

Range Expansion, Pairing Patterns, and Taxonomic Status of Brewster's Booby *Sula leucogaster brewsteri*¹

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Abstract: The Brown Booby (*Sula leucogaster*) is a pantropical seabird that exhibits geographic variation. Brewster's Booby (*S. l. brewsteri*) is the most distinctive form morphologically and genetically. Until recently, Brewster's Booby was restricted to the eastern Pacific Ocean, but it is expanding westward, resulting in increasing sympatry with the Indo-Pacific form, *S. l. plotus*, and greater potential for interbreeding. We compiled observations of Brewster's Booby outside its usual range and we collected data on pairing patterns in the zone of overlap. At least 65 male and 53 female Brewster's Boobies have been observed on 20 islands in the central and western Pacific, with breeding documented on nine islands, mostly since 2000. Pairing by *S. l. brewsteri* and *S. l. plotus* was primarily assortative, with only a few instances of hybridization, all but one of which occurred in locations where no female *S. l. brewsteri* were present. The morphological differences between *S. l. plotus* and *S. l. brewsteri* appear to act as behavioral reproductive isolating mechanisms that restrict interbreeding. The morphological, genetic, and behavioral differences between *S. l. brewsteri* and other forms of the Brown Booby suggest it would be appropriate under all species concepts to consider Brewster's Booby as a distinct species.

Keywords: Brewster's Booby, hybridization, mate choice, range expansion, reproductive isolation

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THE BROWN BOOBY (*Sula leucogaster*) is a pantropical seabird found in the Pacific, Atlantic, and Indian Oceans and exhibits geographic morphological variation. Five subspecies have been described based on differences in color of the plumage, bill, and facial skin (Table 1; Nelson 1978, VanderWerf 2018a, Schreiber and Norton 2020). *S. l. plotus* has the largest geographic range, from the Red Sea and Indian Ocean east to the central Pacific. In both sexes of *S. l. plotus*, the head is dark brown and the bill is yellow (females) or bluish-yellow (males). The nominate subspecies, *S. l. leucogaster*, occurs in the Atlantic and Caribbean and is similar to *plotus* but has a more pinkish bill. The form of Brown Booby occurring in the eastern Pacific, *S. l. brewsteri*, is the most distinctive and originally was described as a separate species called Brewster's Booby (*S. brewsteri*; Goss 1888), but in 1944 it was lumped with other

TABLE 1
Distinguishing Characteristics of Brown Booby Subspecies

Character	<i>plotus</i>	<i>leucogaster</i>	<i>brewsteri</i>	<i>nesiotes</i>	<i>etesiaca</i>
Male head color	Brown	Brown	White head and upper neck	White head and entire neck	White forehead
Female head color	Brown	Brown	Whitish forehead	Whitish forehead	Whitish forehead
Male bill color	Bluish-yellow	Bluish-yellow	Grayish-blue	Grayish-blue	Grayish-blue
Female bill color	Yellow	Pinkish yellow	Pinkish yellow	Pinkish yellow	Pinkish yellow
Ventral lesser wing coverts	White	White	White with brown bar	White with brown bar	?

forms of the Brown Booby (Wetmore et al. 1944). Male *S. l. brewsteri* have a geographically variable white head, a more grayish-blue bill, and a more greenish-blue gular pouch. VanderWerf (2018a) showed that female *S. l. brewsteri* have a pinker bill than female *S. l. plotus* and that the underwing coverts of *S. l. brewsteri* are less extensively white. In the Gulf of California and the western coast of Mexico south to the Revillagigedo Islands, male *S. l. brewsteri* have a white head and a pale silvery upper neck. On islands off Central America and Colombia, the white on the head of males is restricted to the forehead, and this form sometimes is considered a separate subspecies, *S. l. etesiaca*, but also has been grouped with *S. l. brewsteri* (Harrison 1983, Schreiber and Norton 2020). The form breeding on Clipperton Island is the palest, with the entire head and neck white in males, and is sometimes referred to as *S. l. nesiotes* (Heller and Snodgrass 1901, Pitman and Ballance 2002, Schreiber and Norton 2020).

