

SYMPATRY OF LAYSAN AND BLACK-FOOTED ALBATROSSES

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If we assume that albatrosses arose in the Southern Hemisphere where the greatest number of forms occur today, the three species in the North Pacific are derivatives of southern stock. They are isolated from significant ingress of genotypes from the southern species by the broad band of warm, unsuitable waters near the equator. Few southern species are known even as vagrants north of 20° S. The extreme southern record for a North Pacific species is 8° N (Thompson, 1951), and most individuals stay north of 20° N.

The three species of North Pacific albatrosses are: the Laysan, *Diomedea immutabilis*; the Black-footed, *D. nigripes*; and the Short-tailed, *D. albatrus*. The Short-tailed Albatross is outside the scope of this paper because its close affinities appear to lie with the great albatrosses, *D. exulans* and *D. epomophora*, rather than with the Laysan and Black-footed species. It probably represents a northward immigration separate from that of the other two species.

The purpose of this discussion is to present some views of the origin and subsequent sympatry of the Laysan and Black-footed albatrosses over virtually all their breeding range. These two species have much in common, despite the major difference in coloration. The more significant similarities lie in the blood proteins (Brown and Fisher, 1966) and the courtship display, which is more complex than in Southern Hemisphere forms; both sexes regularly participate and exhibit the dorsum rather than the ventrum of the wing to the partner. The species are close in body size, breeding season, incubation period, pattern of sexual participation in incubation, and vocalization. And in many of these features they also show important variations from southern species.

PRESENT HABITAT

Knowledge of the habitat requirements of the two species is necessary for the rationale of the original separation into two forms. The data presented relate solely to the breeding grounds, and primarily to the major colonies in the western Hawaiian Islands, for virtually nothing is known of their ecological distribution or behavior on the high seas.

Both species have, or had within historical times, a similar if not identical breeding range extending from the Hawaiian Islands to Torishima (Bird Island) south of Tokyo and lying approximately between 20° and 30° N (Rice and Kenyon, 1962a). Breeding has been limited to half



Figure 1. Breeding colonies of albatrosses on Midway Atoll. Top: Laysans in the interior of Eastern Island. Middle: Black-footeds on the beach of Sand Island. Bottom: Mixed colony on Eastern Island where wave erosion destroyed Blackfoot colony.

a dozen small islands in the eastern part of the range and even fewer volcanic cinder cones in the west. Where the two species breed on the same islands, and this was true in nearly all instances prior to the intervention of man, the colonies are basically separate and the Laysans are much more numerous than the Blackfoots.

The difference in numbers may be related to two factors; the total habitat suitable for Blackfoots is less extensive and they appear to nest in less dense colonies. The Black-footed Albatross utilizes the exposed sandy beaches and adjacent fringes of islands (Figure 1, middle). Seldom does a Laysan Albatross nest in a wind-blown sandy place on the edge of an island, and when it does the nest is usually unsuccessful. The Laysan nests in the brush-protected interiors of islands (Figure 1, top). Black-footed Albatrosses nest where there is little or no vegetation at or surrounding the nest site. Even when they breed successfully in the vegetated interiors of islands, they do not use grassy spots and do not build the conical nests typical of colonies on sand beaches. The Laysan nests on grass, coral rubble, and patches of sand and dirt between clumps of vegetation. Both species prefer sites that provide loose material the birds can drag together to form the nest cone.

This ecological separation of breeding colonies, except where their edges may meet, is evident on undisturbed atolls such as Lisianski in the Hawaiian Chain. On disturbed islands the habitat of both species has been altered, and care must be taken in assessing the requirements for successful nesting. Military construction has removed the vegetation in many instances and provided newly exposed sandy rubble. The Black-footed Albatrosses often pioneer such areas. Furthermore dredge deposits sometimes provide new shore outside the old Black-footed colonies. On Sand Island of Midway, some Blackfoots nest a quarter of a mile inland, at the site of the original shoreline and separated from the more recently established colonies near the current shoreline. Apparently they are only occupying long-held breeding grounds where, as photographs show, the vegetation has appeared in the last 30 years. The shoreline of Eastern Island of Midway was less disturbed, and only one pair of Blackfoots nests more than 250 yards from the sea. Construction of the concrete runway and its macadam aprons along the south shore of Sand Island preempted some space of former Blackfoot colonies and forced the birds to retreat to the nearest suitable habitat farther inland. Secondary evidence of this is the present crowded condition of these new colonies; nests are much nearer each other than in the seaside colonies.

The natural habitat of the two species is best indicated by the undisturbed conditions on Midway at the turn of the century. Old accounts

refer to Eastern Island as Green Island because of its heavy vegetation, and they indicate that Laysans far outnumbered Blackfoots. Early inhabitants also noted that many Black-footed Albatrosses and but few Laysan Albatrosses nested on Sand Island, which had little vegetation. The Laysan population on Sand Island apparently grew as the vegetative cover increased through the efforts of employees of the Pacific Cable Company subsequent to 1903 (Rice and Kenyon, 1962a).

DIVERGENCE OF LAYSAN AND BLACK-FOOTED ALBATROSSES

As Hutton (1903) and Richdale (1950: 26) point out, the Blackfoot shows closer affinity than the Laysan with the Southern Hemisphere species of albatrosses. The adult Blackfoot is brown to black in color, and the young are dark-downed. Blackfoots raise both wings simultaneously in the courtship wing-lift. The species has a more widespread breeding range than the Laysan. It nests successfully in places where the Laysan fails, and the Blackfoot is known to be successful in occupying Laysan habitat. The Black-footed Albatross appears to be the more adaptable, generalized, and older form. For these reasons it is postulated that *D. nigripes* is closer than *D. immutabilis* to the original stock of albatrosses that formed the Blackfoot-Laysan line.

