Plumage variation and hybridization in Black-footed and Laysan Albatrosses

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INTRODUCTION

Black-footed (*Phoebastria nigripes*) and Laysan (*P. immutabilis*) Albatrosses nest side by side in dense island colonies. Their breeding populations center in the northwestern Hawaiian Islands, with smaller colonies scattered across the subtropical North Pacific. Both species visit nutrient-rich waters off the west coast of North America throughout the year to forage. Black-footeds concentrate in coastal waters from northern California to southern Alaska, while Laysans frequent more offshore and northerly waters in this region. Birders on pelagic trips off the West Coast often encounter significant numbers of one or both of these species, and searching for other, rarer albatrosses among them has proven to be a worthwhile pursuit in recent years (Stallcup and Terrill 1996, Cole 2000).

Albatrosses identified as Black-footed x Laysan hybrids have been seen and studied on Midway Atoll and other northwestern Hawaiian Islands since the late 1800s (Rothschild 1900, Fisher 1948, 1972). In addition, considerable variation in appearance is found within both species, individuals with strikingly aberrant plumage and soft part colors occasionally being encountered (Fisher 1972, Whittow 1993a). Midway Atoll hosts approximately two-thirds of the world's breeding Black-footed Albatrosses (Fig. 1) and one-third of the world's breeding Black-footed Albatrosses. These populations have provided us with many opportunities to study and photograph presumed hybrids and unusual individuals. In this paper, we discuss variation in the plumages of both species and the appearances of aberrant individuals and probable hybrids, as well as the potential pitfalls to identification that such birds may pose. Our observations are based on a collective 21 months on Midway from 1997 to 2000, in addition to the study of thousands of Black-footed and hundreds of Laysan Albatrosses at sea off California.



Figure 1. Midway Atoll hosts significant portions of the breeding populations of both Black-footed and Laysan Albatrosses. Presumed hybrids and aberrant individuals are found regularly in these dense colonies. *Photograph by Peter Pyle*.



A presumed hybrid Laysan x Black-footed Albatross tends a chick at Midway Atoll, 14 February 2000. *Photograph by Peter Pyle.*

BLACK-FOOTED ALBATROSS

Worldwide, the Black-footed Albatross is the less common of the two species, with population estimates ranging from 200,000 to 300,000 individuals (Whittow 1993a, Cousins & Cooper 2000). Adults arrive at colonies in late October, fledging takes place in late June and July, and adults have an incomplete to complete molt during April (non-breeding individuals) or July (breeders) through October. This species is largely dark brown at all ages, with white shafts to the outer primaries. Juveniles have whitish bases to the feathers encircling the bill and to those feathers in a crescent immediately under the eye. The resulting pale areas are obscured at fledging, resulting in wholly dark plumage (Fig. 2) but quickly become visible with wear.

Fledglings usually show well-developed white areas on the face by the time they reach North America in late summer. We have seen one or two breeding adults that lacked the eye crescent and showed limited white around the bill, but these features are obvious on the vast majority of individuals after fledging. Feather edges on the head become very frayed and bleached on birds of all later ages in the summer, and the white area can encompass most of the head on some birds in this state (Fig. 3). Adults with heavily bleached heads from April to August likely represent breeding individuals that have spent significant time at subtropical latitudes, whereas those showing less bleaching probably are prebreeders (ages 2-10 or more years) or birds that skipped breeding that year and remained at temperate or subarctic latitudes, thus being exposed to less intense sunlight. Feather edges throughout the neck and underparts also become bleached and frayed, and on many birds the edges contrast distinctly with dark feather bases and create a scalloped look of tan on brown (see Miller 1940).

White feathering develops on the rump, uppertail coverts, lower belly, vent, and undertail coverts, and its extent has been linked to age and sex (Streets 1877, Bourne 1982, Pyle unpubl. data), old males being whitest. Birds showing areas of white



Figure 2. Juvenile Black-footed Albatross near fledging. Pale areas are already developing on the face, before all the down is lost. Midway Atoll, June 1999. *Photograph by Peter Pyle*.



Figure 5. A leucistic Black-footed Albatross on Tern Island, Hawaii, January 1993. Documented details of the wing and tail pattern indicate that this is the same individual as presented in Figure 4, photographed several years earlier. *Photographs from U. S. Fish and Wildlife Service files.*



Figure 3. An exceptionally worn and bleached adult Black-footed Albatross. The bill is near the pale extreme for the species. Photographed in Monterey Bay, off Santa Cruz, California, 15 October 2000. *Photograph by Michael Donahue*.



