Aspects of the Ecology of Blue-footed and Peruvian Boobies at the Limits of their Ranges on Isla Lobos de Tierra, Peru

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Abstract.—Aspects of nesting and foraging ecology of Peruvian (*Sula variegata*) and Blue-footed (*Sula nebouxi*) boobies were investigated at Isla Lobos de Tierra, at the edges of the breeding ranges of both species. The two species returned from foraging from different directions but did not differ in duration of foraging trip or duration of dive. The Peruvian Booby nested only on flat, windswept areas whereas the Blue-footed Booby nested in a wider variety of habitants. Peruvian Booby nest sites were significantly cooler than those of the Blue-footed Booby. It would appear that these two species are not simple ecological replacements and may be limited by different factors.

Key words.—Allopatry, booby, foraging, nesting, Peru, range, *Sula*, thermal constraints.

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The Blue-footed (*Sula nebouxi*) and Peruvian (*S. variegata*) boobies, have been regarded as ecological replacements of one another, with the Peruvian Booby confined to the cold, very productive waters of the Humboldt or Peruvian Current and the Blue-footed Booby occurring in warmer waters to the north and in upwelling systems in Panama, Ecuador, including the Galapagos, and Mexico (cf. Murphy 1936, Nelson 1978). This paper examines aspects of the ecologies of the two sulid species in their area of overlap. The Blue-footed Booby nests from the Gulf of California south to Lobos de Tierra and Lobos Afuera 06° 54's 80° 43'W off Peru (Fig. 1, Nelson 1978). The Peruvian Booby nests north from islands off the middle part of Chile (33° S) to Punta Aguja, 05° 52'S 81° 06'W, north of Lobos de Tierra (Nelson 1978). The two species nest together on the Lobos de Tierra and Lobos Afuera islands. Nonbreeding Blue-footed Boobies disperse south into the range of the Peruvian Booby (Nelson 1978, Duffy 1981) and nonbreeding Peruvian Boobies have been reported, especially in El Niño years, in the Gulf of Guayaquil, Ecuador (Fuentes 1965), Colombia (Jordan 1958), and Panama (Aid et al. 1985).

METHODS

Field work was conducted during 24 February–3 March 1978 on Isla Lobos de Tierra, (06° 28'S, 80° 50'W). Approximately 9 by 3 km and 1 426 ha in area, the island consists of small, gravelly hills interspersed with extensive plains (Hutchinson 1950). Although some precipitation occurs, very little vegetation is present and most of the island is desert (Murphy 1925).

I observed the direction from which birds of both species returned to their nests after foraging on three evenings: 26-28 February 1978, between 1830-1930 h, dividing the compass into four 90° sectors. Durations of foraging were measured on three days by watching which adults were present at nests from 0530 h to approximately 1500 h. I considered a foraging trip as the time elapsed from the departure

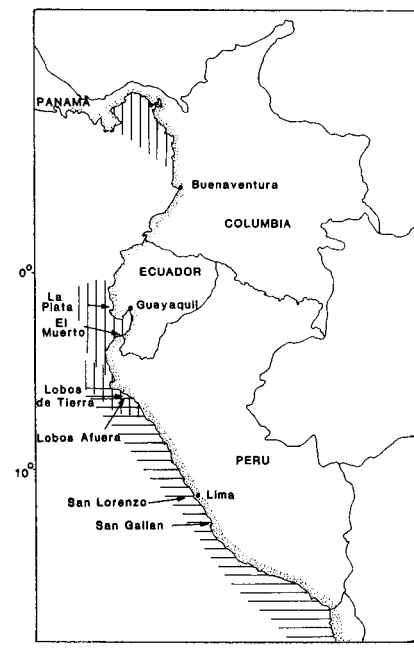

Figure 1. Ranges of the Peruvian (horizontal lines) and Blue-footed (vertical lines) boobies, showing islands mentioned in the text.

of one member of a booby pair from its nest until its return. Limited observations of foraging were made from the island and when I traveled to and from the island by small fishing boat. Plunges were timed from contact with the water until emergence (Duffy 1983a). Diets were not sampled.

