 3 cm	100	—	—
Nest diameter	32 ± 4 cm	100	31 ± 4 cm	100	39 ± 4 cm	11
Nest area (πr^2)	0.08 m ²	—	0.07 m ²	—	1.2 m ²	—
Area occupied by two young	0.06 m ²	—	0.05 m ²	—	—	—

cifics, even if pairs of another species were adjacent.

The actual sequence of events in an interspecific interaction varied greatly. Cormorants or boobies on nests would often jab at a passing bird with no preliminary display. More frequently, jabbing was preceded by "yes head-shaking" (Nelson 1978) by boobies or extended-neck threats by cormorants. Both these behaviors occasionally led to "sky pointing" (Nelson 1978), which itself might precede or follow jabbing. Jabbing occasionally escalated to prolonged fighting in intraspecific encounters, but most interspecific aggressions were brief.

Pelicans rarely jabbed and usually ignored jabbing by the two smaller species. Pelicans would walk obliviously over a jabbing booby or cormorant defending its nest or continue preening while surrounded by jabbing cormorants.

Pelicans were clearly dominant over the other two species. Pelicans displaced another bird in all encounters with boobies ($n = 18$; $P < 0.001$; binomial distribution) and in 99% ($n = 107$) of encounters with cormorants. In interactions between boobies and cormorants ($n = 68$), boobies were the displacers ("won") in 31% of the encounters, and cormorants won 10%, but most (59%) ended as standoffs. The behavioral states of the antagonists were important. Cormorants defending a territory against boobies without territories displaced them or tied in all seven interactions ($P = 0.008$, binomial distribution). With the roles reversed ($n = 11$), boobies displaced cormorants or tied in all encounters ($P < 0.001$). When both species were on territories ($n = 17$), standoffs occurred 95% of the time. When neither was defending a territory ($n = 33$), standoffs occurred 66% of the time, boobies won 21%, and cormorants 12%.

Settlement patterns.—Cormorants and boobies nested at approximately the same time of the year, pelicans slightly later (Vogt 1942). Strong correlations among the monthly frequencies of breeding of the three species (data from Vogt 1942; $n = 12$; boobies and cormorants, $r_s = 0.90$, $P < 0.01$; boobies and pelicans, $r_s = 0.71$, $P < 0.05$; pelicans and cormorants, $r_s = 0.89$, $P < 0.01$) indicate that the three species have not diverged in their breeding seasons.

All three species nested in monospecific subcolonies, but the mechanisms by which neighborhoods were formed differed. Although there was a degree of local synchrony among Peruvian Boobies (Nelson 1978), a pair's egg laying did not depend heavily on the activities of neighbors. Breeding began slowly; pair formation and nest building took more than 1 month (Vogt 1942, Nelson 1978; pers. obs.). Egg laying within a local group spread over more than 1 month (Fig. 2, see also Nelson 1978: fig. 263). The first sites occupied by boobies were

TABLE 2. Numbers of nests, the rims of which were a particular temperature, of the three species. Measurements were made on Isla Macabi on 20 February 1979; ambient air temperature was 24-26°C.

Temperature (C°)	Guanay Cormorant	Peruvian Booby	Brown Pelican
25	1	1	0
26	6	2	0
27	10	7	1
28	9	5	6
29	3	2	2
30	3	6	7
31	1	0	2
34	0	1	0
Mean	27.6°	28.2°	29.2°
SE mean	0.24	0.39	0.28
<i>n</i>	33	24	18