Figure 4. A striking leucistic Black-footed Albatross in Monterey Bay, California, 18 September 1988. The bill shape eliminates Southern Giant-Petrel and Laysan Albatross; the bird also shows a shadow of the Black-footed's facial pattern. *Photograph by Serge LaFrance*.



Figure 6. Leucism often appears in patches, as in this Black-footed with white outer primaries and a white strip across the belly; note also the pale splotching on the feet. The facial pattern is typical of adults. Midway Atoll, 23 June 2000. *Photograph by Peter Pyle.*

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elsewhere on the body due to leucism are very rare but have been photographed in several locations (e.g., Figs. 4, 5, and 6). In extreme cases, such as the mostly white bird in Figures 4 and 5, this can create an appearance reminiscent of a light-morph Southern Giant-Petrel (*Macronectes giganteus*). The distinctive bill structure of *Macronectes*, with external nasal tubes atop the culmen, consistently distinguishes this genus from all albatrosses (Harrison 1983). Roberson (1980) mentioned white in the rectrices and light dusky-yellow feet on some birds. We have seen pale coloration in these areas only on obviously leucistic Black-footeds, so it does not appear to be age-related. Similarly, pale underwings apply only to presumed hybrids and leucistic birds in our experience. Such birds were noted by Stallcup (1976), who felt that it was age-related, and by Roberson (1980), who considered it a feature of aberrant birds or hybrids. The appearance of indistinct pale areas can also be created by the exposure of feather bases of birds in heavy molt in early summer.

The Black-footed's bill is blackish, usually with a pinkish tinge of varying intensity at the base. This color is well developed in some individuals of both sexes, making the bill appear fairly bright pink with a blackish or dark gray nail (Fig. 3), especially in bright sunlight. Pink-billed birds may cause confusion with juvenile Shorttailed Albatross (*P. albatrus*), which has a considerably larger bill. The bill of Shorttailed is dark at fledging (H. Hasegawa, pers. comm. to Pyle), but eventually it develops a bright pink base and pale blue tip. The timing of this change is unknown. Largely dark, pink-billed birds photographed off California in October to December have been regarded as juveniles (e.g., Stallcup and Terrill 1996, *N.A.B.* 52: 203), but these birds show worn, retained feathers, suggesting that the second prebasic molt has taken place. Pink-billed birds photographed in Oregon in March (*N.A.B.* 55: 506) and California in January (McKee and Erickson, in press) may in fact be juveniles, but ageing criteria in this species are still unclear.

Short-tailed Albatrosses slowly acquire an extensively white adult plumage (cf. Roberson 1980, Erickson and Hamilton 2001). Pale areas on the upperwing coverts can be among the first signs of this transition in Short-tailed, but it should be noted that the innermost greater coverts, tertials, and humerals on Black-footed Albatrosses have paler inner webs. When worn, this patch of feathers can contrast with the remainder of the upperwing, creating an appearance similar to Shorttailed. Leg and foot color of Black-footed usually is blackish or dark gray. We have found several individuals with irregular pale splotching on the legs and feet (e.g., Fig 6; these birds often show leucistic plumage as well), but in no case was this extensive enough to resemble the entirely pink feet of juvenile Short-taileds.

LAYSAN ALBATROSS

Although about ten times more numerous than the Black-footed Albatross, with a world population estimated at 2.5 million birds (Whittow 1993b), the Laysan Albatross is not encountered as frequently close to the North American continent. Laysans also arrive at breeding colonies in November, fledge young in July and early August, and have an annual incomplete to complete molt from April to October. This species was named *immutabilis*, meaning unchangeable, because of its lack of obviously different immature and adult plumages (Jobling 1991). While it is true that age-related variation is subtle, this species nonetheless shows a considerable amount of individual variation.