Once this original stock became isolated on two or more islets, the small populations could have diverged simply on the basis of accommodation to breeding on bare sand islands (Blackfoot) or on isles almost completely covered with vegetation (Laysan). Bare sand precedes vegetated sand in the terrestrial succession in atolls, and the geological history of the Hawaiian Islands indicates the continuous presence of low sandy atolls. Thus albatrosses with the habitat preferences of Blackfoots could always find suitable nesting places. The Laysan type of nesting habitat in the North Pacific appeared later and initially must have been limited in extent. No albatross except the Laysan nests at sea level, on flat terrain, and in tall, dense vegetation, much less heavy, woody brush. The Laysan thus utilizes a nesting situation at least partly new for albatrosses. Although both species of this albatross line are relatively small-bodied, the Laysan's body is the smaller, perhaps as an adaptation to movement in the brush.

Considering the geographical isolation of the entire breeding range from invasion by additional forms of albatrosses, the isolation of the atolls within the range, the originally small populations of breeding birds, and the proclivity of the birds to return only to the natal colony to breed (Fisher, MS), divergence and evolution of the two forms may have proceeded rather rapidly. As the birds exploited the predator-free land and the rich energy sources of the northern waters, the populations

may have outgrown the space originally occupied and forced younger birds to seek other suitable islands. Some islands occupied secondarily may have provided satisfactory habitat only for a Laysan-type or for a Blackfoot-type albatross. Thus further reproductive isolation took place and, as population growth caused additional emigrations, other islands were used, islands suitable for colonies of both forms. In this way the Laysan and the Blackfoot came into near sympatry; the colonies were contiguous perhaps but not overlapping. As wave action eliminated the narrow seashore areas occupied by Blackfoot colonies and forced inland the birds bound by tradition to return to that island and colony, and as the vegetational succession began, along with probable increases in the breeding populations of one or both species, the originally sharp borders between colonies of the two species on any single island became obscured. Black-footed Albatrosses nested side by side with Laysan Albatrosses (Figure 1, bottom), and on small islands this zone of overlapping colonies constituted significant sympatry. By this time the two forms were sufficiently distinct that interbreeding seldom occurred.

INTERBREEDING

Today the amount of interbreeding is almost negligible; reports of hybrids are few. Rothschild (1893–1900) found one on Laysan Island, and a member (Palmer) of his party saw a Laysan Albatross feeding what appeared to be a Black-footed chick. Hadden (1941) saw an adult hybrid 25 November 1938, and Blackman (1941) noted one. Five (four on Sand and one on Eastern Island of Midway) were indicated for 1949–50 by Grenville Hatch and Earl and Willadean Sawyer on their joint banding schedule submitted to the U. S. Fish and Wildlife Service. Frings and Frings (1960) saw one in 1960. There is one specimen of a hybrid in the B. P. Bishop Museum in Honolulu.

In some 24 years of interest in these species, including 36 months of intensive field study of the Laysan Albatross in the last 10 breeding seasons, I have found only slight evidence of interbreeding among the approximately 180,000 pairs nesting on the 1,600 acres of land in Midway Atoll. In 1945 I saw one young hybrid and another in 1961. A Laysan and a Black-footed were feeding the 1945 chick (Fisher, 1948); the parents of the 1961 bird were not seen. I recorded nonbreeding hybrids in 1946 (one on Eastern Island), in 1961 (two on Sand Island), in 1964–69 (same bird on Eastern), and in 1964–69 (same individual on Sand). The latter two are banded; one is now (July, 1970) at least 8 years old and the other is at least 10. We see them regularly; each wanders in a limited sector in a colony of Laysans and does not appear to

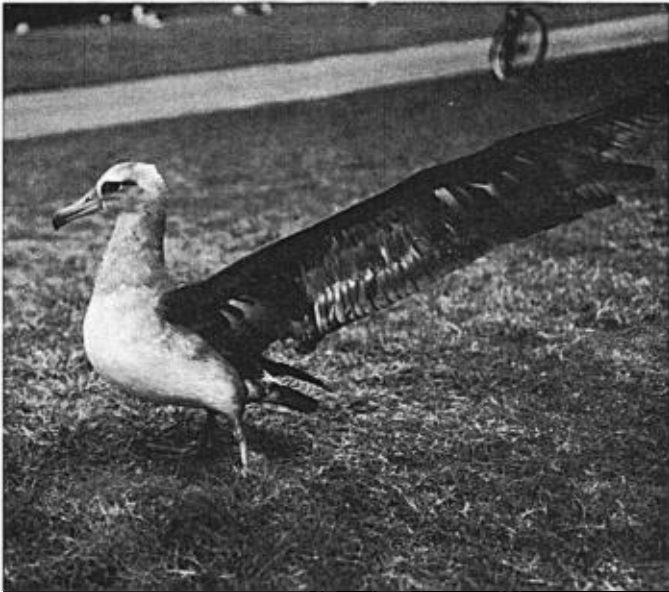


Figure 2. Hybrid albatross: Blackfoot \times Laysan.

be paired. Their areas of activity are less than 100 yards from nesting Blackfoots. No hybrids have been found nesting.

