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GEOGRAPHIC VARIATION AND REASSESSMENT OF SPECIES LIMITS IN THE "MASKED" BOOBIES OF THE EASTERN PACIFIC OCEAN

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ABSTRACT.—Two distinct forms of Masked Booby (*Sula dactylatra*) occur in the eastern Pacific: (1) a yellow-billed form that includes a population on Clipperton Island and islands off western Mexico (*S. d. "californica"*), and another, unnamed, population on Las Islas Desventuradas, Chile, and (2) an orange-billed form [*S. (d.) granti*] that nests almost exclusively on the islands of the Galápagos and on Malpelo Island, Colombia. Quantitative comparisons, including discriminant function analysis (DFA) of standard morphological characters indicated that yellow-billed populations are only marginally different from one another, and neither is consistently separable from *S. d. personata,* a yellow-billed form that ranges over most of the tropical Pacific. Further, we found no consistent differences in bare-part coloration or plumage among yellow-billed populations. In contrast, DFA indicated morphological differences between orange- and yellow-billed populations. The orange-billed bird is smaller with a significantly shorter, shallower bill, shorter tarsus, and longer wings and tail. It is also more sexually dimorphic and has distinct plumage characters. Biological observations also support the distinctness of orange-billed birds. They typically nest on cliffs and steep slopes, whereas yellow-billed forms nest mainly on low, flat areas. A difference in habitat preference at sea resulted in a parapatric distribution: orange-billed birds away from colonies concentrated in nearshore waters off the coast of the Americas, whereas the yellow-billed forms foraged much farther offshore. Most importantly, orange- and yellow-billed birds paired assortatively where they nested sympatrically. Thus, based on morphological and biological differences, including positive assortative mating, we recommend that *Sula granti* be recognized as a separate species, the Nazca Booby.
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Geographic variation in the Masked (or Blue-faced) Booby (*Sula dactylatra*) has been over-described but under-studied. Most of the seven proposed races of this common pantropical seabird date from an era of excessive splitting and were based almost entirely on foot and bill coloration. Plumage and size (with one exception) were ignored, perhaps because few collections contained enough material to allow study of variation in those characters. Although coloration of bare parts (bill, face, legs, feet, and eyes) has been important in sulid systematics (Nelson 1978), conducting comparative studies of these features using only dried museum specimens or notations on specimen labels is almost impossible. Given those complications, and the continued lack of large series of specimens, it is not surprising that no thorough study of geographic variation in this species has ever been attempted. Analysis was further impeded by the residual authority of R. C. Murphy (1936), who was reluctant to accord much weight to color characters in boobies because of their sexual dichromatism as well as individual variation. Murphy's caution was understandable, but it led him to overlook characters that we con-

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FRONTISPIECE. "Masked" boobies from the eastern Pacific Ocean. Above, Masked Booby (*Sula dactylatra*); below, Nazca Booby (*Sula granti*). Both photos taken on Clipperton Island, May 1987 by R. L. Pitman.

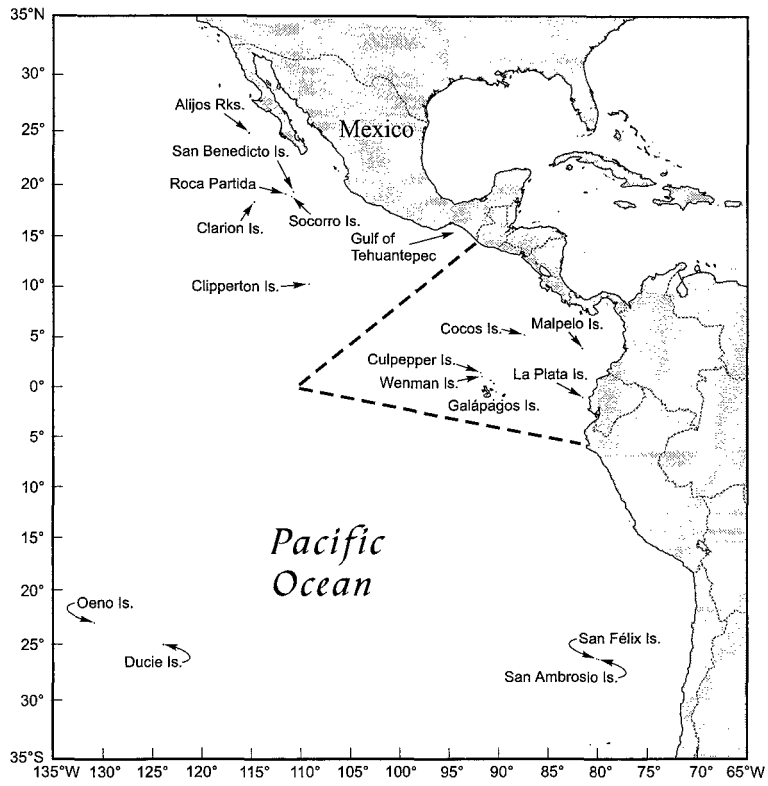

FIG. 1. The eastern Pacific Ocean showing location of "Masked" booby colonies and other sites mentioned in the text. Dashed line separates the major yellow-billed (*Sula dactylatra)* colonies to the north and south from the central orange-billed (*S. granti)* colonies.

sider meaningful, especially because bare-part coloration in Pelecaniformes is clearly important in social signaling and probably in individual recognition as evidenced by interspecific, and often intraspecific, color variation in, for example, cormorant facial skin and iris coloration, tropicbird bills, frigatebird eyerings, pelican and frigatebird pouch coloration, and booby foot, bill and face coloration (Van Tets 1965, Nelson 1978).

This review of geographic variation, which is restricted to Masked Booby populations in the eastern Pacific, was prompted by two sets of field observations. The first was the recognition that there are three clear assemblages that can be defined on the basis of bill color (yellow-billed = YB; orange-billed = OB), and breeding locale: (1) a northern YB population (sometimes recognized as *S. d. californica)* nesting from Clipperton Island to Alijos Rocks; (2) a central OB population [*S. (d.) granti*], nesting mainly on the islands of Galápagos and Malpelo, with much smaller numbers breeding from Isla La Plata, Ecuador, to San Benedicto Island, Mexico, and (3) an unnamed YB population (often incorrectly identified as OB; Murphy 1936, Johnson 1965, Bahamonde 1974, Nelson 1978) on the Islas Desventuradas (San Félix and San Ambrosio), Chile (Frontispiece, Fig. 1). The second and more stimulating observation was that OB and YB birds differ in pelagic distribution and nesting habitat preferences, and, evidently, pair assortatively where they occur sympatrically. In this paper we review the morphological and biological characteristics of these Eastern Pacific populations and argue that *S. granti* is specifically distinct from YB forms.

METHODS

We base this review on: (1) examination of museum specimens (see acknowledgments) of birds taken in the immediate proximity of nesting colonies, or whose

provenance can be determined from characteristics described below; (2) the systematic literature; (3) our field work in the eastern Pacific, which includes visits to all of the known Masked Booby colonies; and (4) an extensive series of photographs of boobies at sea and in the colonies.

