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BREEDING CYCLES AND BEHAVIOR OF LAYSAN AND BLACK-FOOTED ALBATROSSES

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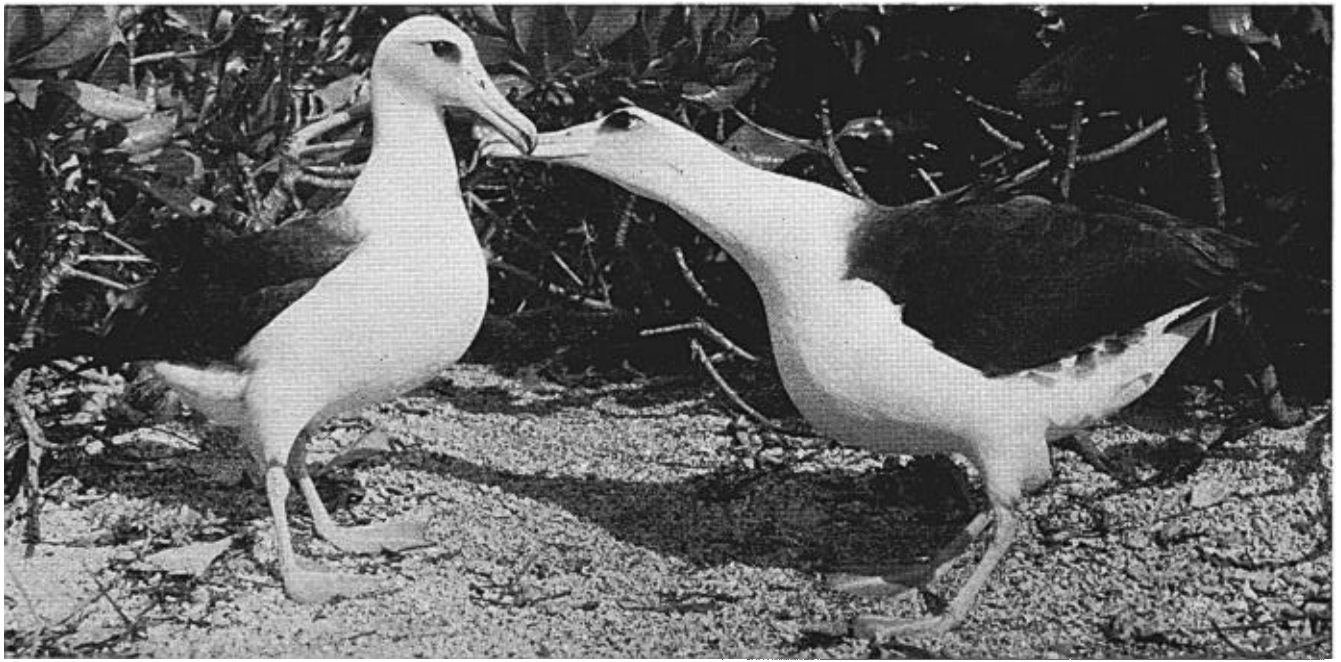
DURING the 1956–1957 and 1957–1958 seasons, we conducted intensive studies on the breeding cycles and breeding behavior of the Laysan Albatross (*Diomedea immutabilis*) and the Black-footed Albatross (*D. nigripes*), as part of a comprehensive study of their biology. Behavior of unemployed birds is not considered in this paper. In a previous publication (Rice and Kenyon, 1962) we treated the breeding distribution and numbers of these birds. Population dynamics and distribution at sea, based on a large-scale banding program, will be treated in a later report. Nesting studies were conducted at Midway Atoll, in the Hawaiian Islands. Rice was in the field from 17 November 1956 until 21 July 1958; Kenyon from 29 December 1956 until 26 June 1957.

Aside from Richdale's (1939, 1942, 1950, 1952) intensive 16-year study of a small colony of Royal Albatrosses (*D. epomophora*), Sorensen's (1950a, 1950b) work on the Royal Albatross and the Light-mantled Sooty Albatross (*Phoebetria palpebrata*), and Rowan's (1951) observations on the Yellow-nosed Albatross (*D. chlororhynchos*), no year-round studies of albatrosses have been conducted. Our studies, although extending over a much shorter period of years than Richdale's, have one advantage in the far greater number of birds under observation.

Our data are reasonably complete through the early post-guard stage (terms relating to breeding behavior follow the usage of Richdale, *op. cit.*). Other duties prevented our making a detailed study of the remainder of the nestling period. Many other aspects of albatross biology can be revealed only by studies extending over many years. We hope that the gaps in our work will indicate to future workers the most profitable fields of investigation, and that our descriptive and experimental studies will lay the groundwork for more detailed experimental analyses of the various phases of the breeding cycle.

The only previous ornithologist to record quantitative observations on



Laysan Albatross on the right illustrates the Gawky-look immediately preceding Billing. KWK 57-2-13.

marked birds was Robert Sheehan (*in* Richdale, 1952). Other published accounts present only general observations on, or cover only certain aspects of, the breeding cycle. These include the successive contributions of Rothschild (1893), W. K. Fisher (1904, 1906), Richards (1909), Dill and Bryan (1912), Bartsch (1922), Hadden (1941), H. I. Fisher and Baldwin (1946), H. I. Fisher (1948, 1949), Bailey (1952, 1956), and Richardson (1957). Recently, experimental studies have been made on salt balance by H. and M. Frings (1959), and on thermoregulation by Howell and Bartholomew (1961); the Frings (1961) have published a few statistical observations.

MATERIALS AND METHODS

The basic data concerning the breeding cycle were obtained primarily from two study plots on Sand Island. During the 1957–1958 season, 116 pairs of marked Laysan Albatrosses and 39 pairs of marked Black-footed Albatrosses, respectively, nested on these two plots. The nests were checked twice daily, at 08:00 and 18:00 (sun noon Midway time—GMT minus 11 hours—is approximately 13:00). (For statistical purposes, we have regarded the time interval as 12 hours, although examinations were alternately 14 and 10 hours apart.) In addition, six experimental study plots containing 419 Laysan Albatross nests, and one control plot, containing 164 Laysan nests, were under frequent observation on Sand Island throughout both the 1956–1957 and 1957–1958 nesting seasons. Other incidental studies were made on nests outside the major study areas, on both Sand and Eastern islands.

All nests under regular observations were either marked with a numbered wooden stake (Figure 1) or were plotted on large-scale maps. Eggs were marked with pen, pencil, or dye. Birds were permanently marked with standard U.S. Fish and Wildlife Service numbered aluminum bird bands, size 7B. To avoid disturbing incubating birds, each sex was distinctively marked with Rhodamine B red dye—red "caps" on females, red "mustaches" on males.

The sex of all marked nesting birds on the permanent study plots was determined by cloacal examination. Up to about 10 days after egg laying, the female of the pair can be distinguished by her distended cloaca. In addition, females are, on the average, slightly smaller and of more delicate build than their mates, with shorter, more slender beaks and smaller heads. Although measurements of 13 males and 19 females overlapped, in any mated pair the male was almost invariably larger than the female. If a pair was together, the general appearance of the two birds enabled us to determine their sex 80 to 90 per cent of the time.

