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HYBRIDIZATION OF THE BLACK-FOOTED AND LAYSAN ALBATROSSES

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ABSTRACT: Although the Laysan (*Phoebastria immutabilis*) and Black-footed Albatrosses (*P. nigripes*) have been known to hybridize for more than a century, little has been published regarding plumage variation of the hybrid progeny. During six months of field work on Laysan, Hawaii, I noted 13 possible hybrids (five presumed F_1 hybrids, three possible F_2 backcrosses with the Black-footed Albatross, and at least four possible F_2 backcrosses with the Laysan Albatross). Apparent F_2 backcrosses with the Black-footed Albatross differ from it most noticeably in their black-and-white underwings and much more extensive white circling the face. Apparent F_2 backcrosses with the Laysan Albatross differ from that species most noticeably in their extensive gray smudging throughout the body and darker underwing coverts. Apparent F_2 backcrosses interbreed with the Black-footed Albatross, the first evidence of any hybrid pairing with that parental species.

The Laysan (*Phoebastria immutabilis*) and Black-footed Albatrosses (*P. nigripes*) have been known to hybridize for more than a century (Rothschild 1900, Fisher 1948). The breeding ranges of these two species overlap widely in the northwestern Hawaiian Islands, particularly on Midway Atoll and Laysan Island (Awkerman et al. 2008, 2009, Pyle and Pyle 2009). Although hybrids receive mention in a few contemporary field guides (Sibley 2000, Dunn and Alderfer 2006), because they are not illustrated or often observed at sea, hybrid phenotypes are not well known to many field ornithologists, though a few photographs were published by Awkerman et al. (2009), Pyle and Pyle (2009), and Howell (2012). Only McKee and Pyle (2002) have discussed the subject of hybridization between the Laysan and Black-footed Albatrosses with regard to plumage variation in each species.

In North American waters, presumed hybrids have been found very infrequently (McKee and Pyle 2002, Howell 2012). Although a few have been reported off California (Debra Shearwater, pers. comm.), none have been confirmed there (Hamilton et al. 2007), and several bleached Black-footed Albatrosses have been misidentified as hybrids (Figure 1; McKee and Pyle 2002). Hybrids have also caused confusion with the Short-tailed Albatross (*P. albatrus*): Roberson (1986) suggested that one of the first Short-tailed Albatrosses reported in California in the 20th century was one of these hybrids (Helm 1980, McKee and Pyle 2002). Despite extensive research, I am aware of just one individual documented at sea, a presumed first-generation (F_1) hybrid photographed by Robert L. Pitman off the Aleutian Islands, Alaska, on 2 June 2002 (Howell 2012: figure A2a.2, Sophie Webb pers. comm.).

In this paper I aim to update and expand upon McKee and Pyle (2002), presenting further photographs of presumed F_1 hybrids, possible second-generation (F_2) backcrosses with both parental species, another bird of indeterminate hybrid origin, and a particularly unusual aberrant plumage aspect of the Black-footed Albatross. These variations may be sources of confusion

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Figure 1. Apparently a very bleached Black-footed Albatross. Aside from the conspicuously pale head, which could suggest hybrid origin, the bill structure and plumage, with brown tones throughout, are consistent with the Black-footed Albatross. West of Kruszof Island, near Sitka, Alaska, May 2012.

Photo by Linda Behnken

with other rare or vagrant albatrosses in the North Pacific (Roberson 1986, McKee and Pyle 2002, Howell 2012).

MECHANICS OF HYBRIDIZATION

Hybridization in tubenoses is very rare (Howell 2012), and—despite being North America’s only well-documented example—successful hybridization between the Black-footed and Laysan Albatrosses is also rare (Fisher 1972, Howell 2012). During six months (September 2011–March 2012) of field work on Laysan, Hawaii, I noted only 13 possible hybrids (five presumed F_1 hybrids, three possible F_2 backcrosses with the Black-footed Albatross, at least four possible F_2 backcrosses with the Laysan Albatross, and one bird of unknown hybrid origin) among approximately 150,000 and 24,000 breeding pairs of the Laysan and Black-footed Albatrosses, respectively (Pyle and Pyle 2009). McKee and Pyle (2002) suspected that hybrids arise through forced extra-pair copulation of male Black-footed with female Laysan Albatrosses, rather than through bonded mixed pairs. Alternatively, it is possible that hybrid progeny originate from females that are willing to accept these extra-pair copulations (Tristan McKee pers. comm.), although there is no direct evidence for either scenario. Brief interspecific courtship dances have

