

IDENTIFICATION AND DISTRIBUTION OF THE BROWN AND COCOS BOOBIES AND THEIR SUBSPECIES

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ABSTRACT: The Brown–Cocos Booby complex occurs in tropical and subtropical oceans worldwide and consists of five named taxa. The Cocos Booby (*Sula brewsteri*), including the subspecies *brewsteri*, *etesiacae*, and *nesiotes*, was split recently from the Brown Booby (*Sula leucogaster*), which retains the subspecies *leucogaster* and *plotus*. Because information about their field identification is limited, especially for females, I evaluated characters distinguishing the five taxa by examining 50 museum specimens and photos of 754 living Cocos and Brown Boobies from 47 locations in the ranges of all five subspecies. The Cocos and Brown Boobies can be distinguished by at least five characters: head color, pattern of the underwing coverts, iris darkness, culmen concavity, and bill color, the importance of which differ by sex and in some cases by subspecies. The white on the head and neck of the male Cocos Booby, which varies by subspecies, is the most obvious difference from the Brown Booby. Female Cocos Boobies also have the head paler brown than in female Brown Boobies. The Cocos Booby has a darker iris and more brown in the underwing coverts. *Sula leucogaster plotus* has a straighter culmen and females have the bill yellow rather than pink, as in all other taxa. The extent of white on the neck of male Cocos Boobies in the Revillagigedo Islands identifies them as *nesiotes* rather than as *brewsteri*. Information about individuals that have dispersed outside the traditional range helps track their movements and in assessing effects of environmental changes on populations.

The complex comprising the Brown Booby (*Sula leucogaster*) and Cocos Booby (*S. brewsteri*) occurs throughout the tropical and subtropical regions of the Pacific, Atlantic, and Indian oceans. Over this wide range, its morphology varies substantially (Nelson 1978, Schreiber and Norton 2020, VanderWerf et al. 2023). Five taxa in the complex are recognized by most authorities (Table 1). Each taxon originally was described as a separate species, starting with *leucogaster* in the Atlantic (Boddaert 1783), then *plotus* in the Indo-Pacific (Forster 1844), followed by three taxa from the eastern Pacific, *brewsteri* (type locality Isla San Pedro Mártir, Gulf of California; Goss 1888), *nesiotes* (type locality Clipperton Island; Heller and Snodgrass 1901), and *etesiacae* (type locality Gorgona Island, Colombia; Thayer and Bangs 1905). The three taxa in the eastern Pacific were based primarily on differences in the amount of white on the head and neck of males, with *nesiotes* having the most and *etesiacae* the least. Wetmore (1939) provided more details on morphological variation and distribution of the three eastern Pacific taxa, but he regarded all of them as subspecies of the Brown Booby, along with *leucogaster* and *plotus*. That taxonomy was formalized when the American Ornithologists' Union's checklist committee lumped all five taxa into a single species (Wetmore et al. 1944).

On the basis of a combination of genetic (Steeves et al. 2003, Morris-Pocock et al. 2011), morphological (VanderWerf 2018), and behavioral evidence (López-Rull et al. 2016, VanderWerf et al. 2023), the Cocos Booby, including the subspecies *brewsteri*, *etesiacae*, and *nesiotes*, was split recently from the Brown Booby, which retains the subspecies *leucogaster* and *plotus* (Chesser et al. 2024,

IDENTIFICATION OF BROWN AND COCOS BOOBIES AND THEIR SUBSPECIES

TABLE 1 Summary of the Ranges and Distinguishing Characteristics of the Subspecies of the Brown and Cocos Boobies^a

	Taxon				
	<i>S. l. leucogaster</i>	<i>S. l. plotus</i>	<i>S. b. brewsteri</i>	<i>S. b. nesiotus</i>	<i>S. b. etesiaca</i>
Usual range	Atlantic and Caribbean	Indo-Central Pacific	Pacific Mexico	Clipperton and Revillagigedo Islands	Pacific Central and South America
Male head color	brown	brown	white head and upper neck	white head and neck	white forehead
Female head color	brown	brown	whitish forehead	whitish forehead	whitish forehead
Ventral wing coverts ^b	white	white	white with brown bar	white with brown bar	white with brown bar
Iris color ^b	Male light to medium, female variable	Male light, female light to medium	Dark	Dark	Dark
Male facial skin color ^b	Orange-yellow	Blue	Blue	Blue	Blue
Female bill color ^b	Pink	Yellow	Pink	Pink	Pink
Culmen concavity	More concave	Less concave	More concave	More concave	More concave

^aAdapted from VanderWerf et al. (2023).

^bVariable character; see figures for more details.

Clements et al. 2024). Information about the identification of the Cocos Booby in field guides is limited and pertains mostly to males, with females often not illustrated or mentioned, or wrongly described as indistinguishable from the female Brown Booby. VanderWerf (2018) described several characters distinguishing adult females of *S. l. plotus* and *S. b. brewsteri* (which at the time were considered conspecific), including head color and bill color (see also Pyle 2008). VanderWerf (2018) also presented anecdotal evidence that the coloration of the underwings of *plotus* and *brewsteri* differs. This character is not mentioned in any field guide and is illustrated incorrectly in some, and a more thorough quantitative examination of this character is needed. Although the extent of white on the head and neck of males is the primary character on which the Cocos Booby's subspecies are based, it has not been assessed systematically or quantitatively.

The purposes of this study are to (1) quantify the characters distinguishing the five taxa constituting the Brown–Cocos Booby complex; (2) quantify four previously undescribed field marks (underwing pattern, iris color, bill color, and bill curvature) distinguishing male and female Cocos and Brown Boobies and their subspecies; and (3) discuss the implications of this information for their taxonomy.

METHODS

I examined 804 Brown and Cocos Boobies, including 50 museum specimens (in the B. P. Bishop Museum, Honolulu, and the Natural History Mu-

seum of Los Angeles County, Los Angeles) and photos of 754 living birds, from 47 locations in all five major geographic regions in which the species occurs (Table 2), and I compiled data on 10 morphological characters. For culmen and mandible concavity, underwing-covert coloration, and extent of white on the head of males, I used both museum specimens and photographs of living birds. For color of the iris, facial skin, and bill I could use only photographs of living birds because the colors quickly fade or change after death. For plumage color of the head, breast, and back, I used only museum specimens because it required direct comparison with standardized color chips. To avoid potential bias in selecting birds for examination, at museums I took all measurements from every specimen unless it was not physically possible because of the condition or posture of the specimen. Most photos from the central Pacific were mine, but I used photographs by other observers from other locations, which I obtained through personal communication with the observer or from the Cornell Lab of Ornithology's Macaulay Library.

I identified each bird's species, sex, and age by previously known criteria, primarily head color and bill color (Pyle 2008, VanderWerf 2018; Table 1). I identified the subspecies of each bird by geography; i.e., I assumed that all individuals were of the subspecies presumed to occur at a given location (Table 2). For birds that were observed outside of their usual range, primarily Cocos Boobies in the central and western Pacific, I did not assign a subspecies and did not include them in analyses of subspecific variation because their origin and ancestry, and thus their presumptive subspecies, were unknown.

I quantified the extent of white on the head and neck of males by classifying each bird into one of five categories based on how far posteriorly the white extended (Figure 1), with higher scores representing more white: 0, none; 1, forehead only (anterior to top of head); 2, head and upper throat; 3, nape and lower throat; 4, most of neck, often with only a narrow pale brown band separating the white belly and whitish neck. I evaluated variation in the frequency of scores among the three Cocos Booby subspecies with a chi-squared test.

I quantified the plumage color of the head (in females) and breast by visually comparing specimens with Munsell color chips (Figure 2; Munsell Color 1994). In the Munsell system a color is defined by three parameters: hue (spectral color or wavelength), value (darkness), and chroma (intensity or saturation). The notation for hue is a letter (Y for yellow, YR for yellow-red, R for red, etc.) preceded by a number from 0 to 10, with higher numbers representing lower wavelengths. Value is measured on a linear scale from 0, for black, to 10, for white. Chroma is measured on a linear scale from 0, for neutral gray, to 20 for an extremely intense color. I measured males' breast color where it was darkest immediately above the white belly, because in some individuals the breast became progressively whiter toward the head (Figure 2). I evaluated variation in color value and chroma by subspecies with a one-way analysis of variance (ANOVA) for each variable. I evaluated differences in color hue between Brown and Cocos Boobies with Kruskal-Wallis tests.