Genetic population structure of Brown Boobies largely matches patterns of morphological variation (Steeves et al. 2003, Morris-Pocock et al. 2010, 2011). Mitochondrial haplotypes are not shared between the eastern and central Pacific or between the eastern Pacific and Caribbean (Steeves et al. 2003), and colonies grouped into four major, genetically differentiated populations; Caribbean, central Atlantic, Indo-central Pacific, and eastern Pacific (Morris-Pocock et al. 2011). The eastern Pacific population is the most different genetically and was estimated to have diverged from all other populations approximately one million years ago (Morris-Pocock

et al. 2011). These populations have diverged because of a combination of physical barriers (the Isthmus of Panama and the Eastern Pacific Basin) and a behavioral tendency in the Brown Booby to forage closer to shore than other booby species (Steeves et al. 2003).

The Eastern Pacific Basin is an enormous, island-free ocean area that for millennia has formed a physical barrier to dispersal and promoted geographic differentiation of many seabirds, including the Brown Booby (Avisé et al. 2000, Steeves et al. 2003, Morris-Pocock et al. 2011). Recently, Brown Boobies have been overcoming the barrier posed by the Eastern Pacific Basin and have dispersed eastward and westward across the Pacific. VanderWerf et al. (2008) documented an increasing number of *S. l. brewsteri* present and breeding in the central Pacific, and Kohno and Mizutani (2011) documented the occurrence and breeding of *S. l. brewsteri* males in Japan. Isla San Benedicto, in the Revillagigedo Islands off the west coast of Mexico, was recolonized by Brown Boobies following a volcanic eruption in 1952, and both *plotus* and *brewsteri* males are present and breeding on the island (Pitman and Ballance 2002, Morris-Pocock et al. 2011).

The increasing sympatry of *S. l. brewsteri* and *S. l. plotus* could result in gene flow and erosion of differentiation between these forms, if they interbreed. A few mixed *brewsteri* × *plotus* pairs have been documented (Kohno and Mizutani 2015), all involving male *brewsteri*, but only in locations where no female *brewsteri* were known to be present. On Isla San Benedicto, where interbreeding has been reported (Pitman and Ballance 2002,

TABLE 2

S. l. brewsteri Records on Islands in the Central and Western Pacific, from East to West

Location ^a	First Year Observed	Max. # Males Observed (Year)	Max. # Females Observed (Year)	Max. # Nests Observed (Year)	Source ^b	Observers
Isla de Pascua, Chile	2017	0	2 (2017)	0		Several
Moku Mana, Maui	2020	12 (2021)	12 (2021)	12 (2021)		M. Frye, E. VanderWerf, J. Penniman
Kiritimati Island	2016	1 (2016)	0	0		R. Pierce
Moku Manu, Oahu	2006	2 (2021)	5 (2022)	1 (2021, 2022)	1	E. VanderWerf
Nuupia Ponds, Oahu	1955	1	0	0	2	R. Pyle
Kaaawa, Oahu	2019	0	2 (2019)	0		H. Franz
Kauai	2015	1	0	0		Bishop Museum
Niihoa	2011	1	0	0		E. VanderWerf
Palmyra Atoll	1996	29 (2014)	21 (2014)	30 (2014)		E. VanderWerf
La Perouse Pinnacles, FFS	2007	1 (2007)	0	0	2	several
Term Island, FFS	2003	2 (2003)	2 (2018)	0	2	R. Sprague, E. VanderWerf
Johnston Atoll	1984	1	0	1	2	D. O'Daniel
Laysan	1994	1 (1984, 1998, 2011, 2018)	1 (1998)	1 (1984, 1998, 2018)	1,2	J. Adams, H. Nevins, B. Becker, C. Rutt, J. Vetter
Lisianski	1997	2 (2000)	0	1 (2000)	2	J. Adams, H. Nevins
Midway Atoll	2001	1 (2001, 2007, 2012, 2020)	0	1 (2020)	2	M. Romano, J. Vetter, J. Plissner
Kure Atoll	2003	1 (2003)	0	0	1	J. & H. Eijzenga
Wake Island	1998	7 (2023)	4 (2023)	4 (2023)	2,3	J. Gilardi, M. Rauzon, E. VanderWerf
Aguigan Island, CNMI	2019	0	1 (2019)	0		R.S. Steffy
Orote Island, Guam	2021	0	3 (2019)	0		R.S. Steffy
Nakanokamishima, Japan	2009	2 (2012–2014)	0	1 (2012–2014)	4	H. Kohno, A. Mizutani
Total number		65	53	52		