We compared morphological characters of specimens from three separate YB populations in the eastern Pacific with OB specimens. These populations were (1) *S. d. californica* (YB), which we will refer to as "Mexican" birds, (2) an unnamed YB population on colonies off Chile, which we will refer to as "Chile" birds, (3) *S. d. personata* (YB), and (4) *S. (d.) granti* (OB). For *S. d. personata,* we used specimens from the nearest adjacent colonies in the central Pacific, Ducie (25° S, 124° W) and Oeno (23° S, 131° W); both are about 4000 km equidistant from Clipperton, the Galápagos, and the Chilean islands. We used the standard morphological characters of bill length, bill depth, bill ratio (depth/length), wing and tail length (Table 1). Boobies are difficult to measure and dimensions obtained by different researchers may not be fully comparable. For example, data in Marchant and Higgins (1990) indicate that museum specimens of *S. d. fullagari* are smaller than living birds, as expected because of shrinkage of skins, but that living *S. d. personata* from Raine Island, Australia, are smaller than skins. For consistency, all original measurements in this report were made by JRJ.

We tested for significant differences in each morphological variable using ANOVA and made multiple comparisons with a Tukey test. We use a discriminant function analysis (DFA) on log-transformed data to determine the effectiveness of five morphological variables (bill ratio excluded) in separating YB and OB forms. In all quantitative comparisons, we treated males and females separately to eliminate variation imposed by sexual dimorphism. We give results of the DFA for males only, because patterns for females were similar. All analyses were performed using SYSTAT (Wilkinson 1989) on an IBM-compatible computer.

We visited all of the known Masked Booby colonies in the eastern Pacific, noting colony size and bill color of roosting and nesting birds (Table 2, Fig. 1). We collected data on at-sea distributions from nine research cruises between 1983 and 1990 (prior to that no distinction was made between YB and OB birds). Details of at-sea methods are outlined in Pitman (1986). Note that cruises on which the forms were distinguished are seasonally biased in that 94% of the survey days (n = 266) on which sightings were made were in the second half of the year.

RESULTS

A brief taxonomic review.—Geographic variation in Masked Boobies, as understood early in this century, was summarized by Mathews and Iredale (1931:75): "Rothschild in 1915 proposed five subspecies as follows: *S. d. dactylatra* (Lesson [1831]) from Ascension Island and South Atlantic coasts with bill horny blue-gray, very slender, feet and legs yellow; *S. d. melanops* Hartlaub [1859], from Western Indian Ocean, with bill greenish-yellow, slender, feet and legs slaty-blue to dull black; *S. d. personata* (Gould [1846]) from Western Pacific with bill yellow, very stout and large, feet and legs greenish-blue; *S. d. californica* Rothschild [1915], from Coasts of California and Central America, with bill bright yellow, very thick, feet and legs orange; and *S. d. granti* Rothschild [1902], with bill red and feet bluish-green from Galápagos Islands." An additional form, *S. d. bedouti* from Bedout Island, off western Australia, was ignored by Rothschild; it was said to differ from *S. d. personata* "in its much smaller size, especially in the bill; and in having blue feet" (Mathews 1913:189). Recently, O'Brien and Davies (1990) described *S. d. fullagari* from Lord Howe, Norfolk, and the Kermadec islands, which was characterized as having a dark eye. These characters, as well as those of the Chile birds, are summarized in Table 3.

Early in this century there was confusion about the identity of *S. (d.) granti* from the Galápagos, because it was originally identified as a Peruvian Booby, *S. variegata* (e.g., Rothschild and Hartert 1899, Snodgrass and Heller 1902, Beck 1907, Gifford 1913). Rothschild (1902) corrected the mistake and designated the originally misidentified specimen as the type of a new species, *Sula granti.* According to Sharpe and Ogilvie-Grant (1898: 435) the bill in the dry skin was "red, paler toward the tips of the mandibles" and the legs were "yellowish brown." [Note that these characters differ somewhat from those reported by Mathews and Iredale (1931, above)]. The label of the type specimen (AMNH 729,228) contains no information on coloration.) Snodgrass and Heller (1902:512) wrote that Galápagos boobies were "identical in plumage" to those from Clipperton and the Revillagigedos but differed in bill color; they also alleged "some differences in proportions." Gifford (1913:92–93) expanded on this, reporting that Galápagos birds had "a decidedly longer wing, and . . . a relatively shorter tarsus . . . than has the average *Sula cyanops* [=*S. dactylatra*]." Even so, Rothschild (1915:44)—without acknowledging his peers or presenting any morphometric infor-

TABLE 1. Dimensions of "Masked" boobies (*Sula granti* and *S. dactylatra*) (measurements in mm). Locality of specimens and references are listed below each population.

	Male				Female			
	n	$\bar{x}$	Range	SD	*n*	$\bar{x}$	Range	SD
S. granti[a]								
Galápagos; Malpelo; at sea off Ecuador, Guatemala, Peru, Gulf of Panama (this study)								
Bill length	19	101.9	96.3–107.2	3.12	16	105.0	100.0–113.2 100.0[b]	3.79
Bill depth	20	33.3	30.4–35.8	1.88	15	35.4	33.5–38.0 34.5[b]	1.56
Bill ratio[c]	19	0.32	0.29–0.36	0.017	15	0.34	0.32–0.34 0.34[b]	0.018
Wing	20	437.8	410–467	17.02	16	460.8	438–483 438[b]	16.06
Tail	20	175.4	165–185	6.09	16	179.9	160–194 176[b]	8.76
Tarsus	20	54.1	50–60.4	3.02	16	57.43	52.3–63.0 55.9[b]	2.61
S. d. californica[a]								
Alijos Rocks, Revillagigedos, Clipperton (this study)								
Bill length	12	103.0	99.5–106.5	2.61	9	102.1	98.8–109.2 100.5[b]	2.96
Bill depth	12	36.3	33.5–40.5	1.69	9	37.2	35.2–39.8 38.5[b]	1.66
Bill ratio[c]	12	0.35	0.33–0.38	0.016	9	0.36	0.35–0.40 0.38[b]	0.018
Wing	12	434.3	405–462	19.70	9	433.2	405–450 450[b]	16.38
Tail	12	174.8	160–197	13.62	9	175.6	163–196 196[b]	10.91
Tarsus	12	56.4	53.5–60.3	2.35	9	57.9	53.0–61.8 55.9[b]	2.93
S. d. "Chile"[a]								
Chile: San Félix, San Ambrosio (this study)								
Bill length	4	105.1	102.1–107.5	2.28	8	106.2	101.9–110.0	3.16
Bill depth	4	36.2	33.8–38.5	2.19	8	37.1	35.5–38.2	1.05
Bill ratio[c]	4	0.35	0.33–0.38	0.021	8	0.35	0.34–0.35	0.008
Wing	4	445.6	434–462	10.97	8	466.1	455–481	8.98
Tail	4	183.2	178–192	5.76	8	187.2	165–196	10.08
Tarsus	4	60.7	57.5–64.7	2.85	8	62.4	58.5–65.8	2.81
S. d. personata[a]								
Ducie, Oeno (this study)								
Bill length	4	104.4	95.5–109.5	6.38	8	105.8	102.8–110.8	2.68
Bill depth	4	36.8	34.5–38.5	1.7	8	38.2	35.7–42.8	2.25
Bill ratio[c]	4	0.35	0.34–0.37	0.015	8	0.36	0.34–0.39	0.018
Wing	4	436.5	430–445	6.56	8	453.5	442–460	6.78
Tail	4	180.2	157–195	16.40	8	185.5	176–196	6.37
Tarsus	4	58.2	52.5–60.7	3.82	8	60.0	56.8–63.2	2.02
S. d. bedouti								
Bedout Is., Australia (O'Brien and Davies 1990)								
Bill length	3	104.3	103–106	1.2	3	103.9	101.0–105.8	2.1
Wing	3	413	401–420	8	3	425	422–430	3
Tail	3	171	165–175	3	3	177	172–186	6
Tarsus	3	53.9	51.0–51.7	2.8	3	54.4	52.0–58.4	2.8