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been reported (Fisher 1972, McKee and Pyle 2002), yet I never witnessed any such dances on Laysan, nor did I detect any evidence of bonded mixed pairs, supporting the hypotheses of either forced or voluntary extra-pair copulations.

HYBRIDS

In addition to being intermediate in plumage aspects, hybrids differ from the parental species in vocalizations, bare-part coloration, and behavior (Fisher 1972; Table 1). Behaviorally, the two species have numerous differences in their courtship dances (Fisher 1972). The Black-footed and Laysan Albatrosses also walk with noticeably different postures; Black-footed Albatrosses walk with the neck partially extended in front of the body and the head held low, while Laysan Albatrosses maintain a nearly vertical neck posture and the head held high (Fisher 1972). Furthermore, preferences for breeding habitat differ: the Laysan Albatross prefers the vegetated, interior portions of islands, the Black-footed Albatross more exposed outer sandy beaches (Fisher 1972). All of these reported behavioral differences were consistent with my observations on Laysan.

When possible in the field, I attempted to assess apparent hybrids' plumage aspect, bare-part coloration, walking posture, colony composition, and breeding behavior. Unfortunately, my departure in March precluded the opportunity to determine whether chicks successfully fledged and prevented documentation of plumages of hybrid progeny. Without marking of individuals or genetic confirmation, these observations of phenotypes are all necessarily tentative. Categorizations of presumed hybrids, especially of possible backcrosses, are inferences.

“CLASSIC” PRESUMED F_1 HYBRIDS

In all respects—physically, behaviorally, and reproductively—the five presumed F_1 hybrids appeared more closely aligned to the Laysan than to the Black-footed Albatross. If the forced-copulation hypothesis is correct—a female Laysan Albatross being fertilized in an extra-pair copulation with a male Black-footed Albatross—it could explain the behavioral and reproductive associations with the Laysan Albatross, as an F_1 chick would have been raised by a pair of Laysan Albatrosses (McKee and Pyle 2002). The main physical difference between F_1 hybrids and the Laysan Albatross was the former having pearly to smoky gray head and neck feathering (Figure 2), which ended rather abruptly on the lower breast, contrasting markedly with the white belly. The pale patterning on the head, with a white nose band and lower white eye-arc, was more reminiscent of the Black-footed Albatross, but the white across the forehead was more extensive and extended into the eyebrow. Structurally, the bill shape matched that of the Laysan Albatross, appearing longer and narrower than that of the Black-footed Albatross (Pyle 2008) and having a more obvious saddle to the culminicorn. Bare parts were generally darker than those of a Laysan Albatross; the bills of F_1 hybrids had a dusky tip (darker than the blue-gray of an average Laysan Albatross) and a dark base to the culminicorn, lacking the yellowish-orange base of the bill of an adult Laysan Albatross. The legs of F_1

Table 1 Criteria Distinguishing the Three Main Phenotypes of Presumed Hybrid Laysan × Black-footed Albatrosses from the Parental Species