Some hybrids reported in the literature and by local residents are probably simple aberrations or age-related changes in plumage. All reports of "hybrid Blackfoots" made to me by residents of Midway were of individuals with unusual amounts of white on the abdomen, at the base of the tail, at the base of the bill, and scattered white feathers among the contour feathers on the body. In Black-footed Albatrosses these areas may become increasingly white with age.

Two albinistic Laysans were found on Laysan Island in 1891 (Rothschild, 1893-1900; Munro, 1941a, 1941b), and Munro (1946) reported an albino on Eastern Island. We found one albino Laysan chick on Eastern in 1961, one in 1969, and another in 1970, but never have we seen an adult albino of either species. Plumage aberrations in the Laysan Albatross occur most frequently in the gray mantle and on the dorsum of the wings. Examination of six such living specimens and one collected by Eugene Kridler on Pearl and Hermes Reef in February 1969 produced an impression of speckling on the back and wings; the Kridler specimen also had an unusually extensive spread of pastel gray over the side of the head. The speckle is produced in different ways: 1) white or buffy bases on otherwise normal gray major and minor coverts of

primary, secondary or tertial remiges; 2) all-white feathers scattered in the scapular and dorsal spinal tracts; 3) a one-eighth- to one-half-inch white trim on the edges of the flight feather coverts; and 4) silvery, prismatic-colored feathers in the mantle, some with brown edges. (The bird showing this last variant was the only albatross with aberrant plumage found nesting.) As in all instances the color pattern was typically Laysan Albatross, it appears unlikely that these birds were either primary or secondary hybrids.

The two true hybrids we have observed are pearl gray, darker on the back, and almost white in places, particularly the ventral surfaces of the neck and belly. The smokey, pearl gray is superficial; the slightest ruffling exposes the underlying white. The shape of the bill is intermediate; its color is black in one bird, not the rosy-yellow of the adult Laysan, and it is part black and part gray in the other hybrid. Both hybrids have the Black-footed pattern of white at the base of the bill, but the white is more extensive, moving onto the forehead and supra-orbital area. One bird has one black leg and foot and one light gray leg and foot (Figure 2); the other bird's legs and feet are typically those of the Blackfoot. The hybrid thought to be the older is browner, less dusky gray than it was 6 years ago. The body is upright, more the posture of the Laysan Albatross, and the walking gait is more that of a Laysan than a Blackfoot's head-down waddle.

The "sky-moos" of these hybrids are intermediate in general, but at times the sounds are clearly those of a Laysan or a Black-foot—a low clear "ooo" versus a hoarse and throaty "aaw," respectively. The "sky-moo" was the only sound heard from either hybrid, perhaps because neither one had an associate.

Neither hybrid could be sexed positively and neither maintained a station or territory as a typical male of either species does at a comparable age; both wandered over an area perhaps 100 feet in diameter. Both rather obviously "thought" of themselves as Laysan Albatrosses for they ignored several Black-footed Albatrosses within range of their movements and attempted to socialize only with Laysans. However they seldom could proceed beyond a touch of the bill, the initial greeting of the two species, before the Laysan moved on. The hybrid sometimes followed the Laysan for a few steps. Rejection of the hybrids by Laysan Albatrosses is also indicated by the solitary state of the hybrids, for both are several years beyond the age when a normal juvenile begins to associate with another bird.

Where the nesting colonies overlap, a Laysan and a Black-footed Albatross may sit side by side, as members of a pair customarily do. They may even preen each other. Close follow-up observations have

failed to show that these couples became more intimately involved; most likely they were juveniles, which are known to seek company, especially at night. Nor is the presence of a member of one species incubating an egg with a member of the other species standing alongside indicative of a pair in the crowded zone of overlapping colonies. Only once have I seen a Laysan and a Blackfoot attempt a courtship dance, although not infrequently a member of one species will bow to, or circle, a dancing twosome of the other species. These are the only indications I have of more than casual social relations between members of the two species.

One might speculate that a few hybrids could result from successful rape attempts, a behavior observed in both species and that I recently (1971) described for the Laysan Albatross. This is not impossible, but no actual interspecific rapes have been seen. A 2-week interval separates the peak seasons for copulation in the two species, and I found no evidence of insemination during rape attempts by Laysan males. Consequently it is assumed, from the evidence presented, that mixed pairs do occur. Why are they so rare? And why are so few hybrids found?

POSSIBLE ISOLATING FACTORS DURING SYMPATRY

SPATIAL

Although geographical separation was an important isolating mechanism originally and is still operative for most individuals of the two species, physical separation is not complete. The 5- and 6-year-old juveniles do return to congregate and to socialize within a colony of their own kind rather than on its edges, and these mate-seeking birds are, therefore, most often in contact with conspecific albatrosses. But this can be operative in actual pair formation only when there is room within the colony for the young male to establish a territory. If the colony is crowded, and the zone of overlap of the colonies is frequently the most crowded, he may be forced to establish himself in a place partly or wholly occupied by the other species and thus expose himself to more females of that species. Even if he is inside a colony of his own kind, an itinerant female of the opposite species may approach him in her meandering between males of her own species. As eligible females apparently pick the males to dance with, the females are probably most responsible for the formation of mixed pairs.