I examined the color pattern of the underwing coverts in photos of birds in flight and from a few museum specimens with spread wings. The extent of brown and white in the lesser and greater underwing coverts was variable, and I scored the amount of brown color and resulting pattern on a scale from 1 to 5, using the following definitions, with higher scores representing less

TABLE 2 Sample Sizes and Locations of Specimens ($n = 50$) and Photos ($n = 754$) of Living Brown and Cocos Boobies Examined

Region and location	Male	Female	Total
Atlantic			
Ascension Island	2	8	10
Brazil (Fernando de Noronha)	10	7	17
Cape Verde	13	12	25
French Guiana	0	1	1
São Tome and Principe	3	8	11
Caribbean			
Bahamas	1	13	14
Netherlands Antilles	1	4	5
Cayman Islands	14	11	25
Cuba	0	3	3
Curaçao	0	1	1
Mexico	2	10	12
Navassa Island	1	0	1
Tobago	2	7	9
United States (vagrants in eastern states)	1	4	5
Virgin Islands	0	1	1
Central and western Pacific			
American Samoa	1	1	2
Japan (Bonin Islands)	2	1	3
Hawaiian Islands	50	40	90
Johnston Island	1	0	1
Kiritimati Island	6	4	10
Palmyra Atoll	58	48	106
Mariana Islands	0	3	3
Marquesas Islands	0	1	1
Solomon Islands	0	1	1
Wake Island	19	15	34
Eastern Pacific			
Chile (incl. Rapa Nui)	0	7	7
Clipperton Island	34	23	57
Colombia	8	13	21
Costa Rica (incl. Cocos Is.)	53	71	124
Ecuador (incl. Galapagos)	4	3	7
El Salvador	0	6	6
Guatemala	1	8	9
Mexico (incl. Revillagigedo Is.)	37	19	56
Nicaragua	3	7	10
Panama	15	23	38
Peru	0	6	6
Indian Ocean			
Chagos Islands	0	3	3
Christmas Island	18	10	28
Cocos (Keeling) Islands	0	1	1
Djibouti	1	4	5
Egypt	2	1	3
Eritrea	1	1	2
Madagascar	10	0	10
Oman	0	2	2
Saudi Arabia	3	3	6
Seychelles	0	1	1
Yemen (Socotra Island)	2	2	4
Total	380	424	804

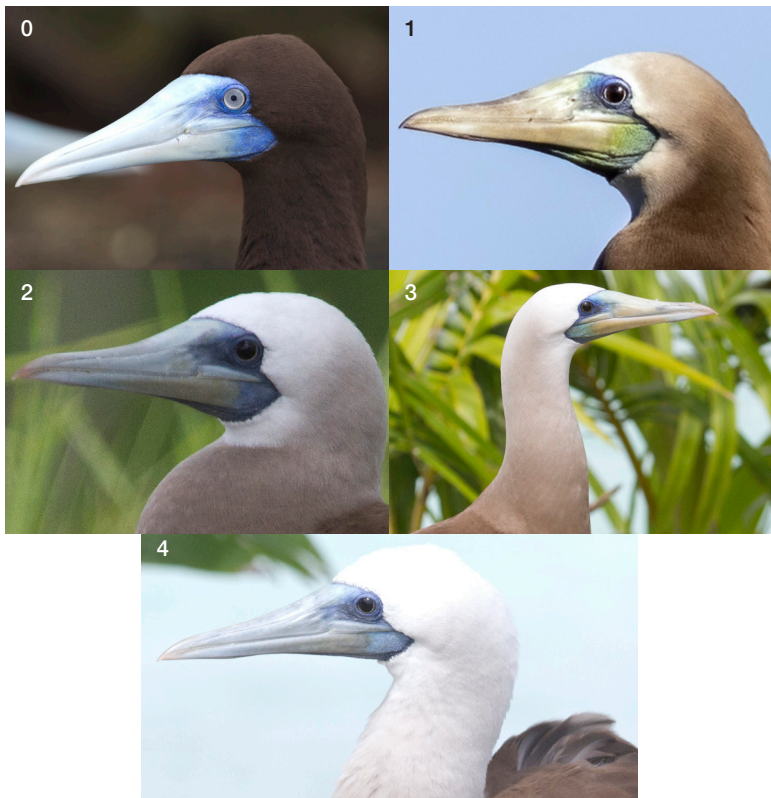


FIGURE 1. Categories quantifying the extent of white on the head and neck of male Brown (0) and Cocos (1–4) Boobies. 0, Palmyra Atoll; 1, Corcovado, Costa Rica; 2, male, Palmyra Atoll; 3, Palmyra Atoll; 4, Palmyra Atoll.

Photos by Eric VanderWerf (0, 2, 3, 4) and Sandy and Bob Sipe (1)

white and more brown (Figure 3): 1, lesser coverts entirely white, forming an entire white polygon with the white median and greater coverts; 2, some lesser coverts brownish, forming an indistinct brown bar that extended a short distance into the white polygon; 3, more lesser coverts brownish, forming a distinct brown bar with moderate extension into the white polygon; 4, broad brown bar with long extension into white polygon; 5, lesser coverts mostly brown and greater coverts also brownish, causing the median coverts to appear as a narrow white stripe. I evaluated variation in the frequency of scores among all five subspecies of the Brown and Cocos Boobies with a chi-squared test.

I scored iris darkness on a scale from 1 (lightest) to 5 (darkest), using only individuals in which the iris was clearly visible, was not obscured by shadow, and in which the pupil was not so dilated that only a small amount of the iris

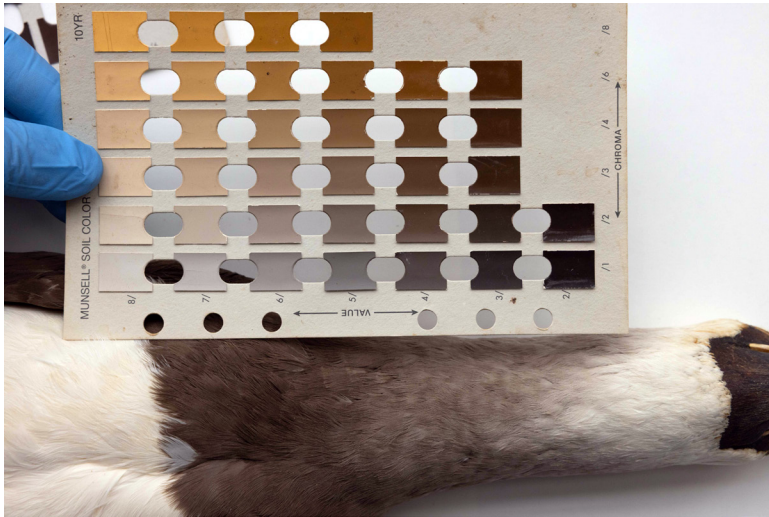


FIGURE 2. Method of measuring plumage color with Munsell color chips.

was visible (Figure 4). I evaluated variation in the frequency of scores among all five subspecies of the Brown and Cocos Boobies with a chi-squared test.

To measure concavity of the culmen, I used a computer to digitally overlay a circle on a photograph of the head, then adjusted the size of the photo until it matched the curvature of the circle (Figure 5). I then drew lines from the center of the circle to the base of the bill and the inflection point where the curvature changed toward the bill tip. I measured the angle formed by those lines (the central angle of the circle, A in Figure 5) by using a protractor on the computer screen, which is the same as the curvature of the bill (the intercepted arc, B in Figure 5). I used the same method to measure concavity of the mandible from the base of the bill to the gonydeal angle. I used only photographs in which the bill was parallel to the plane of the image because the apparent curvature changes with the viewing angle. I tested for variation in culmen and mandible concavity with a one-way analysis of variance (ANOVA) for each, with subspecies as the factor.