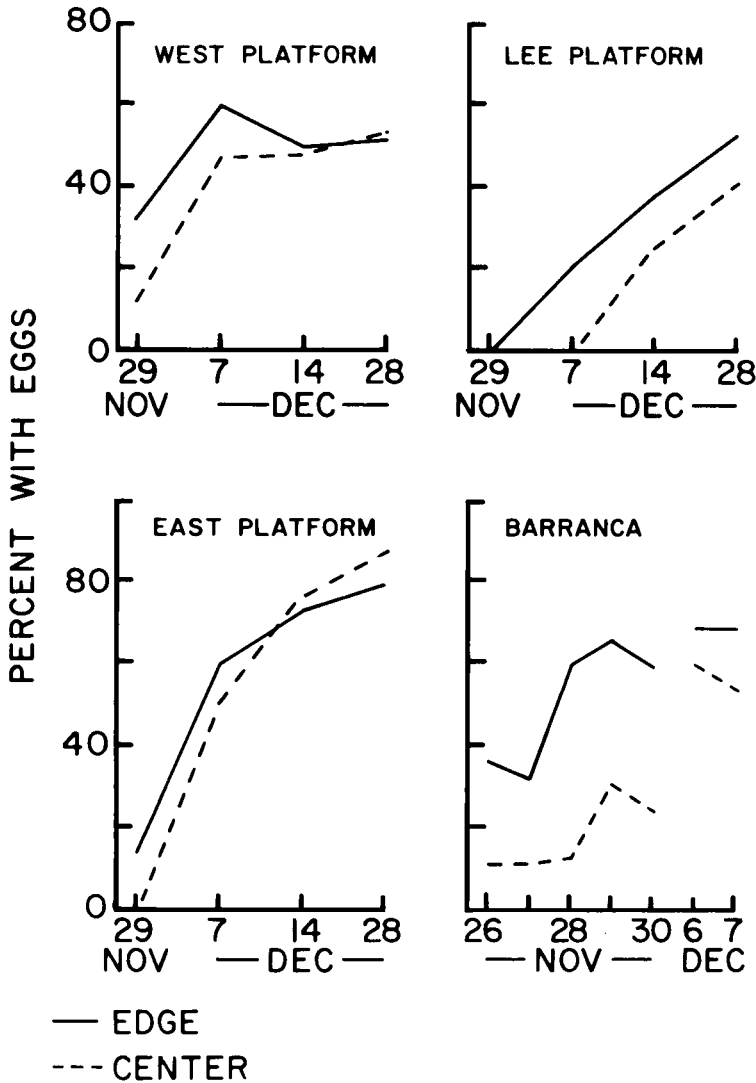


Fig. 2. Comparative settlement at edge and interior nest sites by Peruvian Boobies at four study sites (see Methods for sample sizes).

on the edges of drop-offs and ledges of cliffs. Later pairs nested away from the edges (Fig. 2). Pairs rarely were able to establish territories in occupied areas. Neither habitat consistently produced more nestlings per active nest on four islands (Table 3). Nesting groups of boobies ranged from 2 or 3 pairs on isolated cliff-ledges to tens or hundreds of thousands nesting on smoothly sloping hillside.

In contrast, nesting groups of Guanay Cormorants always exceeded 1,000 pairs (Vogt, cited by Hutchinson 1950, said 10,000 was the minimal size). The breeding of cormorants

seemed to begin whenever food became sufficiently abundant that a number of males remained on the island instead of departing with the fishing flock in the morning. These birds stayed to defend sites and to build closely packed nests. Males gathered next to each other to form a colony nucleus on a windswept slope. Gradually other males set up territories on the periphery, so that the colony expanded with the newest nests always on the outside (Vogt 1942). Pairs never settled into occupied areas.

