

NEST SITE SELECTION BY MASKED AND BLUE-FOOTED BOOBIES ON ISLA ESPAÑOLA, GALÁPAGOS

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ABSTRACT.—On Punta Suarez, Isla Española, Galápagos Islands, Masked Boobies (*Sula dactylatra*) nested at the edge of a cliff while Blue-footed Boobies (*Sula nebouxii*) nested farther inland. Elsewhere in the Galápagos, Blue-footed Boobies nested near cliff edges at seven of eight sites where Masked Boobies were absent. Masked Boobies appeared to have difficulty taking flight except from the cliff edge, while Blue-footed Boobies were able to take off from the interior. Neither species appeared dominant in interspecific interactions or could displace the other from occupied nest sites. Blue-footed Boobies may avoid nesting near cliff edges where Masked Boobies are present in order to avoid more frequent conflicts caused by a restricted habitat. Any such competition which occurs seems to involve only a small percentage of either species and seems unlikely to limit the numbers of breeding birds or the total population.

Boobies (*Sula* spp.) nest in habitats that range from tree-tops to cliffs, although most of the species nest on level ground (Nelson 1978). I investigated how two of these species, the Masked or White (*S. dactylatra*) and Blue-footed (*S. nebouxii*) boobies, share nesting habitat in the Galápagos Islands.

Nelson (1978:892) suggested that "With a few local exceptions, such as the crater on Daphne Major, there are no habitats suitable for the blue-foot, but not for the brown [*S. leucogaster*] or white boobies." He felt that either no "important" competition takes place or the Masked Booby is dominant over the Blue-footed Booby. He mentioned Punta Suarez, Isla Española, Galápagos Islands as an example of a place where habitat partitioning occurs. The Masked Boobies there occupy a "strip facing the open sea" and the Blue-footed Boobies nest farther inland. I decided to investigate the following questions in the Galápagos:

1. Do the two species actually differ in the distance between their nests and the sea at Punta Suarez?
2. Is the Masked Booby dominant over the Blue-footed Booby?
3. Do the two species differ in their behavior while taking flight, a factor that might affect choice of nesting site?
4. Does the Blue-footed Booby nest closer to the sea in the absence of the Masked Booby at other locations in the archipelago?

STUDY AREAS

Isla Española is the southeastern-most of the Galápagos Islands. Punta Suarez, its western point, is a major nesting area for Waved Albatross (*Diomedea irrorata*), Masked, and Blue-footed boobies (Nelson 1968, 1978). I

made my observations at the southern part of the point, along about 100 m of cliff edge and extending about 50 m inland. The terrain is level, with guano-covered rocks at the top of a 7-m cliff giving way to low herbaceous vegetation and scattered rocks farther inland. Except for a few 1-m bushes, the vegetation is not tall enough to obstruct the perambulations of boobies (cf. fig. 220b in Nelson 1978:522 which shows habitat similar to the study area). The site was not visible from tourist trails and remained undisturbed except for my visits.

I also visited 10 other booby nesting areas during 1980-1981. Isla Isabela—Tagus Cove, Beagle Crater, Islas Marielas in Elizabeth Bay, Caleta Iguana, and Punta Vincente Roca; Isla Española—Punta Cevallos; Isla Seymour Norte; Isla Floreana—Punta Cormorant; Isla Daphne Major; and Isla Fernandina—Cabo Douglas. Blue-footed Boobies nested at all these sites but Masked Boobies nested only at Punta Cevallos and Daphne Major.

METHODS

Approximately 90 Masked and 40 Blue-footed boobies were present at the study area on Punta Suarez during 2-6 May 1981. Most Masked Boobies were either feeding large young or at-

TABLE 1. Distance from nests to cliff edge for Blue-footed and Masked boobies at Punta Suarez.

Distance (m)	Blue-footed Booby (n = 20)	Masked Booby (n = 40)
0-2 m	0	40
3-5 m	10	22.5
6-10 m	20	25
11-20 m	20	7.5
>20 m	50	5

TABLE 2. Colonies visited, nesting habitats used, and population estimates for Blue-footed and Masked boobies (colony size estimates are numbers of adult individuals; cliff nests are those within 2 m of a cliff; inland nests are those farther than 2 m from cliffs).