^a Location abbreviations: FFS = French Frigate Shoals; CNMI = Commonwealth of the Northern Mariana Islands.

^b Sources: 1 = VanderWerf et al. 2008; 2 = Pyle and Pyle 2017; 3 = Rauzon et al., 2008; 4 = Kohno and Mizutani 2011 and 2015. If no source is given it has not been unpublished previously.

TABLE 3

Pairing Patterns of Brown Boobies by Subspecies, Including Only Cases in Which the Identity of Both Parents Was Known

Location	Year	Male <i>plotus</i> + Female <i>plotus</i>	Male <i>plotus</i> + Female <i>brewsteri</i>	Male <i>brewsteri</i> + Female <i>plotus</i>	Male <i>brewsteri</i> + Female <i>brewsteri</i>
Palmyra Atoll ^a	2014	~200	1	0	8
Moku Mana	2021	6	0	0	12
Moku Manu	2021	93	0	0	1
Laysan	1998	~70	0	0	1
Midway ^b	2020	15	NA	1	NA
Wake Island	2023	301	0	0	4
Nakanokamishima ^b	2009	~900	NA	1	NA

^aAt Palmyra 30 nests were observed with at least one *brewsteri* parent, but some nests were attended by a single parent and the identity of the mate was unknown.

^bAt Midway and Nakanokamishima no female *brewsteri* were present so there was no chance of a mixed pair.

Morris-Pocock et al. 2011), it is unclear whether any female *plotus* were present, and thus whether the male *plotus* really formed mixed pairs. To assess mate choice and potential genetic introgression between *S. l. brewsteri* and *S. l. plotus* adequately, information is needed about mate choice when males and females of both forms are known to occur together.

The purposes of this paper are to: (1) further document the range expansion of *S. l. brewsteri* into the central and western Pacific, including first records for several areas; (2) examine mate choice and the extent of interbreeding between *S. l. brewsteri* and *S. l. plotus* as their ranges increasingly overlap; and (3) explore the implications of mate choice and information about breeding biology on the taxonomic status of Brewster's Booby.

METHODS

We compiled our observations of Brown Boobies in the central and western Pacific Ocean and reports by other observers in the scientific literature, eBird, social media, and personal communications (Table 2). We visited several Brown Booby breeding colonies in the central and western Pacific and recorded the following data: number of males and females of each subspecies present; number of males and females of intermediate appearance; number of nests; and identity of

parents attending nests. We photographed many individuals to document their appearance, especially birds on nests and individuals of intermediate appearance. We used data from Moku Mana and Palmyra to test whether mate choice was random using chi-squared tests (Table 3). We could not test mate choice patterns at other locations because too few *S. l. brewsteri* were present.