TABLE 1. Continued

	Male				Female			
	n	$\bar{x}$	Range	SD	*n*	$\bar{x}$	Range	SD
S. d. fullagari								
Lord Howe Is. (O'Brien and Davies 1990)								
Bill length	14	108.3	104–114	3.3	7	109.9	105.0–115.4	3.1
Wing	14	442	429–455	6	7	452	430–468	12
Tail	11	187	175.0–202.7	11	12	190	174–205	12
Tarsus	14	58.9	53–65	3.3	7	61.0	54–65	3.51
S. d. dactylatra								
Ascension, Fernando de Noronha (Murphy 1936)								
Bill length	9	95.6	92.6–97.2		7	95.7	91.6–99.0	
Wing	9	424	406–433		7	429	417–440	
Tail	9	166	153.0–173.2		7	164.6	151.3–180.0	
Tarsus	9	54	53.0–56.2		7	53.4	52.0–54.6	
S. d. melanops								
Red Sea, Indian Ocean (Brown et al. 1982)								
Bill length	6	100.7	97–104					
Wing	6	421	407–430					
Tail	6	176	169–180					
Tarsus	6	56	51–58					

[a] Measured by J.R.J.
[b] Dimensions of type specimen.
[c] Bill depth/bill length.

mation to the contrary—reversed his earlier stand and decreed there was "absolutely no other difference" between *S. granti* and *S. d. californica* except bare-part coloration. He reduced *S. granti* to subspecies rank, a position subsequently adopted by Murphy (1936) and Nelson (1978).

Yellow-billed populations in the eastern Pacific.—The yellow-billed Masked Booby that breeds north of the equator in the eastern Pacific, sometimes recognized as *S. d. californica* (e.g., AOU 1957), nests from Alijos Rocks, Mexico, south to Clipperton Island. [A single YB individual nesting among a colony of OB boobies on La Plata Island in September 1989 (Table 2) was of unknown provenance]. The total population is on the order of 65,000 individuals, 95% of which occur on Clipperton (Table 2).

Rothschild (1915:43–44) described *S. d. californica* from an adult female taken at San Benedicto Island (measurements of type specimen in Table 1). Asserted characters were "bill bright yellow, very thick; feet and legs orange." Rothschild's leg color description is inconsistent with our observations: YB Masked Boobies that currently nest on Clipperton and San Benedicto have legs that are either blue or greenish blue, or greenish yellow (Table 3). Rothschild also wrote that *S. d. californica* had a "much larger and stouter bill" than *S. d. dactylatra.* He made no comparisons with *S. d. melanops* or *S. d. personata,* although he characterized the latter as "bill yellow, very stout and large; feet and legs greenish blue."

South of the equator, James P. Chapin in 1935 discovered Masked Boobies nesting on Las Islas Desventuradas (San Ambrosio and San Félix), Chile (Murphy 1936). The colony is small, comprising several hundred (Bahamonde 1974) to perhaps a few thousand pairs, all yellow-billed (Jehl 1973, unpubl. data). Bare-part coloration in this population as described by Bahamonde (1974) is evidently paraphrased from Murphy's (1936) description of *S. d. granti* (in which Murphy mistakenly included the Chilean population) and cannot be credited as independent or authoritative.

Our quantitative and qualitative comparisons support the view that the YB populations

TABLE 2. Location, dates of visits, and size of breeding colonies and roosting sites of "Masked" boobies in the eastern Pacific Ocean. Listed are number of individual birds (+ = present). Dashed horizontal lines separate primarily orange-billed (OB = *Sula granti*) colonies from yellow-billed (YB = *S. dactylatra*) colonies to the north and south (see Fig. 1).

Site	Number of YB individuals (% of population)	Number of OB individuals (% of population)	Comments	Source
Alijos Rocks	+	+	Oct 1983; 100 breeding, mostly YB; a few OB roost, some may breed	Pitman 1985, R. L. Pitman, unpubl. data
Clarión	757–937 (>99)	min 3 (<1)	Feb 1988	Howell and Webb 1989, 1990
San Benedicto	1,166–1,196 (>99)	4 (<1)	Feb 1988	Howell and Webb 1990
	2,450 (98)	50 (2)	Nov 1990	R. L. Pitman, unpubl. data
Roca Partida	+	+	Aug 1987, Feb 1988, Aug 1989; both forms roost, neither confirmed breeder; max. roosting numbers 5 Aug 1989: 48 YB, 5 OB	Howell and Webb 1990, R. L. Pitman, unpubl. data
Socorro Island	+?	+?	Not breeding; up to 10 individuals roosting; bill color not recorded	Wehtje et al. 1993, R. L. Pitman, unpubl. data; J. Jehl, unpubl. data
Clipperton Island	61,339 (99.8)	150 (0.2)	4 visits, 1986–1990	Pitman et al., unpubl. data
Cocos Island	0	0	Oct 1989; 3 YB roosting; no breeding	Slud 1967, R. L. Pitman, unpubl. data
Malpelo Island	0	24,034 (100)		Pitman et al. 1995
Galápagos	0	50,000–100,000 (100)	YB individuals occasionally occur on northern islands (Wenman and Culpepper); breeding status unknown	Nelson 1978, D. J. Anderson, pers. comm.; R. L. Pitman, unpubl. data
La Plata	1 (<5)	794 (>95)	Both forms breed; minimum 1 YB Sept 1989	Ortiz-Crespo and Agnew 1992, R. L. Pitman, unpubl. data
San Félix, San Ambrosio	hundreds–perhaps several thousand (100)	0	Jun 1970; breeding on both islands	Jehl 1973, unpubl. data; Bahamonde 1974

are not distinct. No consistent differences in bare-part coloration (Table 3) or plumage (see below) differentiate the three YB populations. Similarly, there were no significant differences in size among males, and in females the only difference was that Chilean birds had larger wings than Mexican birds ($F = 10.168$, $P < 0.001$). In neither sex did DFA indicate any consistent differences in size or shape among these three YB populations (Table 4, Fig. 2).