I described the color of each bird's facial skin, noting blue, slate blue, blue-gray, blue-green, green, pink, yellow, yellow-gray, and yellow-green (Figure 6). The bill was often more than one color, so for each bird I recorded a dominant bill color and a secondary bill color, noting blue, slate blue, blue-gray, blue-green, gray, gray-yellow, orange-yellow, pink, pink-brown, pink-orange, pink-yellow, yellow, and yellow-green (Figure 6). To simplify analyses and because of low sample size of some colors, I combined some similar colors into fewer categories. For example, I combined blue-green and blue-gray with blue, gray-yellow with gray, and pink with pink-brown.

For analyses of color, I used only data from adults, not immature birds. In each analysis, to account for multiple comparisons, I applied a Bonferroni correction to *p*-values.

IDENTIFICATION OF BROWN AND COCOS BOOBIES AND THEIR SUBSPECIES

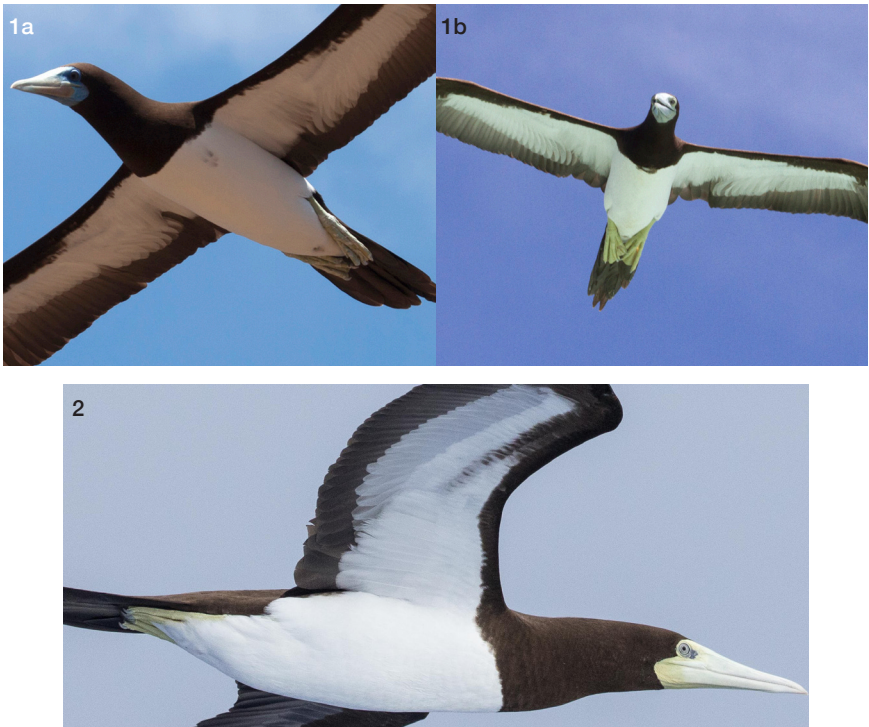


FIGURE 3. Categories quantifying the pattern of the ventral wing coverts. Category 1, entire white polygon with no brown bar. 1a, male Brown Booby Lehua Islet, Hawaii; 1b, female Brown Booby, Palmyra, Line Islands. Category 2, indistinct brown bar with short extension into white polygon. Brown Booby, Tern Island, Hawaii. Category 3, distinct brown bar with moderate extension into white polygon. 3a, male Cocos Booby, Palmyra, Line Islands. 3b, male Cocos Booby, Ixtapa, Mexico. Category 4, Distinct brown bar with long extension into white polygon. Greater coverts somewhat brownish. 4a, female Cocos Booby, Ixtapa, Mexico. 4b, male Cocos Booby, Ixtapa, Mexico. Category 5, lesser coverts mostly brown, greater coverts also brownish, causing median coverts to appear as a narrow white stripe. 5a, Chocó, Colombia. 5b, Puntarenas, Costa Rica.

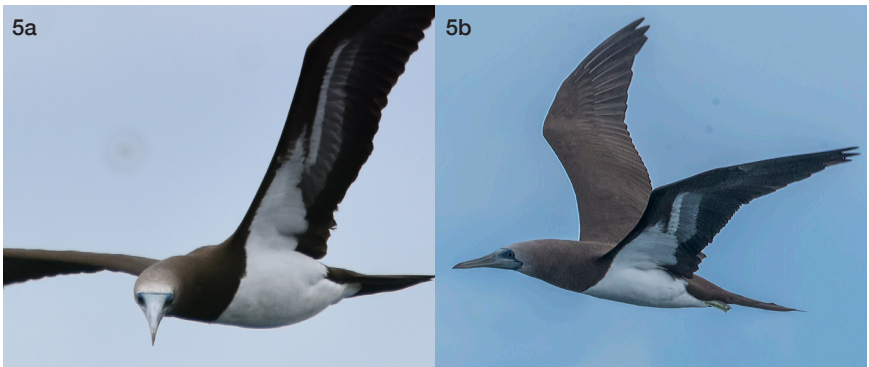
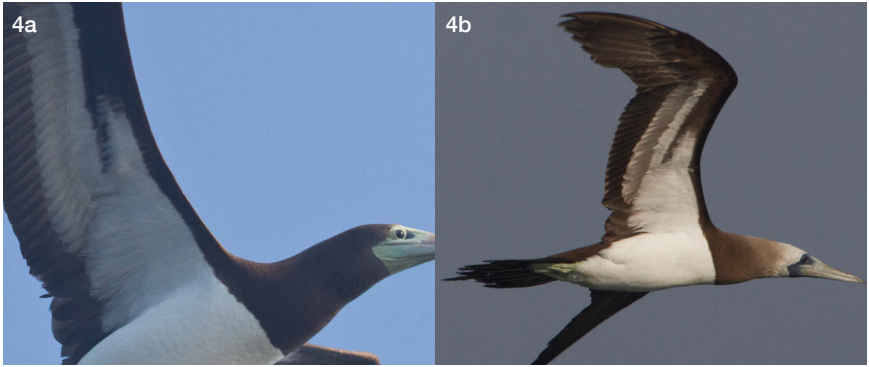
Photos by Eric VanderWerf (1–4), Rodolfo Dodero (5a), and Leandro Arias Salazar (5b)

RESULTS

Extent of White on Head of Males

The extent of white on the head and neck of male Cocos Boobies differed by subspecies ($\chi^2 = 96.3$, $df = 6$, $p < 0.001$), but there was overlap (Figure 7). The white was most extensive in *nesiotes*, least in *etsiaca*, and intermediate in *brewsteri*, which overlapped with that in both *nesiotes* and *etsiaca*. The scores of males from the Revillagigedo Islands (mean $2.8 \pm SE 0.3$), which have been

IDENTIFICATION OF BROWN AND COCOS BOOBIES AND THEIR SUBSPECIES



ascribed previously to *brewsteri* (Wetmore 1939, Nelson 1978, Schreiber and Norton 2020), did not differ from scores of *nesiotes* males from Clipperton Island (mean $3.4 \pm \text{SE } 0.12$; Mann–Whitney *U*-test, $W = 308$, $p = 0.150$), but did differ from scores of males of *brewsteri* (mean 2.0 ± 0.08 ; Mann–Whitney *U*-test, $W = 322.5$, $p = 0.04$). Males from the Revillagigedo Islands accounted