Pelican nesting groups were generally small,

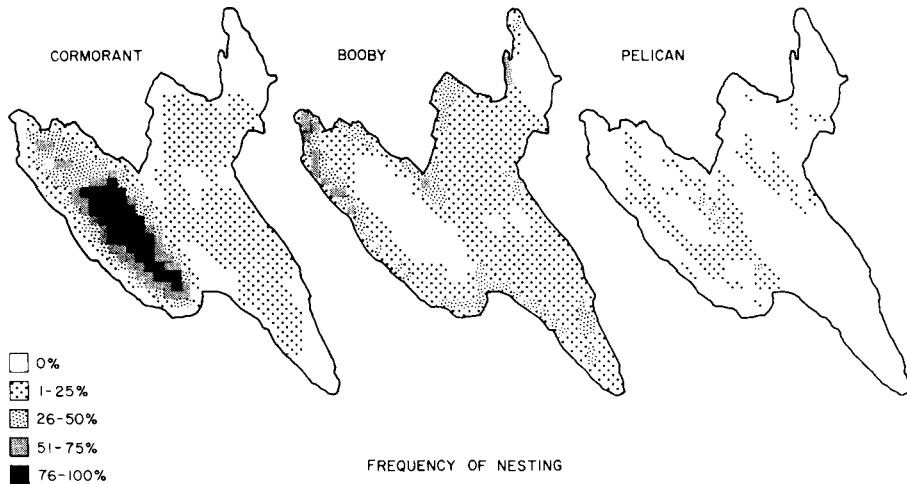


Fig. 3. Frequency of nesting by the species on Isla Mazorca (530 quadrats; 30 breeding seasons).

ranging from 10 to several hundred pairs. Subcolonies were highly synchronized; groups made up of mated pairs arrived overnight and settled in the midst of nesting boobies and cormorants, expropriating their nests.

Overlap between species.—While the three species showed preferences for certain areas year after year on Mazorca and Macabi (Figs. 3 and 4), the overlap was high (Table 4), suggesting that most areas are suitable for nesting by more than one species. On Mazorca, exclusive use of nesting areas was only 19% for cormorants, 21% for boobies, and 4% for pelicans. On Macabi, the levels were 21% for cormorants and zero for the other two.

DISCUSSION

The increase in safe nesting space during the 1940's resulted in an increase in the combined populations of the three species and in their annual rate of increase. This clearly demonstrated that usable nesting space had limited

the combined populations. Sufficient food and other resources were available to support the subsequent populations.

Several millennia or more (Hutchinson 1950) of limited nesting space would have produced a strong interspecific competition for access to breeding sites. Alternatively, the species could have diverged to reduce competition by choosing different habitats or by nesting at different times of the year.

The species differ in their apparent nesting preferences. Boobies prefer edges, presumably to facilitate take-offs and landings. Pelicans require flat areas, perhaps because their large wingspans do not permit safe landings on edges or steep slopes. Their nest scrapes may also be insufficient to retain eggs and young on slopes. Cormorants seem to prefer the middle portions of windy hillsides, perhaps to facilitate take-offs, to cool their dense colonies, or to allow large continuous colonies to form the "phalanx" effect of cormorant breaks against aerial predators such as the Kelp Gull (*Larus domini-*

TABLE 3. Comparison of the mean number of nestling Peruvian Boobies in nests on cliffs and on flat areas at four nesting islands.

Island	Month	Age	Cliff		Flat	
			\bar{x}	<i>n</i>	\bar{x}	<i>n</i>
Mazorca	Feb. 1978	6 weeks	1.97	360	2.03	377
	Mar. 1978	10 weeks	1.78	348	1.84	154
Guañape Norte	Feb. 1979	4-8 weeks	1.63	65	1.71	65
Macabi	Feb. 1979	8 weeks	1.86	29	1.77	57
Ballestas	Mar. 1979	8 weeks	1.47	36	1.30	50