Colony	Blue-footed Booby			Masked Booby		
	Habitat		Colony size (individuals)	Habitat		Colony size (individuals)
	Cliff	Inland		Cliff	Inland	
Tagus Cove	X		10 ²			0
Beagle Cr.	X	X	10 ³			0
Cal. Iguana	X	X	10 ²			0
Is. Marielas	X		10 ²			0
Vincente Roca	X	X	10 ³			0
Pta. Cevallos		X	10 ² -10 ³	X	X	10 ³
Seymour N.	X	X	10 ³			0
Pta. Cormorant		X	10 ²			0
Daphne Major	X	X	10 ³	X	X	10 ²
Cabo Douglas	X	X	10 ³ -10 ⁴			0
Punta Suarez		X	10 ³	X	X	10 ³

tending nest sites in pairs. Pair-maintenance behavior (e.g., Sky-pointing, Parading, Mutual Jabbing, Allopreening, and Symbolic Nest Building, cf. Nelson 1978) was common. Most Blue-footed Boobies had eggs, although pairs in all stages of breeding were present, from courting pairs to those with large downy young.

To determine if the distribution of nests of the two species differed at Punta Suarez, I recorded the distance to the windward seacliff for 20 Blue-footed and 40 Masked booby pairs. Distances were divided into five classes: 0-2 m; 3-5 m; 6-10 m; 11-20 m; and >20 m. To see if the species differed in the locations used for take-offs, I spent 247 min on four afternoons estimating the distance between the cliff edge and the locations where the two species took off within the study colony. Take-offs were divided into cliff take-offs that occurred within 2 m of the cliff edge, or interior take-offs that occurred more than 2 m from the edge. For birds that did not take off from the nest sites, I estimated the distance walked before taking flight. During the four observation periods, the wind was from the southeast, striking the cliff face directly at an estimated speed of 20-30 kph.

I also watched for interspecific interactions in order to see if they might determine nesting locations of the two species. I considered Yes Head-shaking, Jabbing, and Wing-flailing displays (Nelson 1978:551) as interspecific aggression when these behaviors appeared to be directed at the other species. Outcomes of these encounters were divided into two categories, based on whether site-holders retained or lost possession of their sites. Site-holders were single birds or pairs that had eggs or young, or were pairs associated with nest depressions. Birds without sites were those wandering

through the nesting areas or loafing away from any apparent nest site.

The other colonies were visited only briefly, during the course of other field work. I made rough estimates of colony size. If I saw boobies of either species at nest sites within 2 m of cliff edges or steep (>30 degrees) drop offs, I considered these as cliff-edge nesters. Since boobies frequently roost on cliff ledges, I did not count birds but only nests with eggs or young. Although I considered cliff nesting to occur within a colony if even a single pair nested within 2 m of an edge, in all cases more than one pair was involved.

RESULTS

At Punta Suarez, over 70% of Masked Booby pairs occupied sites within 10 m of the cliff edge (Table 1); 32% of all pairs nested within 2 m. In contrast, 70% of all Blue-footed Boobies nested more than 10 m from the cliff and none were within 2 m of the cliff edge. The distributions differed significantly ($P < 0.001$; 5×2 contingency table; $\chi^2 = 19.36$; Siegel 1956).

In 21 take-offs by Blue-footed Boobies, all occurred more than 2 m from the cliff. In 28 take-offs by Masked Boobies, 24 occurred within 2 m of the cliff edge. The difference is highly significant ($P < 0.001$; 2×2 contingency table with correction for continuity; $\chi^2 = 31.93$). Of the 24 Masked Boobies that walked to the cliff edge before taking off, 16 traveled a mean distance of 1.9 m (SD = 1.3). Four that took off inland walked a mean distance of 7.5 m (SD = 2.9). Two of these birds had great difficulty in remaining airborne and they did not gain more than 0.5 m in altitude until they reached the updraft at the cliff edge.

Significantly more Masked Boobies took off

TABLE 3. Measurements of Blue-footed and Masked boobies (data from Nelson 1978:322, 511).