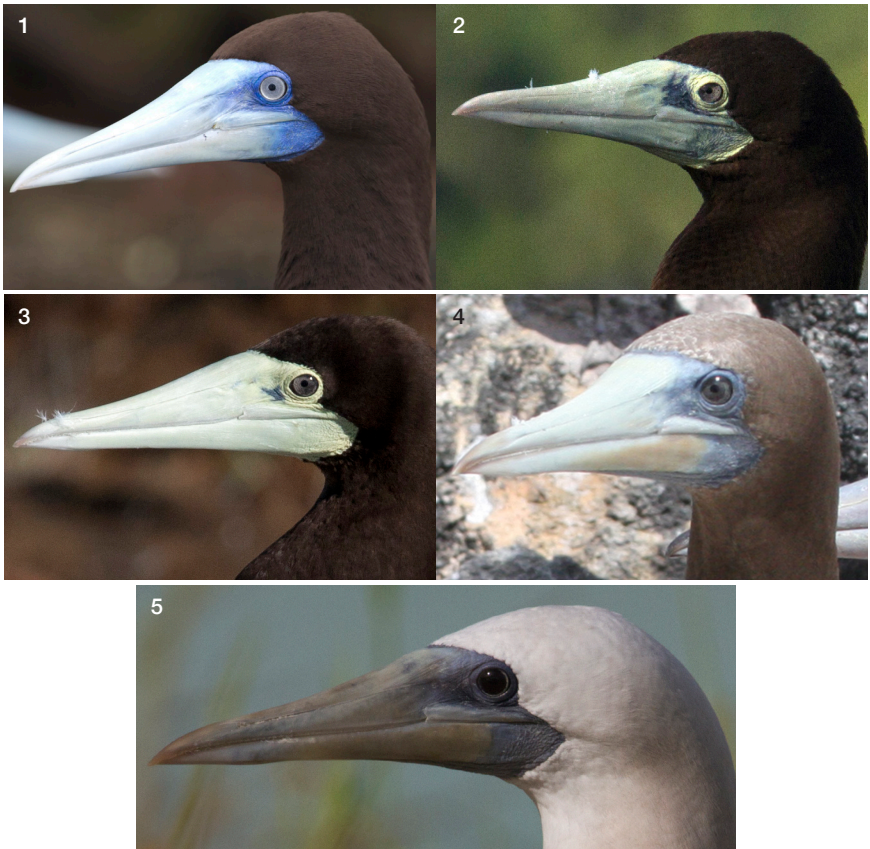


FIGURE 4. Categories quantifying iris color, from 1 (lightest) to 5 (darkest). Category 1, male Brown Booby, Palmyra Atoll; category 2, female Brown Booby, Palmyra Atoll; category 3, female Brown Booby, Lehua Islet, Hawaii; category 4, male Cocos Booby, Moku Manu, Hawaii; category 5, male Cocos Booby, Palmyra Atoll.

Photos by Eric VanderWerf

for most (6 of 7) scores of 5 in *brewsteri* when defined to include the Revil-lagidedo Islands (Figure 7). Scores of males from southwestern Mexico, including the states of Nayarit, Colima, Guerrero, Oaxaca, and Chiapas (mean 2.0) were similar to those of *brewsteri* from northwestern Mexico. Scores of males from northern Central America, including Guatemala, Nicaragua, and El Salvador (mean $1.3 \pm SE 0.25$), were similar to those of *etesiaca* from southern Central America and South America.

Plumage Color

The head color of females varied among the subspecies and was lighter in *S. b. nesiotus* (mean Munsell value 4.7 ± 0.3) and *S. b. brewsteri* (mean Munsell

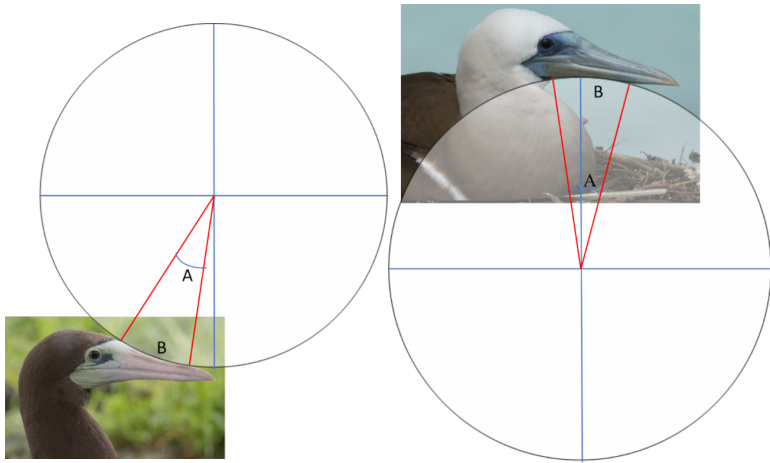


FIGURE 5. Method for measuring curvature of the culmen and mandible. I placed a circle over a photograph of the bill and adjusted the size to match the bill shape. I measured the central angle of the circle (A) with a protractor, which is the same as the curvature of the bill (the intercepted arc, B).

value 3.4 ± 0.2) than in *S. b. etesiaca* (mean Munsell value 3.0 ± 0.0) and *S. l. plotus* (mean Munsell value 3.0 ± 0.06 ; $F_{16,19} = 18.00$, $p < 0.001$; see Figure 2 for examples of values). Similarly, the breast color of males varied by subspecies and was lighter in all three Cocos Booby subspecies (mean Munsell values 5.8 ± 0.4 in *nesiotes*, 4.7 ± 0.2 in *brewsteri*, and 4.0 ± 0.0 in *etesiacca*) than in *S. l. plotus* (2.9 ± 0.08 ; $F_{17,20} = 30.8$, $p < 0.001$). The hues of females' heads and males' breasts in the two species differed, tending to be slightly more yellow (10YR) in the Cocos Booby and more red (7.5YR) in the Brown Booby (Kruskal-Wallis $H = 5.73$ and 13.35 , $df = 1$ and 1 , $p = 0.017$ and < 0.001 , respectively).

Wing Pattern

The color pattern of the underwing coverts of the Brown and Cocos Boobies differed, and the differences were similar in females and males of each species (Figure 8; $\chi^2 = 197.5$, $df = 12$, $p < 0.001$). In the Brown Booby, most individuals had an entire white polygon on the underwing formed by the lesser, median, and greater ventral wing coverts (score of 1); about 30% had a white polygon with only an indistinct brown bar between the lesser and median coverts (score of 2), and a few individuals of *leucogaster*, mostly females, had a score from 3 to 5 (Figure 8). There was no overall difference in the frequency of the ventral wing covert pattern between the subspecies *leucogaster* and *plotus* ($\chi^2 = 2.58$, $df = 1$, $p = 0.11$), but variation in *leucogaster* was wider. In the Cocos Booby, almost all individuals had more brown color in the lesser coverts, forming a distinct brown bar within the white polygon. The pattern in the three subspecies varied, *etesiacca* more often having mostly brown lesser and greater coverts, causing the median coverts to appear as a narrow white stripe (Figure 9; $\chi^2 = 31.2$, $df = 4$, $p < 0.001$).