Albatrosses are ideal birds to work with because of their inherent tameness. Incubating birds often allow themselves to be gently scratched

Figure 1. Stakes were driven into the ground to identify individual nests on study plots. Feathers of certain individuals were marked with dye, as illustrated on the breast of the bird at right. The edges of Laysan Albatross nests were usually built up several cm above the substratum as illustrated here. KWK 57-1A-8.

on the head (some even seem to enjoy this). Eggs are easily examined by gently nudging the incubating bird until it rises sufficiently to reveal the egg. No birds deserted their nests because of handling (except during nest-displacement experiments).

MATURITY

Age at First Return

In May and June of 1957, on Eastern Island, we marked 3,786 Laysan and 1,000 Black-footed albatross chicks with standard aluminum leg bands and red plastic leg bands; on Sand Island, 50 Laysan chicks were marked with yellow-enameled aluminum bands. In May and June 1958, on Eastern Island, 4,000 Laysan and 600 Black-foot chicks were marked with standard bands and yellow plastic bands.

During the 1957–1958 breeding season we made an intensive search for the birds color banded the previous season. Unfortunately, no one could be present to search for color-banded birds during the 1958–1959 season. Chandler S. Robbins of the U.S. Fish and Wildlife Service visited Midway in the spring of 1960, and made an intensive search for color-banded birds between 22 March and 6 April; a local cooperator, Ralph Stockstad, made

TABLE 1
SUMMARY OF RETURNS OF LAYSAN AND BLACK-FOOTED ALBATROSSES BANDED AS CHICKS

Species	*Year class*	*Number of returns*			
		1957–1958[a]	*1958–1959*[b]	*1959–1960*[c]	*1960–1961*[d]
Laysan	1956–1957	0	2[e]	22	1[f]
Black-foot	"	0	0	9	4
Laysan	1957–1958	X	0	0	2
Black-foot	"	X	0	(2)[g]	3

[a] Intensive search all season.
[b] No search made for color-banded birds.
[c] Intensive search 22 March–5 May.
[d] Intensive search 24–28 January.
[e] 7 May and 30 June.
[f] 25 May.
[g] Two Black-foots with yellow leg bands were observed, but they could not be captured.

an intensive search on 5 May. In the winter of 1960–1961, Robbins again visited Midway and searched for color-banded birds between 24 and 28 January. Their returns, plus a few others reported by other observers, are summarized in Table 1. A few additional color-banded Black-footed Albatrosses were seen in both the 1959–1960 and 1960–1961 seasons, but they evaded capture.

From these returns, it may be concluded that no appreciable segment of any year class returns to the breeding islands until the third season after hatching. Quantitative data on the age at first return may be obtained only if observations are carried on systematically throughout each succeeding breeding season after banding.

Comparison of the 1959–1960 returns with those of 1960–1961 indicates that, as in other pelagic species of birds, and in northern fur seals (*Callorhinus ursinus*), the innubile individuals tend to reach the breeding grounds relatively late in the season, the number of returns increasing as the season advances.

Age at Sexual Maturity

The only direct information on the age at which Laysan Albatrosses first nest is the record of a bird banded as a chick in 1951 and found incubating in December 1957, seven seasons after hatching. It is probable that this bird did not nest the previous season, as all nesting birds on that area were thoroughly checked repeatedly during the incubation period in 1956. It is possible, but unlikely, that it may have nested prior to 1956.

During an experimental control program by the U.S. Navy, 14 Laysan Albatrosses banded as chicks seven seasons previously were killed. All of them were apparently unemployed birds when killed. They included seven males, five females, and two of unknown sex. Only three (two males, one

TABLE 2
RELATION BETWEEN NESTING SUCCESS AND NESTING THE FOLLOWING SEASON BY LAYSAN ALBATROSSES

Nesting, 1956–1957			*Returned, 1957–1958*	
Fate of nest	*No. of nests*	*No. of birds*[1]	*No. of birds*	*Per cent*
Egg lost early in incubation	89	167	145	87
Egg lost late in incubation	73	144	108	75
Egg sterile	75	147	128	87
Chick died during guard stage	64	126	99	79
Chick died during post-guard stage	43	86	70	81
Chick successfully fledged	75	150	94	63

[1] Number of birds does not always equal twice the number of nests, because in several instances one member of the pair was not banded the first season, or was not recaptured the second season.

female) had bare incubation patches, suggesting that they may have nested that season.

All banded birds, two to six years of age, that have returned have apparently been unemployed birds.

These data suggest that seven years is the earliest age at which Laysan Albatrosses (and probably Black-foots also) nest. This agrees closely with Richdale's (1950) data for Royal Albatrosses.

FREQUENCY OF BREEDING

To determine if Laysan Albatrosses nest in consecutive years, 497 nesting pairs were banded during the 1956–1957 season. These included 164 pairs on a control plot, and 333 pairs on experimental plots where the eggs or chicks were destroyed at different stages in the breeding cycle. Seventy-eight nests were eliminated from consideration for various reasons, leaving 419 nests for calculating the correlation between nesting success one season and nesting the following season. Of these 419 nests, on 18 only one bird could be used in the calculations, as the other pair member either was not marked the first season, or was not recaptured the second season. Thus, the results are based on 820 individual birds of known nesting success.

The results in Table 2 show that a large proportion of Laysan Albatrosses nesting in any one season, whether or not they are successful in rearing a chick, return to nest the following year. Presumably the same is true of Black-footed Albatrosses, although we have no data for that species.

The proportion of birds returning and nesting the second year varied from 87 to 63 per cent. The affinity for an established nesting site (see Territory: Maintenance) precludes the probability that birds that failed to return nested elsewhere. There may be a decreasing tendency to nest the following year with an increase in the length of the portion of the breed-

ing cycle that is successfully completed. Birds that lost their eggs early in the 1956–1957 incubation period showed the highest percentage of nesting the following season, while those that successfully fledged a chick in 1956–1957 showed the lowest percentage of nesting in 1957–1958. Additional data are required to determine if the difference is statistically significant.

ARRIVAL AT THE BREEDING GROUND

Time of Arrival

In the 1957–1958 season the first Black-footed Albatross arrived at Sand Island on 18 October, the first Laysan Albatross on 1 November. On several selected areas, counts of all albatrosses were made daily at 12:00–13:00. The results in Figure 2 show the buildup and variation in numbers from the time of first arrival until the end of the egg-laying period. Both nesting and unemployed birds were included in the counts.

On one small area the earliest arriving Laysan Albatrosses were banded. Their sexes were subsequently determined after egg laying. The first male arrived on 4 November, and five more followed on 6, 8 (2 birds), 9, and 10 November. The first female did not arrive until 10 November. This suggests that females tend to arrive a few days later than males.