Laysans at fledging are white throughout the head and underparts, with a small black patch surrounding the eye (Fig. 7). They lack the gray wash across the auriculars of adult birds (Fig. 8). The exact time at which gray in the face develops is unknown. Procellariiformes typically do not molt between fledging and the second prebasic molt (see Howell and Corben 2000) during the following breeding season, so gray auriculars are not likely acquired before then. Our observations off California confirm that juveniles can remain white-faced at least until December. The gray wash normally is quite evident, though variable, by the time birds return to colonies, many of which are three to four years old (bands examined). Ageing is not always straightforward at sea, because the gray wash of adults can be difficult to discern in bright sunlight. Its extent also is reduced by wear, and some birds take on a facial pattern like that of the juvenile by late summer, just before the prebasic molt. The heavily worn mantle feathers of these birds readily distinguish them from fresh



Figure 7. Juvenile Laysan Albatross, showing white auriculars; adult bill color begins to develop near fledging. Midway Atoll, June 1999. *Photograph by Peter Pyle.*



Figure 8. A Laysan with rather pale underwings, showing narrow black margins. Midway Atoll, May 1999. *Photograph by Tristan McKee.*



Figure 9. A Laysan toward the dark end of the spectrum, with black areas merging on the underwings. Midway Atoll, February 2000. *Photograph by Tristan McKee.*



Figure 10. A leucistic Laysan Albatross, near fledging at Midway Atoll 25 June 1999. One or two mostly white chicks are found almost every year on Midway. *Photograph by Peter Pyle.*



Figure 11. Laysan Albatross chicks showing a scaly or barred pattern to the upperparts, another regular occurrence in large colonies. The bird on the left was photographed at Midway Atoll, 21 May 1997, the bird at right 30 May 1993. *Photograph by Peter Pyle (left) and from U. S. Fish and Wildlife Service files (right).*



Figure 12. Aberrant Laysan Albatross. Such birds can show a pale gray shadow of the typical Laysan underwing pattern of dark margins and humerals. Midway Atoll, April 1993. *Photograph from U. S. Fish and Wildlife Service files*.

juveniles. All ages have a dark brown back, upperwings, and rectrices and show white shafts to the outer primaries. The bill is dark grayish on young chicks, but a dull pink base and bluish-gray nail begin to develop before fledging.

The underwing pattern of this species usually is distinctive, but there is substantial variation in the amount of black versus white (National Geographic Society 1999, Sibley 2000). Preliminary observation of known-age birds on Midway has indicated that underwing variation is not strongly related to age, but more study is needed to confirm this. Black is present on the leading edge of the underwing, the flight feathers, the primary coverts, and usually in a triangular patch on the humerals. Near the palest extreme for birds that otherwise appear normal (but cf. leucistic birds), the black borders are very narrow and the humeral patch limited to a few blackish streaks or a grayish shadow. The humeral patch is absent or invisible in the field on a few birds, which appeared to represent less than 0.01% of the overall population at Midway. They could create confusion with the Shy Albatross (*Thalassarche cauta*) complex (Cole 2000), but size, structure, and bill shape differences are easily visible and should be used to confirm any Shy Albatross in the North Pacific.

Toward the darker side of the underwing spectrum, the black areas merge, sometimes to the extent that white is limited to the outer secondary coverts (Fig. 9, cf. Fig. 20). A few individuals show no white on the underwing, with either a gray shadow of the latter pattern or entirely dark underwings. It is not known whether these are at the dark extreme for the species or if this is strictly the result of introgression with the Black-footed Albatross (see below). The amount of dark on the rump is also variable and often loosely mirrors that of the underwing. The darkest birds have a dark rump with only a thin U-shaped white area on the uppertail coverts, contrasting with the dark tail, while the palest show a straight line of contrast, even with the trailing edge of the wings, between the dark back and an entirely white rump. Most birds fall between these two extremes, showing a patchy dark area extending into the center of an extensively white rump (Fig. 20). Laysans show a variable amount of dark smudging around the thighs, which is discussed below.

As in Black-footeds, leucism and other plumage aberrancy is occasionally noted in Laysans. One or two mostly white chicks (e.g., Fig. 10) are found on Midway almost every year, and some have been followed to fledging, but none have been known to return as adults. These birds again could cause confusion with giantpetrels until bill structure is noted. Bill structure also is an important feature for determining which of the Phoebastria is involved when dealing with leucistic birds: with experience, the shorter, thicker bill of Black-footed is distinguishable in the field from the relatively slimmer bill of Laysan, which shows a more concave culmen (cf. Figs. 6 and 13). Figures 11, 12, and 13 illustrate some of the other ways leucism and/or other types of plumage aberrancy can be manifested in this species. A variable amount of gray or whitish in the mantle feathers, often in a uniform pattern, is the most commonly encountered example. This can involve a scaly pattern of contrasting feather edges, various internal bars, or dark anchor-shaped markings on pale-based feathers. Fisher (1972) described such birds, and we have found a small number regularly on Midway. Such plumages may be caused by schizochroism (the lack of a pigment throughout) or dilution (reduction in quantity of a pigment), but the specific cause is difficult to determine without precise genetic information (Buckley 1969; P. A. Buckley, pers. comm.).