IDENTIFICATION OF BROWN AND COCOS BOOBIES AND THEIR SUBSPECIES

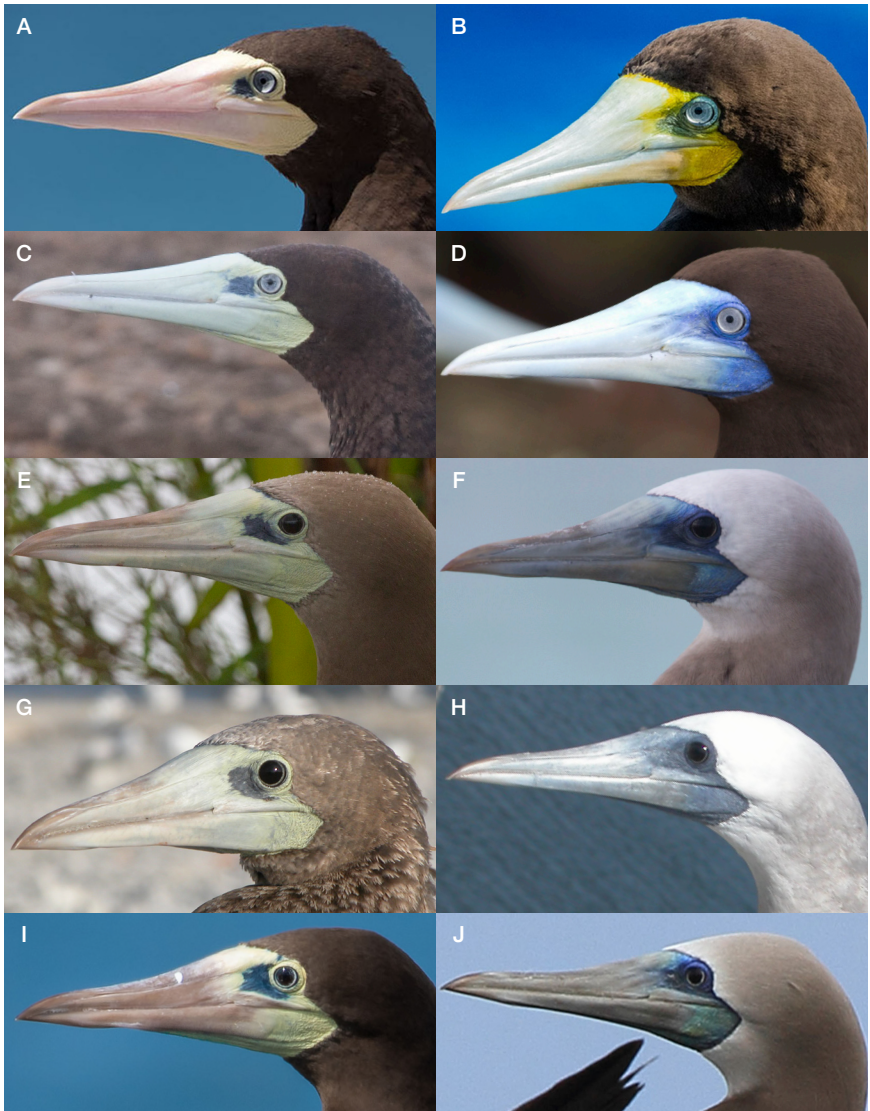


FIGURE 6. Typical colors of the head, facial skin, and bill of the Brown and Cocos Boobies. Females in the left column, males in the right column. A and B, *Sula leucogaster leucogaster*, Cayman Brac. C and D, *S. l. plotus*, Lehua Islet, Hawaii (C) and Palmyra Atoll (D). E and F, *Sula brewsteri brewsteri*, Palmyra Atoll. G and H, *S. b. nesiotes*, Clipperton Island. I and J, *S. b. etesiaca*, Corcovado, Costa Rica (I) and Coiba Island, Panama (J).

Photos by Denny Swaby (A), Nicole Martin (B), Eric VanderWerf (C, D, E, F), Henri Weimerskirch (G, H), Rio Dante (I), and Fabio Olmos (J)

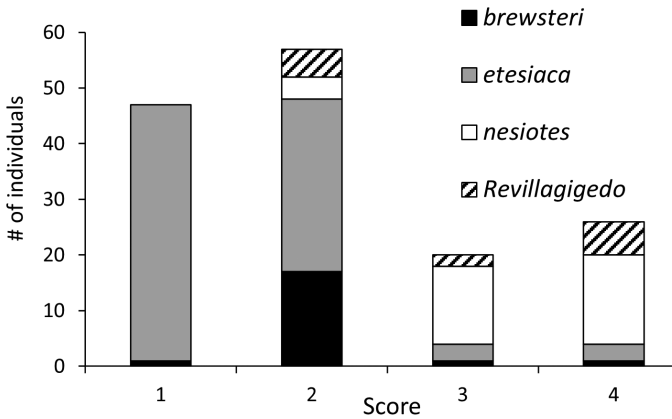


FIGURE 7. Extent of white plumage on the head and neck of male Cocos Boobies by subspecies, with birds from the Revillagigedo Islands shown separately.

Iris Color

In all three subspecies of the Cocos Booby the iris was darker than in most Brown Boobies (Figure 10), in both males ($\chi^2 = 279.2$, $df = 4$, $p < 0.001$) and females ($\chi^2 = 203.6$, $df = 4$, $p < 0.001$), but there was some overlap, especially in females. Almost all male Cocos Boobies had a dark iris (99% scoring 4 or 5), and almost all male Brown Boobies had a light iris (92% scoring 1 or 2); in just a few individuals was the iris color intermediate. In females, overlap was greater because the iris color of female Brown Boobies was variable, distributed fairly evenly among all five scores (13% to 31%; Figure 10). Within the Brown Booby, subspecies *leucogaster* and *plotus* differed (Figure 11), in both males ($\chi^2 = 45.9$, $df = 4$, $p < 0.001$) and females ($\chi^2 = 46.5$, $df = 4$, $p <$

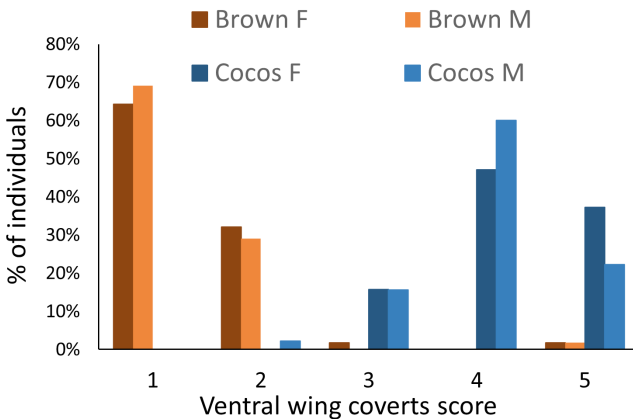


FIGURE 8. Histogram of scores for ventral wing covert pattern in male and female Brown and Cocos Boobies. See Figure 2 for photographs representing each score.

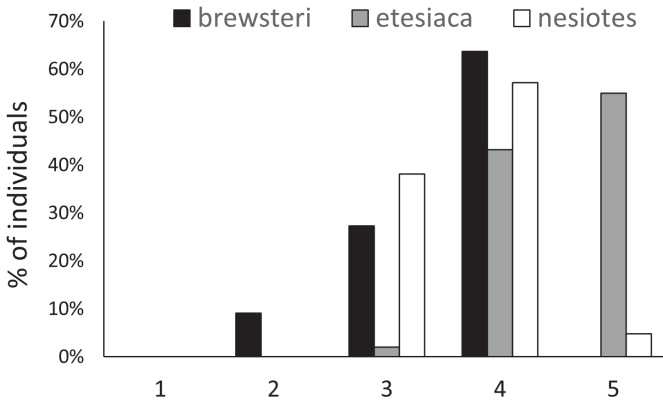


Figure 9. Histogram of scores for ventral wing covert pattern in the Cocos Booby by subspecies.

0.001), with wider variation in both sexes of *leucogaster*. Within the Cocos Booby, variation ($\chi^2 = 16.2$, $df = 4$, $p = 0.03$) was due solely to a few examples of *etesiaca* that had a moderately dark iris (score 3), a score that was not observed in any *brewsteri* or *nesiotus*.

Bill Shape

On average, the culmen was less concave in *Sula leucogaster plotus* than in the other four taxa, which did not differ significantly from each other ($F_{4,359} = 127.4$, $p < 0.001$; Figure 12). There was a small amount of overlap in culmen curvature between *plotus* and the other taxa, but the interquartile ranges (which represent the median 50% of individuals) did not overlap, and

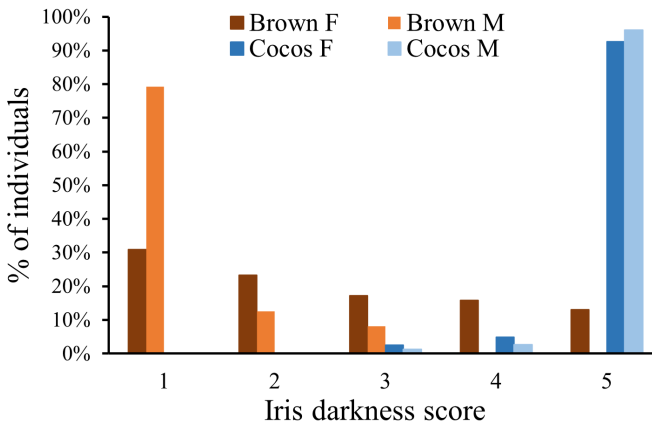


FIGURE 10. Iris darkness scores in male and female Brown and Cocos boobies. In each sex, the iris averages darker in the Cocos Booby than in the Brown Booby, but there is more overlap between the species in females.

