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Nesting distributions of Galápagos boobies (Aves: Sulidae): an apparent case of amensalism

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Abstract Blue-footed boobies (*Sula nebouxi*) in the Galápagos Islands nest at coastal sites such as cliff edges if Nazca boobies (*S. granti*) are absent. However, if sympatric with nesting Nazca boobies, they nest nearby, but farther inland, in areas with little topographical relief. Nazca boobies nest at the coastal sites whether blue-footed boobies are present or not. The segregated nesting pattern of these two species offers a model system to investigate factors influencing community structure. We tested a non-interactive hypothesis, in which different fundamental niches generate the non-overlapping distributions, and an interactive hypothesis, in which the two fundamental niches overlap and an interaction between the two species causes the segregation. Data on three factors considered as likely parameters differentiating fundamental niches (nest microclimate, nature of the nesting substrate, and ease of taking flight from nest sites) failed to support the non-interactive hypothesis. These results suggest that the two species have indistinguishable fundamental niches with respect to these parameters, but different realized niches. Researchers studying resource partitioning by ecologically similar species often only consider competition (a “-/-” interaction) to explain situations like this, ignoring the more parsimonious amensal (0/-) possibility. Nesting segregation in this situation is apparently caused by attacks of non-breeding adult Nazca boobies on blue-footed booby nestlings, injuring nestlings and ultimately preventing them from fledging. The interaction does not result in any discernible costs or benefits (i.e., effects on fecundity or survival) for the adult Nazca boobies, so it is

best described as an amensal interaction. This interaction provides a sufficient explanation of the observed nesting segregation, and precludes present competition for nesting space.

Keywords Amensalism · Blue-footed booby · Competition · Nazca booby · Resource partitioning

Introduction

From the early developmental stages of the science of ecology, many researchers have argued that competition is the most important factor determining community organization, frequently to the exclusion of other possible interactions (reviewed by den Boer 1986; Ekschmitt and Breckling 1994). Others suggest that the relative importance of competition has been overestimated (Connor and Simberloff 1979, 1983; den Boer 1986; Ekschmitt and Breckling 1994; Dodds 1997; Gotelli et al. 1997), and that the influence of other interactions on community structure has not been well studied (Dodds 1997). These conclusions about the role of competition are frequently derived from studies of distributions of species, inferring process through analysis of pattern, and employing null models based on random distribution of species over a given area (e.g., Connor and Simberloff 1979, 1983; Dodds 1997). While this method promotes rigorous hypothesis testing, it is often difficult to achieve the statistical power necessary to reject a null model, and it is difficult to decide which null model to use (Gilpin and Diamond 1982; Harvey et al. 1983; Abrams et al. 1986; Roberts and Stone 1990).

An alternative approach analyzes the putative structuring processes themselves, and lies at the interface of population ecology, community ecology, and behavioral ecology. Ecologically similar species pairs with segregated distributions or resource uses provide excellent opportunities for studying ecological and behavioral interactions suspected as influences on community structure (Begon et al. 1996 and references therein). Of particular interest

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are situations in which clear null models, lacking interactions between members of a species pair, can be contrasted with alternative models implicating species interactions (Connor and Simberloff 1983). This contrast may be difficult to obtain from the distributional data that are frequently used in studies of community structure (e.g., Diamond 1975; Ricklefs and Schluter 1993). For this reason, a focus on the behavioral interactions that may mediate resource partitioning has recently gained favor (Fryxell and Lundberg 1998), involving a productive collaboration between community and behavioral ecology techniques. In this paper we adopt this perspective, using both pattern- and process-based approaches to investigate the nesting distributions of two seabirds.

The study system

Nelson (1978) and Duffy (1984) studied two species of ground-nesting seabirds in the Galápagos Islands with contiguous, but non-overlapping nesting distributions. Both researchers noted that blue-footed boobies (*Sula nebouxii*) nest at coastal sites such as cliff edges if Nazca boobies (*S. granti*) are absent. However, if sympatric with Nazca boobies they nest nearby, but farther inland, in areas with little topographical relief. Nazca boobies nest at the coastal sites whether blue-footed boobies are present or not. Both species forage at least 35 km from the nesting colony during breeding (Anderson and Ricklefs 1987) to obtain their similar diets of fish (Anderson 1989a) by plunge diving. The distances separating coastal and inland nest sites (<200 m) are trivial in comparison with the distances traveled daily by breeders to find food, so food distribution is unlikely to influence nesting distributions. Nelson (1978) and Duffy (1984) both minimized the role of competition in creating the exclusive nesting distributions, but neither evaluated other factors that could produce such a distribution.

In this paper, we re-visit the system described by Nelson (1978) and Duffy (1984), applying a more extensive hypothesis-testing approach. First, we test the hypothesis that the nesting distributions are in fact different, with a larger data set than Duffy (1984) used. In search of segregating mechanisms, we test a non-interactive hypothesis, invoking different habitat requirements (i.e., different fundamental niches) that generate the exclusive distributions against an alternate interactive hypothesis, which holds that the two fundamental niches overlap and that interactions between the two species cause the segregation. Regarding the non-interactive hypothesis, these congeners have morphological and behavioral similarities in addition to their similar foraging biologies, and Nelson (1978) and Duffy (1984) considered it unlikely, based on casual observation, that different terrestrial habitat requirements would lead to segregation. We systematically examined variation in three habitat variables that we considered most likely, based on our past experience with these populations, to differentiate the two fundamental niches: nest microclimate, nature of the nesting substrate,

and ease of taking flight from nest sites. A priori support for the interactive hypothesis is suggested by blue-footed booby occupancy of coastal sites on islands in the Galápagos lacking Nazca boobies (Duffy 1984), consistent with exclusion of blue-footed boobies from preferred coastal sites by Nazca boobies where they co-occur. Competition (a “-/-” interaction) is not the only possible interaction responsible for this spatial structure, and as Gordon (1997) suggested, we gave general consideration to the behavior of individuals and to the spectrum of potential structuring factors. Predation (a +/- interaction) and amensal interactions (0/-) could also exclude one species from their mutually preferred habitat. The term “amensal” may be unfamiliar to some readers. Amensal interactions are asymmetrical: the existence of species A has a negative effect on species B (for example, elephants may inadvertently trample the habitat of a number of other species), but species B's existence has no effect on species A. In contrast, competitive interactions involve negative effects of each species on the other.