RESULTS

Range Expansion

At least 65 male and 53 female *S. l. brewsteri* have been observed on 20 islands in the central and western Pacific, mostly since 2000 (Table 1). Breeding by at least one *S. l. brewsteri* has been documented on nine islands (Table 1). In addition, at least 11 other *S. l. brewsteri* have been photographed at sea in the region, including (from east to west): 2,000 km southwest of Galápagos on 6 May 2017 (Greenfelder 2017); 1,650 km northeast of the Marquesas on 30 January 2020 (Pennington 2020); 1250 km and 830 km east of Hawaii Island on 9 and 10 January 2016 (Mathre 2016a,b); from Makapu'u Point, Oahu, on 13 July 2022 (Apuna 2022); off Barber's Point, Oahu on 8 March 2009 (C. Babbitt unpubl.); 250 km west of Kauai on 5 April 2018 (VanderWerf 2018b); 340 km west of Kure Atoll on 23 September 2017 (Ü 2017); off Saipan in 2018 (Ü unpubl.); 13–35 km east of Miyako, Iwate, Japan on 18

and 23 July 2020 (Muzika 2020a), and 10 km southwest of Mikurajima, Japan on 12 July and 17 October 2020 (Muzika 2020b,c).

Several of these observations constitute first records of *S. l. brewsteri* for the locality, some of which are shown in Figure 1. The breeding pairs on Moku Mana are the first records for Maui County, Hawaii. A male that was found injured and eventually died in a rehabilitation facility on 26 January 2015 is the first record for K auai County, Hawaii. A male photographed on Kiritimati Island by R. Pierce in 2016 is the first for that island and the Republic of Kiribati. A male photographed east of Saipan by A.   in 2018 is the first record for the Commonwealth of the Northern Mariana Islands (CNMI). The females photographed by R. S. Steffy in 2019 and 2021 are the first records for Aguiguan, CNMI, and Guam, respectively. A male of the *S. l. etesiaca* subspecies photographed on Moku Manu islet off Oahu by E. VanderWerf on 26 June 2008 is the first record of that subspecies in Hawaii and away from its usual breeding range off Central America and Colombia (Figure 1B). Conversely, a male *S. l. plotus* photographed on Isla Clari n on 20 February 2017 is the first

record for that island (Figure 1E; Montejo 2017).

On Isla de Pascua (Easter Island), Chile, there were 10 reports of single Brown Boobies in eBird starting in March 2017, which are the first records for that island. None of the reports identified the individual to subspecies, but seven reports included photos in which the subspecies could be identified, and all were female *S. l. brewsteri* based on the bill color, head color, and underwing pattern (Figure 1). Two photos in March and April 2017 showed an adult female and an immature female, respectively, indicating at least two females were present.

Pairing Patterns and Mate Choice

Quantitative and anecdotal evidence indicated pairing by *S. l. brewsteri* and *S. l. plotus* was primarily assortative (Table 2). At Moku Mana, Maui in 2021, there were fewer mixed pairs (zero), than expected by chance ($X^2 = 18.00$, $df = 1$, $P < 0.001$). On Palmyra, there also were fewer mixed pairs than expected by chance ($X^2 = 181.1$, $df = 1$, $P < 0.001$), though the sample size was small. On Wake Island, M. Rauzon observed a male



FIGURE 1. Photographs of Brown Boobies that represent new records of the *brewsteri*, *etsiaca*, and *plotus* subspecies for various locations. (A) *Brewsteri* male and chick (on right, with three *plotus* on left) Moku Mana, Maui, March 2021, by E. VanderWerf. (B) Male *etsiaca* with chick, Moku Manu, Oahu, 6 June 2008, by E. VanderWerf. (C) Female *brewsteri*, Orote Island, Guam, July 2021, by R. S. Steffy. (D) Female *brewsteri*, Aguiguan, CNMI, 2019, by R. S. Steffy. (E) Female *brewsteri*, Isla de Pascua, Chile, 13 January 2019, by F. D az. (F) Male *plotus*, Isla Clari n, M xico, 20 February 2017, by J. Montejo. (G) Male *brewsteri* specimen collected on Kauai, 2015, photographed at Bishop Museum by E. VanderWerf.