TIME

Breeding Black-footed Albatrosses arrive on the islands 2 or 3 weeks before the breeding Laysan Albatrosses, but this difference cannot be a primary isolating factor. Their pair bonds were established nearly 2 years before, in most instances. From February through April, unpaired

juveniles of both species and of proper age to pair are on the island at the same time. Older birds, surviving members of pairs broken by death, begin seeking mates in late egg-laying time (mid-November for Blackfoots, early December for Laysans) and would be more likely to form mixed pairs. But the paucity of such pairs indicates an isolating mechanism other than differences in times of arrival of different age groups of the two species.

BEHAVIOR

In many ways the behavior of the two species appears to be sufficiently similar to permit more than the observed infrequent interbreeding. For example, on 1 December 1962 we exchanged 25 eggs between nests of the two species. Fledging success in both instances equaled that of undisturbed colonies of both species. Also, chicks up to the age of 4 weeks were adopted interspecifically when exchanged between nests. It is evident that differences in the behavior, voice, and appearance of chicks do not always present secondary barriers to continued introgression.

However Black-footed Albatrosses are more aggressive and intense. They are quick to strike vigorously and repeatedly at avian or human intruders, which a Laysan Albatross seldom does. Laysans seem not to defend the mate, only self, territory, nest, or egg. An incubating Blackfoot may leave the egg to attack a human being; I have never seen a Laysan do this. Even juvenile Black-footeds disturbed at night or interrupted in their dancing lash out with the bill. Young Laysans walk or run away. It is impossible to ascribe specific isolating functions to general temperament, but the fundamental differences just described underlie much of the behavior.

Posture and gait.—Differences are at once apparent to the human observer, and they must be to the birds. The Laysan holds the head high on a nearly vertical neck when standing or walking (Figure 3, top); the breast is higher than the abdomen. Black-footed Albatrosses walk with the neck partly extended forward and the head kept low; the body is nearly horizontal, and the gait is straddling or waddling (Figure 3, bottom). The standing Blackfoot often holds the head up in the Laysan position. Males of both species apparently recognize the interspecific differences even in distant females and do not entice those of the other species.

Sounds.—Although one may use the same syllables to describe the same vocalizations of the two species, and the same types of vocalizations are produced, the sounds are different in pitch, intonation, intensity, and duration. The species can always be identified by an experienced

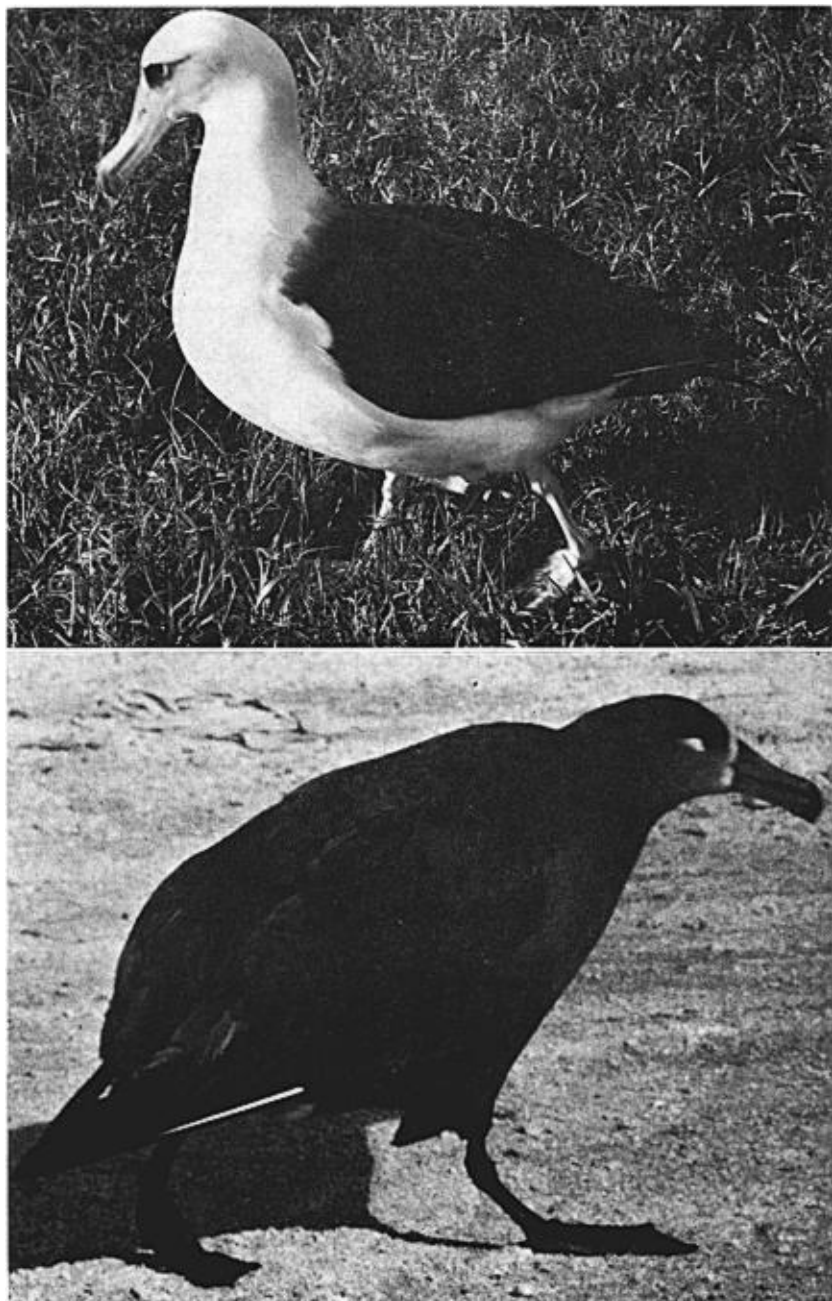


Figure 3. Differences in posture and locomotion. Top: Laysan Albatross. Bottom: Black-footed Albatross.