The Nazca boobies of the Galápagos have traditionally been considered masked boobies (*Sula dactylatra granti*), but recent analyses of morphological and breeding data (Pitman and Jehl 1998), and of mtDNA differentiation (Friesen et al. 2002) support elevation of the Galápagos and some nearby populations to species status. In this paper we follow the nomenclature of the American Ornithologist' Union (2000) and refer to these birds as Nazca boobies (*Sula granti*).

Materials and methods

We studied Nazca and blue-footed booby nesting biology at Punta Cevallos, Isla Española, Galápagos Islands (1°23'S, 89°37'W), between 1986 and 1995 in conjunction with other long-term research on these species. Anderson and Ricklefs (1987) provide details of the study site. Approximately 3,500 Nazca booby pairs (Anderson 1993) and a variable number, up to 1,000 pairs (unpublished data), of blue-footed boobies breed at Punta Cevallos. Nazca boobies breed seasonally at Punta Cevallos, with eggs laid October–February and fledging occurring March–June. Nazca booby fledglings and 50–80% of the adults vacate the colony during the non-breeding season (Anderson, unpublished data). In contrast, blue-footed booby breeding is temporally unpredictable and apparently opportunistic, (i.e., when supply of prey is adequate). During the years that we collected data for this study, the breeding seasons of these species overlapped to some degree.

Nest site distribution

Nazca boobies nest in minimally vegetated coastal areas in a broken strip starting 1 km north of Punta Cevallos and extending south and then west (Huyvaert and Anderson, submitted). We characterized the nesting distributions of the two species by establishing transects perpendicular to the coast at 100-m intervals, covering 6 km of the coastline beginning at the eastern end of the colony and following the coastline south and west. The transects extended to the point at which inland vegetation was too thick for boobies to nest, and ranged from 5–210 m in length. Each of the 61 transects was 10 m wide and divided into 5-m blocks along its length; each block thus enclosed 50 m². This scale is appropriate for the phenomenon under study: at Punta Cevallos, the average radius of blue-footed booby nests is 175 mm and of Nazca booby

nests is 127 mm (Anderson 1995), with small nearest neighbor distances between nests (Nazca booby: median=2 m; blue-footed booby: median=7 m; Anderson, unpublished data). Within each block we counted the numbers of Nazca and blue-footed booby nest sites present during the period 2–8 April 1986, when peaks of breeding by both species coincided.

To characterize booby nesting patterns in the entire Galápagos Archipelago, we used data from Duffy's (1984) paper and our own observations of Nazca and blue-footed booby nest sites on islands with breeding populations. We used a contingency table to determine if blue-footed boobies nested in coastal nest sites when masked boobies were also present on a particular island. We considered nest sites coastal if they were within 10 m of the coast (Duffy 1984) or on the steep, ocean-facing, outside slopes of volcanic cones.

Parameters of fundamental niches:

Nest microclimate and thermoregulation

Ground temperatures at this equatorial location could affect nest site preferences by imposing thermal stress on incubating boobies around mid-day (Bartholomew 1966). We compared the thermal loads imposed by Nazca and blue-footed booby nesting areas by measuring operative temperature with a modification of the technique of Walsberg and Weathers (1986). We suspended Hobotemp (Onset Computer, Pocasset, Mass.) miniature dataloggers in the center of copper toilet floats (painted white) and mounted the floats on wooden dowels. The center of the float was 20 cm above the ground surface, the location of an adult booby's neck during normal incubation and of the breast when standing over the clutch (during the hot part of the day, boobies frequently stand over the eggs, shading but not incubating them). We placed six units at randomly selected nest sites in the Nazca booby nesting area and six more in randomly selected sites in the adjacent blue-footed booby area, during the periods 1–6 December 1993, and five units per species during 6–11 July 1994. Each day the units were moved to a different set of nests. The dataloggers recorded the air temperature within the floats at 6-min intervals. We also measured wind speed at each location with a hot wire anemometer at 1000 hours, 1200 hours, and 1400 hours, every 5 s for 1 min. The average of these readings was taken as the wind speed at a given site for a given time period. On 22 November 1994, we measured the cooling effects of wind (wind chill) by recording operative temperature at six Nazca booby sites and six adjacent shielded sites. Rectangular 22.7-l (5-gal) jugs served as windshields.

Boobies attempt to lose heat at midday by postural adjustments, urohydrolysis (defecating on the feet), and gular flutter (rapid vibration of the hyoid muscles and bones in the throat to speed evaporative heat loss via the mouth; Gill 1995). We used gular flutter as an easily observed indicator of thermal stress in boobies. An observer on a raised vantage point simultaneously monitored 10 Nazca booby and 10 blue-footed booby adults at their respective nest sites during the hottest part of the day (0900–1600 hours) on 7 December 1992. The observer's position was ≥ 20 m from the nearest nest and did not affect the behavior of the focal birds. All adults were incubating eggs and judged to be at species-typical nest sites. At 15-min intervals the observer recorded the percentage of adults of each species that were exhibiting gular flutter at any time during a 40-s period of observation.