FIGURE 1. (Continued)

S. l. brewsteri paired with a female *S. l. plotus* in 2012, and one individual of intermediate appearance has been present on the island since then and may be an offspring from that hybridization. On Wake Island in 2021, J. Gilardi observed 301 *S. l. plotus* pairs, six *S. l. brewsteri* males, and one *S. l. brewsteri* female, which was paired with one of the male *S. l. brewsteri*. The other five male *S. l. brewsteri* on Wake that year did not attract a mate despite the presence of many unpaired *S. l. plotus* females. On Wake in 2022, J. Gilardi observed that the *brewsteri*-*brewsteri* pair remained together and raised another chick, but the

other five *brewsteri* males were unpaired. On Wake in 2023, J. Gilardi observed seven male and four female *brewsteri*; all 4 *brewsteri* females were paired with *brewsteri* males, and three single *brewsteri* males built nests but had no mate. On Moku Manu, Oahu in May 2021, E. VanderWerf observed 93 *S. l. plotus* pairs and only one male and one female *S. l. brewsteri*, which were paired with each other and had a large chick. In September 2022, E. VanderWerf observed five *S. l. brewsteri* females on Moku Manu, all of which were unpaired. On Laysan, a nest with a male *brewsteri* and female *plotus* was reported in



FIGURE 1. (Continued)

1998 (VanderWerf et al. 2008), but re-examination of photos using identification criteria from VanderWerf (2018) revealed that the female was *S. l. brewsteri*, representing another instance in which a male and female *brewsteri* paired with each other amid large numbers of male and female *plotus*. On Tern Island, only males were reported in 2003 and only females were observed in 2018 by E. VanderWerf, and no nests were found

in either year. On Midway, J. Plissner observed a male *brewsteri* × female *plotus* pair that raised a chick in 2020, but no female *brewsteri* were present. At Nakanokamishima Island, Japan, one *brewsteri* male paired and raised offspring with a *plotus* female from 2012 to 2014, but a second *brewsteri* male was not able to attract a mate despite frequent courtship attempts with *plotus* females (Kohno and Mizutani 2015).

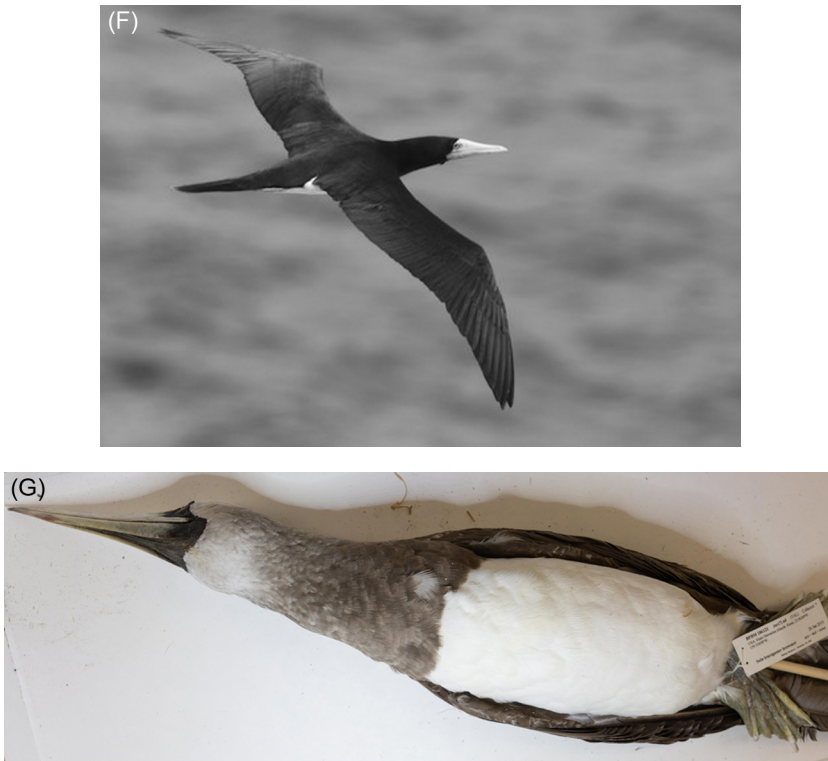


FIGURE 1. (Continued)