Indistinct white bars on dark feathers are particularly common in chicks (Fig. 11) and may be exaggerated growth bars resulting from metabolic changes during feather growth (see Michener and Michener 1938). The adult in Figure 12 takes gray in the mantle to the extreme. Several aberrant Laysans on Midway have returned to specific areas year after year, retaining the same patterns of abnormal pigmentation through repeated molts.

The unusual coloration of the bird in Figure 13 is evident in both the plumage and the soft parts. The bill is exceptionally bright pink, the gray wash is lacking on the face, and the upperparts show a considerable amount of white. This bird superficially resembles a near-adult Short-tailed Albatross in coloration, but size and structural features identify it readily.

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HYBRIDS

In 1997-2000, we observed up to 20 different presumed first-generation (F1) hybrids on Midway. Although no hybrid between these species has yet been confirmed genetically or through parentage, presumed hybrids are intermediate between Black-footed and Laysan in plumage, soft-part, behavioral, and vocal characters (Fisher 1972), and they would be difficult to explain as resulting from variation in either parental species. As also reported by Fisher (1972), all presumed hybrids we observed were interacting with Laysan Albatrosses, many being found among the pure Laysan populations in the central portions of the islands. We have witnessed male Black-footed Albatrosses involved in "rapes" (Fisher 1971) of female Laysans, and, contra Fisher (1948, 1972), we believe that hybrids between the two species are most likely products of these extra-pair copulatory events rather than of naturally occurring mixed pairs, something we have seen no evidence of on Midway. This would explain why hybrids seemed to be imprinted upon Laysan rather than Black-footed Albatrosses: they were likely raised by a pair of Laysans, the male unwittingly not the father. We have seen occasional attempts at interspecific courtship dancing, but these rarely lasted more than a few seconds (see also Whittow 1993b). It should be noted, however, that Fisher (1971) examined Laysans after intraspecific extra-pair copulation and found no physical evidence of successful copulation.

Because of the intermediate nature of their displays, most attempts of hybrids at courtship with Laysans appear unsuccessful. We observed two presumed hybrids incubating eggs and raising chicks with Laysan mates during the 1999-2000 season (frontispiece); hybrids have been observed on eggs on several other occasions. The chicks from these pairings appeared to have thicker bills and darker first-basic plumage than Laysan chicks from adjacent nests. Blood from hybrids and these apparent F_2 (second-generation) back-crosses has been taken by U. S. Fish and Wildlife biologists for DNA sampling (N. Hoffman, pers. comm.). If confirmed, this would represent the first documented record of a hybrid albatross successfully breeding (cf. Whittow 1993b), although our observations of suspected back-crosses (see below) indicate that this probably has occurred before. Actual parentage is difficult to confirm in the field because "adoption" of various objects, including displaced eggs and young chicks, is common in these dense colonies.

Most presumed F_1 hybrids are quite distinctive, with strong gray tones setting them apart from both species (Figs. 14, 15, 16, 17). Structural and behavioral features, soft part colors, courtship displays, and vocalizations are variably intermediate. The head and neck are gray on most birds, varying from a pale pearl gray to a dark, smoky-brown color. White areas around the bill and under the eye are often more extensive and diffused at the edges than on fresh Black-footeds, giving the face a frosty appearance. The gray wash on the neck can give way to white on the breast or continue down onto the lower breast, sides, and flanks. The undertail coverts and lower flanks often show some dark gray, even on pale hybrids. A large white area remains on the belly, usually more extensive than on Black-footeds.