To examine interspecific differences in gular flutter, we conducted an experiment on 6 December 1992 in which adults were confined in plastic mesh crates (63 × 57 × 37 cm) along a transect perpendicular to the coastal cliff edge and their gular fluttering monitored. We used only non-breeding females to standardize thermoregulatory physiology as much as possible. Four females of each species were caged (one individual per cage) at each of three sites: within the Nazca booby nesting area (3 m from edge), between the two areas (18 m from edge), and within the blue-footed booby nesting area (33 m from edge). At 10-min intervals between 1000 hours and 1300 hours we recorded the percentage of birds,

within site and species, exhibiting gular flutter at any time during a 20-s period of observation. Birds were placed in the cages at 0600 hours to allow them time to adjust to the experimental situation. During the monitoring, the birds stood quietly in the cages, their observable activity confined to looking about and, at times, gular fluttering.

Substrate hardness

The nest shapes of these two species differ in association with differences in social systems. Nazca boobies lay 1–2 eggs per clutch and are obligately siblicidal; if both eggs hatch, the first-hatched nestling pushes its sibling from the nest scrape within days, and the victim dies from exposure or depredation (Anderson 1989b). Blue-footed boobies lay 1–3 eggs, and while facultative siblicide may occur among older nestmates during food shortages (Drummond et al. 1986; Drummond and Chavelas 1989), the early siblicide typical of Nazca boobies does not occur. Nazca boobies nest in scrapes that are unusually flat for a ground-nesting seabird, and we have suggested elsewhere that this feature is an adaptation to facilitate efficient siblicide (Anderson 1995). In contrast, blue-footed boobies nest in bowl-shaped scrapes, which may limit the success of the ejection behaviors of which blue-footed booby hatchlings are capable (Anderson 1995; Loughheed and Anderson 1999). Moreover, blue-footed booby parents seem to closely regulate the shapes of their scrapes (Anderson 1995), and show "some tendency to choose a softish substrate" (Nelson 1978, p 523). We hypothesized that nesting distributions are influenced by the distributions of nesting substrates. Specifically, the blue-footed booby social system may require substrate that is loosely packed, or easily compacted or excavated, while Nazca boobies may require substrate with opposite qualities.

We assessed the compaction of nesting substrate by drilling a steel concrete-reinforcing bar into the ground. Spearman correlations between penetration depths of the drill and a three-clawed gardening tool, that imitates the action of a booby's foot, indicated that drilling for 10 s could serve as a non-destructive proxy for 10 s of digging by Nazca boobies ($r=0.96$, $n=12$, one-tailed $P<0.001$) and by blue-footed boobies ($r=0.51$, $n=12$, one-tailed $P=0.04$). An assistant, who was unaware of the hypothesis being tested, penetrated the substrate as deeply as possible in 10 s by rotating the stake and pushing it downward, attempting to use equal effort at all sites. We paired 12 occupied blue-footed booby nest scrapes with 12 randomly selected sites in the Nazca booby area to determine whether the substrate chosen by blue-footed boobies was available in the Nazca booby area.

Flight initiation

Nazca boobies take flight from a cliff edge or elevated rock, 0.2–2.2 m from their nest (T. Santander, unpublished data); breeding blue-footed boobies at Punta Cevallos also typically take flight from an elevated rock within 2 m (mean=0.9 m) of the nest (D. Anderson, unpublished data). In view of this use of elevated perches to take flight, and our impression that the importance of such perches increases further inland, we hypothesized that nesting distributions are influenced by spatial variation in the difficulty of becoming airborne. To test boobies' ability to take flight, we captured Nazca and blue-footed boobies (four males and four females of each species) and moved each bird to the same unfamiliar part of the blue-footed booby nesting area, 60 m from the nearest cliff edge. We released each bird 60–90 s after capture and measured the time to take flight (become airborne). In all 16 cases the bird was alarmed and made vigorous efforts to take flight immediately after release. We measured the mass and wing wrist-to-tip distance and used the guidelines in Pennycuik (1989) to calculate each subject's wing loading; however, to correctly calculate wing loading it is necessary to determine the wing area, which is time-consuming. Rather than determine the wing area for the subjects of the experiment and possibly affect their performance by

imposing additional stress on the birds, we measured the wing chord (flattened wrist-to-tip distance). We measured both wing chord and wing area for another set of 19 Nazca boobies and 18 blue-footed boobies. We used the regression of the square root of the wing area on wing chord to estimate wing area and wing loading in experimental birds. We examined the Spearman rank correlation between wing loading and time to take flight and used a MANOVA (to reduce type I error) and a two-way ANOVA by ranks (Zar 1984) to determine species and sex differences in these variables.

Species interactions and realized niches

Nest site selection by blue-footed boobies

We established a grid system that allowed us to locate sites in a 7.5-ha rectangular section of the colony, which included a 500-m length of coastline and all nesting habitat inland of that length. We used the grid system from May to November 1994 to map the locations of each nest, the inland edge of the Nazca booby nesting area (as determined by our nesting records), and the high tide line. We used this map to calculate the least squares linear regression of y coordinates (north-south) on the x -coordinates (east-west). The regression line closely paralleled the straight coastline in that area. The residual of each nest's location was classified into one of three groups based on nest initiation date, which included: (1) nests initiated before 30 April (during high density Nazca booby nesting); (2) nests initiated in May (a period of decreasing Nazca booby nesting); and (3) nests initiated after May when most Nazca booby fledglings and adults had left the island. We used one-way ANOVA of the residuals to detect any shifts of blue-footed booby nest locations toward the coastline as Nazca booby density declined across the three time periods. Of the original 486 nests marked for the map, 102 markers were missing in November, probably due to their use by frigatebirds (*Fregata* spp.) and fledgling blue-footed boobies as playthings. We are unaware of any bias introduced by loss of these markers.