DISCUSSION

Range Expansion

The westward range expansion of *S. l. brewsteri* across the North Pacific has continued since observations were compiled by VanderWerf et al. (2008), with observations in the Hawaiian Islands, Line Islands, Wake Island, Mariana Islands, and Japan, and additional observations at sea. The largest number of *S. l. brewsteri* have been observed at Palmyra, where there were at least 51 individuals and 30 nests in June 2014, though the actual number probably was higher because some nests were attended by a single adult and the identity of their mates was unknown. Moku Mana Islet off the north coast of Maui is a particularly interesting case. It was colonized by Brown Boobies recently, with the first nest documented in 2004 by J. Penniman. In 2021, the colony held twice as many *S. l. brewsteri* pairs as *S. l. plotus* pairs,

with no mixed pairs. This is the easternmost location in the Hawaiian Islands where Brown Boobies breed, and the colonies were formed by individuals dispersing from the east (*S. l. brewsteri*) and west (*S. l. plotus*), much like the situation on Isla San Benedicto (Pitman and Ballance 2002).

Recent observations of *S. l. brewsteri* on Isla de Pascua indicate the westward range expansion is also occurring in the South Pacific. Isla de Pascua is a particularly remote island and could provide a stepping-stone across the East Pacific Basin toward other parts of Polynesia, where *S. l. plotus* currently is the usual form. If the range expansion continues as it has in the North Pacific, *S. l. brewsteri* can be expected to occur in the Pitcairn Island Group, which are the next islands west of Isla de Pascua, and in French Polynesia.

Several other seabird species that historically have been restricted to the eastern

Pacific have begun crossing the East Pacific Basin more often and have been observed recently in the central Pacific for the first time or with greater frequency, including the Red-billed Tropicbird (*Phaethon aethereus*; [VanderWerf and Young 2007](#)), Nazca Booby ([VanderWerf et al. 2008](#)), Pink-footed Shearwater (*Ardenna creatopus*) and Wedge-rumped Storm-Petrel (*Oceanodroma tethys*; [Pyle and Pyle 2017](#), [VanderWerf et al. 2018](#)), and Inca Tern (*Larosterna inca*; [VanderWerf 2022](#)). The movement shifts in these ecologically diverse seabirds probably are related to more than one oceanographic or atmospheric parameter, and the cause(s) underlying these changing patterns warrant further investigation.

Mate Choice

As *S. l. brewsteri* has expanded in range westward across the Pacific Ocean, it has become increasingly sympatric with *S. l. plotus*, and the potential for interbreeding between these taxa has increased. However, information on pairing patterns from this study indicates that *S. l. brewsteri* and *S. l. plotus* prefer mating with individuals of their own form, which appears to have restricted hybridization thus far. Only a single mixed pair has been observed in situations when both sexes of both subspecies were known to be present; all other instances of mixed pairing occurred where no female *brewsteri* were present, such as on Midway Atoll and Nakanokamishima Island, Japan. Mixed pairs consisting of male *plotus* and female *brewsteri* have been reported on Isla San Benedicto, and only male *plotus* have been reported on Isla San Benedicto ([Pitman and Ballance 2002](#), [Morris-Pocock et al. 2011](#)), but the criteria for distinguishing females of *plotus* and *brewsteri* were not known during those studies and thus the pairing patterns there are unclear. [Morris-Pocock et al. \(2011\)](#) speculated that introgression of *S. l. plotus* mitochondrial haplotypes into the eastern Pacific population has been limited because dispersal or realized gene flow occurs only in males. However, they genetically sampled a chick that had a white-headed father yet had primarily central Pacific mtDNA, indicating

a female *S. l. plotus* must have been present at some time. Continued monitoring of pairing patterns across the Pacific will help to reveal whether hybridization remains rare, and further examination of pairing patterns on Isla San Benedicto is needed to clarify mate choice there.