Orange-billed boobies.—Orange-billed boobies nests by the tens of thousands in the Galápagos Archipelago and Malpelo Island, in much smaller numbers on Isla La Plata, and in only token numbers on the islands of Clipperton and San Benedicto, and possibly Alijos Rocks (Table 2, Fig. 1). All turn-of-the-cen-

TABLE 3. Soft part coloration of *Sula granti* and *S. dactylatra.*

Race (locality)	Coloration			Reference
	Iris	Bill	Legs and feet	
S. granti				
(Galápagos)	orange	rosy pink in females; more orange in males	olive or khaki in males; lead or olive in females	Nelson 1978
(Malpelo)	orangish	pinkish-orange, more yellow toward tip	yellowish-olive in males; blue-gray with hint of magenta in females	R. L. Pitman, unpubl. data
(San Benedicto)		deep orange	gray	Howell and Webb 1990
(Clipperton)	orangish	orange-pink	blue-gray or greenish-yellow	R. L. Pitman, unpubl. data
S. d. californica				
(San Benedicto)	yellow	bright yellow to greenish-yellow	pale green with blue tinge or olive with yellow tinge; webs paler	R. L. Pitman and J. Jehl, unpubl. data
S. d. Chile				
(San Félix and San Ambrosio)	yellow	yellow to greenish-yellow	khaki yellow, light olive, or greenish	J. Jehl, unpubl. data
S. d. personata				
(Kure)		bright yellow, brighter in breeding males	olive drab to bluish-gray	Kepler 1968
(New Zealand)		yellowish	greenish-blue	Oliver 1930
(W. Australia and Indian Ocean)	yellow to yellowish gray; brighter in males	yellow in males; yellowish-gray in females	dull olive in males; lead-gray in females	Marchant and Higgins 1990
S. d. bedouti				
(Bedout, Australia)			blue	Mathews 1913
S. d. fullagari				
(Lord Howe, Norfolk, Kermadecs)	sepia	buff yellow	varied grayish; feet and webs dull chrome yellow	O'Brien and Davies 1990
			greenish-gray	Oliver 1930
S. d. dactylatra				
(Ascension)		straw	dull orange (range from rich orange in some males to dull olive in some females)	Dorward 1962
S. d. melanops				
(Red Sea, Indian Ocean)	yellow	orange-yellow to yellow-green	lead gray	Brown et al. 1982

TABLE 4. Loadings on discriminant function axes based on five morphological measurements for three yellow-billed populations (*Sula dactylatra "californica"*, *S. d. personata*, and *S. d.* "Chile") and one orange-billed population (*S. granti*). Data are for males only.

Variable	Axis 1	Axis 2	Axis 3
Bill length	0.078	0.390	0.058
Bill depth	0.795	−0.679	0.104
Wing	−0.425	−0.103	−0.756
Tail	−0.140	0.429	1.083
Tarsus	0.506	0.755	−0.395
Canonical correlation	0.701	0.374	0.101
% Variance explained	76.8	19.6	3.6

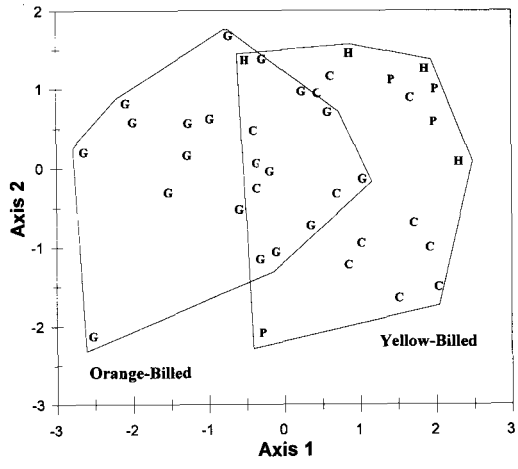

FIG. 2. Discriminant function analysis on morphological measures of four populations of "Masked" boobies (males only). Letters indicate population identity of specimens: (C) *Sula dactylatra* californica; (H) *S. d.* "Chile"; (P) *S. d. personata*; (G) *S. granti*. Polygons circumscribe yellow- and orange-billed forms.

tury ornithologists who visited both Clipperton Island and the Galápagos recognized their distinctiveness. Although similar to YB boobies (Frontispiece), they differ in size and proportions, as first noted by Snodgrass and Heller (1902) and Gifford (1913).

In contrast to comparisons among YB populations, our quantitative comparisons between YB and OB populations indicate that OB birds are distinct. Univariate comparisons indicated that OB birds have a significantly shallower bill ($F = 9.129$, $P < 0.04$ for males from all populations; $F = 5.478$, $P < 0.01$ for *S. d. personata* females), thinner bill ($F = 7.361$, $P < 0.03$ for males from *S. d. californica* and *S. d. personata*; $F = 6.125$, $P < 0.02$ for females from *S. d. californica* and *S. d. personata*), longer wing ($F = 10.168$, $P < 0.001$ for female *S. d. californica* only), and shorter legs ($F = 6.483$, $P < 0.01$ for male *S. d.* "Chile"; $F = 5.906$, $P < 0.01$ for female *S. d.* "Chile"). Discriminant function analysis showed that OB birds are generally smaller, having shallower bills, shorter tarsi, and longer wings (Table 4, Fig. 2). The smaller size of OB birds is further indicated by body mass, which averages 12–14% lighter than *S. d. personata* (Anderson 1993). They are also more sexually dimorphic in bill, wing, and tarsus than YB boobies (Fig. 3).

Plumage.—The full plumage sequence in boobies remains to be worked out. Because Masked Boobies do not breed until age 3–4 years (E. A. Schreiber, pers. comm.), they probably require several years to attain the definitive black-and-white adult plumage. Since a similar range of variation occurs in both OB and YB forms, we presume that the sequence of plumages develops on about the same schedule.

Despite some variation with each plumage type (age group?), there are consistent differences between OB and YB birds (Figs. 4, 5). In juvenile OB birds the dorsal areas are grayish brown, as compared to dark chocolate to blackish. Also, the upper back is usually dark, lightening with age; if a white collar is present it is narrow or incomplete. In YB birds the upper back is white, usually forming a broad and conspicuous collar. In OB birds feathers on the head and neck tend to be uniform grayish brown with diffuse flecking; in YB birds they are darker brown and appear blotchy. In addition, the central rectrices in OB birds tend to be pale at the base, as if dusted with flour, and the extent increasing with age, so that some older sub-adults appear white-rumped; in YB populations the rectrices average darker, and whitish bases, if present, are usually concealed by the upper tail coverts. In definitive plumage, OB and YB forms are similar, except that the dark areas tend to be