Significance of the Timing of the Annual Cycle

The nesting cycles of North Pacific albatrosses begin at about the same time of year, and thus at the opposite season, as the nesting cycles of the southern hemisphere albatrosses. It is frequently stated that the North Pacific species have simply "retained" the November laying season of their presumed southern hemisphere ancestors. However, there is no evidence to indicate that an entirely endogenous annual rhythm could be maintained during the long period of time that the Laysan and Black-footed albatrosses have surely occupied their present North Pacific habitat.

Laysan and Black-footed albatrosses occupy lower latitudes, and thus a warmer climate, than do any of the southern hemisphere albatrosses. Their breeding cycle seems to be timed to ensure that the chicks are fledged prior to the period of maximum summer heat (see Development of Young: Temperature Regulation). The work of Howell and Bartholomew (1961) supports this hypothesis.

PAIRING

Formation of the Pair Bond

Formation of the pair bond in albatrosses apparently takes a considerable period of time. As stated above, birds may return to the island when three years old, but do not nest until at least seven years old. Many birds that we thought to be innubile because of their delicate build and dusky

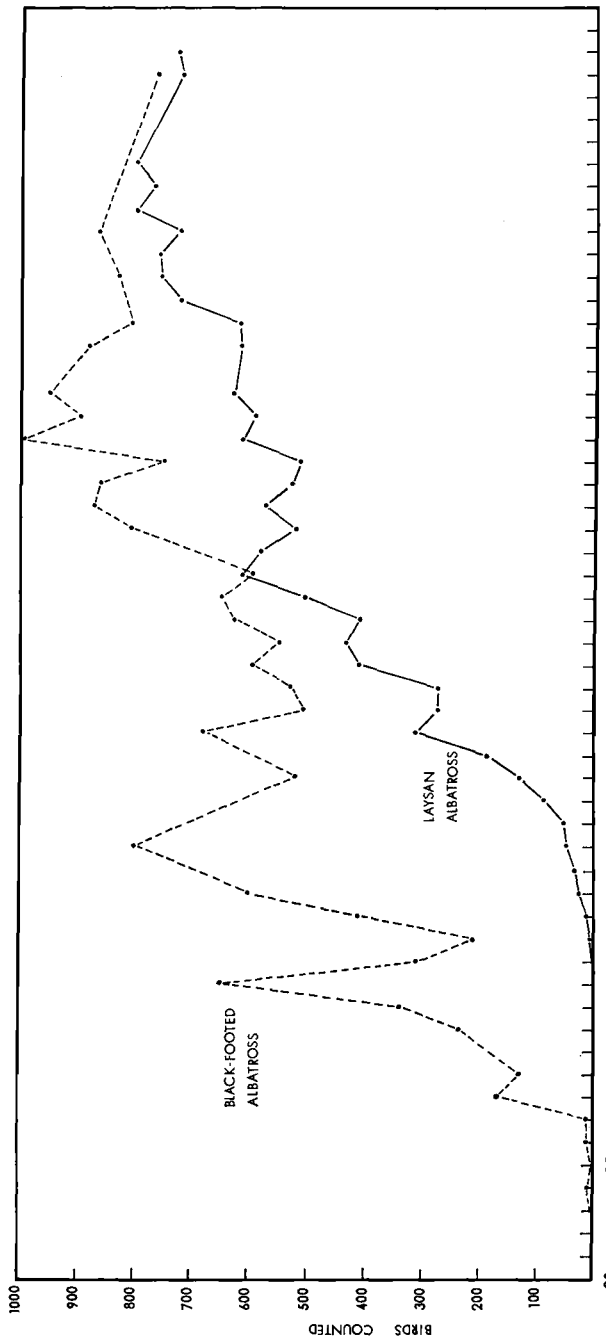


Figure 2. Daily counts of Laysan and Black-footed albatrosses on sample plots at Midway Atoll from time of arrival until the end of the egg-laying period.

TABLE 3
MAINTENANCE OF PAIR BOND FOR TWO SEASONS IN 341 MARKED PAIRS OF LAYSAN ALBATROSSES

Status of pairs	*Number*	*Per cent*
Pairs returned intact	323	94.7
Pairs returned divorced (both birds with new mates)	7	2.1
Only one member returned (with new mate)	11	3.2

feathers on their thighs were found "keeping company," dancing, and sometimes building nests, but not breeding.

On one experimental study plot, the mates of 76 incubating birds were killed. The following season only 10 (13 per cent) had acquired new mates and nested. At least 29 of the remaining 66 birds returned as unemployed birds to the same area. This indicates that a year or more may be required to consummate a pair bond after loss of a mate.

In one unusual case a male whose mate's egg was destroyed was discovered a few days later on another nest incubating an egg newly laid by another female. He and the new female incubated and hatched this egg.

Duration of the Pair Bond

The pair bond normally remains intact until broken by the death or disappearance of one of the partners; divorces are very rare. On several study plots, 341 marked pairs of Laysan Albatrosses were followed through two nesting seasons (1956–1957 and 1957–1958). The status of the pairs during the second season is shown in Table 3.

DISPLAYS AND VOCALIZATIONS

The principal ritualized display postures are described below. The terminology of Richdale (1949, 1950) has been retained insofar as it was possible to determine homologies from his descriptions and photographs (Richdale's terms are marked with an asterisk in the following account). We found several display postures that have not been previously described for other species of albatrosses: Whinnying, Head-up-and-whine, Head-up-and-clap, and possibly Bowing. We did not observe the following postures in the Laysan and Black-footed albatrosses: Wing-stretching, Wailing, Gulping, Bill-clashing, Tattooing; nor did we observe any aerial activity connected with social relationships. If any of these postures are present in Laysans and Black-foots, they have been so modified that their homologies are not obvious.

Vocalizations

Homologous calls are used by Laysan and Black-footed albatrosses. The calls of the Black-foot have a decided nasal quality and are louder, lower

pitched, and hoarser than those of the Laysan. The primary calls of the adult are the following:

Whinny. This is a wavering wail greatly resembling the whinny of a horse. It is frequently used by Laysans, rarely by Black-foots.

Whine. This is a smooth, long drawn-out scream: *Wheeeeee* in the Laysan, *Haaaaaw* in the Black-foot. It is given with the Head-shake-and-whine and the Head-up-and-whine posture. A similar sound is uttered when a bird is grabbed by a wing tip and prevented from escaping.

Moo. This is a cowlike moo uttered only from the Sky-call posture (Figure 3).

Double-call. This is a high-pitched *eh-eh* in the Laysan, and a donkey-like braying *haw-haw* in the Black-foot. It is uttered chiefly from the Yapping posture.

Yammer. This is a rapidly repeated series of snorting honks habitually given by the Black-foot during aggressive displays, rarely by Laysans.

Displays

All of the display postures described are used by both Laysan and Black-foots. The Black-foot, unlike the Laysan, often keeps its wings slightly fanned while performing the various displays. Minor variations between the two species are noted below.

Bowing. Bowing may be homologous to the Scooping action of Buller's Albatross (Richdale, 1949). It differs in that the tail is not spread. Bowing is performed by bobbing the head, neck, and foreparts up and down.