Character	Laysan Albatross	Black-footed Albatross	Presumed F ₁ hybrids	Possible F ₂ backcrosses with the Black-footed Albatross	Possible F ₂ backcrosses with the Laysan Albatross
Underwing pattern	Extensive white underwing coverts with variable amounts of black in the humerals and primary coverts	Uniform dark brown	Like Laysan, but with reduced white and more extensive black, particularly in the humerals	Like Laysan, with strikingly white underwing coverts and black humerals and primary coverts	Like Laysan, but with reduced white and more extensive black (one individual even appeared to have largely to wholly dark underwings)
Underparts	White chest and belly	Dark brown overall with a variably paler belly, sometimes appearing whitish at the pale extreme	Pearly to smoky gray neck and breast, contrasting sharply with white belly	Like Black-footed, but more gray-brown with a contrasty white belly	Like Laysan, but with gray smudging along the wingband and especially on the lower belly
Face pattern	White head with contrasting gray auriculars (excluding young immatures, which lack gray auriculars)	Dark brown with a paler auricular, white noseband, and white lower eye-arc	Reminiscent of Black-footed (white nose band and lower eye-arc), but with pearly to smoky gray and more extensive white across forehead and eyebrow	Much more extensive white than Black-footed, with white encircling the face	Like Laysan, but with gray smudging on the crown and lower hindneck
Bill coloration	Pinkish with a yellowish-orange base and grayish tip	Dark, ranging from blackish to dusky pinkish	Like Laysan, but darker, having a dark base to the culminicorn in place of the yellowish-orange base	Significantly paler than an average Black-footed; drab, pale pink with a dark base to culminicorn	Like Laysan
Bill structure	Relatively long and narrow with a more obvious saddle to the culminicorn	Comparatively stout (averaging shorter and thicker) with a reduced saddle	Like Laysan	Like Black-footed	Like Laysan
Vent, undertail coverts, and uppertail coverts	White	Variably dark brown to white, depending on age and sex	Like Laysan, but with fairly extensive dark gray smudging around legs and flanks	Like Laysan	Like Laysan, but with extensive gray smudging in all three regions
Legs and feet	Pinkish	Dark (grayish black)	Like Laysan, but darker and more blue-gray with gray or dark purplish feet	Dark gray to flesh-colored with pale/dark mottling on the legs	Like Laysan, but perhaps with some added light blue tones
Walking posture	Neck nearly vertical; head held high	Neck partially extended in front of body with head held low (crouching walk)	Like Laysan	Like Black-footed	Like Laysan

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hybrids were darker than those of the Laysan Albatross and more blue-gray, with gray or dark purplish feet, generally lacking pink tones. These hybrids also showed fairly extensive dark gray smudging around the legs and flanks, areas that are cleanly white on a typical Laysan Albatross. Finally, the underwings of F_1 hybrids that I was able to observe showed reduced white and more extensive black, particularly in the humerals (upper photo on this issue's back cover).

Behaviorally and reproductively, these F_1 hybrids were also more similar to the Laysan Albatross. F_1 hybrids walked with the head held high, like a Laysan Albatross. Minimal observations of these hybrids' courtship dances also suggested they were more like those of the Laysan Albatross (Fisher 1972). Similarly, their territories were in locations dominated by Laysan Albatrosses (average 76% of the nearest neighboring birds); one hybrid was in a predominantly Black-footed Albatross colony (nearest neighbors 28% Laysan Albatrosses), whereas three were located in the more vegetated interior of the island, in areas occupied almost exclusively by Laysan Albatrosses.

I detected only one of the five F_1 hybrids engaged in successful reproduction (Figure 3). It was paired with a Laysan Albatross and was incubating and/or brooding a chick from 24 December 2011 through at least 11 February 2012.

POSSIBLE BLACK-FOOTED ALBATROSS BACKCROSSES

In order for this phenotype to be generated, I speculate that F_1 hybrids bred with a Black-footed Albatross. And as with the origin of F_1 hybrids, I hypothesize that this backcrossing resulted from extra-pair copulations of a male Black-footed Albatross with a female hybrid, as all the aforementioned evidence suggests an otherwise strong affinity of F_1 hybrids for the Laysan Albatross.