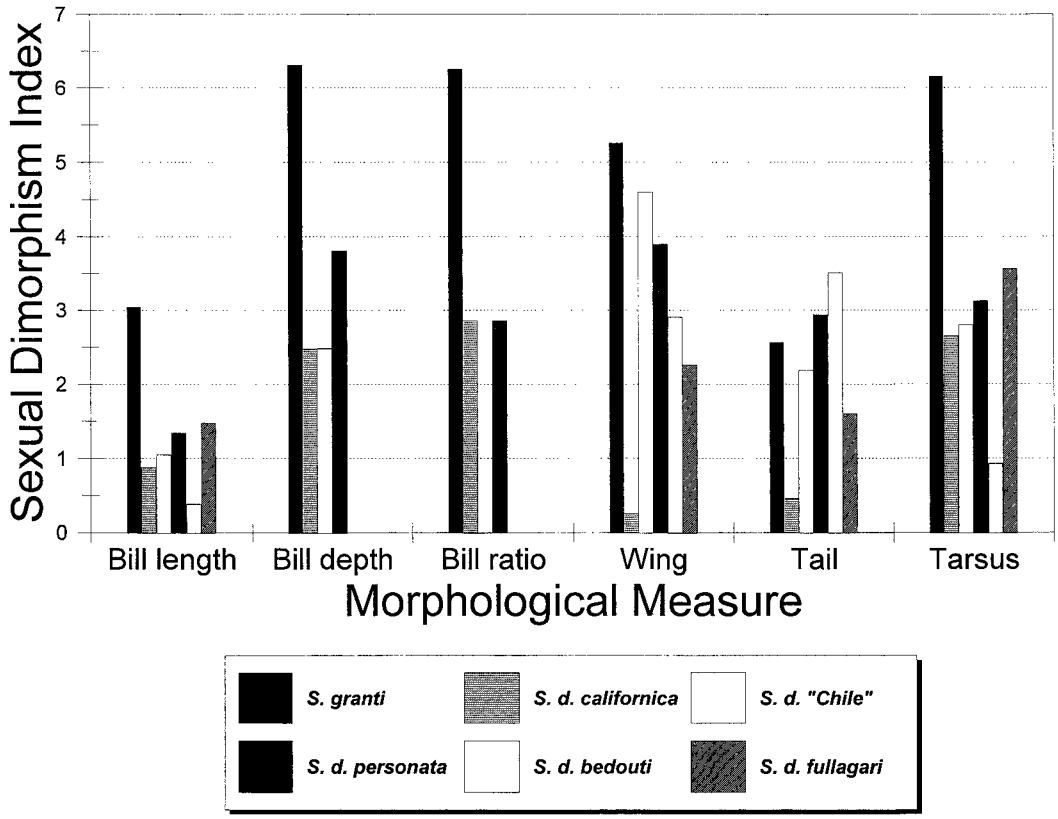

FIG. 3. Indices of sexual dimorphism among populations of "Masked" boobies calculated as: |male − female|/male × 100.

a rich chocolate brown with a reddish tinge in OB birds, compared to dark brown to blackish in YB birds, and the central rectrices average paler and may be almost entirely white, a condition that is rare in all YB populations.

Biology.—Several biological characteristics also differentiate OB and YB boobies. The first is that they pair assortatively on breeding islands. Although we could not analyze it statistically because often only one adult was present at the nest during the day, RLP observed only positive assortative pairing in colonies where both forms occur. Specific counts of OB birds include up to eight mated pairs on San Benedicto Island in November 1990, single roosting pairs on Roca Partida in August 1987 and August 1989, and at least six different pairs at Clipperton Island in May 1987 and November 1990 (Table 2). Considering that there are currently over 60,000 YB birds on Clipperton as compared to 150 OB, the presence of OB—but not mixed—pairs is further evidence of mate preference. Furthermore, both forms have apparently nested at Clipperton at least since the turn of the century (Beck 1907, Sachet 1962, this study), evidently with little or no interbreeding as parental forms still predominate there. Moreover, RLP observed no mixed pairs in any colony, although he did note two birds with intermediate-colored bills, one at San Benedicto on 14 March 1988, and another, paired with a YB, on Clipperton on 5 May 1987, suggesting that some hybridization may occur. There was an observation of a possible mixed pair on Clipperton in 1901 (Beck 1907) and a definite mixed pair on San Benedicto in 1988 (Howell and Webb 1990).

A second difference is preferred nesting habitat. In our experience YB birds use flat, open terrain, such as Clipperton Island, the Chilean islands, and the flat top of San

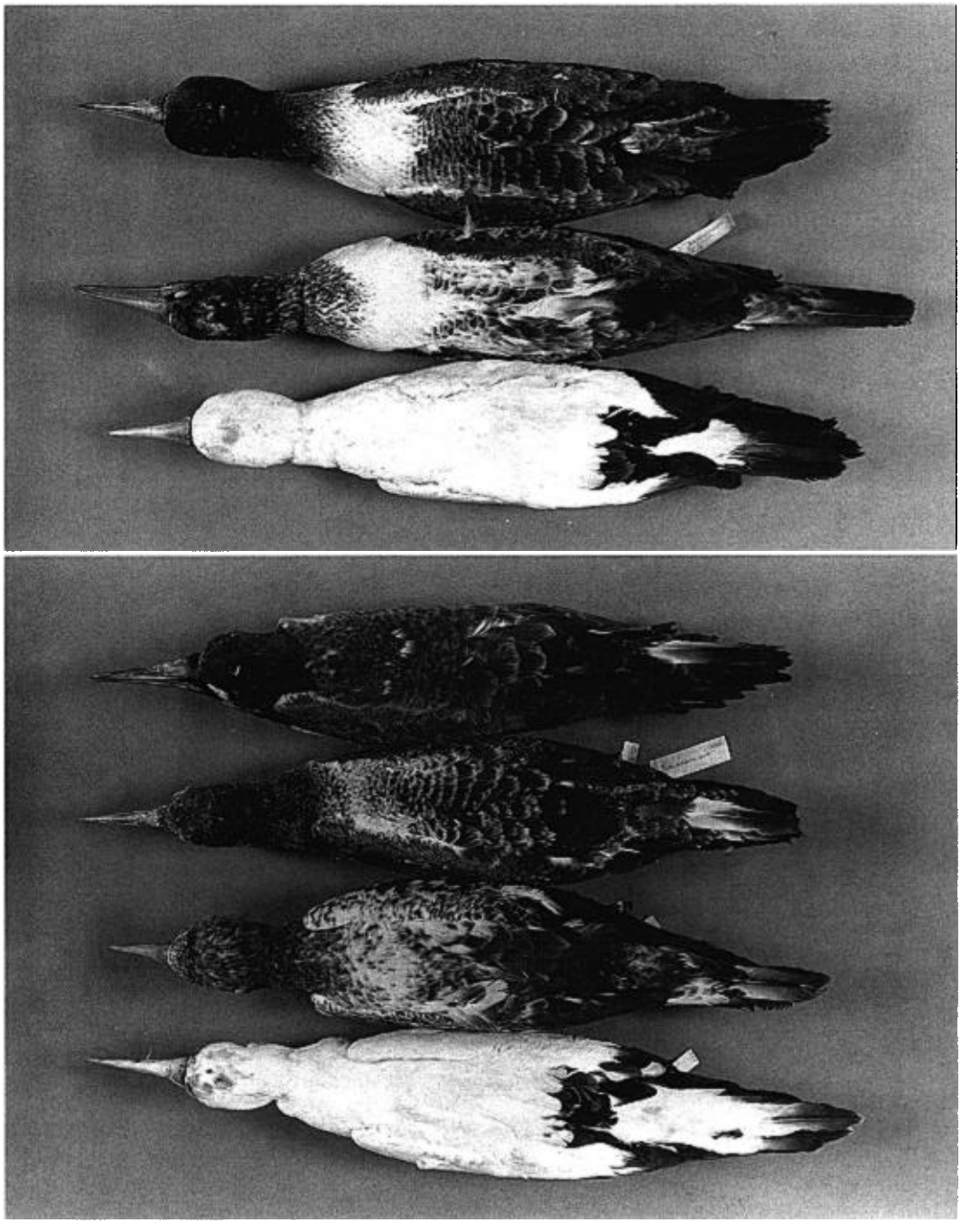

FIG. 4. Dorsal view of plumage sequences in yellow-billed (top) and orange-billed (bottom) "Masked" boobies. Above, top to bottom: *Sula dactylatra personata,* ANMH nos. 18900, 18899, 18901; below, top to bottom: *S. granti,* AMNH nos. 729,234, 729,238, 720,338, and 407,818.