In 1994, the breeding seasons of the two species overlapped only slightly: as the Nazca boobies were finishing their breeding season, the blue-footed boobies were beginning. If the observed nesting segregation results from interspecific competition, then when little or no temporal overlap of breeding occurs and vacant coastal sites exist, blue-footed boobies should use any vacant coastal nest sites if they are, in fact, preferred over inland sites. As more coastal sites become available, blue-footed boobies should occupy them. In the 7.5-ha section of the colony described above, we marked the locations of all blue-footed booby nests containing newly laid eggs during the period 25 May–5 July 1994. At the beginning of this period we also marked all existing blue-footed booby nests and back-calculated the date of egg-laying (by noting when the egg hatched or by relationships between nestling wing length and age: Anderson, unpublished data).

Attacks on nestlings

Some non-breeding Nazca booby adults regularly approach and interact with conspecific nestlings (Nelson 1978; Curry and Anderson 1987; Anderson 1993). Since 1984, we have observed 2,651 such events, during which non-breeding adult visitor (NAVs) Nazca boobies attend the nestling, often show courtship behaviors, and in 35.2% of events physically attack it (Anderson et al., in preparation). We have also observed several NAV interactions (all attacks) with blue-footed booby nestlings. These attacks cause injuries to the nestling's neck and wings, the principal sites bitten by NAVs along with the rump. In the case of blue-footed booby nestlings, the humeral-ulnar joint of the wing was severely injured or broken during the attacks that we witnessed. We monitored one blue-footed booby nestling for several days after the attack and observed it holding its twisted wing limply away from its body. This posture and injury was identical to that of other juve-

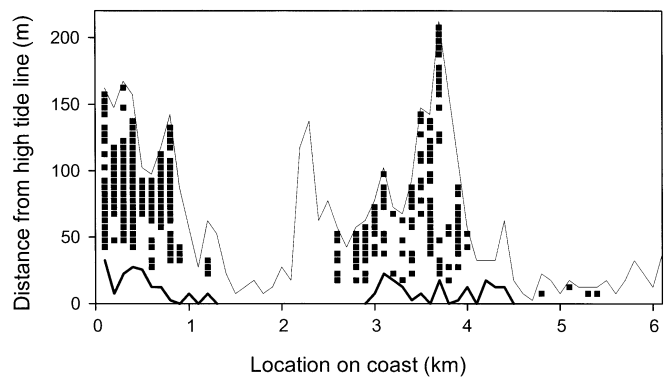


Fig. 1 Distribution of nest sites of Nazca (*Sula granti*) and blue-footed (*S. nebulosus*) boobies, April 1986. The farthest inland Nazca booby sites are represented by the *thick solid line*. Transects with blue-footed boobies at nests are *solid blocks*. The *thin solid line* represents the point at which vegetation was too thick for booby nesting

nile blue-footed boobies noted in both previous and later years. These nestlings never become independent because they cannot fly, and eventually starve when their parents abandon them. We hypothesized that NAV attacks on blue-footed booby nestlings select against blue-footed booby parents that nest near or within Nazca booby colonies. To test this hypothesis, we recorded the distance between all nests with a twisted-wing juvenile blue-footed booby ($n=5$) and the nearest Nazca booby nest in November 1993, when both species bred at high density. For comparison, we also recorded the distance between nests with an uninjured blue-footed booby nestling and the nearest Nazca booby nest in nine of the transects in this area (the transects at 3.0–3.8 km in Fig. 1).

In July 1994, during the Nazca booby non-breeding season, we tested this hypothesis experimentally by placing a nestling blue-footed booby (30–60 days post-hatching) as a stimulus within 10 m of a non-breeding Nazca booby. The stimulus nestling was seaward of the high tide line, in an area without nests and where boobies are not typically found, so any attacks on these nestlings could not be interpreted as defense or other interest in a nest site. If no response was observed within 20 min we returned the nestling to its nest. When an adult Nazca booby did respond, it walked directly toward the nestling with the intense staring that is characteristic of NAVs prior to attacking conspecific nestlings (Anderson 1993). In these cases, we interrupted the interaction just prior to a physical attack. Nonetheless, we are certain that the NAV would have proceeded with a physical attack on stimulus nestlings had we not interceded, based on the similarity between the behavior we induced and that of non-experimental NAVs. We conducted 14 such stimulus response experiments, as well as eight controls with rolls of toilet tissue stacked and painted white, roughly the size and shape of a blue-footed booby nestling. No Nazca booby was involved in more than one experiment.

Results

Nest site distribution

In 1986, 21 of the 61 transects contained nests of both species. In all 21, distributions of Nazca booby and blue-footed booby nests did not overlap, and in all 21 transects blue-footed boobies nested inland of Nazca boobies (binomial probability <0.001). No 50-m² block contained nests of both Nazca and blue-footed boobies. All Nazca booby nests were within 35 m of the high tide line (Fig. 1). In 1994, mean distance of Nazca booby nests from the high

Table 1 Habitat use and population size estimates of colonies in the Galápagos Archipelago. Coastal nests are those within 2–3 m of coast or cliffs; inland nests are >3 m from coast or cliffs (after

Duffy 1984). The asterisk (*) denotes locations where inland sites likely receive high levels of wind, because of topography or location with respect to prevailing southeasterly and easterly winds