I counted the number of young aged 10-12 weeks per nest, using criteria of Galarza (1968) and Duffy and Ricklefs (1981); I observed the general locations and sizes of Blue-footed and Peruvian Booby nesting aggregations on Lobos de Tierra; and measured temperatures of guano nest-rims of both species at three different sites at three different times of day between 28 February and 1 March 1978 (cf. Duffy 1983b). Guano nest rims are relatively similar in color and substrate and thus more likely to reflect differences in the thermal microclimate than interspecific differences in nest structure. Means and their standard errors are given for all data.

RESULTS

Foraging Ecology

The two species differed significantly in direction of return ($\chi^2 = 439.4$, df = 3, $p < 0.001$; the three sample periods combined. Over 90% of the Peruvian Boobies returned from either the south or east. Blue-footed Boobies returned about equally from the north, south, and west (Fig. 2). Returns within each species were not randomly distributed (Peruvian Booby: $\chi^2 = 606.8$; df = 3; $p < 0.001$; Blue-footed Booby: $\chi^2 = 69.8$, df = 3; $p < 0.001$).

The durations of foraging were similar for both species (Blue-footed Booby, 133 ± 12.9 min, n = 21; Peruvian Booby, 115 ± 11.2 min, n = 19, t = 1.04, $p < 0.05$). To the south, where the Peruvian Booby occurs alone, its foraging trips were almost 50% shorter: 60.1 min at Isla Mazorca 11° 23′S 77° 45′ W (Duffy 1983c). In the Galapagos Islands, Blue-footed Boobies had mean absences of 159 min for males and 106 min for females (Nelson 1978: 530).

The Blue-footed Booby had slightly longer submergences during plunges (4.04 ± 0.126 sec; n = 72) than the Peruvian Booby (3.69 ± 0.36 sec, n = 10) but the difference was not significant (t = 0.96, $p > 0.05$). Peruvian Booby plunges around Lobos de Tierra were similar to those at Isla Mazorca (3.01 ± 0.05 sec: Duffy 1983a; t = 1.93, $p > 0.05$) and in central Chile 29–33° S, at the southern edge of its

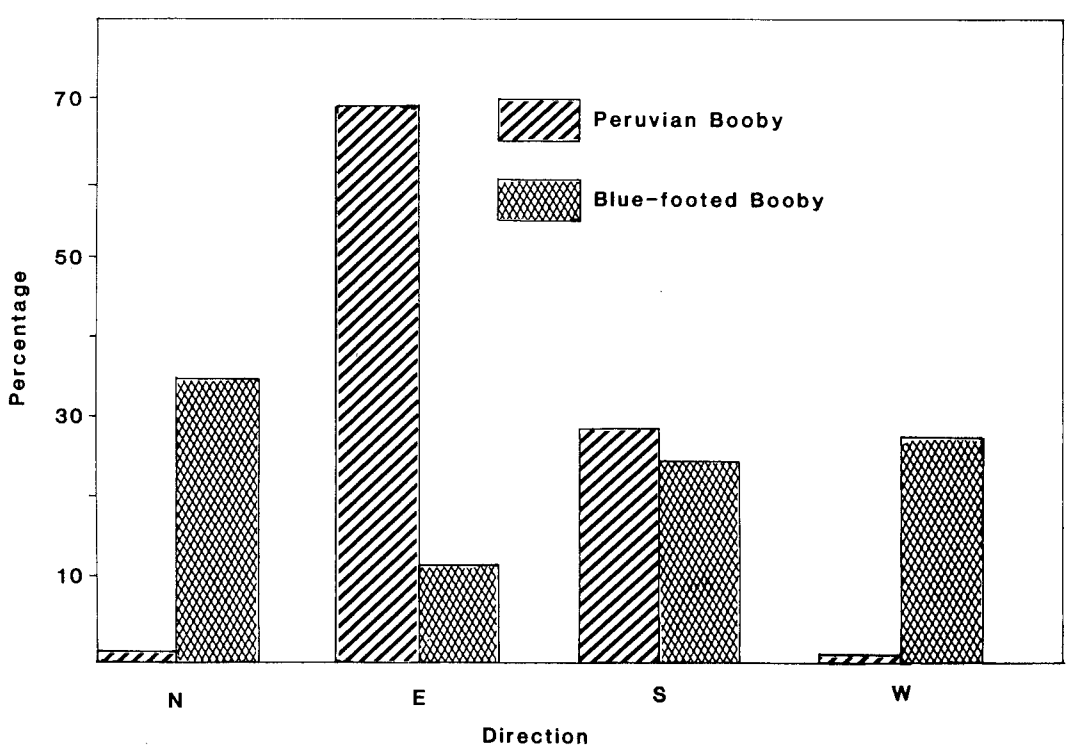

Figure 2. Directions of return of Blue-footed and Peruvian boobies to nesting colonies at Isla Lobos de Tierra, Peru.

range (3.89 ± 0.81 sec, n = 9: pers. obser.; t = 0.234; p > 0.05).