*Gawky-look.** This distinctive stance, with the head forward, is often assumed by one bird while watching its partner performing, and is assumed in the intervals between other postures in the dance. It also precedes Billing (cf. Frontispiece).

*Billing.** Richdale (1949) also calls this the Rapier action in reference to the Buller's Albatross. It begins with the Gawky-look. The bird then extends its head and bill forward and gently touches the bill of the partner with the tip of its bill. This may be followed by the two birds gently nibbling each other's bills. We were often able to elicit this reaction by pointing a finger toward a bird. The bird would then gently nibble the tip of our finger.

*Mouthing.** This could better be called mutual preening, but we retain Richdale's (1950) term. It is usually performed from the sitting position by mated pairs or birds keeping company. One bird gently nibbles the other on the head, particularly on the cheeks and chin. The partner tilts and turns its head to expose better the parts being nibbled. Often we were able quietly to approach a sleeping bird and simulate Mouthing

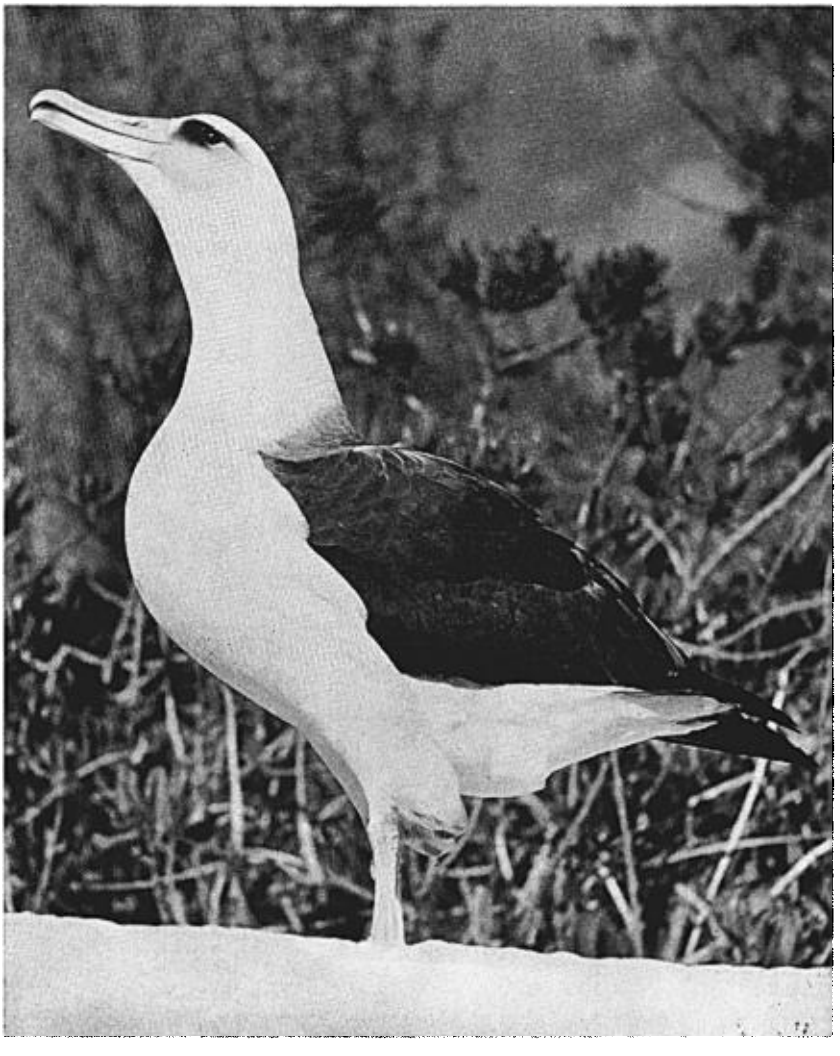


Figure 3. Laysan Albatross showing the Sky-call posture and uttering the Moo. KWK 994.

by gently scratching the bird on the cheek. This would elicit the head turning and tilting, which would continue until the bird opened its eyes.

*Yapping.** Yapping usually is performed from a crouching position. The neck is drawn in; the bill is pointed straight down, or inclined back toward the feet. The Double-call is repeatedly uttered. In the Laysan and Black-footed albatrosses, Yapping differs from the Yapping of Royal Albatrosses (Richdale, 1950) and the Croaking and nodding of Buller's

Figure 4. Yapping is illustrated by the albatross immediately after being disturbed during incubation. Birds always exhibited Yapping behavior when returning to the nest, and often at other times. KWK 57-6-0.

Albatross (Richdale, 1949); however, when its relationship to the birds' activities is considered, their homology seems reasonably certain. Yapping occurs chiefly between pairs keeping company; between mated pairs on their breeding territory, whether nesting or not; and between a bird and its egg or chick (Figure 4).

*Snapping.** From either the sitting or the standing positions, Snapping is performed by sharply closing the bill a few times. It may be performed alone, or in the presence of another bird. Occasionally it is performed in flight. A more intense variation of Snapping is used as threat display toward men, dogs, and other albatrosses; in Black-footed Albatrosses it is often accompanied by the Yammering call.

*Clappering.** The bill is repeatedly opened and closed so rapidly that the lower mandible is blurred. This makes a sound similar to the drumming

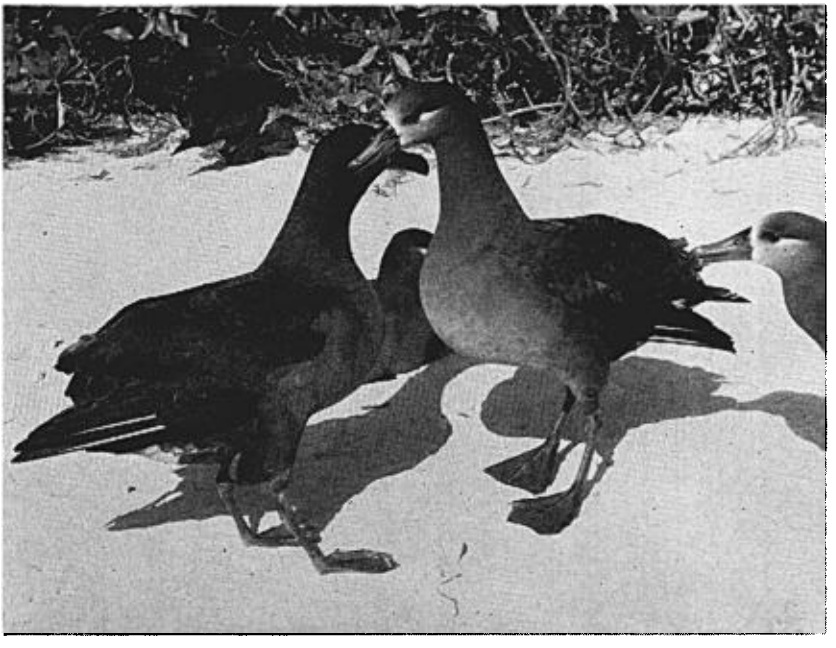


Figure 5. Black-footed Albatrosses exhibiting the Clappering position during the dance ceremony. In the Laysan Albatross the birds face each other in the Clappering position. KWK 57-4-17.

of a woodpecker. When Clappering, Laysan Albatrosses face each other and pull their heads and necks back and hold their bills at a downward angle, nearly parallel to the necks. Black-footed Albatrosses hold their heads side by side, arch their necks forward, and hold the bills downward (Figure 5).