The grayish head and underpart color of even most dark hybrids, such as the bird in Figure 16, is distinguishable from the dark brown of Black-footed. Figure 19 shows the only hybrid-like bird we have on record in which the distinction from Black-footed was unclear. Without behavioral information, this bird's identification must be left unresolved. The line between pale hybrids and Laysans is less clear. We have encountered a small number of adults that appear to be intermediate between hybrids and typical Laysans. Individuals such as the one depicted in Figure 18, which showed extensive dark smudging on the flanks, a very faint gray wash on the head, and very dark underwings, may be F2 back-crosses. In 2000, we were able to follow one of the chicks attended by an adult hybrid and a pure Laysan through to fledging, and it resembled the bird in Figure 18 in its extent of extralimital darkness. On the other hand, such birds could represent anomalous plumages or extremes in variation among pure birds or hybrids. We have observed similar individuals with more extensively dark bellies or slightly darker heads than this bird, so there is no clear line separating "typical" gray hybrids from paler individuals. We have also seen birds that are slightly paler and more Laysan-like than the bird in Figure 18, making the dark extreme in "pure" Laysans difficult to pinpoint. The



Figure 13. This Laysan shows reduced pigment in both the plumage and soft parts; note the superficial resemblance to a subadult Short-tailed Albatross. Midway Atoll, 8 February 2000. *Photograph by Peter Pyle.*



Figure 14. This is a "classic" hybrid with a contrasting gray head and breast and extensively white underparts. This bird shared incubation duties with a Laysan Albatross in December 1999 at Midway. *Photograph by Jennifer W. Schramm.*



Figure 15. Presumed hybrids typically associate with Laysan Albatrosses. This bird shows a fairly even gray wash through the head and underparts. Midway Atoll, March 1999. *Photograph by Tristan McKee*.



Figure 16. Although this presumed hybrid is at the dark extreme, the grayish cast to the head still distinguishes it from Black-footed. Midway Atoll, March 2000. *Photograph by Tristan McKee*.



Figure 17. A much paler presumed hybrid, showing a pearl-gray wash on the head and breast. Midway Atoll, March 2000. *Photograph by Tristan McKee*.

amount of dark smudging on the thighs, flanks, and undertail coverts of Laysan shows a considerable amount of variation. Unlike Whittow (1993b), we have found no evidence, based on examination of known-age birds, that this smudging is more extensive on juveniles than adults. There appears to be a continuous gradation or overlap between typical Laysans and suspected back-crosses in both flank color and underwing pattern (Fig. 20), and the increased pigmentation of most notably dark individuals is evident in both areas. Birds retaining the pure white head, belly, and upper flanks and some pattern on the underwing probably fall within the range of variation of pure Laysans, but those showing more extensive darkness are difficult to categorize.

Hybrids also present a potential source of confusion with other albatross species. George Watson (in Wahl 1970) discussed the identification of these birds in comparison with an immature Short-tailed Albatross photographed off Washington, citing white feathers on the underwings and the darker bill and feet of hybrids (see also Roberson 1980). Older Short-taileds develop pale underwings, but like Blackfooted, they always lack the distinctive gray cast of hybrids. Size and structural features are also diagnostic. Although Wahl later expressed doubts about the identity of the Washington bird (Helm 1980, Roberson 1986), we feel that the plumage pattern and structural features visible in the photograph strongly support his original conclusion. On the other hand, we concur that the photograph published in Helm (1980), originally identified as a Short-tailed but later as a Black-footed or Blackfooted x Laysan hybrid (Roberson 1986), is a worn Black-footed. This bird's neck,



Figure 18. This bird shows a very faint gray wash to the head and extensive dark smudging on the flanks; it may be an F₂ backcross. Determining the dark extreme for pure Laysans is problematic. Midway Atoll, April 1999. *Photograph by Tristan McKee.*



Figure 19. Unidentified albatross on Laysan Island, February 1995. This bird superficially resembles other suspected hybrids, but the head and neck are brownish, closer in color to Black-footed. The bluish bill tip, pale feet, and extent of white on the belly are unusual in our experience for Black-footed but might appear on a leucistic bird. Note also the lack of gray in the auriculars, normally present in adult Laysans and presumed hybrids. *Photograph from U. S. Fish and Wildlife Service files.*

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Figure 20. Underwing and rump patterns of Laysan Albatrosses and presumed hybrids. Laysans that are apparently "pure" can show any of these underwing patterns, although (1) is extremely rare and (4) may suggest introgression with Black-footed in some cases. Most presumed F₁ hybrids show patterns similar to (3) and (4) or even darker. All three rump patterns are common in Laysan, while hybrids tend to be closest to (C). Sketch by Tristan McKee.

breast, and upper belly are considerably darker than any hybrid we have encountered, and the bill color, head pattern, and extent of white on the lower underparts appear to be within the range of variation of Black-footed.