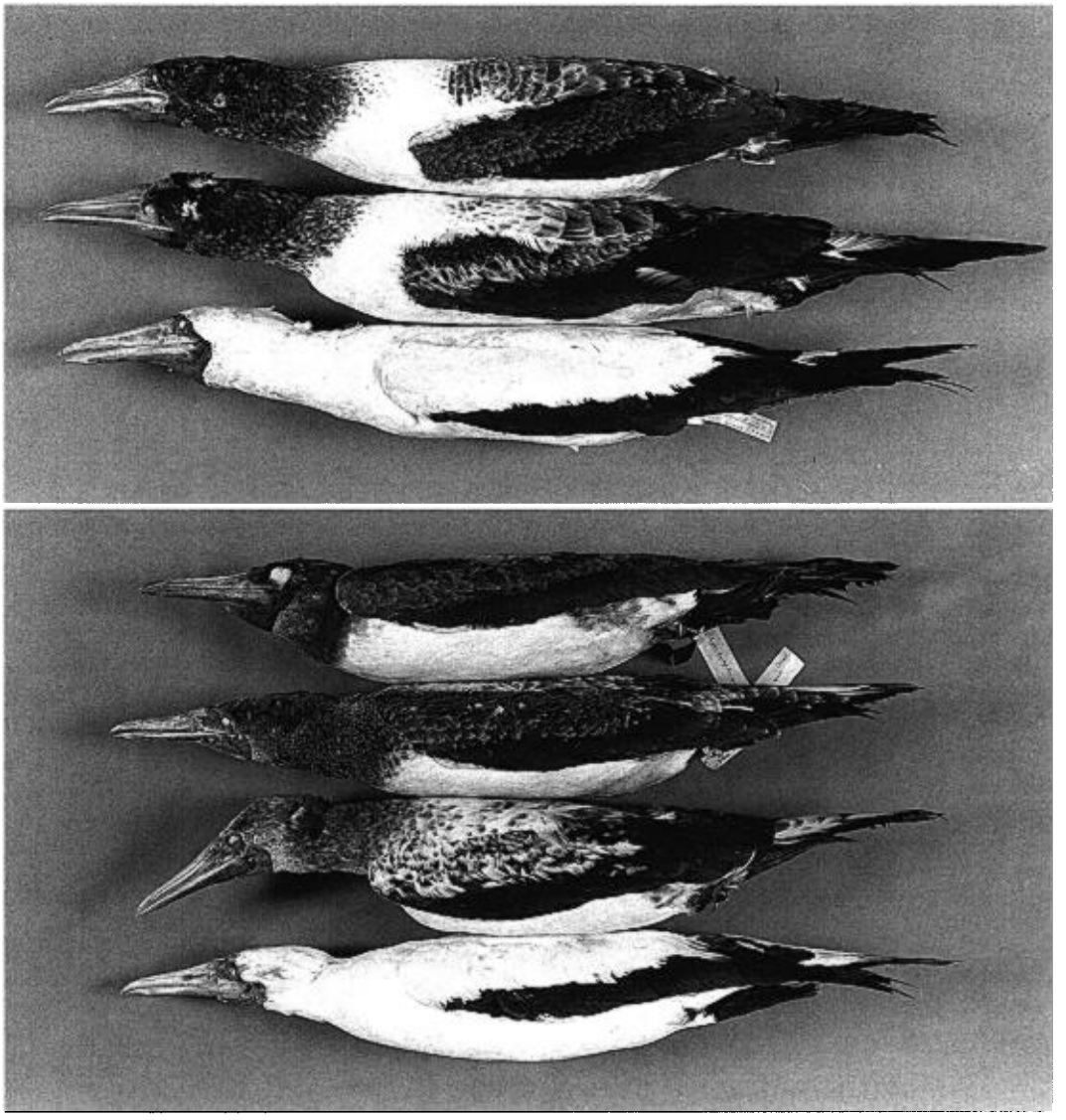

FIG. 5. Lateral view of plumage sequences in yellow-billed (top) and orange-billed (bottom) "Masked" boobies; specimens as in Figure 4.

Benedicto Island, whereas OB birds nest on steep cliffs of high islands like Malpelo, and Wenman and Culpepper, the northernmost Galápagos islands (Fig. 6; Nelson 1978, Duffy 1984, Gibbs et al. 1987). The difference was particularly evident at San Benedicto, where nearly all YB boobies nested on the flat upper surface of the island (mostly on the floor and around the flat rim of Herrera Crater), while the small OB colony (about 25 birds) was on the edge of a sloping cliff and at least 150 m from the nearest nesting YB individuals. The same preferences extend to roosting habitat. At Roca Partida, a tiny rock formed by two nearly vertical peaks that each rise 30 m above the sea with a low saddle joining them, YB birds roosted only on the flat saddle, where-