Colony	Blue-footed booby		Colony size (Individuals)	Nazca booby		Source	
	Habitat			Habitat			
	Coastal	Inland		Coastal	Inland		
Santa Fe*			0	X		10	Pers. obs.
Tortuga			0	X		10 ²	Pers. obs.
Caldwell*			0	X	X	10	Pers. obs.
Darwin*			0	X	X	10 ³	Pers. obs.
Genovesa*			0	X	X	10 ³	Pers. obs.
Isla Marielas	X		10 ²			0	Duffy 1984
Tagus Cove	X		10 ²			0	Duffy 1984
Beagle Cr.	X	X	10 ³			0	Duffy 1984
Cabo Douglas	X	X	10 ³ –10 ⁴			0	Duffy 1984
Cal. Iguana	X	X	10 ²			0	Duffy 1984
Pta. Vincente Roca	X	X	10 ³			0	Duffy 1984
Gardner (Floreana)*		X	10 ²	X		10	Pers. obs.
Champion		X	10 ²	X	X	10	Pers. obs.
Daphne Major*		X	10 ³	X	X	10 ²	Duffy 1984, Pers. obs.
Pta. Cevallos*		X	10 ² –10 ³	X	X	10 ⁴	Duffy 1984, Pers. obs.
Pta. Pitt		X	10 ²	X	X	10 ² –10 ³	Pers. obs.
Pta. Suarez*		X	10 ³	X	X	10 ³	Duffy 1984

tide line was 11.8 m (SD=7.66 m, range 0–39 m, $n=46$), and all blue-footed boobies nested inland from the nearest Nazca booby nest site. In 1994, the minimum separation between a blue-footed booby nest site and a Nazca booby site was 8.7 m. Thus, the nesting distributions of these congeners at Punta Cevallos were segregated and a clear zonation of the two species was apparent.

In 1986, some transects contained only blue-footed booby nests, and these nests were in coastal locations (i.e., within 10 m of the coast) that would normally be occupied by Nazca boobies had Nazca boobies been present (Fig. 1). However, transects containing only Nazca booby nests did not show Nazca boobies occupying sites typical of blue-footed boobies in other transects.

At the archipelago scale, blue-footed boobies nested in coastal sites on 6/6 islands lacking Nazca boobies, but on 0/5 islands where Nazca boobies did nest (Fisher's Exact Test, $P=0.001$; Table 1). In all but two cases, Nazca boobies only used inland nest sites if those sites were exposed to relatively high wind levels (Table 1).

Parameters of fundamental niches

Nest microclimate and thermoregulation

In December 1993, Nazca boobies nested at sites that had higher wind speeds ($F=368.75$, $df=1$, $P<0.001$) and lower temperatures ($F=101.88$, $df=1$, $P<0.001$) than the typical blue-footed booby nest sites did, regardless of time of day (Fig. 2, top row). In July 1994, wind speeds were higher ($F=115.34$, $df=1$, $P<0.001$) and operative temperatures were lower ($F=200.91$, $df=1$, $P<0.001$) in Nazca booby nest sites (Fig. 2, bottom row). Additionally, temperatures at sites shielded from wind (mean=28.9°C, SD=0.35,

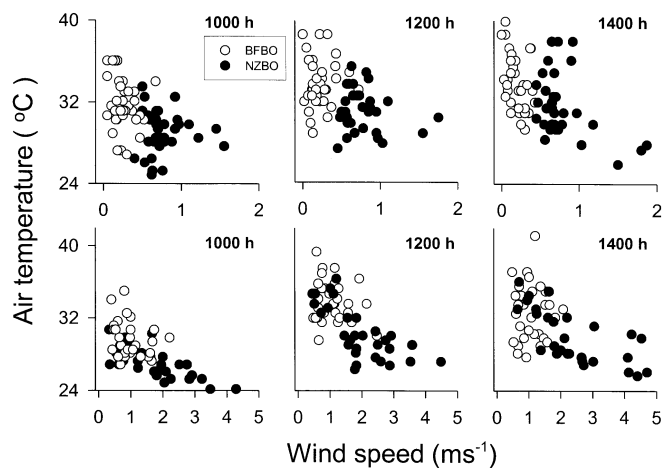


Fig. 2 Top row: December 1993 wind speeds and operative temperatures at typical nest sites of Nazca (NZBO) and blue-footed boobies (BFBO) at 1000 hours, 1200 hours, and 1400 hours. Bottom row: July 1994 wind speeds and operative temperatures at typical nest sites of the two species at 1000 hours, 1200 hours, and 1400 hours

$n=5$) were higher than those at open sites mean=27.9°C, SD=0.33, $n=5$; $F=41.71$, $df=1$, $P<0.001$). The inland sites occupied by blue-footed boobies thus imposed a higher thermal load than the coastal Nazca booby sites did, due at least in part to the lower wind speeds at inland sites.

Log-linear analysis of the frequencies of gular flutter during the caging experiment showed an effect of distance from coastal cliff ledge on proportion of birds fluttering ($\chi^2=73.72$, $df=32$, $P<0.001$) with more birds fluttering at warmer inland sites (Fig. 3). The species \times distance effect was not significant ($\chi^2=1.07$ $df=32$, $P=1.00$). The similarity of thermoregulatory response of the two species is notable in the actual nesting areas of Nazca

Fig. 3 Thermoregulation by Nazca (*NZBO*) and blue-footed boobies (*BFBO*) in December 1992, estimated by incidence of gular fluttering, in coastal (3 m) and inland (18 and 33 m) areas. The 3-m site was within the Nazca booby nesting area, the 33-m site was within the blue-footed booby nesting area, and the 18-m site was between the two areas ($n=12$ of each species)