Unlike F_1 hybrids, possible F_2 backcrosses with the Black-footed Albatross were physically, behaviorally, and reproductively more similar to that species. These F_2 hybrids appeared paler than the whitest extreme of the oldest male Black-footed Albatrosses (lower photo on this issue's back cover). The head and neck of these hybrids were gray-brown, and they had more gray in the upperparts as well. A white face encircled the eye and bill (not limited to a white nose band); this bold facial pattern may seem novel for this species pair, yet it mirrors the paler cheeks of the Black-footed Albatross. The belly of F_2 hybrids was white, with a cutoff to the darker gray neck as in F_1 hybrids (Figure 4). Compared to that of F_1 hybrids and Laysan Albatrosses, the bill appeared comparatively stout and lacked the distinct saddle to the culminicorn, matching the Black-footed Albatross. The bill was significantly paler than that of the average Black-footed Albatross, being drab, pale pink with a dark base to the culminicorn, again as in F_1 hybrids. Their dark gray or flesh-colored legs and feet were also paler than those of a Black-footed Albatross, with some mottling. Although I obtained only a single look at one of these hybrids' underwings, it had strikingly white coverts with black primary coverts and humerals, much as in a pure Laysan Albatross, and very unlike a Black-footed Albatross. These three apparent F_2 hybrids all closely matched an "unidentified albatross" photographed on Laysan in 1995, McKee and Pyle's (2002) figure 19, which those authors cautiously

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left unresolved without the aid of any behavioral information. Although not previously described well, these hybrids are not just of recent occurrence; Peter Pyle (pers. comm.) photographed a similar bird on Laysan as early as 1984.

In addition to their plumage characteristics, these hybrids acted like and associated with Black-footed Albatrosses. I observed all three of these possible F_2 hybrids walk with a crouching posture, like a Black-footed Albatross. Additionally, one of these hybrids engaged in an extended bout of courtship dancing with a Black-footed Albatross (upper photo on this issue's inside back cover), matching the style, complexity, and tempo of the Black-footed Albatross's display and unlike that of a Laysan Albatross (Fisher 1972). These possible F_2 hybrids were strongly associated with Black-footed Albatrosses, which were 93% of their nearest neighbors. If these birds were, in fact, the result of hybridization, these observations belie the previously reported preference of hybrids to socialize only with Laysan Albatrosses (Fisher 1972, McKee and Pyle 2002), an observation based solely upon F_1 hybrids. All of these F_2 hybrids were found on exposed outer sandy beaches typical of the Black-footed Albatross's habitat.

Two of these three F_2 hybrids were paired with Black-footed Albatrosses and shared parental duties (Figure 5), successfully hatching chicks (26 December 2011–17 February 2012; 20 November 2011–17 February 2012). No evidence of a hybrid successfully breeding with a Black-footed Albatross has been reported previously (Awkerman et al. 2008).

POSSIBLE LAYSAN ALBATROSS BACKCROSSES

Identifying possible F_2 backcrosses with the Laysan Albatross was difficult, as it was impossible to delineate the extreme in darkness of a genetically pure Laysan Albatross (McKee and Pyle 2002). Because of this lack of clear distinction, multiple F_2 backcrosses with the Laysan Albatross may have passed unnoticed—unlike the other hybrid phenotypes, which were very conspicuous. Individuals into which Black-footed Albatross DNA may have introgressed from an interspecific hybrid of a past generation had more extensive gray smudging overall, including the cheek, crown, lower hindneck, bend of the wing, uppertail coverts, and particularly around the lower belly, vent, and undertail coverts (lower photo on this issue's inside back cover). Additionally, multiple birds showed reduced white in the underwing coverts, and one individual appeared to have largely dark underwings. Otherwise, these birds suggested a dark Laysan Albatross.

UNKNOWN HYBRID COMBINATION

On 8 March 2012, I observed briefly in flight a fourth type of possible hybrid. Its head and neck were like those of a Laysan Albatross, but it had a sooty body and undertail coverts, dark underwings, and grayish uppertail coverts, much like an apparent hybrid photographed on Midway Atoll 28 December 2006 (Figure 6).

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Figure 2. The most commonly detected hybrid phenotype, a presumed F₁ hybrid. These hybrids looked and acted much like the Laysan Albatross, but note the largely pearl gray head and neck, with white facial patterning like that of a Black-footed Albatross. Laysan Island, 18 December 2011.

Photo by Cameron Rutt



Figure 3. Another presumed F₁ hybrid, this was the only individual engaged in successful reproductive behavior (here seen incubating), although actual parentage of the chick is unknown. This hybrid shared duties with a Laysan Albatross and successfully hatched a chick. Laysan Island, 25 December 2011.