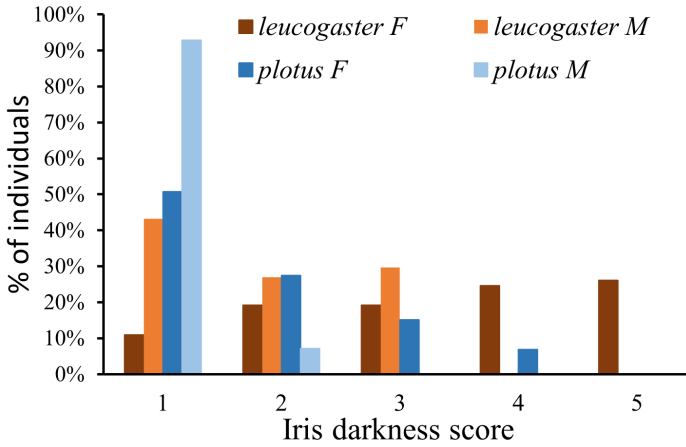


FIGURE 11. Difference in iris color between the two subspecies of the Brown Booby. In both sexes, variation in *S. l. leucogaster* is wider than in *S. l. plotus*.

only 4 of 227 (<2%) examples of *plotus* had a culmen as concave as 25% of examples of *brewsteri* (Figure 12). Mandible concavity also differed statistically by subspecies ($F_{4,348} = 49.3, p < 0.001$), but the pattern was different, with *brewsteri* and *nesiotes* having a more concave mandible than the other three taxa. However, the differences in average mandible curvature among subspecies were smaller (4.3° or less) and harder to distinguish visually than the differences in culmen curvature (7.2° or more), and there was broader overlap, with the interquartile ranges of all five subspecies overlapping to various degrees.

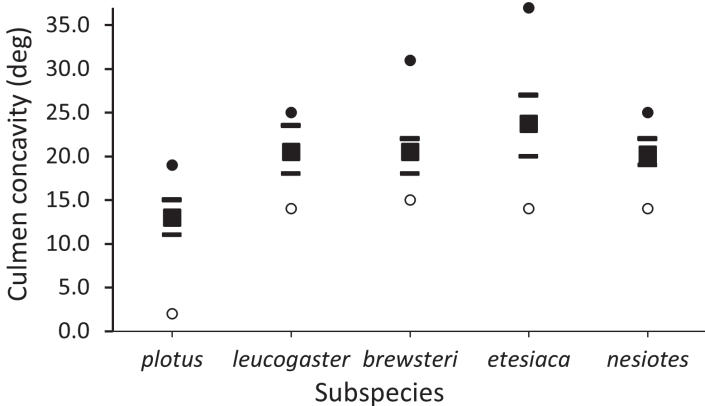


FIGURE 12. Concavity of the culmen in the Brown and Cocos Boobies by subspecies. The culmen is less concave in *Sula leucogaster plotus* than in the other four taxa. The black square is the median, the black bars are the interquartile range, the black circle is the maximum, and the open circle is the minimum.

Face and Bill Color

The facial skin was yellow in most (89–100%) females of all subspecies, with 6% to 11% of females having an orange-yellow face in *leucogaster* and a gray-yellow face in *plotus* and *brewsteri* (Figure 13). In males, the facial skin was blue in most individuals of all subspecies except nominate *leucogaster*, in which the face was most often orange-yellow (Figure 13). The face was a dark slate blue in 50% of male *plotus* from the Indian Ocean; this color was not observed outside the Indian Ocean and was particularly common on Christmas Island.

The dominant bill color in female Cocos Boobies was pink-brown in all subspecies (Figure 14), sometimes with yellow or gray-yellow as a secondary color. In females of *S. l. leucogaster*, the dominant bill color was bright pink, with some individuals having yellow or gray-yellow as the dominant color and pink as the secondary color. In females of *S. l. plotus*, the dominant bill color was yellow, sometimes with pink-brown as a secondary color toward the tip. That subspecies had less pink in the bill than in any other taxon ($F_{4,348} = 481.6, p < 0.001$; Figure 15). In female *plotus*, the bill was never more than

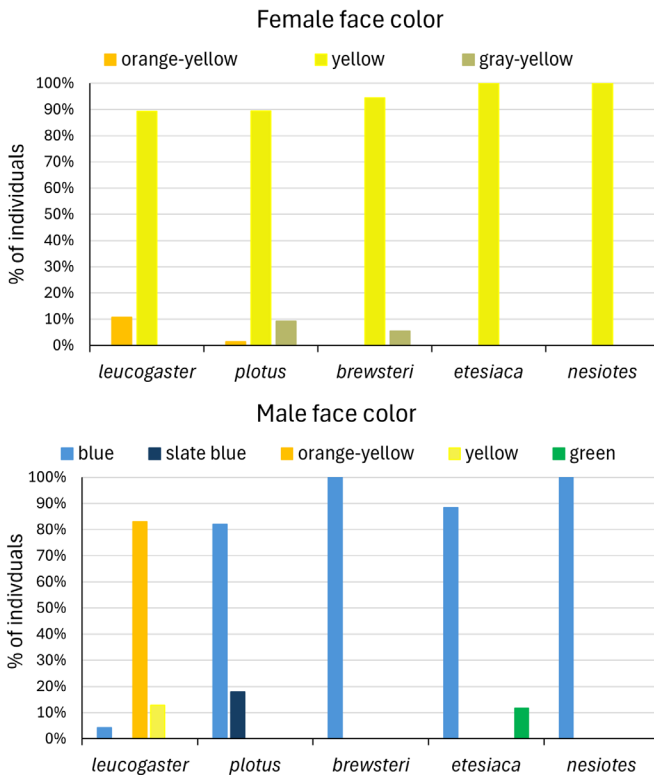


FIGURE 13. Facial skin color in the Brown and Cocos Boobies by sex and subspecies.

half pink-brown, and the transition from yellow to pink-brown was usually gradual, whereas in female Cocos Boobies there often was an abrupt transition from yellow to pink-brown, giving the bill a distinctly two-toned appearance (Figure 6).

DISCUSSION

The Cocos and Brown Boobies can be distinguished by at least five characters: head and breast color, color pattern of the ventral wing coverts, iris darkness, culmen curvature, and bill color, the importance of which differ by sex and in some cases by subspecies (Table 1). The variation in head color of males is widely recognized and was the primary basis for the original descriptions of some taxa (Goss 1888, Heller and Snodgrass 1901, Wetmore 1939). The differences between the Brown Booby and Cocos Booby in head color of females was first mentioned by Pyle (2008), and this character and the color of the ventral wing coverts were more fully described by VanderWerf (2018). The differences in iris darkness, culmen concavity, and bill color have not been described previ-

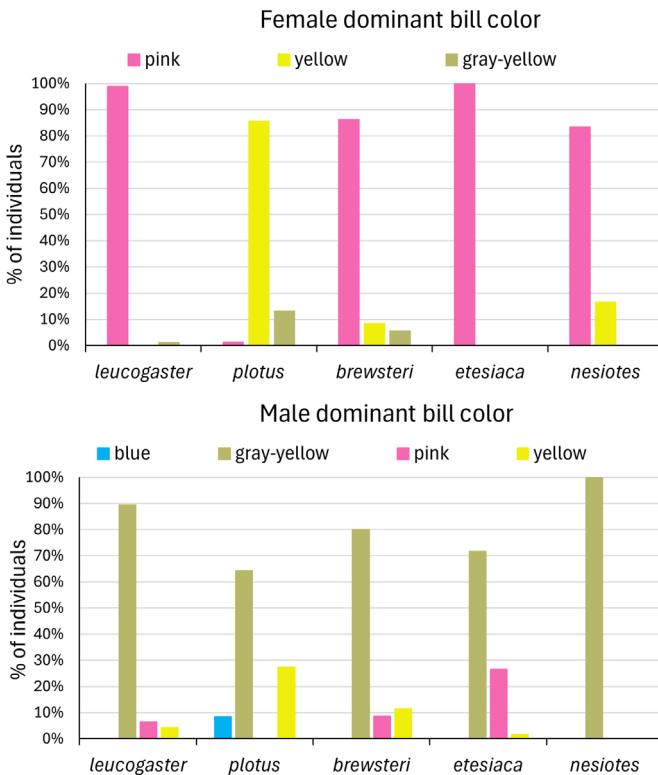


FIGURE 14. Dominant bill color in the Brown and Cocos Boobies by sex and subspecies.