Figure 4. The bill-touch greeting of Laysan Albatrosses.

listener. As Rice and Kenyon (1926b: 524) note, "The calls of the Blackfoot have a decided nasal quality and are louder, lower pitched, and hoarser than those of the Laysan."

The double call is the basic syllabification of both species; it is the primary sound from which other calls are derived. In the Laysan it is "eh eh," in the Blackfoot "haw haw." It is the greeting between mates, between young and adults, and on occasion between strange individuals. It is also the most used vocalization of the male on territory and attempting to attract a female, mate or otherwise, and of both sexes in communicating with the unhatched offspring. In the latter behavior, the male or female parent bends toward the egg and with the bill near the egg, double calls. If this is indeed a communication with the advanced embryo, as I suggest, it is probable that before hatching the chick learns the basic vocalization of the species, as well as the individuality of the parent's voice, before the chick can be visually or otherwise aware of other species. If so, it is a powerful factor acting against mixed pairing later. This fundamental difference in the double call makes it difficult, if not impossible, I believe, for males to attract females of the other species or to greet them properly if they do approach.

One other attraction call, the "whinny," is an ululating high-pitched



Figure 5. The rushing, tiptoe approach in the dance of the Black-footed Albatross.

cry similar to the whinny of a horse. It is made frequently by male Laysans on station, seldom by Blackfoots. The "sky-moo" indicated earlier is perhaps a displacement vocalization, but, when uttered by a male on his territory after being ignored by a passing female, it sometimes causes the female to return. The interspecific difference may prevent females from responding to a male of the other species.

Courtship dance.—Attention is focused only on certain aspects that appear to play some part in preventing successful dancing between members of different species. The comments apply only to courtship behavior in full action, not the often atypical and abortive displays of immatures or of males not successful in holding a partner for at least 10 minutes.

Initial greeting.—Touching of the bills is an almost universal behavior when two Laysan Albatrosses first come near each other. It is always a precursor and a repeated part of the courtship dance. It is less general in the Blackfoot. A Laysan male on territory and approached by a female extends his head and bill on arched neck to meet her bill, which is somewhat lower and on a horizontally held neck. The touch of



Figure 6. The posture in the Laysan dance in which the male (on left) determines his height dominance over the female.

bills is gentle and usually soundless; sometimes the curved tip of the upper ramus touches the inside surface of the floor of the partner's mouth (Figure 4). When the bill touch occurs in Black-foots it usually comes later, following mutual head raising, and is often a rough, hard side-to-side slap that sometimes can be heard 30 feet away.

Two field observations show how effective the difference is as a barrier to any interspecific social behavior. On 15 December 1968 I watched a "female Blackfoot making advances to a male Laysan on his territory. She extended neck, head low, and tried to bill-touch; male stood his ground but avoided contact by turning head to side; female came closer and tried again, uttering Blackfoot double call; male backed up; female persisted, advancing and 'growling'; male 'uneasy,' turned and started to walk away; female followed. Every few feet male stopped to stand his ground but was pursued by female walking with head low and extended." The female Blackfoot followed the male Laysan on a circuitous route until, some 40 feet from his territory, she was distracted by a male Blackfoot. After 2 or 3 minutes the Laysan slowly returned to his territorial station, turning several times to watch the female.

On 9 February 1969 a Blackfoot of unknown sex rapidly approached a young territorial Laysan and attempted to greet it. The male Laysan

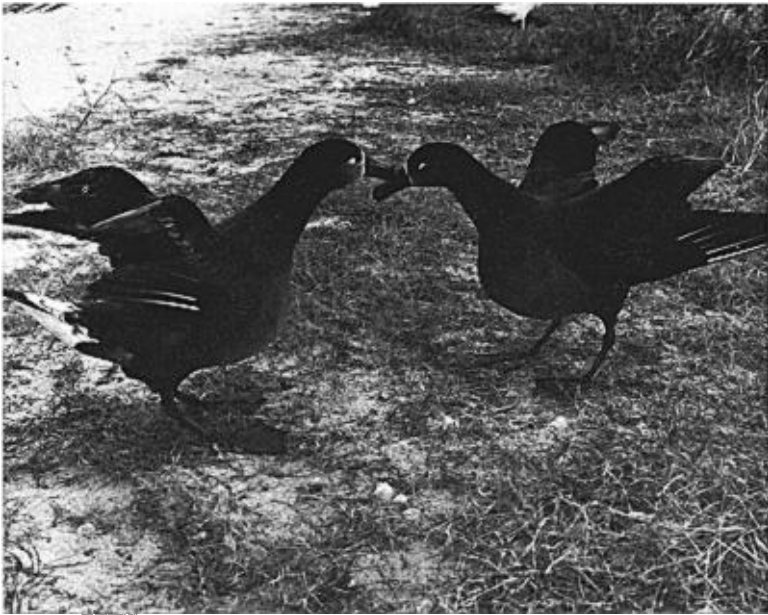


Figure 7. Dancing Black-footed Albatrosses simultaneously lift both wings to display the dorsal wing surface.

stopped all enticement activity when the Blackfoot came within a couple of yards and recoiled a step or two when the Blackfoot extended its bill.