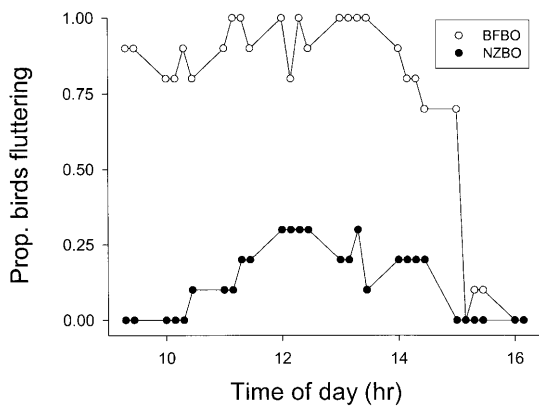
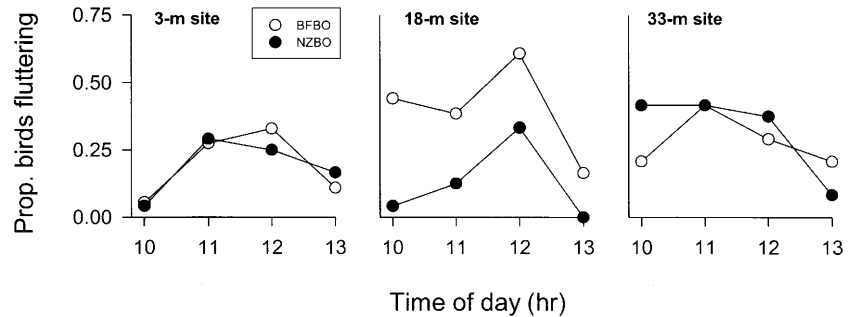


Fig. 4 Proportion of incubating birds engaging in gular flutter in December 1992 ($n=10$ of each species)

boobies (the 3-m site) and blue-footed boobies (the 33-m site; Fig. 3). This result indicates that adults of the two species experienced similar levels of physiological stress under a given thermal load in the present nesting areas.

Observations of undisturbed birds at natural nest sites showed that blue-footed boobies used gular fluttering much more frequently than Nazca boobies did (Fig. 4); time-of-day effects were held constant by using a Wilcoxon matched pairs test ($T=0.00$, $Z=4.37$, $n=28$, $P<0.001$). Since the species had similar responses to a given thermal load (see above), and gular flutter indicates heat stress, inland nest sites imposed higher heat stress on blue-footed boobies than did coastal nest sites on Nazca boobies. Furthermore, if blue-footed boobies nested in Nazca booby sites, they would apparently experience the same lower level of thermal stress that Nazca boobies did (e.g., Fig. 3).

Substrate hardness

The mean drilling depth achieved in blue-footed booby nesting areas was 98.9 ± 89.2 cm ($n=12$) and in Nazca booby nesting areas was 82.2 ± 99.8 cm ($n=12$; paired t -test $t=0.19$, $df=11$, $P=0.86$).

Flight initiation

A significant effect of species on morphology (wing chord and wing area) was observed (Wilk's lambda=0.40,

Table 2 Wing loading and time taken to initiate flight by species and sex. Median and range are given for each group ($n=4$ in each case)

Species, sex	Wing loading (Nm^{-2})	Flight initiation (s)
Blue-footed, male	47 (45–52)	19.0 (15–35)
Blue-footed, female	52 (49–61)	74.5 (20–385)
Nazca, male	74 (73–82)	267 (105–423)
Nazca, female	84 (80–92)	387.5 (333–626)

$n=37$, $P<0.001$), so we used species-specific linear regression equations to estimate wing area from wing chord data; for Nazca boobies, $\sqrt{\text{area}}=0.682 \times \text{length}+0.164$ ($r=0.44$, $n=19$, $P=0.06$), for blue-footed boobies, $\sqrt{\text{area}}=1.293 \times \text{length}-0.121$ ($r=0.71$, $n=18$, $P<0.001$). The effect of sex was not significant (Wilks' lambda=0.81, $n=37$, $P=0.25$).

MANOVA showed a significant effect of species (Wilks' lambda=0.36, $n=16$, $P=0.003$) and sex (Wilks' lambda=0.36, $n=16$, $P=0.003$) on wing loading and flight initiation rank scores, so we could proceed using a two-way ANOVA by ranks to examine the species and sex effects on these variables separately. The species and sexes differed in wing loading (species effect: $F=153.60$, $P<0.001$; sex effect: $F=38.40$, $P<0.001$) and time to flight initiation (species effect: $F=18.11$, $P<0.001$; sex effect: $F=6.03$, $P=0.030$; Table 2). Additionally, the wing loading estimate was correlated with time taken to initiate flight (Spearman $R=0.79$, $n=16$, $P<0.001$).

Species interactions and realized niches

Nest site selection by blue-footed boobies

Blue-footed boobies that initiated breeding after the seasonal departure of most Nazca boobies did not nest significantly closer to the coast than did pairs nesting earlier (Table 3; $F=1.46$, $df=2$, one-tailed $P=0.12$), nor did they nest within the vacated Nazca booby nesting area (Fig. 5).