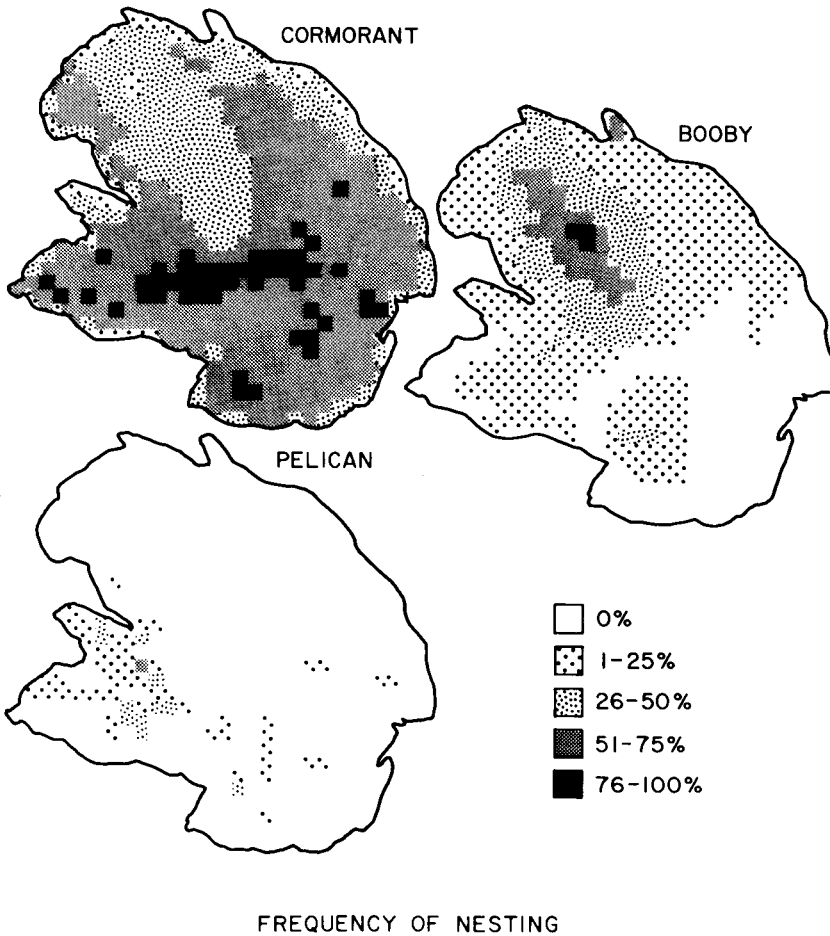


Fig. 4. Frequency of nesting by the three species on Isla Macabi (450 quadrats; 31 breeding seasons).

canus). These differences between the species, however, are not sufficient to prevent large overlaps between the species.

All three species nest at approximately the same time of the year. Initially, all three settle on their preferred nesting habitats until these are full. Cormorants begin nesting on the slopes, boobies on the edges. Their colonies expand toward the habitat of the other. The failure of either species to displace the other when both are defending nest sites (ties = 95%) suggests that when they meet, they stop, neither species displacing the other. Occupancy of a particular area depends on which species reaches it first. This depends in turn on proximity to the initial nesting areas and the numbers of each species seeking to nest.

In contrast, pelicans are clearly dominant over

the two smaller species. As is common in such cases (Morse 1974), however, the pelican has a narrower range of acceptable nesting habitats than do the other two species so that usurpation of the nests of cormorants or boobies can only occur on level ground. Such terrain is scarce on most guano islands. Even so, pelicans have rarely filled all the available flat areas on any one island and have not even nested on many islands every year (Fig. 4). This suggests that some other factor, such as food, keeps the population of pelicans below that level at which all the available nesting space could be used.

Nelson (1978: 589) suggested that a species excludes the others from "traditional" areas "merely by its presence." Occupancy of an area, however, would be interrupted annually or biennially by guano extraction; by desertions

TABLE 4. Percentage of nesting area ever used by Species A overlapping with that ever used by Species B on Isla Mazorca (30 breeding seasons) and Isla Macabi (31 seasons).

		Species A		
		Booby	Cor-morant	Pelican
Isla Mazorca	Booby	—	79%	36%
	Cormorant	71%	—	83%
	Pelican	20%	28%	—
Isla Macabi	Booby	—	80%	74%
	Cormorant	100%	—	100%
	Pelican	17%	14%	—

caused by food shortages during El Niños, which occur at approximately 5-yr intervals (Duffy 1983b); and by desertions caused by outbreaks of ticks (Duffy 1983a). Partitioning of nesting areas under present conditions is thus an almost annual event. Even before guano extraction, repartitioning would have occurred once or twice a decade during El Niños. Competition for space is thus much less static than suggested by Nelson (1978).