Spacing, speed, and posture of dancers:—The dance of the Black-footed Albatross is speedier, more intense, more vigorous. The birds approach each other rapidly in the dance sequences, sometimes running toward each other and touching breast to breast. Their heads are held high, and the birds mince forward on tiptoes (Figure 5). Laysans also hold the head high and rise on tiptoes, but only when posing statue-like, not when approaching each other, and their breasts are usually a foot apart (Figure 6). Figures 5 and 6 show that the Blackfoot uses only the distal phalanx on each toe in the tiptoe position; the Laysan uses the penultimate phalanx as well.

As male Laysans require that their mates be shorter and have shorter bills (Figure 6 and Fisher, MS), as this sexual difference is less than the increase in height produced by standing on tiptoes, and as a female Blackfoot on tiptoes is taller than most male Laysans, I believe male Laysans in most instances would cease courting and attack Blackfoot females. At least they do attack prospective Laysan mates that present a



Figure 8. Dancing Laysan Albatrosses lift only one wing in the wing-lift-bill-tuck and the partners often take turns in the action; they also alternately lift the right and left wings.

higher tip of the bill. Female Laysans might be attracted by the intensified and impressive height of a Blackfoot male on tiptoes, but the latter's forward rush and vigorous contacts probably repel them.

Wing-lift:—Blackfoots of both sexes elevate both wings simultaneously (Figure 7). Laysans raise but one wing and alternate right and left (Figure 8). When the wing or wings come up and flare out laterally, the dancing Blackfoot or Laysan puts its bill near and below the base of the elevated wing; this is the bill-tuck. The bird is rigid, strained, and holds the posture several seconds as the bill nibbles on the surface of the feathers. This is probably a derivative of the scapular action described by Richdale (1950: 18). Two dancing Blackfoots wing-lift together (Figure 7), but bill-tuck on opposite sides of the body so that the birds are bill-tucking in the same direction. They do not always bill-tuck after a wing-lift as Laysans do, and the latter do not always wing-lift at the

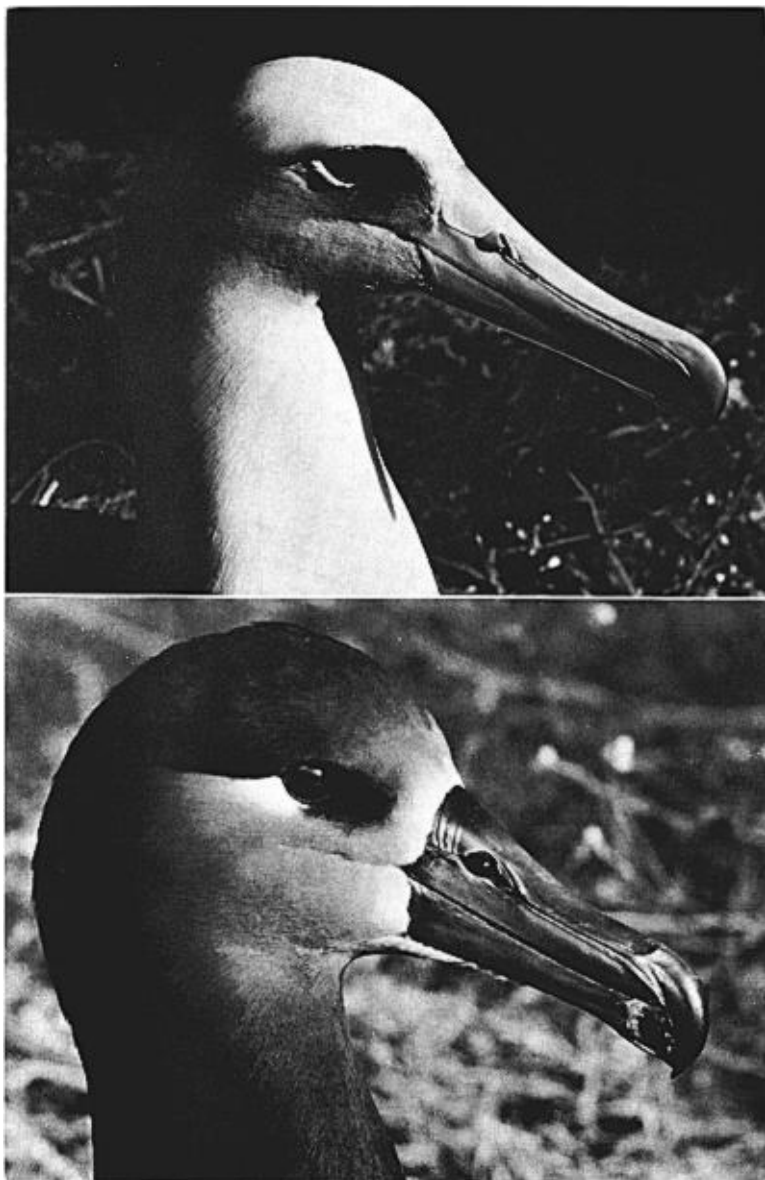


Figure 9. Lateral view of bill and head coloration. Top: Laysan Albatross. Bottom: Black-footed Albatross.



Figure 10. The female Laysan (on right) stares at the posing male just before attempting to touch his breast.

same time. The members of the Laysan pair characteristically wing-lift and bill-tuck alternately (Figure 8).