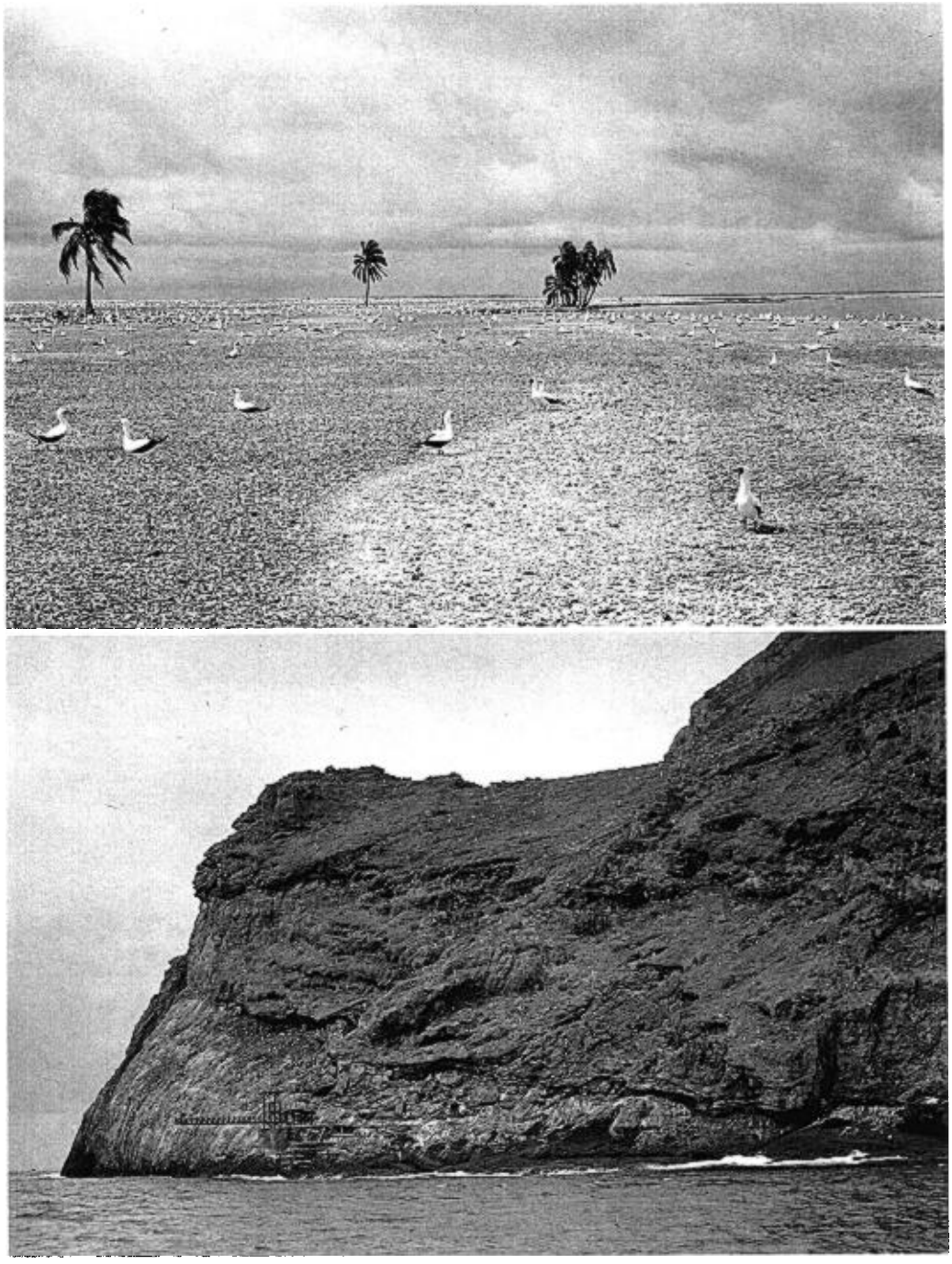

FIG. 6. A comparison of breeding habitats on (a) Clipperton Island, where over 60,000 *Sula dactylatra* breed, and (b) Malpelo Island, home to 24,000 *S. granti* (hundreds of nesting boobies are visible only as white dots in this photo). Photos by R. L. Pitman.

as OB birds roosted (and possibly nested: Howell and Webb 1990) only on the sides of the peaks. Duffy (1984) suggested that OB birds in the Galápagos preferentially nest near cliff edges because they may have problems taking flight from flat areas.

Finally, the two forms have different pelagic realms. YB boobies north of the equator tended to concentrate around, and to the west of, the Clipperton/Revillagigedos colonies (Fig. 7a), whereas OB boobies, including at least some banded individuals from the Galápagos, move northward from Galápagos/Malpelo to an area off Middle America (Anderson 1993), where they concentrate along the coast from Colima, Mexico, southward to Ecuador (Fig. 7b). Recent observations by RLP indicate that they also occur in small numbers throughout Gulf of California. The pelagic range of the Chilean birds is conjectural. YB birds south of the equator in Figure 7a are possibly of central Pacific (see Pitman 1986) or Chilean origin. Jehl (1973) observed occasional Masked Boobies, presumably from Islas Desventuradas, up to 200 km to the southeast.

DISCUSSION

Yellow-billed Masked Boobies in the eastern Pacific are geographically variable, being smallest in the north (*S. d. "californica"*; Clipperton and Mexican islands) and largest in the south (Chile). However, the differences are not statistically significant, and are within the range of variation of the geographically intermediate populations in the central Pacific. Thus, only one YB race, *S. d. personata,* can be recognized in this general area, and its relationship to the other named Masked Booby populations awaits review. The OB booby, on the other hand, differs from all YB populations in so many ways that we consider it to comprise a distinct species, *Sula granti.* These differences include mate preference, breeding habitat, and oceanic range that would be relevant to a biological species definition; as well as size, shape, degree of sexual dimorphism, bill color, and plumage pattern, which would support distinctiveness under a morphological species concept.

Bare-part coloration is an important distinguishing character of sulids in general (Nelson 1978) and Masked Boobies are no exception: the orange bill of *S. granti* separates it from all other forms of *S. dactylatra* (Table 3). At sea, adult *S. granti* and many juveniles are readily separable from YB forms by bill color alone (Howell and Engel 1993; RLP, pers. obs.). Even in long-dried museum specimens, the bill color of adult *S. granti* is usually apparent. This difference likely promotes species recognition. Foot color, despite its historical use in characterizing the various subspecies, has never been adequately described (Nelson 1978) and its taxonomic significance, as questioned by Murphy (1936), will only be resolved after seasonal, sexual, ontogenetic, and geographic factors are considered. Sex differences, at least, are involved: when RLP visited Malpelo Island in November, 1987, he could readily sex *S. granti* (verified by vocalizations: Nelson 1978) based on foot color alone (Table 3).

Pitman (1986) presented at-sea sightings data for over 10,000 Masked Boobies from the eastern tropical Pacific collected on cruises that occurred mainly during the first half of the year. At that time he did not distinguish between OB and YB boobies and the results showed a widespread distribution with no obvious pattern, except for dense concentrations within daily foraging ranges of the main colonies. Subsequent observations, however, in which the two forms were differentiated, although limited to the second half of the year, show that both forms prefer highly productive waters but in different areas (Figs. 7a, b). The concentration of OB boobies off southern Mexico (see also Anderson 1993, Howell and Engel 1993) corresponds to an area of seasonally strong, coastal upwelling off the Gulf of Tehuantepec (Blackburn 1962, 1963). The northern YB boobies concentrated along the 10° N latitude west of Clipperton Island, which corresponds to the northern boundary of the Northern Equatorial Countercurrent, a particularly rich feeding area for higher vertebrates (Wyrtki 1966, Reilly 1990). The significance of these habitat preferences is suggested by the fact that the Gulf of Tehuantepec is actually closer to Clipperton than it is to Galápagos or Malpelo; nevertheless, Clipperton boobies apparently prefer to forage farther offshore.