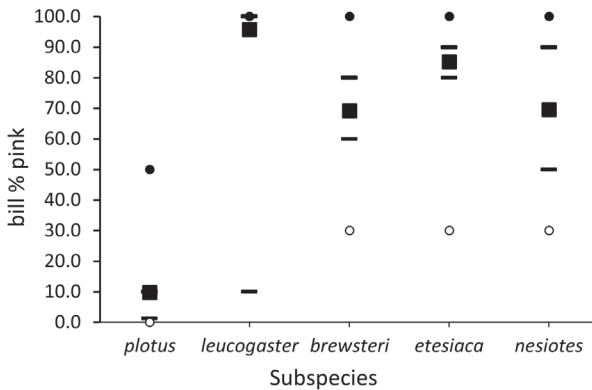


FIGURE 15. Proportion of the bill pink in female Brown and Cocos Boobies, by subspecies. The black square is the median, the black bars are the interquartile range, the black circle is the maximum, and the open circle is the minimum.

ously and are useful new field marks for identification of these species. Most of these characters vary to some extent, and, especially for females, it is better to rely on a combination of field marks for species identification.

All these field marks apply only to adults; more research is required to determine which, if any, field marks can be used to identify juvenile and first-year birds. The pattern of the underwing coverts is known to not be useful for identifying juveniles, all of which have the underwing pattern of the Cocos Booby, with a brownish bar—see VanderWerf (2018) for an example. Adults of both sexes of both species have a completely white belly with a sharp line between the white belly and the brown breast. Juveniles and first-year birds have a brownish wash over the entire belly, and second-year and third-year birds have brown spots or patches of brown on the belly and can be aged by this and molt patterns (Pyle 2008). The face and bill color may begin to develop before definitive plumage is acquired, and this can be useful in attempting to identify some second-year and third-year birds.

The subspecies of both species also can be identified by several characters, but there is variation and overlap, and a conclusive subspecific identification may not be possible in some cases, which is to be expected with subspecies (Patten and Unitt 2002, Patten 2015).

Summary of Identifying Characters

Head color. This is the most important and obvious character for distinguishing the Brown and Cocos Boobies, especially in males and to a lesser degree in females. In the Brown Booby, all adult males and females have a uniformly dark brown head and neck (Figure 6A–D). In the Cocos Booby, adult males have a variable amount of white on the head and neck (Figure 6F, H, J), and adult females have some pale brown color on the forehead and occasionally on the entire head (Figure 6E, G, I). The extent of white on the head and neck also is useful for distinguishing the subspecies of the Cocos Booby;

in most males of *nesiotes*, the white extends onto the lower neck (Figure 6H). In most males of *etesiaca*, the white is restricted to the forehead, sometimes as just a narrow band around the face (Figure 6J). The extent of white in males of *brewsteri* is more variable but typically intermediate between *nesiotes* and *etesiaca*. The white head of a male Booby often is visible at a long distance and in poor light, but the slightly paler brown forehead of a female Cocos Booby often is visible only at close range and in good light. Males of *nesiotes* also have a paler brown breast and lower neck than males of *brewsteri* or *etesiaca*.

Throughout the range of the Cocos Booby, I found some males in which the extent of white on the head and neck was not typical of the subspecies expected in the area (Figure 7). For example, in Mexico and on Cocos Island, where *brewsteri* and *etesiaca* are the expected subspecies, respectively, there was a small proportion of males in which the head and most of the neck were white, which is more typical of *nesiotes*. It is not clear if such individuals represent variation within a local population or had dispersed outside the usual range of their subspecies.

In the Revillagigedo Islands, the extent of white on the neck of males is similar on average to that in *nesiotes* and greater than in *brewsteri*. Traditionally, *nesiotes* has been regarded as occurring only on Clipperton Island, though Wetmore (1939) suggested it may range to Isla Isabel and the Tres Marias Islands. Results of my study indicate that Cocos Boobies in the Revillagigedo Islands should be classified as *nesiotes* rather than *brewsteri* and also demonstrate that *nesiotes* is distinct and valid, which had been questioned previously (Nelson 1978).

Van Rossem (1938) described an additional subspecies, *albiceps*, from Isla Isabel, between the mainland of Nayarit and the Tres Marias Islands, but seemed unaware of the previous description of *nesiotes*. Wetmore (1939) stated that the specimens from those islands he examined did not differ from *nesiotes*. I have not seen the original type specimens of *albiceps* designated by van Rossem (1938), but when I examined photos of birds from Isla Isabel and the Tres Marias Islands (e.g., <https://ebird.org/checklist/S199839266>), almost all males were typical of *brewsteri*, not *nesiotes*, with white on the head and upper neck but not extending onto the lower neck. Both van Rossem (1938) and Wetmore (1939) appear to have been wrong about the subspecific classification of birds from these islands, unless the appearance of birds on these islands has changed over time or there has been immigration of *brewsteri* from other locations. Regardless, the birds currently breeding on those islands do not differ from *brewsteri* and there is no support for recognition of the subspecies *albiceps*.

The range boundary between *brewsteri* and *etesiaca* appears to occur roughly at the border of Mexico and Guatemala, an area with few islands suitable for breeding and relatively few reports in <https://eBird.org>. This taxonomy makes intuitive biogeographic sense, with *nesiotes* occurring on the remote oceanic islands in the eastern Pacific, *brewsteri* breeding on islands closer to the coast of continental Mexico, and *etesiaca* occurring in Central and South America. The status of the Cocos Booby on Guadalupe Island, where it began breeding only recently, warrants further investigation. Guadalupe is an oceanic island but is closer to the mainland than the Revi-

llagigedo Islands. I have seen male Cocos Boobies on Guadalupe, but only distantly; all appeared to have white that extended onto the lower neck, as in *nesiotes*, but closer views and more observations are needed to confirm this.

The subspecific identity of Cocos Boobies documented in the central and western Pacific has not been determined previously (VanderWerf et al. 2023). On the basis of the extent of white on the head and neck in 59 males observed in the central and western Pacific, it is likely that 29 of them were *nesiotes* (score 3 or 4), one was *etsiaca* (score 1), and the subspecific identity of the remaining 29 males (score 2) is less clear but more likely to be *brewsteri*. There still is no known way to identify female Cocos Boobies to subspecies, so the subspecific identity of the females observed in the central and western Pacific remains unknown.

Ventral wing coverts. This character is reliable for distinguishing most male and female Brown and Cocos Boobies. It can be seen only when the bird is in flight or when stretching the wings, and it may be the most useful character for birds in flight. Brown Boobies usually have a complete or nearly complete white polygon formed by the lesser, median, and greater ventral wing coverts. Cocos Boobies have more brown in the lesser coverts and sometimes the greater coverts, resulting in a more irregular white shape or striped pattern (Figure 3). However, a few *leucogaster* Brown Boobies, mostly females, have a ventral wing covert pattern like that of the Cocos Booby (Figure 8), so this character should be used in conjunction with others. The ventral wing coverts also are useful for identifying some individuals of *Sula brewsteri etsiaca*; almost all Cocos Boobies with brownish greater coverts, forming a striped pattern on the underwing, were of this subspecies. A few birds had less white in the coverts than expected for their identity based on other characters (Figure 8), and this may be related to molt. Some individuals that are replacing the wing coverts may appear more extensively brown because the dark brown remiges are not covered and are thus more visible.

Iris color. In the original description of *brewsteri*, Goss (1888) noted that characteristics of the species included “a dark brown iris with a narrow outer ring of grayish-white,” but this character has been overlooked since then. Iris color can be useful for distinguishing male Brown and Cocos Boobies, but it is more variable and less useful for identifying females. All Cocos Boobies, both males and females, have a dark iris that often looks essentially black. All males of *Sula leucogaster plotus* have a pale iris. Most females of *plotus* have a pale iris, but some have a somewhat darker iris and there is some overlap with female *brewsteri*. Iris color is useful primarily for distinguishing the Cocos Booby from *S. l. plotus*. In *S. l. leucogaster*, the iris color is more variable, especially in females, and cannot be used to distinguish that taxon from the Cocos Booby, though the ranges of those taxa are not known to overlap. Lighting conditions can affect appearance of the eye; less of the iris is visible when the pupil becomes dilated in dim light, which can cause the eye to look darker. If the iris is pale, at least some light color should be visible at all times.