Whinnying. Richdale (1950) confused Hadden's (1941) description of Whinnying in the Laysan Albatross with the Head-shake-and-whine. Whinnying has not been reported in other species of albatrosses. It is used frequently by the Laysan, rarely by the Black-foot. It is performed from the same position as Clappering, and is accompanied by the Whinny call, uttered with the bill nearly closed.

*Head-shake-and-whine.** Head shaking is done from the same stance as Clappering and Whinnying. The head rapidly swings from side to side several times with the beak open, while the Whine is uttered. It is given infrequently.

*Sky-call.** When Sky-calling, the birds rise on the tips of their toes, stretch their necks and point their bills upward. From this position the Moo call is given once with the bill very slightly open (Figure 6). The Sky-call is used frequently in the dance. Single birds may exhibit a less

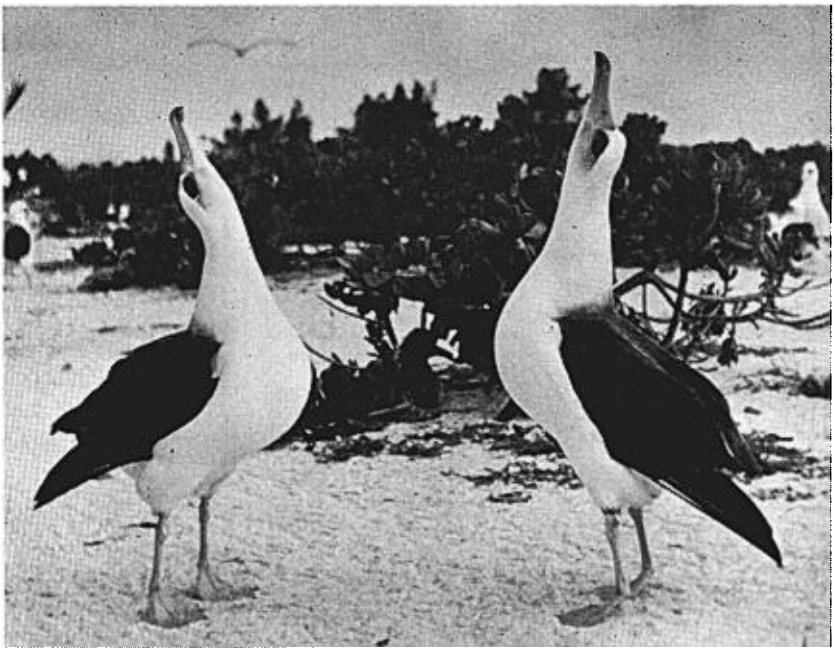


Figure 6. Laysan Albatrosses displaying the Sky-call position. DWR 997.

intense version, in which they may not raise their heads so high, nor stand up on their toes (Figure 3). We have also seen it performed at sea by Black-foots resting on the water. It is never used to call to a bird flying overhead.

Head-up-and-whine. This is given from the same posture as the Sky-call, but the bill is widely opened and the Whine is uttered (Figure 7). It is sometimes given by a bird immediately after it has chased away another bird, and is also given during the dance.

*Scapular-action.** In this posture, the tip of the bill is placed near the bend of the wing and the bill is lightly clappered for one or two seconds. Black-foots fan both wings forward (keeping them partially folded) during this display, but Laysans fan only the wing on the side on which the action is performed (Figures 8 and 9).

Head-up-and-clap. This posture has not been described for other species of albatrosses. It invariably follows the Scapular-action, and is not given at other times. The bird assumes the same posture as for the Sky-call, but snaps the bill once, instead of Mooing. The Head-up-and-clap may be homologous to the Wail of Buller's Albatross (Richdale, 1949), as both usually follow the Scapular-action.

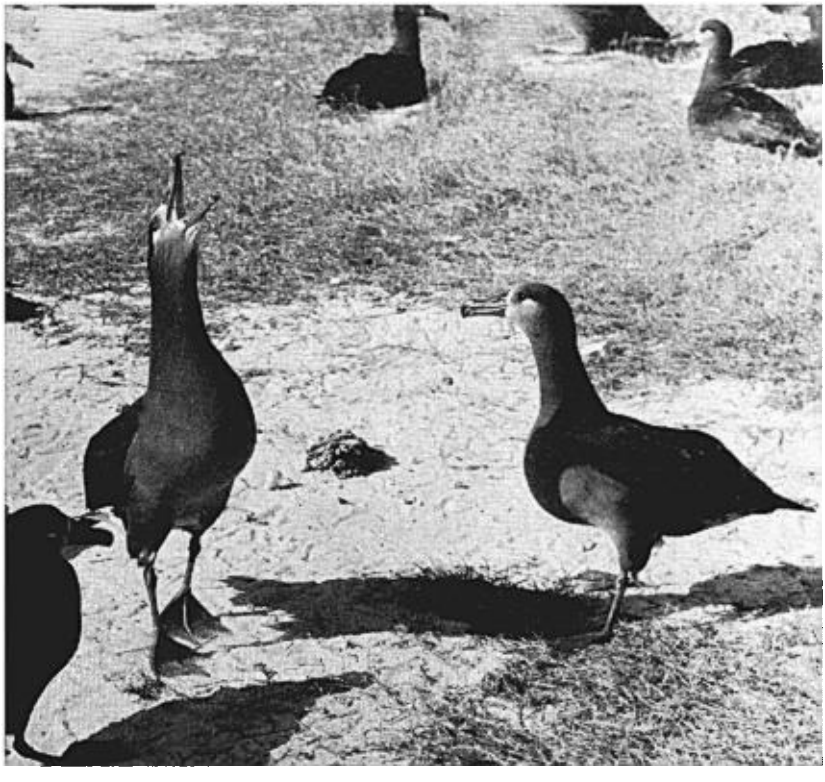


Figure 7. The Black-footed Albatross on the left demonstrates the Head-up-and-whine posture while its dancing partner on the right approaches the Gawky-look. Note that the incubating birds in the background have not built up the edges of their nests to the extent usually done by the Laysan Albatross. KWK 57-4-14.

The Dance

Richdale (1950) terms the dance the "Ecstatic Ritual." The dance is a mutual gamosematic and/or epigamic display. On 6 February 1958 we killed six dancing pairs, and one dancing trio, of Laysan Albatrosses, all apparently unemployed birds. Autopsy revealed that each pair consisted of a male and a female; the trio included one male and two females. Dancing begins with the arrival of the birds on the breeding ground and is discontinued only by mated pairs after nest building has begun. Unemployed birds continue to dance during the entire breeding season, but the frequency of dancing is reduced as the season advances.