Measurement	Blue-footed Booby		Masked Booby		
	Male	Female	Male	Female	
Wing length (mm):	mean	432	457	451	484
	range	406–438	432–470	445–457	457–495
	sample	9	8	6	5
Mass (g):	mean	1,283	1,801	1,627	1,881
	range	1,100–1,580	1,450–2,230	1,220–1,970	1,470–2,350
	sample	23	28	48	37
Ratio of mass to wing length	2.97	3.94	3.61	3.89	

from the cliff edge than would be expected from the distribution of nests ($P < 0.001$; 2×2 contingency test with correction for continuity; nest data reduced to two classes: less than and more than 2 m; $\chi^2 = 12.39$).

I saw few interspecific interactions. In nine conflicts at nest sites, all were “standoffs” with neither species being displaced. When at nest sites, Masked Boobies displaced non-nesting Blue-footed Boobies in all five cases ($P = 0.031$; binomial distribution with $P = 0.5$). In the reverse situation, Blue-footed Boobies on nests displaced non-nesting Masked Boobies twice and “standoffs” occurred twice. Nest-site holders of both species were never displaced by intruders. I saw no conflicts between the species away from nest sites at Punta Suarez.

Only Blue-footed Boobies nested at 8 of the 11 colonies visited, including Punta Suarez. At seven of these eight colonies where Masked Boobies were absent, Blue-footed Boobies nested within 2 m of cliff edges (Table 2). Blue-footed Boobies did not nest near cliffs at two colonies where both species were present, and only a few did so at the third colony, on Isla Daphne Major. Nests on this island were situated on the upper crater floor, where Masked Boobies do not nest (T. Price, pers. comm.).

DISCUSSION

Why did Masked Boobies nest at cliff edges while Blue-footed Boobies nested farther inland? The distribution of take-offs by Masked Boobies strongly favored the cliff edge. Masked Boobies nesting inland often walked to the cliff edge. Those that took off inland had difficulty staying aloft. At wind speeds less than 20–30 kph, take-offs would have been even more difficult. Blue-footed Boobies generally took off from their nest sites, even when well inland. I surmise that the difference in choice of take-off locations was related to differences in wing shape and wing loading. In relation to wing

length, male Blue-footed Boobies are lighter than female Blue-footed Boobies and both sexes of the Masked Booby, which appear similar (Table 3). Hence, female Blue-footed Boobies should have the same difficulty with take-offs as do Masked Boobies. Female Blue-footed Boobies may have wider wings, giving them greater lift at lower speeds; they appear, however, to have more difficulty becoming airborne than do males (Nelson 1978).

Although difficulty in taking off inland may explain why Masked Boobies prefer to nest close to the cliff, it does not explain why Blue-footed Boobies do not nest on the cliff edges at Punta Suarez. This species uses ledges and cliff edges elsewhere in the Galápagos where the Masked Booby does not nest, suggesting that the latter preempts cliff nesting at Punta Suarez.

Aggressive conflicts were rare between the species. I saw no indication that Masked Boobies were dominant over Blue-footed Boobies at nest sites, as suggested by Nelson (1978: 892). Territory holders could not be displaced by the other species: site tenure, rather than species, determined the outcome of aggressive encounters. Blue-footed Boobies may simply avoid the higher densities at cliff edges where Masked Boobies are present, rather than being actively displaced.

On Punta Suarez, only small percentages of the two species were exposed to each other, primarily in the zone 3–20 m from the cliff. Within this area of overlap, competition seemed not to be aggressive but rather a “scramble” (Miller 1967), or perhaps totipalmate waddle, to occupy nest sites. Any interspecific competition for space that occurs is likely to have little effect on total breeding numbers. The situation described here agrees with suggestions by Ashmole (1963) and Nelson (1978) that nesting space rarely limits populations of tropical seabirds.