At first glance, hybrids may recall gray-headed forms of the Shy Albatross complex, but their underwing patterns, as well as size and structure, should prevent confusion. More critically, many presumed hybrids show a superficial resemblance to immature Black-browed (Thalassarche melanophrys) and Gray-headed (T. chrysostoma) Albatrosses. The underwing pattern of some hybrids maintains a recognizable resemblance to the "average" Laysan pattern, but others retain only an indistinct pale strip on the underwing coverts (e.g., see Fig. 2 in Fisher 1972), appearing nearly identical to dark immature Black-browed and Gray-headed Albatrosses in this respect. The head pattern of hybrids can be a close match for these species as well, although the two southern species are more likely to retain a dark partial collar, while hybrids usually show some suggestion of the Black-footed's facial pattern. Thalassarche species differ noticeably at sea from Phoebastria in their greater caudal projection, that is, longer projection of body and tail behind the trailing edge of the wings (S. N. G. Howell, pers. comm.). The feet of the former do not extend noticeably beyond the tail tip. The feet of North Pacific Phoebastria project well beyond the tail tip when they are extended, but these species often fly with the feet tucked into the contour feathers. Another important feature is rump color, which is pure white in Black-browed and Gray-headed (Morlan 1985, Marchant and Higgins 1990). Only the palest Laysans show this pattern, and we have never seen a hybrid without a noticeable intrusion of dark onto the upper rump (cf. Fig. 20). Considering that old male Black-footeds can also be white-rumped, however, this pattern is not inconceivable on hybrids.

Other potentially useful features to examine on confusing birds are exact bill and tail colors. Very young Black-browed and Gray-headed Albatrosses initially show blackish bills, but birds of this age are unlikely to be encountered in North America. The bill of Black-browed quickly develops a dull pinkish cast at the base, before changing to yellowish or horn with a dark tip (S. N. G. Howell, pers. comm.; cf. Patteson et al. 1999). During the brief period when dull pink is evident, the bill appears very similar to that of presumed Black-footed x Laysan hybrids. Developing yellow or horn coloration is indicative of Black-browed, but beware of hybrids illuminated by low-angle sunlight, which can appear to have yellow tints to their bills. Gray-headeds develop yellowish or horn coloration along the culmen and at the tip of the maxilla, a pattern that is easily distinguished from that of

Phoebastria species. The tails of Black-browed and Gray-headed are grayish when fresh (Marchant and Higgins 1990), while hybrids share the dark brown tails of Black-footed and Laysan. Worn birds of both genera have similarly dark, brownish tails. Good views of a combination of these features should allow the identification of nearly all birds. Observers are strongly encouraged to photographically document any "gray-headed" albatrosses appearing off North America, including suspected Black-footed x Laysan hybrids, which to our knowledge have not yet been documented near the continent.

Despite being large and generally easy to identify, albatrosses show complex agerelated and geographic variation in their plumages. This can cause confusion, especially when encountered in their, but not our, element: rough seas. It does not help that two of the more genetically stable species, the Black-footed and Laysan Albatrosses, show extensive individual variation, which is further complicated by apparent hybridization. We hope this paper will stimulate others to continue to document and understand variation in albatross plumages throughout the seven seas

Acknowledgments

We extend special thanks to the people of Midway, including U. S. Fish and Wildlife Service personnel Rob Shallenberger, Ken Neithammer, Nanette Seto, Nancy Hoffman, Keith Larson, and Aaron Gallagher, as well as Birgit Winning of the Oceanic Society, who all facilitated our presence and work on the atoll. We are indebted to Debra Shearwater, who has made it possible for us to spend a considerable amount of time offshore California studying albatrosses on Shearwater Journeys trips; she also provided valuable photos for use in this paper. We thank Rich Stallcup, Michael Donahue, Jennifer Schramm, James Aliberti, and the Northwestern Hawaiian Islands National Wildlife Refuge for contributing useful photographs and permission to publish them, and we are most grateful to Cindy LaFrance for granting permission for us to use the photograph of the late Serge LaFrance. Kimball L. Garrett, Steve N.G. Howell, Hiroshi Hasegawa, and Joseph Smith have added helpful and interesting discussion or information relating to these species. Steve N. G. Howell and P. A. Buckley reviewed drafts of the manuscript and added many helpful suggestions.

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