Attacks on nestlings

Blue-footed booby nest sites with an injured nestling were significantly closer (median=3 m, range 2–8 m, $n=5$) to the nearest Nazca booby nest than were 40 other nest sites with healthy nestlings in nine transects (medi-

Table 3 Summary of residuals of blue-footed booby nest locations (see text) in relation to seasonal change in Nazca booby density. Units are meters. Negative residual indicates that the nest was closer to the coast than was the regression line based on all nest locations

Nest initiation period	Mean	SD	<i>n</i>
Before May	3.45	24.62	78
May	-0.74	22.00	225
After May	-3.60	25.90	39
All groups	-0.11	23.11	342

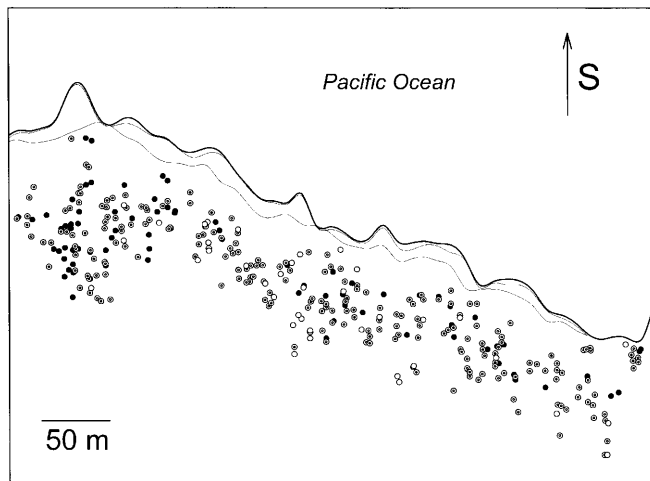


Fig. 5 Map of nest sites of Nazca and blue-footed boobies in 1994. The *hairlines* along the coastal high tide line enclose the Nazca booby nesting areas. *Black circles* represent blue-footed booby nests initiated before 30 April, *grey circles* are nests initiated in May, and *white circles* are nests initiated after May. This area corresponds to kilometers 3.0–3.7 in Fig. 1

an=58.5 m, range 8–145 m, $n=40$; Mann-Whitney $U=0.5$, $P<0.001$). The ranges of injured and healthy blue-footed booby nestlings were nearly non-overlapping: the five blue-footed booby nests with injured nestlings were all among the six nests closest to Nazca booby nests.

In experimental presentations of blue-footed booby nestlings to adult Nazca boobies, the attack response of NAVs was elicited in 6/14 trials. However, no Nazca boobies (0/8) attacked an inanimate object of similar size and shape in the same locations (Fisher's Exact Test, $P=0.04$), indicating that the blue-footed booby chick itself elicited the behavior when it was presented in a coastal location, in view of Nazca booby adults, rather than unseen at the usual inland blue-footed booby nest site.

Discussion

Nazca and blue-footed booby nests were distributed within adjacent but completely non-overlapping bands at Punta Cevallos in both 1986 and 1994; during our 17 years of work at the site this pattern has not varied. The non-interactive hypothesis based on different fundamental nesting niches received little support from our data. Blue-

footed boobies nested in coastal areas if Nazca boobies did not nest there at any time of year, indicating that the abiotic characteristics of the coastal sites were suitable. Adults of the two species responded physiologically in a similar manner to a given thermal load, and inland sites imposed a higher thermal load, indicating that coastal sites provided a better thermal environment for both species. The two species differed in ease of taking flight in low wind inland conditions, in association with differences in wing loading, so the fundamental nesting niche of blue-footed boobies is broader than that of Nazca boobies in this respect. However, non-breeding blue-footed boobies roost in numbers within the Nazca booby colony, and take flight with ease from that location (personal observation), so wing-loading considerations contribute to an explanation of how blue-footed boobies can occupy more inland sites than masked boobies, but not why they do not use coastal sites near Nazca boobies. Finally, nesting substrates chosen by both species were available in the nesting area of the other species. Coastal sites seem to be a part of the fundamental niche of both species; however, they are not a part of the realized niche of the blue-footed boobies when the two species are sympatric.

The interactive hypothesis did receive support. Booby nesting patterns in 17 colonies in the Galápagos Archipelago (Table 1, Fig. 1) suggest that nest site segregation is due to some interaction, with blue-footed boobies replacing Nazca boobies in coastal sites lacking Nazca boobies. A number of segregating mechanisms could produce this pattern, including predation of Nazca on blue-footed boobies, competitive exclusion, and a negative amensal effect of Nazca on blue-footed boobies. Nazca boobies are not known to eat other birds (Nelson 1978; Anderson 1989a; unpublished data); we consider predation an unlikely mode of interaction between these species. When Nazca boobies ceased breeding in 1994, their density in their nesting habitat declined markedly; some males remain in this habitat during the non-breeding season, but most Nazca boobies vacate the island or show much reduced attendance (Anderson, unpublished data). At this time, coastal sites were available to blue-footed boobies, but blue-footed boobies did not occupy them (Fig. 5), as would be expected if competition for nest sites acted as a structuring mechanism. Furthermore, behavioral interactions between adults of the two species are extremely rare; in 17 years of work at this site we have seen less than five interactions between adults of these species, because their spatial zonation largely precludes behavioral contact. Thus, we have little confidence in a role for current interspecific competition for space as a structuring mechanism. Additionally, during nine interactions observed by Duffy (1984) nest-site holders of either species were never displaced by congeners.

An amensal interaction excluding blue-footed boobies from coastal nest sites did receive positive support. Both experimental and non-experimental evidence implicates attacks by some adult Nazca boobies on nestling blue-footed boobies as a segregating mechanism. Nazca booby NAVs attacked blue-footed booby nestlings during

the Nazca booby breeding season, inflicting fatal injuries; they also responded to experimental presentations of blue-footed booby chicks between Nazca booby breeding seasons. Since blue-footed booby chicks are at risk from NAVs year-round, selection should act on blue-footed boobies to nest in a manner that separates or conceals them from Nazca boobies year-round. In the open habitat of Punta Cevallos, this requires nesting inland of the coastal strip occupied by Nazca boobies.