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RECENT PUBLICATIONS

The Marine Ecology of Birds in the Ross Sea, Antarctica.—David G. Ainley, Edmund F. O'Connor, and Robert J. Boekelheide. 1984. Ornithological Monographs No. 32, American Ornithologists' Union, Washington, DC. 97 p. Paper cover. \$9.00 (\$8.00 to AOU members). Source: Frank R. Moore, Assistant to the Treasurer, Department of Biology, University of Southern Mississippi, Southern Station Box 5018, Hattiesburg, MS 39406; orders must be prepaid and include a \$0.50 handling charge. This monograph attempts "to explain the factors that determine seabird occurrence and distribution in the Ross Sea during summer." Data from seabird censuses on six cruises are correlated with oceanographic measurements and dietary information from collected specimens. Text and charts describe the environment and give the findings for 21 species (Emperor Penguin to Arctic Tern). These results are analyzed and discussed with regard to the birds' feeding behavior, trophic relations, community composition and biomass, and the factors affecting seabird occurrence. The study reaches important conclusions about prey selection and the importance of food abundance as a limiting factor for high latitude Antarctic bird populations in summer, ideas that may well apply elsewhere. Robert Cushman Murphy would be proud to see how far his light has carried. References, appendixes.

Nature Through Tropical Windows.—Alexander F. Skutch, illustrated by Dana Gardner. 1983. University of California Press, Berkeley. 374 p. \$19.95. "It took Kropotkin to take the edge off Darwin," Alexander Skutch has said, voicing profound dissatisfaction with a vision of nature red in tooth and claw. In his latest book Skutch invests his always painstaking, always valuable accounts of natural history with a sense of his perplexity over the relative importance of competition and cooperation in evolution. The dissonance between graceful descriptions of what he sees as cooperation and reflections on current views of the selfish nature of social behavior make the book worth thinking about. Lyric writing and elegant illustrations reflect forty years of unhurried days spent watching the disappearing tropical world. Although the writing evokes shades of eighteenth and nineteenth century naturalists, it would be a mistake to dismiss Skutch as an isolated eccentric, a relic of Natural Theology. In this book, which addresses—more explicitly than earlier works—his concerns about allowing the predictions of population genetics to dominate our explanations of social behavior, Skutch is frequently successful at revealing how highly contrived some of our currently fashionable selfish-gene ideas may be.—M. F. Lawton.

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Charles Darwin Research Station, Isla Santa Cruz, Galapagos Islands, Ecuador. Present address: Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7700, South Africa. Received 7 May 1983. Final acceptance 17 January 1984.

A Field Guide to the Grand Canyon.—Stephen Whitney. 1982. Quill, New York. 320 p. Paper cover. \$12.50. This easily-carried volume offers a little of everything about the natural history of the Grand Canyon. At least for birds and their habitats, its treatment is not very successful. The five pages of text on birds are less than illuminating, while the 15 plates of bird illustrations are uneven, with mostly stiff and generalized poses. By contrast, the plates of butterflies and herptiles are convincing and accurate. Provides 87 plates, 17 figures, index.—J. Tate.

Myology of the Purple-throated Carib (*Eulampis jugularis*) and Other Hummingbirds (Aves: Trochilidae).—Richard L. Zusi and Gregory Dean Bentz. 1984. Smithsonian Contributions to Zoology No. 385, Smithsonian Institution Press, Washington, DC. 70 p. Paper cover. This report describes and illustrates the gross morphology of all the muscles attaching on the axial, appendicular, or hyoid skeletons, and the integument. The condition in the principal species is compared with those in six other species, chosen to represent the major taxonomic subdivisions within the family. These findings are discussed with regard to systematic studies within the Trochilidae and phylogenetic relationships of that group to other birds. The authors have indicated the wealth of structural adaptations that are yet to be examined in hummingbirds, and their paper is a solid place to begin. Line drawings, references, index.

Migration: Paths Through Time and Space.—R. Robin Baker. 1983. Hodder and Stoughton [England]. 248 p. \$15.95 paperback, \$32.50 hardcover. Available: Holmes and Meier Publishers, Inc., IUB Building, 30 Irving Pl., New York, NY 10003. This is a sequel to, and offspring of, Baker's *The Evolutionary Ecology of Animal Migration* (1978; noticed in *Condor* 81:121). In this book, ethologists are taken to task for their insensitive dissection of programmed reflex responses, while population ecologists are criticized for their calculated descriptions of dispersion, gene flow and population regulation mechanisms. To replace these concepts, we are offered the "individual": less than a population, but more than a set of measurable responses to stimuli. Migration theory, according to Baker, is the description of the life path of an integrated, quite anthropomorphic organism making its way through life, across great distances, while remaining true only to itself. Illustrative material identical to the earlier book. Glossary, references and author indices.—J. Tate.