In many respects, the dances of the Laysan and Black-footed albatrosses are similar. The differences, however, are apparent to even the casual observer, and are such that birds of the two species, although they may

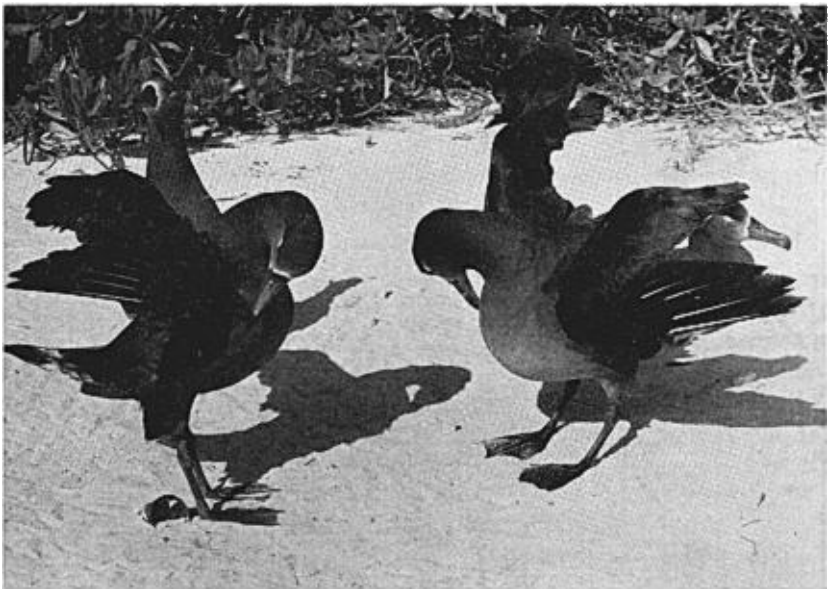


Figure 8. During Scapular-action the Black-footed Albatross fans both wings. KWK 57-4-19.

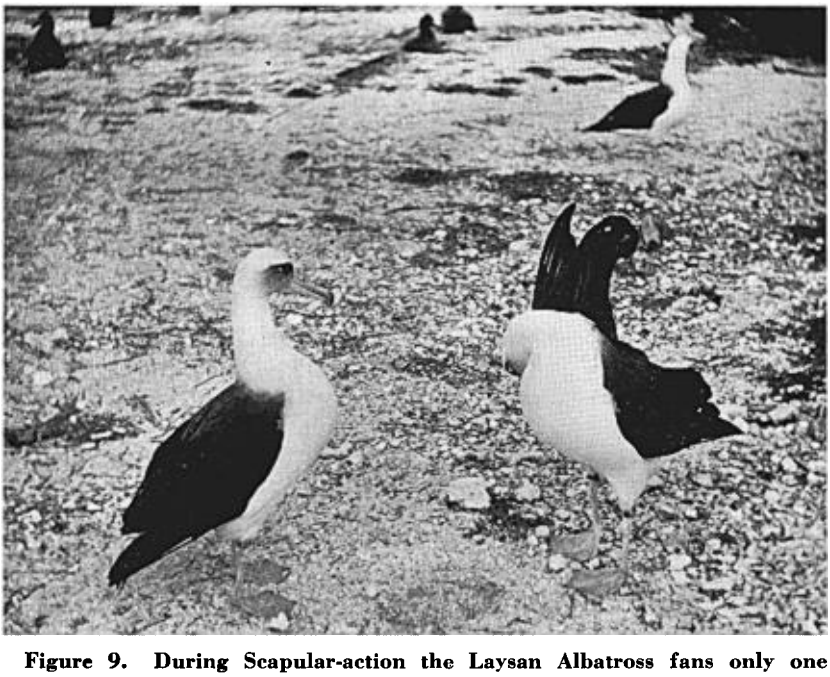


Figure 9. During Scapular-action the Laysan Albatross fans only one wing. DWR 996.

start to dance together, invariably discontinue the affair with shrieks and an attack by one on the other.

A dance begins when two birds face each other, assume the Gawky-look posture, and engage in Billing and Bowing. The displays and vocalizations (as detailed previously) follow in varying sequence. The most frequent displays are Clappering, Whinnying, and Scapular-action, usually terminating with the Head-up-and-clap. The Head-shake-and-whine, Sky-call, and Head-up-and-whine are also performed during the dance. Clappering is usually performed in unison by the two birds, but the other displays are not necessarily synchronized. The most apparent differences in the dances of the two species are in the so-called Scapular-action (Figures 8 and 9), and in Clappering. All actions, however, differ in degree, and a detailed study would reveal rather noteworthy quantitative differences in all analogous rituals of the two species.

TERRITORY

Breeding territory of albatrosses may be classified as Type C of Hinde (1956). It is confined to the immediate vicinity of the nest, and is used only for mating and nesting. In densely occupied areas, nests are far enough apart only to permit a bird (or man) to walk between them without being pecked by setting birds on either side.

Establishment

No albatrosses banded as chicks have been found nesting in subsequent years at the site where they were hatched. On the other hand, two Laysan Albatrosses have been found nesting at some distance from their hatching sites. One hatched on Sand Island in 1937 was found nesting 500 meters away, on the same island, in 1957–1958. Another hatched on Eastern Island in 1951 was found nesting on Sand Island, five km away, in 1957–1958. Of 45 two-, three-, and four-year-old birds recaptured (see Age at First Return), 44 were on the island on which they were hatched (24 Laysans and 18 Black-foots on Eastern Island; 2 Laysans on Sand Island), mostly not far from their hatching sites; one Laysan Albatross hatched on Eastern Island was found dead on Sand Island two seasons later. Of 97 banded Laysans that hatched on Eastern Island in 1951, 14 were killed on Sand Island in 1958, seven seasons later, during a control program on that island; these were apparently mostly unemployed birds (see Age at Sexual Maturity). These records indicate that innubile birds wander and eventually establish territories some distance from their hatching sites.

Apparently very few settle down on other atolls, however. Thousands of albatrosses have been banded on Midway, but, despite diligent search,

TABLE 4
DISTANCE BETWEEN NESTING SITES IN THE 1956–1957 AND 1957–1958 SEASONS, OF 101 MARKED PAIRS OF LAYSAN ALBATROSSES

Distance moved (meters)	*Number of pairs*	*Per cent*
0–1	44	43.5
1–2	34	33.7
2–3	11	10.9
3–4	7	6.9
4–5	3	3.0
5–6	2	2.0
6+	0	0

none of these have been found on Laysan Island, and only one Black-footed Albatross was found at Kure Atoll.

General observations suggest that territory is initially established during the pair-formation period. Many pairs "keeping company" but not nesting show a strong attachment for a particular site, and may even build play nests.

Maintenance

Adult albatrosses, once they have established a breeding territory, return to it season after season. No marked albatross has ever been found nesting at widely separated sites in different years. Many birds banded as adults in 1938 on Sand Island at the site of Gooneyville Lodge (the old Pan-American Airways hotel, destroyed in 1957) were still nesting there during the 1956–1957 and 1957–1958 seasons; none have been found nesting elsewhere.