Colors:—The bill, head, and breast appear to be the areas where color differences would be of most importance, although one cannot dismiss the difference in color of the flared wing or the general impression of whiteness in the Laysan and of blackness in the Blackfoot.

The bill plays such a noticeable role in the initial bill-touch, and later in bill clapping and buzzing in the dance, that its rosy-yellow horn color in the Laysan and its blackness in the Blackfoot must be important (Figure 9). The bill is usually directed toward the other bird or upward and, made more visible by the motions of clapping, buzzing, and bowing, it becomes a center of attention.

The breast is the largest and most obvious part of the male's body, at the level of the female's head. The size and curved fullness of the breast in both sexes of both species are accentuated in three ways during the dance: 1) the breast is thrust forward and up by tilting the rear of the body downward; 2) the neck is drawn posteriorly over the back

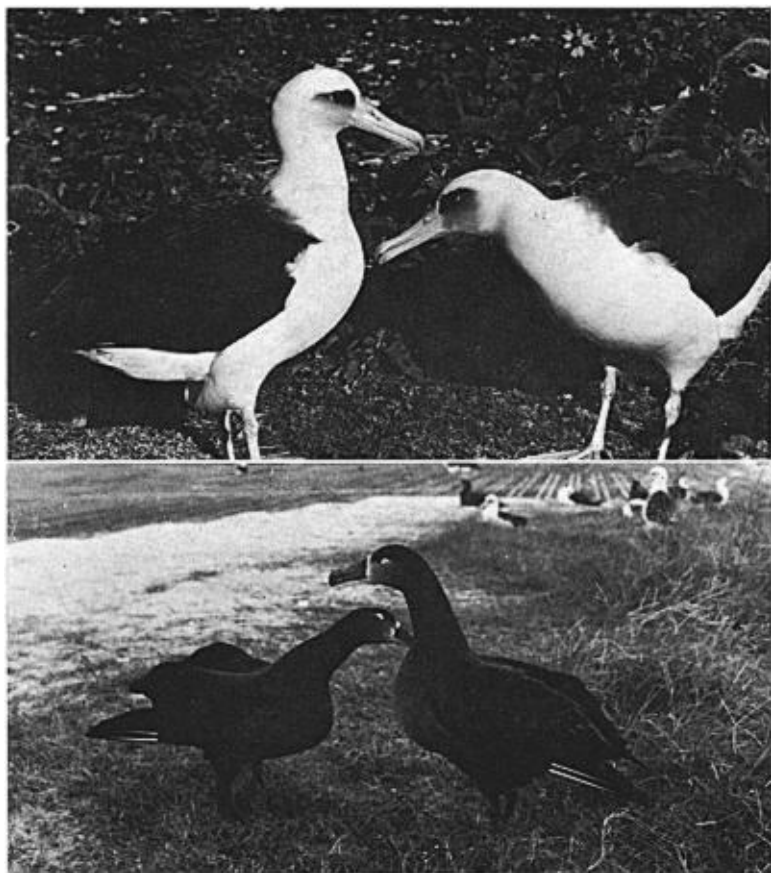


Figure 11. Female albatrosses touching the breasts of quiescent male Laysan (top) and posing male Blackfoot (bottom).

(Figure 10); and 3) as the birds bow low, especially the male, the breast is alternately visible and hidden. Consequently, the females of both species concentrate a great deal of their attention on the male's breast as the two face each other (Figure 11). The female Laysan stares at it while the male poses in the sky-call and bill-tuck, then tries to touch it with her bill (Figure 10). The female Blackfoot may touch the male's breast as a substitute for the initial mutual bill-touch.

Further, the snowy Laysan breast and the brown-black Blackfoot breast are probably the most impressive objects in the lives of newly hatched chicks, and consequently in post-hatching imprinting. It is not surprising, then, that the breast should play a critical role in adult behavior. The female shows this influence as just described; the male

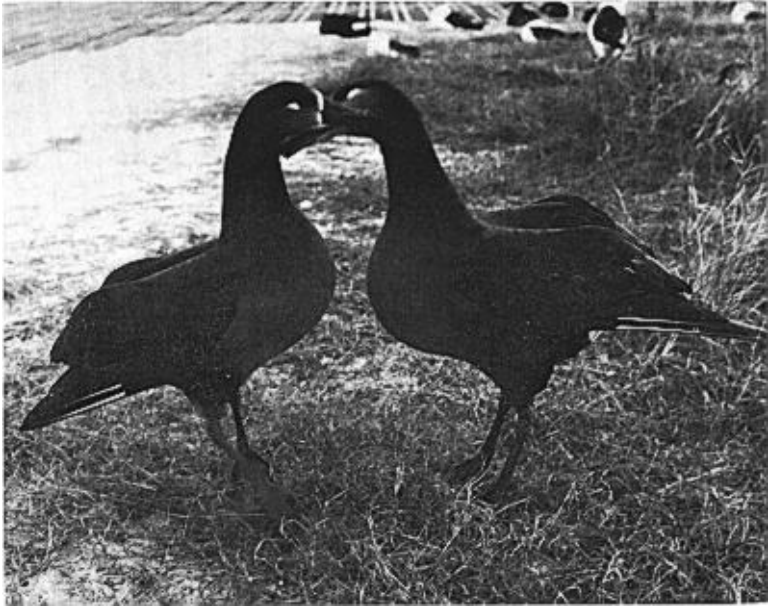


Figure 12. Black-footed Albatrosses bill-buzzing in the courtship dance.