Studying the effects of competition on long-lived, mobile animals in complex environments can be difficult. For example, both Mazorca and Macabi have been covered by nesting birds over the years. With large areas suitable for both cormorants and boobies, occupancy by one species should have prevented nesting by the other. Except for occasional bouts of sparring by pairs at borders between the species, however, there were almost no interspecific interactions, aggressive or otherwise. Agonistic encounters were a poor measure of competition.

From a single year's study of the species' nesting distributions, one might conclude that cormorants prefer slopes and boobies prefer edges. Without detailed maps of nesting distributions on Mazorca and Macabi over the years, one might never realize the extent of overlap.

Measuring competition by assessing its effect on the populations of the three species is also likely to be unproductive. Birds unable to obtain nesting space would either go to less suitable habitats, which were not full, or would not breed (Ashmole 1963). The massive adult mortalities during El Niño phenomena (Murphy 1925, Vogt 1942, Jordan and Fuentes 1966) are likely to have more of an effect on the dy-

namics of the populations than does limited nesting space on any one island. Even before the expansion of nesting space in the 1940's, limited space acted as a damper on the increase of the population, not as an absolute limit.

The importance of competition between bird species remains a source of controversy. It is to be hoped that studies such as this one serve to illustrate the complexities that must be understood before the issue can be resolved.

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LITERATURE CITED

- ASHMOLE, N. P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103: 458-473.
- DUFFY, D. C. 1980. Comparative reproductive behavior and population regulation of seabirds of the Peruvian coastal current. Unpublished Ph.D. dissertation. Princeton, New Jersey, Princeton Univ.
- . 1983a. The ecology of tick parasitism on densely nesting Peruvian seabirds. *Ecology* 64: 110-119.
- . 1983b. Environmental uncertainty and commercial fishing: effects on Peruvian guano birds. *Biol. Conserv.* 26: 227-238.
- GALARZA, N. 1968. Informe sobre estudios ornitológicos realizados en el laboratorio de La Puntilla (Pisco) en Setiembre de 1965/66. *Inf. Esp. Instit. Mar Perú—Callao* 31: 1-20.
- HUTCHINSON, G. E. 1950. Survey of contemporary knowledge of biogeochemistry. 3. The biogeochemistry of vertebrate excretion. *Bull. Amer. Mus. Nat. Hist. New York* 96: 1-554.
- JORDAN, R., & H. FUENTES. 1966. Las poblaciones de aves guaneras y su situación actual. *Inf. Instit. Mar Perú—Callao* 10: 1-31.
- LAVALLE, J. A. 1918. Estudio sobre los factores que influyen sobre la distribución de los nidos de las aves productoras del guano. *Mem. Comp. Admora. Guano* 9: 207-213.
- MORSE, D. H. 1974. Niche breadth as a function of social dominance. *Amer. Natur.* 108: 818-830.
- MURPHY, R. C. 1925. *Bird islands of Peru*. New York, Putnam.

- . 1936. *Oceanic birds of South America*. New York, Amer. Mus. Nat. Hist.
- NELSON, J. B. 1978. *The Sulidae: gannets and boobies*. Oxford, University Press.
- SIEGEL, S. 1956. *Non-parametric statistics for the behavioral sciences*. New York, McGraw-Hill.
- TOVAR, H. 1978. Las poblaciones de aves guaneras en los ciclos reproductivos de 1969/70 a 1973/74. *Inf. Instit. Mar Perú—Callao* 45: 1-13.
- VALDIVIA, J. 1978. The anchoveta and El Niño. *Rapp. P.-v. Reun. Cons. int. Explor. Mer* 173: 196-202.
- VOGT, W. 1940. Una depresión ecológica en la costa del Perú. *Bol. Comp. Admora. Guano* 16: 307-329.
- . 1942. Aves guaneras. *Bol. Comp. Admora. Guano* 18: 1-132.