During the 1956–1957 season, the locations of the nests of 166 marked pairs of Laysan Albatrosses were plotted on a large-scale map. The following year, 1957–1958, 101 of these pairs returned intact and nested. The locations of their nests were again mapped. The two seasons' maps were compared, and the distances the birds moved their nest sites between subsequent seasons were measured. Over 50 per cent of all pairs constructed their nests within 1.3 meters of the previous year's site; none moved farther than six meters (Table 4). In general, those nesting adjacent to an obvious landmark, such as a tree or bush, showed less deviation than those that nested in the middle of a large, open area.

During the nesting season, the adult albatross maintains such a strong affinity for its exact nest site that it will not feed its chick until the latter returns to within a few meters of the nest site (see Parental Care: Recognition between Parents and Young).

Experiments in Displacement of Nests and Chicks

The proposition has been presented that as an aid to reducing the bird

TABLE 5
RESULTS OF EXPERIMENTAL NEST DISPLACEMENT 5 FEBRUARY 1957

Nest No.	*Nest contents*	*Distance moved (meters)*	*Results*[1]		
			5 February	*8 February*	*11 February*
1	Pipped egg	1.0	Move accepted	Move accepted	Move accepted
2	Newly hatched chick	1.5	Move accepted	Move accepted	Move accepted
3	Newly hatched chick	2.0	Not accepted; parent flew off	Chick dead; parent at old nest site	Adults at original nest site
4	Pipped egg	2.0	Move accepted	Chick dead; parent on nest	Adults at original nest site
5	Newly hatched chick	2.0	Move accepted	Chick dead; parents gone	Adults at original nest site

[1] On 14 February area was bulldozed.

populations on Sand Island, Midway Atoll, albatrosses (adults and chicks) might be moved to other islands where they would not interfere with human activities.

Although general observation of albatrosses and ethological studies of other species would indicate that nesting albatrosses could not be successfully displaced any significant distance from their original nest sites, the following experiments were conducted to determine whether or not the Laysan Albatross would accept its nest (and egg or young) after it had been displaced from the original nest site.

On 5 February 1957 the nests and eggs or chicks of five pairs of Laysan Albatrosses were carefully slipped onto a sheet of plywood, and displaced one to two meters from their original sites. Immediately after being moved, three of the adult birds returned to the original nest site (Table 5), although all signs of the nest had been removed and the spot where the nest had been was made to look like its surroundings. The birds were then picked up and replaced on the nest in its new location. Two individuals had to be replaced on their nests two or three times in a period of about 15 minutes, and one parent, becoming quite upset, fled from the area. Four birds, however, appeared to have accepted the new nest position an hour after the displacement. The parent that fled returned to the original nest site, but not to its chick at the new site two meters away. The newly hatched chick died of exposure during the night. Two of the new nest sites, moved respectively 1.0 and 1.5 meters, were ultimately accepted. The fourth and fifth nests, which had been displaced 2.0 meters, appeared for nearly two days to have been accepted. However, the adults then returned to the old nest sites, and by 8 February both chicks were dead. The adults belonging to the three nests that had been moved two meters, and whose chicks had died, were seen at the original nest sites until 14

February, when the study area was unexpectedly bulldozed for building construction.

On 8 February 10 nests containing young, one to two weeks old, were moved distances of 1.0, 2.0, 3.0, 3.5, and 4.0 meters. With one exception the parent present at each nest when it was moved was induced to accept the nest in its new location. The parents occupying nests moved more than two meters had to be induced repeatedly to leave the original nest sites and return to the nest in its new position. On 14 February building construction on the area terminated the experiment so that it was impossible to ascertain the ultimate results of nest displacement.

The questions left unanswered in the experiments are: (1) Would the parent that was originally forced to accept the nest displacement return and feed its chick at the displacement site after going to sea? (2) Would the adult that was at sea when the nest was moved return to the old nest site, and fail to feed its chick at the displacement site?

In addition to the above displacement experiments, we made observations on two instances of accidental displacement:

On 14 February 1957 construction crews began work on a new building. Before bulldozing the area, the crews removed all young and parent albatrosses from the working area. We were not present when this was done, but a crew member told us that when possible parents and young were moved together, and he showed us where they had been placed, at distances of 20 to 100 meters from the original nest sites. Approximately 100 young were displaced; we marked 25 with red dye. The displaced chicks were immediately deserted by their parents. Within a few hours each chick had constructed a new nest. The parents continued to ignore them and returned as nearly as possible to the original nest sites. During the day when construction was in progress they rested outside the construction zone, but each day after working hours they returned to spend the night at or near the old nest sites. At intervals of two to three days during the following weeks we visited the displaced young. Although adults often wandered about near them, none was seen feeding a young bird. The young were not weighed, but it soon became apparent that they were starving. Several of the youngest died in early March. Four died on 17 March and six on 21 March, the remaining 10 to 15 within the next week. The last, nearly dead, was observed on 27 March. Death from starvation thus ranged from about 20 to 42 days.

On 9 March 1957 a *tsunami* washed many five- to six-week-old young Laysan Albatrosses from their nests and deposited them 20 to 50 meters away. A few of the larger individuals returned to their original nest sites, where they were successfully reared. Four individuals that remained where the wave had deposited them, near the bases of trees along a route we often

took, were observed almost daily until they died, two on 10 April and the other two on 14 April, 32 and 36 days respectively after displacement.

From these experiments and observations we conclude that helpless young albatrosses (newly hatched to 10 days old) may be displaced approximately one meter from the original nest site with only moderate danger of desertion or neglect by parents, if parents are moved with the young. If helpless young are moved greater distances, they will usually not be recognized by their parents and will ultimately starve.

Well-fed young, displaced 50 or more meters from their original nest sites at the age of three to six weeks, are usually unable to find their way back to the original nest site, and remain at the new location. They are not recognized or fed by their parents, which continue to frequent the original nest site. All young thus observed died of starvation in approximately a month to six weeks.

Because they survive for a long period without food after being displaced, casual observers at Midway believed that displacements were successful; they failed to associate the eventual death of the young with displacement from the nest site, which took place weeks earlier. Older chicks, which are able to return to the nest site, will survive when displaced for moderate distances if they are not physically prevented from returning to the nest site to be fed. Displaced chicks that cannot return to the original nest site stand a poor chance of successful fledging.

Defense

Albatrosses do not vigorously defend their breeding territories. They will attack an intruder that gets in their way, but they will not leave the nest while they are incubating or brooding. At this time, defense consists only of snapping at or pecking other birds or human intruders that come close to them.

In general, albatrosses get along well with their established neighbors. Defense is directed largely toward unestablished birds that are seeking territories, and mainly serves to establish a minimum distance between nests.

A ritualized display, the Head-up-and-whine, often follows the expulsion of an intruder.

NEST BUILDING

Both sexes participate in the construction of the nest. Nest building begins only one to three days before the egg is laid.