At sea, the two species fed in both large and small groups, frequently with dolphins (cf. Brown 1981) and, at times, together. There appeared to be no difference in group size between the species, but quantitative data were not collected. Blue-footed Boobies frequently fed in small groups or alone, as reported in Galapagos (Parkin et al. 1970, Nelson 1978), but larger groups of 40 to 200 were seen. These were comparable in size to the largest group (76) of Blue-footed Boobies I observed in Galapagos. When this species occurs off central Peru where it is rare (Brown 1981, Duffy 1981), individuals feed alone or at the edges of large groups of other species (Duffy 1983a). The very large feeding groups of hundreds to thousands of Peruvian Boobies seen farther south (Duffy 1983a) were not observed near Lobos de Tierra.

Nesting Ecology

Data on breeding seasons of the two species on Lobos de Tierra are few. Nelson (1978: 541), after a review of earlier reports, suggested that the Blue-footed Booby nests there throughout the year, but could not determine if there are seasonal peaks. At nesting sites south of Lobos de Tierra, Vogt (1942) found Peruvian Boobies nesting throughout the year but with a strong seasonal peak in the austral summer.

Blue-footed Booby nests were scattered over Lobos de Tierra in sand and gravel flats, rocky outcroppings, gullies, tops of hills: everywhere but steep slopes. Peruvian Boobies nested only on smooth, windswept "pampas" or sand flats. Peruvian Booby nests on Isla Lobos de Tierra had a density of 2.1/m^2 (Duffy and Duffy 1986) compared to slightly lower densities of 1.5 - 1.9/m^2 at islands to the south where they nested on cliffs and slopes, as well as on flat areas (Vogt 1942, Nelson 1978, Duffy 1983b). Blue-footed Booby nests on Lobos de Tierra were often 10–30 m or more apart, and rarely closer than one m from each other, densities comparable to those on the Galapagos Islands (Nelson 1978).

Temperatures at Blue-footed Booby nests on Lobos de Tierra were significantly higher than those of Peruvian Booby (Table 1). Temperatures of Peruvian Boobies nests (mean 31.8°) were hotter than those on Isla Mazorca (mean 28.2°, Duffy 1983b), as were ambient air temperatures (Lobos: 27°; Macabi: 24–26°).

Heat tolerances and growth of young of the two species appeared approximately equivalent on Lobos de Tierra (Duffy and Ricklefs 1981) and growth rates appeared similar to growth measured from Peruvian Boobies taken on Isla Chincha Norte (Galarza 1978) and Blue-footed Boobies in the Galapagos Islands (Nelson 1978, Ricklefs et al. 1984), although quantitative comparisons were not possible because of the small sample sizes.

The numbers of 10–12 week old young per nest were not statistically different for the species (p > 0.005; χ^2 = 2.328, df = 2; Blue-footed Boobies, mean = 1.7: nests with one young, 76; two young, 113; three young, 11. Peruvian Booby, mean = 1.6: nests with one young, 87; two young, 107; three young 6). Mean number of young of the same age per nest (1.9, n = 703) was slightly higher for Peruvian Boobies nesting on flat areas at Isla Mazorca (Duffy 1983b). In Galapagos, Nelson (1978: 538) found a brood size of only about 1.3/nest for Blue-footed Booby young of 8+ weeks age, but this was partially during a period of food shortage.