Photo by Cameron Rutt

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Figure 4. This possible F_2 backcross with a Black-footed Albatross looked noticeably grayer than that species in flight, and it had an obvious white face. The underwing pattern was strikingly unlike that of a Black-footed Albatross, with largely white underwing coverts and black primary coverts and humerals like those of a Laysan Albatross. Laysan Island, 12 November 2011.

Photo by Cameron Rutt



Figure 5. Another possible F_2 backcross with a Black-footed Albatross, this was one of two that paired with a Black-footed Albatross and successfully hatched chicks. If these birds are correctly identified as hybrids, this is the first documentation of a hybrid breeding with a Black-footed Albatross. Laysan Island, 11 February 2012.

Photo by Cameron Rutt

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Figure 6. Although this presumed hybrid could at first suggest a different species, the bill structure and color, as well as the head pattern, are all consistent with a Laysan Albatross. It is unclear how this phenotype might arise, although it appears most similar to an extremely dark version of a possible F_2 backcross with a Laysan Albatross. The pattern of the underwings would help categorize it. Midway Atoll, 28 December 2006.

Photo by Ryan DiGaudio

ABERRANT BLACK-FOOTED ALBATROSSES

Two albatrosses on Laysan had plumage aspects that could suggest hybridization; however, they seem more likely to represent aberrant Black-footed Albatrosses (Figures 7 and 8). Nearly identical, these birds were like pale, scaly, and frosty versions of a Black-footed Albatross, looking largely beige and silver. Their white faces recalled the pattern of a Black-footed Albatross and were much like those of the possible F_2 backcrosses with the Black-footed Albatross, but their bills were bright pink. Unlike these F_2 hybrids and the Laysan Albatross, however, their upperwings had dark patches and their underwings appeared much like a uniform, paler version of a Black-footed Albatross's. The underwing pattern may be critical in distinguishing these birds from possible F_2 backcrosses with the Black-footed Albatross, which could appear similar, particularly at sea, where other details would be less apparent. These individuals were remarkably similar to a leucistic Black-footed Albatross photographed off Santa Barbara, California (Howell 2012: figure 25); one may have been the same individual. McKee and Pyle (2002) addressed aberrant plumage aspects of the Black-footed and Laysan Albatrosses more exhaustively.

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Figure 7. Initially thought to be a hybrid, this aberrant Black-footed Albatross had the white face of possible F_2 backcrosses with the Black-footed Albatross (Figure 8) but lacked any other characteristics of the Laysan Albatross. It associated with Black-footed Albatrosses and walked with that species' crouching posture, as did the bird pictured in Figure 8. Laysan Island, 27 November 2011.

Photo by Cameron Rutt



Figure 8. An individual different from that in Figure 7, though nearly identical, distinguishable by different apparent molt limits (or, perhaps, leucism) in the primaries. This aberrant Black-footed Albatross could cause confusion at sea, but it lacked the white and black underwing pattern of all presumed F_1 and possible F_2 hybrids. Laysan Island, 15 December 2011.

Photo by Cameron Rutt

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CONCLUSION

Although rare on their breeding grounds and scarcely observed at sea, presumed hybrid Black-footed × Laysan Albatrosses may be categorized by at least three different but consistent phenotypes. Table 1 outlines criteria for distinguishing these three phenotypes from the parental species. In particular, underwing pattern may be critical in revealing hybrids or classifying problematic individuals. Most previous documentation of hybrids stems from Midway, so my observations on Laysan Island complement those descriptions. Further observation of hybrids may reveal that at sea their distribution tracks that of the Laysan rather than the Black-footed Albatross, concentrated in the Gulf of Alaska and around the Aleutians. In any case, birders throughout the North Pacific should watch for these birds and document them when possible, as hybrid albatrosses are truly rare at sea.

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Philip Unitt



“Featured Photos” by © Cameron Rutt of Blooming Glen, Pennsylvania: hybrid Laysan × Black-footed Albatrosses (*Phoebastria immutabilis* × *P. nigripes*) on Laysan, northwestern Hawaiian Islands. Top, presumed F₁ hybrid; bottom, presumed F₂ backcross to the Black-footed Albatross, paired with a likely female Black-footed Albatross.