Mate choice and breeding biology of Brewster's Booby have been studied extensively in Mexico, and this literature is important for understanding the pairing patterns observed in the central Pacific. For example, [López-Rull et al. \(2016\)](#) showed that male *S. l. brewsteri* with their head painted brown to look like male *S. l. plotus* were treated aggressively by their mate and that the level of aggression was higher at a colony closer to the zone of overlap. They concluded that female dislike of foreign males may function as a reproductive barrier in populations close to contact zones, where the risk of possibly maladaptive hybridization is highest. [Montoya et al. \(2018\)](#) showed that the carotenoid-based greenish-blue color of the gular pouch of males was energetically expensive to maintain, that its chroma peaked during courtship, and that it may serve as a reliable signal of individual quality. [Michael et al. \(2018\)](#) showed that color of the gular pouch in Brown Boobies in México was related to foraging range and location, with individuals in poor body condition constrained to low-cost, short-distance foraging trips closer to shore, where they were unable to obtain the pelagic diet necessary for production of the carotenoid-rich gular pouch ornament important in mate attraction. Cumulatively, this research indicates that the morphological differences between *S. l. brewsteri* and *S. l. plotus* act as an isolating mechanism that inhibits interbreeding.

Taxonomic Status

Brewster's Booby originally was described as a species, *S. brewsteri*, by [Goss \(1888\)](#) based on type specimens from San Pedro Mártir Island, Mexico. In 1944, *S. brewsteri* was lumped with other forms of the Brown Booby without any explanation ([Wetmore et al. 1944](#)). The morphological and genetic

differences between *S. l. brewsteri* and other forms of the Brown Booby meet the standards for species recognition under the typological (or morphological) and phylogenetic species concepts, respectively (Mayr 2000, Wheeler 2000). The behavioral evidence described in this study, increasing sympatry with primarily assortative mating and rare interbreeding, meets the standards of the biological species concept (Mayr 2000). Cumulatively, all three forms of evidence suggest it would be appropriate to consider Brewster's Booby as a separate species again.

Occasional hybridization between *S. l. brewsteri* and *S. l. plotus* and the presence of some individuals of intermediate appearance does not constitute evidence that they are conspecific. Similar situations exist in two other pairs of booby species, Blue-footed Booby (*S. neobuxii*) and Peruvian Booby (*S. variegata*), and Masked Booby (*S. dactylatra*) and Nazca Booby (*S. granti*). Blue-footed and Peruvian boobies are largely allopatric, but breeding colonies occur together on two islands off Peru, where mating is primarily assortative, with few instances of hybridization, resulting in genetic differentiation and only limited introgression (Figueroa and Stucchi 2008, Taylor et al. 2012). Nazca Booby was considered a subspecies of Masked Booby but was split into a separate species based on morphological differences and assortative mating (Pitman and Jehl 1998), which subsequently was supported by evidence of genetic differentiation (Friesen et al. 2002). Another similar example is the spread of the Glossy Ibis (*Plegadis falcinellus*) into North America over the past two centuries, resulting in range overlap and occasional hybridization with White-faced Ibis (*P. chibi*), but little introgression (Arterburn and Grzybowski 2003, Oswald et al. 2019).

Previous genetic analyses showed *S. l. brewsteri* was a distinct phylogenetic unit (Steeves et al. 2003, Morris-Pocock et al. 2011), and hybridization has remained rare despite recently increasing breeding sympatry. Continued monitoring of Brown Boobies in the eastern, central, and western Pacific will help to determine whether the range

expansion of *S. l. brewsteri* continues, and whether the morphologically-based behavioral barriers to interbreeding remain sufficient to limit hybridization and genetic introgression with other forms of the Brown Booby.

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