Bill concavity. The culmen is less concave in *Sula leucogaster plotus* than in *S. l. leucogaster* or any subspecies of the Cocos Booby. The culmen of some examples of *plotus* appears to be essentially straight. A photograph or a close view often is needed for this field mark to be useful. This difference is analogous to that between between the Nazca Booby (*Sula granti*), which

has a more concave culmen, and the Masked Booby (*S. dactylatra*), which has a straighter culmen, and this was one of the characters described by Pitman and Jehl as differentiating the species (1998). The differences in mandible curvature among the subspecies of the Cocos Booby, though statistically significant, are smaller, less consistent, and probably not useful as a field mark.

Bill and facial skin color. The color of the bill and facial skin is important for identifying the sex, which often is a prerequisite for identifying the species. In females of all taxa, the skin at the base of the bill and around the eye is yellow (sometimes a darker grayish or brownish yellow or a brighter orange-yellow). In males, the facial skin is blue in all taxa except *leucogaster*, in which it usually is bright orange-yellow, brighter than the facial skin of female *leucogaster* (Figure 6). In males of all taxa, the dominant bill color is gray-yellow, sometimes with blue, green, yellow, pink, or pink-brown as a secondary color on less than half the bill. In females of *plotus*, the bill is yellow, usually the same color as the facial skin (Figure 6A), sometimes gradually transitioning to pink-brown toward the tip, but always with less than half the bill pink. In females of all three subspecies of the Cocos Booby and in *S. l. leucogaster*, the dominant bill color is pink, bright pink in *leucogaster* and darker pink-brown in the Cocos Booby (Figure 5). In female Cocos Boobies, the base of the bill is sometimes yellowish, but at least half of the bill is pink-brown, often with an abrupt boundary between the yellow and the pink (Figure 6).

Female Brown and Cocos Boobies have an irregular dark patch in the bare skin in front of the eye, sometimes called a loreal spot (Pyle 2008), which males do not have, and this is useful in determining the sex. Some females of *S. l. leucogaster*, however, appear to lack the loreal spot, so the best field mark for identifying the sex in that subspecies of the Brown Booby is bill color, which is usually pink in females and gray-yellow in males. Males of *S. l. leucogaster* sometimes have a dark area in front of the eye, but it is not as distinct or as large as that in females.

In male Cocos Boobies, the color of the facial skin, particularly the gular pouch, varies seasonally and individually with the bird's diet and foraging location, being brightest blue-green during courtship, the color likely playing a role in mate selection (Michael et al. 2018, Montoya et al. 2018). It is possible that similar seasonal and individual variation occurs in all populations of both species, and this may be the cause of some of the variation in face and bill color I observed in photographs. Individual variation in the color and brightness of the facial skin should be considered in any attempt to identify boobies, particularly outside their usual range.

Extralimital Records and Geographic Identification Challenges

The range of Cocos Booby is expanding to the west, north, and south, probably in response to changing environmental conditions and corresponding changes in the distribution or availability of prey. The species is being observed with increasing regularity and breeding in several areas of the central and western Pacific (VanderWerf et al. 2008, 2023). It is regularly seen in California and in 2017 began breeding on Sutil Rock in the Channel Islands (Howard et al. 2024), following colonization of Los Coronados Islands off Tijuana in 2005 (Whitworth et al. 2007). It has been documented in eBird as far south as 32.687° S in Chile since 2022 (<https://ebird.org/>)

checklist/S123340208) and at Rapa Nui since 2017 (e.g., <https://ebird.org/checklist/S121474959>). As I describe below, a few Brown Boobies have been observed in the eastern Pacific, and it is possible others have been overlooked. Information about identifying individuals that have dispersed outside their usual range is useful for tracking their movements and assessing effects of environmental changes on populations.

Their white head makes identifying male Cocos Boobies in the central and western Pacific easy, though the extent of white is variable. To identify female Cocos Boobies in the central Pacific, observers should look for the slightly paler brown forehead, darker iris, brown bar in the white ventral wing coverts, and bill that is more than half pink-brown, often with an abrupt boundary between yellow and pink.

To identify Brown Boobies in the eastern Pacific, observers should look for the following combinations of field marks: an entirely dark brown head and either blue facial skin (indicating a male) or entirely or mostly yellow bill (indicating a female). Other field marks that can help confirm the identification as the Brown Booby are the entire white polygon on the ventral wing coverts and the straighter culmen.

The first Brown Booby documented in the North American Pacific was an adult male that landed on a boat in the Bering Sea on 13 July 2000; the bird died and was collected and is now in the University of Alaska Museum (specimen number 11555, <https://ebird.org/checklist/S91575499>). It was identified as an adult male *plotus* at that time, and the identification can be confirmed from the specimen by the completely brown head and dark bluish face. Gibson and Withrow (2015) thought it was unlikely to have reached the Bering Sea without human assistance. A male Brown Booby was photographed by Jorge Montejo off Isla Clarión, Mexico, on 20 February 2017, as previously reported by VanderWerf et al. (2023). While examining photos in the Macaulay Library for this study, I found two more Brown Boobies from Mexico; a female off Isla Socorro on 17 February 2017 (A. McAndrews and J. Montejo, <https://ebird.org/checklist/S34761482>) and a male off Isla Socorro on 7 April 2023 (J. Montejo and A. McAndrews, <https://ebird.org/checklist/S133873688>). The female off Isla Socorro on 17 February 2017 preceded the male near Isla Clarión by three days and thus represents the first documented Mexican record. A booby found dead and photographed by Greg Troutman on Frances Beach, Half Moon Bay, California, on 25 August 2018 appeared to have a white belly, brown head, and yellow bill with a very straight culmen, suggesting it was an adult female Brown Booby, but the poor condition of the carcass made confirmation difficult and it apparently was not saved (P. Pyle pers. comm). Searches of the Macaulay Library by Peter Pyle and me yielded no Brown Boobies in California or elsewhere farther north.

The ranges of the Cocos Booby and subspecies *leucogaster* of the Brown Booby are separated by a relatively narrow barrier of unsuitable, sometimes mountainous, terrestrial habitat in Mexico and Central America. The most likely way for a booby to cross this barrier would be along the Panama Canal, and photos in the Macaulay Library indicate this has happened. A male Cocos Booby of subspecies *etesiacae* was photographed at sea off Colón, Panama, by Alice Horst on 31 March 2024, close to the Atlantic terminus of the canal (<https://ebird.org/checklist/S166714313>). Female Cocos Boobies have been

photographed near Barro Colorado Island, roughly in the middle of the canal, on 15 October 2022 (<https://ebird.org/checklist/S120795753>) and on 10 December 2023 (<https://ebird.org/checklist/S156108547>) by Jorge Moisés Herrera. I did not find any photos in the Macaulay Library of Brown Boobies on the Pacific side of the Panama Canal, though it seems plausible they do occur there. Both species are commonly reported along the canal, with the Cocos primarily on the Pacific side and the Brown on the Atlantic side, and it would seem easy for a bird to continue along the canal instead of returning in the direction from which it came. All photos in the Macaulay Library of vagrant Brown Boobies in eastern North America represent *Sula leucogaster leucogaster*. To identify Cocos Boobies in the Caribbean, Atlantic, and eastern North America, observers should look for males with white on the head and for females with a bill that is dark pink-brown and sometimes partly yellow, instead of bright pink. To identify *S. l. leucogaster* in the eastern Pacific, observers should look for an entirely dark brown head and either orange-yellow facial skin (males) or a bright pink bill (females; not dark pink-brown as in the female Cocos).

In the Mediterranean region, where the species occurs only rarely, adult Brown Boobies could be identified to subspecies by the color of the bill and facial skin. In males, the facial skin would be blue in *plotus* and orange-yellow in *leucogaster*. In females, the bill would be yellow in *plotus* and pink in *leucogaster*. It might be possible to identify second-year birds that have begun to develop the face and bill color of adults, but it currently is not possible to identify the subspecies, or even the species, of juveniles or first-year birds.

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