Tick (*Ornithodoros amblus*) densities at Peruvian Booby nests in areas away from mass nest-desertions on Lobos de Tierra were 8.2/500 mL sample, within the range (7.2–85.4 ticks/500 mL) for 'healthy' Peruvian Booby nests at other islands to the south (Duffy 1983c). No ticks were found in nests or seen on young Blue-footed Boobies at Lobos de Tierra, but low-intensity parasitism almost certainly occurs as it does in Galapagos (Duffy and Duffy 1986)

DISCUSSION

The foraging of two species seemed to differ primarily in the direction of return, with Peruvian Boobies foraging south and east of Lobos de Tierra and Blue-footed Boobies foraging to the west, north and south. Brown(1981) found a similar pattern during 1977, with Blue-footed Boobies commonest to the north and Peruvian Boobies to the southeast. The inshore

Table 1. Temperatures (means plus standard errors) of nest-rims of Blue-footed and Peruvian Booby nests at different times of day on Isla Lobos de Tierra, Peru.

			Temperatures at nests (°C)			
Date	Time	Wind (km)	Ambient	Peruvian	Blue-footed	t[1]
28 February	10:30	5	27	30.1 (0.22)	31.1 (0.18)	3.492**
	14:30	20	27	30.9 (0.16)	32.4 (0.27)	4.829***
1 March	10:30	0	27	34.4 (2.04)	35.6 (0.36)	2.033*

[1]n = 20 for each species in each sample. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

waters east of Lobos de Tierra are typically colder than waters in other directions (Zuta and Urquizo 1972).

Almost nothing is known of the diet of the Blue-footed Booby. Regurgitations in Galapagos contained mackerel *Scomber japonicus* and sardina (*Sardinops sagax*) (pers. obs.). Nelson (1978) summarized literature reports of "flying fish (*Exocoetus* spp.), sardines, several species of anchovies, and Pacific mackerel" as prey species. Peruvian Boobies at Isla Chincha Norte (Galarza 1968) and Isla Mazorca (pers obs.) predominately took Peruvian anchoveta, with smaller amounts of mackerel and other species.

The Peruvian anchoveta is found inshore, at low temperatues of 14.5–21° C (Jordan 1971). Horse mackerel (*Trachurus murphyi*) and sardina (*Sardinops sagax*) occur offshore, over the edge of the continental shelf (Johannesson & Vilchez 1980) and the sardina typically occurs in waters warmer than 19° C and farther offshore than the anchoveta (Santander 1980). The Peruvian Booby may be an anchovy specialist, foraging inshore, while the Blue-footed Booby forages at the edge of the upwelling on a variety of warm-water species (cf. Nelson 1978).

Peruvian Boobies nested only on flat, windswept plains that were cooler than the more varied nesting habitats of Blue-footed Boobies. The higher nest densities of Peruvian Boobies led to greater tick numbers (Duffy and Duffy 1986), but nesting success did not differ between the species, based on number of young per nest. The Peruvian Booby may be under thermal constraints that limit its choice of nesting habitat on the island. Vogt (1942) suggested that such constraints limit the species' nesting habitat even on islands farther south. Similarly, Hand et al. (1981) suggest thermal constants may be important in determining nest sites and even breeding ranges of gulls (*Larus* spp.).

Islands north of Lobos de Tierra (such as El Muerto 03° 09'S 80° 04'W in the Gulf of Guayaquil or Isla La Plata 01° 14'S 81° 04'W, north of Punta Salinas, Ecuador) may be too warm for successful nesting by Peruvian Boobies. On the other hand, it seems unlikely that temperatures farther south of Lobos de Tierra are too low for nesting Blue-footed Boobies. Sheltered areas and the leeward sides of many guano islands can be very warm (ground temperatures: 30.1–50.1° C, Vogt 1942) and would appear suitable.

While ambient temperatures and anchoveta distribution may limit the northward range of the Peruvian Booby, no such limits can be identified at present for the Blue-footed Booby.This suggests that the two species are not simply ecological replacements along an environmental gradient such as heat or productivity, but rather that the factors that limit their ranges differ.

Future visits to Lobos de Tierra should look more closely at adult and nestling tolerance to heat and wind chill, diet of the two species, and breeding cycles. At sea, information is needed on interactions of the two species and use of different sizes of food patches. Similar studies of species' replacements among seabirds are needed to examine the relative roles of competition and intrinsic species' physiological or behavioral limits. Such studies are perhaps more likely to identify the critical features of individual species' life histories than are studies at the centers of species' ranges.

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