Evidence of reproductive isolation between *S. granti* and *S. dactylatra* is provided by ob-

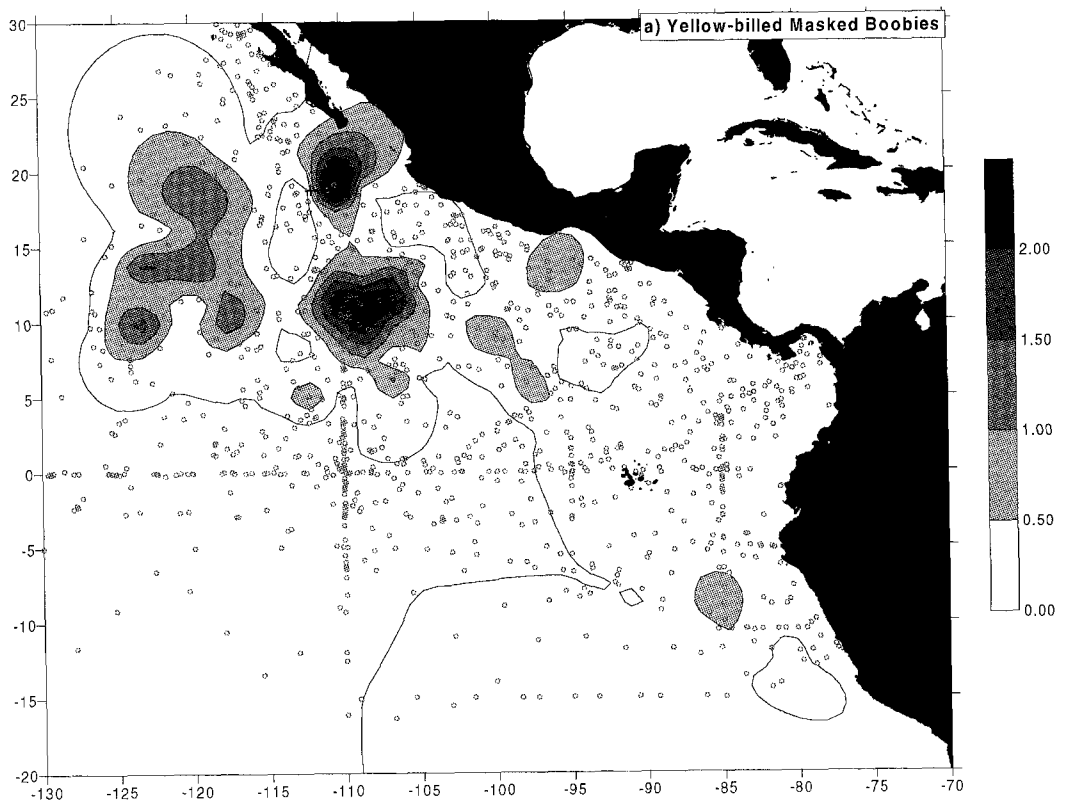

FIG. 7. Pelagic ranges of (a) yellow-billed (*Sula dactylatra*) and (b) orange-billed (*S. granti*) "Masked" boobies in the eastern Pacific identified on the basis of bill color. The average number of individuals of each form seen per hour is calculated for each 2° block of longitude and latitude in which they were recorded and the results contoured using Surfer (Keckler 1995). Noon ship positions for days when no bird was seen is indicated by an open circle. Sample sizes: OB = 701, YB = 243 (Pitman, unpubl. data).

servations of positive assortative mating within colonies where they occur together. Genetic analyses that extend our knowledge of booby evolution will be of great interest, as will observations that clarify any isolating mechanisms that allow these forms to avoid interbreeding. Also of interest are the selective forces that have modified body shape and increased sexual dimorphism of *S. granti* versus *S. dactylatra.* The increased dimorphism may be related to the fact that Galápagos is the only place in the world where "Masked" and Blue-footed (*S. nebouxii*) boobies breed sympatrically. Blue-foots are highly sexually dimorphic and substantially smaller than any of the YB populations [average mass of Blue-foot females is 1801 g, males 1283 g (Nelson 1978)]. In the Galápagos, Blue-foots feed mainly on sardines (*Sardinops sagax*; Anderson 1989), whereas YB boobies throughout the tropics feed mainly on flyingfish (Anderson 1993). During most years *S. granti* in the Galápagos feed mainly on sardines, but they can successfully switch to flyingfish during El Niño years when the sardines are unavailable and the Blue-foots starve (Anderson 1989). Perhaps *S. granti* is smaller and more sexually dimorphic than YB boobies because it has converged on Blue-footed Booby ecologically and morphologically as an adaptation to prey availability and variability within the Galápagos environment (see Boersma 1978).

Snow and Nelson (1984) pointed out that the Galápagos has the highest incidence of seabird endemism of any island group in the world and our study indicates that the otherwise pantropical Masked Booby has not been exempted from the modifying influence of

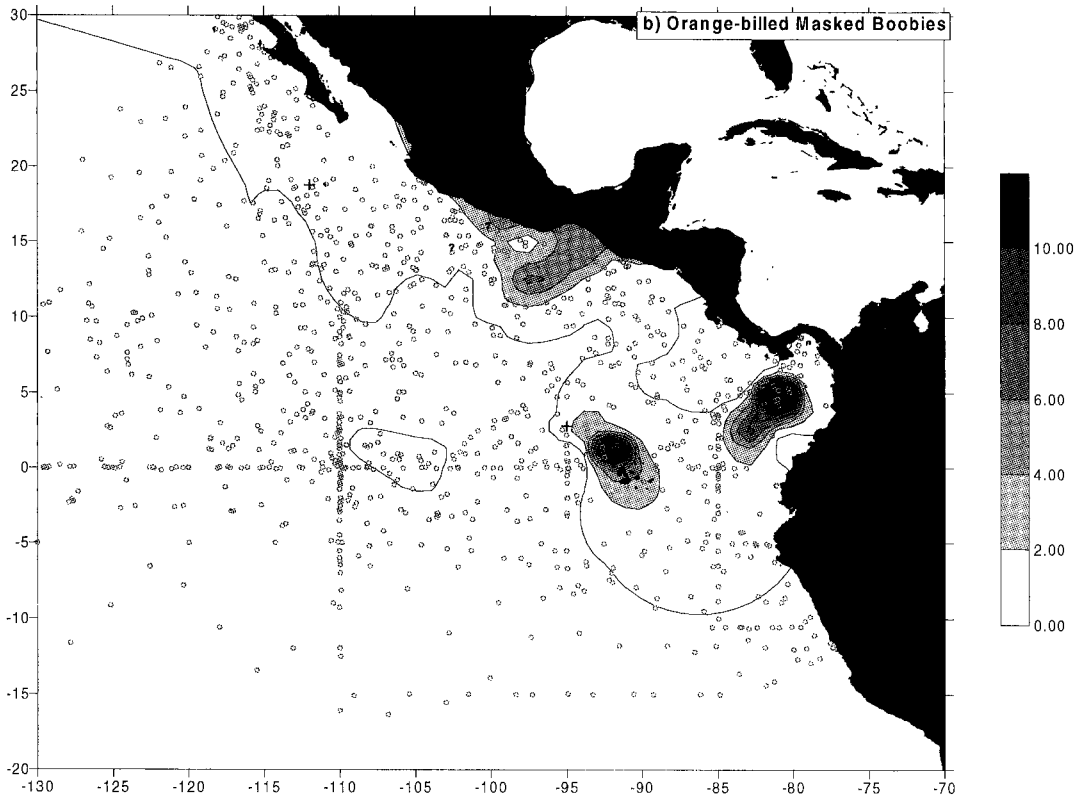

FIG. 7. Continued.

that environment. As a common name for *Sula granti* we propose Nazca Booby, which recognizes that the current breeding range and probably evolutionary history of this species is closely associated with the Nazca Crustal Plate.

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