Laysan later exhibits his focus on the breast by attempting to touch the female's in precopulatory behavior (Fisher, 1971). It would seem, therefore, that the solid white versus solid brown-black color on the breast may constitute one of the fundamental barriers to interspecific socializing.

The role of head coloration may be similar, but the head is presented frontally to the partner (Figure 8) and its area is relatively small. The white at the base of the bill and behind the eye of the Blackfoot and the pastel gray in the suborbital and loreal areas on the Laysan are most obvious in lateral view (Figure 9), which is primarily but only briefly displayed to the partner in the clapper behavior described below.

Rapid bill clapper:—This sound, produced by a rapid opening and forceful closing of the mandibles, is like two pieces of seasoned wood striking together. The Laysan uses it more frequently. Rapid repetition of the sound in the dance makes it into a buzz—softer and more irregular in the Laysan. The major interspecific differences lie not so much in the sound itself as in the position and posture of the birds making it. Black-footed Albatrosses buzz simultaneously and repeatedly alongside the partner's head, first on one side and then the other, and almost touching (Figure 12). As they buzz, both birds lift both wings very slightly. Laysans sometimes buzz alongside the partner's head, but usually

the buzz comes as the head is thrown forward, downward, and sidewise away from the vicinity of the partner's head. Seldom do they buzz simultaneously; the male buzzes more often than the female; and neither wing is flared as in the wing-lift, although one wing may be twitched slightly upward for a moment.

Simultaneous action by both members:—The greater frequency of the same behavior at the same time by Blackfoots is worthy of further emphasis. They wing-lift, buzz, sky-call, tiptoe, and approach each other at the same time, and do all these things with greater speed and vigor. Laysan Albatrosses tend to alternate specific acts between the partners. To human eyes, it appears simpler for the Blackfoot pair to perform simultaneous acts than to remember the cues for alternate or one-member performances as found in the Laysan Albatross. This suggests that the Laysan has a more intricately developed courtship dance.

One further feature of albatross behavior may be a final or corrective barrier to the formation of interspecific pairs. In the Laysan Albatross (Fisher, MS) and perhaps in some of the southern albatrosses (Richdale, 1950; Tickell, 1968), there is a long prenesting period of association between the members of newly formed pairs. Seldom does a pair nest in the first breeding season after formation of the pair; the occasional exceptions are pairs in which at least one member is pairing for a second time, having lost the previous mate by death. This "engagement" period in the Laysan is at least 1 year and sometimes 2. As most pairs are formed in the spring months, the "engagement" period generally extends from March or April of one year to November of the subsequent year. The associating birds are usually and frequently together on the male's territory, testing or firming the pair bond for several months in each of two breeding seasons before they attempt nesting. They may be together at sea during the remaining months of this period, but we do not know. In any event, this long period of courtship activity provides time for any hasty misalliances (certainly interspecific ones) to be broken by malappropriate behavior on the part of either member.

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SUMMARY

The three species of North Pacific albatrosses represent two lines of emigration from the Southern Hemisphere—the Short-tailed Albatross and the Blackfoot-Laysan lines. The Black-footed and Laysan albatrosses are similar in blood proteins, complexity of courtship, sexual

participation in courtship and incubation, and patterns and chronology of behavior, including breeding. But, compared to the Laysan Albatross, the Black-footed Albatross is more primitive in habitat, behavior, and color, and more representative of the hypothesized progenitor of the Laysan-Blackfoot line.

Once this Blackfoot-type progenitor established itself on North Pacific atolls, it was isolated from significant genetic ingress from the south by the warm equatorial waters. The growing populations on small islets were eventually forced to occupy additional islands. The new populations evolved rapidly on islands in different stages of vegetative succession, the change being aided by small numbers, spatial isolation of breeding colonies, and the strong tendency of young to breed on the island of their own natality and of adults to maintain life long territories. One group, the Black-footed, was or became a breeder on exposed, sandy islands; the Laysan group occupied a new niche on more densely vegetated islands. Population density caused the occupation of still more islands and the use of marginal habitat. The Blackfoots and Laysans began to breed on the same islands—Blackfoots on the barren beaches and Laysans in the brushy interiors. Increasing numbers caused the colonies to coalesce along their edges, and the constant reshaping of the sandy shores by wind, waves and water currents sometimes forced the Black-footed colonies inland into the Laysan colonies. But by this time the two forms were morphologically distinct and behaviorally separated.

Little evidence of hybridization exists at the present time. It is too rare to be of taxonomic significance, and, as the hybrids appear to be unsuccessful in gaining mates, hybridization is of no continuing biological significance. The two species are now reproductively isolated, not as originally by geography, habitat or chronology, but by their inability to enter interspecific behavior. The most important barriers to the formation of mixed pairs include differences in posture and gait, temperament, and courtship behavior. In the latter, it is postulated that initial greeting ceremony, sounds, wing-lifts, bill-tucks, posture, color of bill and breast, and complexity of dance pattern include the more probable isolating differences. One factor that is impossible to describe is the almost overpowering vigor and intensity displayed by dancing Black-footed Albatrosses.

The long period of association between members of a new pair before copulation occurs not only increases the probability of an eventually firm pair bond, but provides an opportunity for correction of interspecific alliances. It is, thus, a basic and final part of the isolating mechanism.

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