The Nazca booby non-breeding season, exemplified by the situation in June and July 1994, is the critical period to discriminate the competition and amensal hypotheses. Competition for nesting space should have been minimized in the Nazca booby area and maximized in the blue-footed booby area at this time, when most of the Nazca boobies were absent from Isla Española and blue-footed booby nesting density was unusually high. In spite of the asymmetry between intra- and inter-specific competition for nest sites within the blue-footed booby population, blue-footed boobies did not move into vacated Nazca booby space, as would be predicted if current inter-specific competition excluded blue-footed boobies. This result is expected if interspecific attacks on nestlings structure the nesting distributions, because some non-breeding Nazca boobies were present in their area, and blue-footed booby nestlings in the Nazca booby area would not be concealed from these birds. We cannot exclude past competition combined with strong philopatry as an explanation for this observation, but we have no positive evidence in favor of this hypothesis. In contrast, we have presented positive evidence of an amensal exclusion of blue-footed boobies from coastal sites. Applying strong inference (Platt 1964), the amensal hypothesis is more strongly supported than are hypotheses of present and past competition; furthermore, the amensal hypothesis provides a sufficient explanation of the nesting zonation in these two species.

Nazca booby NAVs attack conspecific nestlings much more frequently than they do blue-footed boobies (e.g., Curry and Anderson 1987). The causation of this behavior is currently under investigation; preliminary data indicate that NAVs are typically young adults that have not yet bred, and they receive no obvious benefit from performing the behavior (Anderson et al., in preparation; Porter and Anderson, in preparation). In the case of attacks on blue-footed booby nestlings, our observations and experimental presentations of blue-footed booby nestlings indicate that these congeners provide a target for NAV behavior that is as acceptable as are conspecific nestlings. We can exclude several conceivable types of benefit that NAVs might accrue from attacks on blue-footed booby nestlings: they do not acquire the nestling's nest site (because it is outside the Nazca booby colony), they do not cause the nestling to regurgitate food that could then be eaten by the NAV, and they do not depredate the nestling. NAVs experience no apparent cost due to the behavior either. In the absence of any indication that survival and fecundity of Nazca boobies are affected by the interaction, but clear indication that survival of blue-footed boobies is affected, the inter-

action mediated by NAV behavior meets the requirements of an amensal (0/-) interaction.

Blue-footed boobies show high natal philopatry (Osorio-Beristain and Drummond 1993), so current adaptations can be expected to reflect past local conditions. Within the Galápagos, blue-footed boobies nest jointly with Nazca boobies in many colonies (Table 1), and attacks by Nazca booby NAVs on conspecific nestlings occur commonly throughout the archipelago (Nelson 1978; Anderson, unpublished data). Thus, the selective agent that we identified on Española is likely to act throughout the Galápagos Archipelago, accounting for the segregated nesting on other islands. While the majority of blue-footed boobies nest in Galápagos, two other populations exist on the west coast of equatorial South America and on the west coast of Central America/Mexico (Nelson 1978). We have not studied the latter population; on the Ecuadorian coastal island of Isla de la Plata, Nazca boobies occupy coastal sites, blue-footed boobies occupy inland sites (Anderson, unpublished data), and Nazca booby adults show NAV behavior (A. Pincay, personal communication), as in Galápagos. We suspect that the amensal interactive hypothesis provides a general explanation for the segregated nesting pattern shown by these two species.

Our data implicate amensalism as a factor influencing community structure. While amensal events should theoretically be a common interspecific interaction, few instances have been documented. Dodds (1997) searched *Biological Abstracts* from 1993–1995 and found amensalism was referred to in only one article, while competition was referred to in 139 articles. We searched *Biological Abstracts* from 1996 to 1999 using Dodds' protocol and found amensalism in nine articles and competition in 491 articles. Additionally, from 1990 to 1999, amensalism involving vertebrate populations was not the subject of any article. We found that amensalism was mentioned in only three of nine major ecology textbooks (Colinvaux 1993; Brewer 1994; Krebs 1994; Pianka 1994; Begon et al 1996; Kormondy 1996; Ricklefs 1993; Krohne 1998; Stiling 1999); allelopathy was mentioned in all nine texts, but authors did not agree as to whether allelopathy is considered an amensal or a competitive interaction. Brewer (1994) devotes three pages to amensalism and allelopathy and suggests that "it is possible that the term 'amensalism' should be more widely applied and, further, that not all cases of interference should be equated with competition".

Amensal interactions may be important for understanding community structure, as we conclude for two booby species, but the importance of amensalism in general cannot be assessed without more attention by researchers. Historically, ecologists have invoked competitive interactions to explain habitat segregation by ecologically similar species, often congeners (examples in Begon et al. 1996; Schoener 1974); however, much of the support for the competitive exclusion as a mechanism for niche differentiation is weak. As Begon et al. (1996) noted, "... interspecific competition is a process that is often associated, ecologically and evolutionarily, with a particular pattern (niche differentiation), but interspecific com-

petition and niche differentiation (the process and the pattern) are not inextricably linked.” In fact, the competitive exclusion principle is difficult to test, because current levels of competition between species might be indiscernible, the competition having been resolved through past interactions. The “ghost of competition past” (Connell 1980) can be readily invoked to explain patterns, but hypotheses dealing with this phenomenon cannot be easily tested. In the system we studied, current levels of amensal interactions between two species are discernible (through direct observation and through observation of characteristic injuries to blue-footed booby chicks), and, assuming that the current behavior and ecology of the two species has remained fairly constant throughout the history of interactions between the two species, we can infer that the evolutionary effects of the amensal interaction have led to the current differentiation of habitat. The strength of our approach is to study both pattern and process to understand the factors producing community structure.

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