The nests of both species are of the directly adaptive type, consisting primarily of a depression in the sand or humus, with the rim built up to a variable extent. The nest is formed by scraping the material of the substratum backward with the feet. The body is rotated in the depression,

forming it to the shape of the bird, and producing a raised, craterlike edge. The Laysan Albatross, to a greater degree than the Black-foot, uses the bill to rake sand, twigs, and leaves to the rim of the nest; this material is pressed down and compacted with the side of the bill. Material is gathered only while the bird is sitting on the nest. As a result, a ring-shaped moat up to five cm deep often encircles the nest. The hard rim of the nest may project 15 cm above the surrounding surface. The outside diameter of a nest (including moat) is about one meter. The nests of Black-foots are much less built up than those of the Laysan, probably because of the nature of the substratum. In areas of loose sand, most frequently used by Black-foots, nests are little more than scooped-out hollows in the sand.

Albatrosses continue to improve their nests throughout the incubation period and guard stage. Heavy rains always initiate a flurry of nest-building activity by incubating birds, perhaps because the substratum is easier to work when wet.

Newly hatched chicks, particularly the Black-foots, begin kicking sand out of the nest immediately after hatching (Figure 10). The instinctive kicking of sand from the nest by this predominantly open-beach nesting species has survival value during wind storms; if a storm is prolonged, young birds which become exhausted are buried alive.

During the guard stage when chicks become too large to be comfortably brooded, they frequently leave the nest and build a miniature nest of their own, adjacent to and confluent with the original nest on which the parent is sitting.

During the post-guard stage, chicks often build one or more additional nests within 30 meters of the original nest. If the original nest is exposed to sunlight, they may build a nest in the shade for use during the day, and return to the original nest at night. Chick nests never reach the proportions of the better-constructed adult nests.

Nests are often built by nonbreeding pairs, or birds "keeping company."

EGG LAYING

Length of Pre-egg Stage

The interval between the arrival of the first birds and the laying of the first eggs, and the interval between the date when approximately 50 per cent of the birds have arrived and the modal date for egg laying, is 14 to 16 days for the Laysan Albatross, and 18 to 21 days for the Black-footed Albatross.

The length of the pre-egg stage for seven individual Laysan Albatrosses was determined. For six males it varied from 13 to 21 days, with a mean of 16.5. For the one female it was 12 days. A shorter pre-egg stage is indi-

Figure 10. Almost from the moment of hatching, young albatrosses use their feet to kick sand from the nest. This is a survival factor, particularly during wind storms, and is exhibited to a greater extent by the predominantly beach-nesting Black-foots than by the Laysans. DWR 1003.

cated for females, because they tend to arrive on the breeding grounds later than the males.

Clutch Size

Laysan and Black-footed albatrosses lay only one egg per year. Very rarely we found a second egg outside a nest, or even in a nest, but it usually differed in size, shape, and markings from the one in the nest, indicating that it had been dropped by another bird (human interference was responsible for many of the observed cases of two eggs at one nest).

On one study plot the eggs of 95 marked pairs of Laysan Albatrosses were destroyed early in the incubation period. In only two cases did apparent relaying take place. One egg was destroyed on 30 November while the male was incubating; on 2 December a new female was found on the nest, incubating a new egg, with the male beside her. The female that laid the original egg was not in the vicinity. At another nest the egg was

destroyed on 3 December while the male was incubating; on 7 December he was found incubating a new egg. Unfortunately, this egg was accidentally broken, so we were unable to determine which female laid it.

In another experiment the eggs of 70 marked pairs of Laysans were destroyed late in the incubation period. In no instance was a second egg found in any of their nests.

Factors Controlling Clutch Size

To determine if a pair of albatrosses can hatch more than one egg, we gave second eggs to a number of birds at various times during the incubation period. The bird's incubation patch can accommodate only a single egg. Setting birds appear very "uncomfortable" with two eggs, and usually push the second egg out. If it remains in the nest, it does not receive enough heat to develop. Sometimes it will be partially buried in the floor of the nest. In no case did two eggs hatch. In a few instances the presence of two eggs resulted in neither hatching, apparently because alternate incubation of each egg was insufficient to permit them to develop. It is obvious that albatrosses are unable to incubate two eggs.

To determine if a pair of albatrosses can raise two chicks simultaneously, 18 pairs of Laysans were each given a chick in addition to their own. This was done on 11 February when the chicks averaged nine days old. At this early age adult albatrosses will readily accept foster chicks if their own is lost. The chicks were examined at three- to four-day intervals until 21 May.

In at least nine nests both chicks were subsequently fed by the parents. In most cases one chick grew faster than the other. As the chicks grew older, they became increasingly aggressive toward each other, and one usually drove the other several meters away from the nest. On two observed feedings the larger and more aggressive chick received all the food from the parent.

At 15 nests both chicks died. At one nest a single chick survived. At two nests both young survived but one set was so emaciated that their survival to fledging was improbable. Thus out of 18 nests containing a total of 36 chicks, possibly three chicks were fledged. On the average, 18 normal nests (containing one chick each) would fledge about 12 or more chicks. It appears that a clutch of one is the optimum that produces the highest number of fledged chicks per nesting pair.

To determine if a single parent can successfully raise a chick, one member of each of 16 marked pairs of Laysan Albatrosses was killed on 11 and 14 February. The presumed average age of their chicks was 9 to 12 days, and all were at least three days old. The chicks were examined at three- to four-day intervals until 25 July. Three of the chicks were accidentally

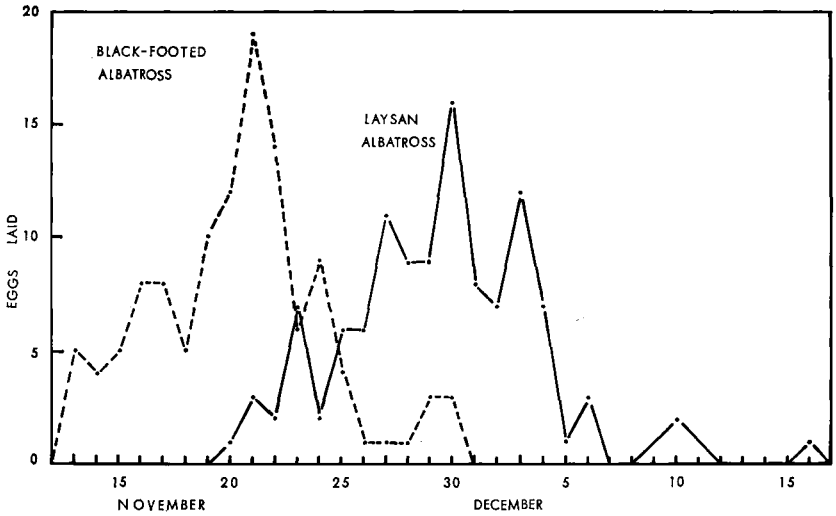


Figure 11. Egg-laying dates of 115 Laysan and 118 Black-footed albatrosses at Midway Atoll in 1957.

killed. Of the remaining 13, only one was fed regularly; the other 12, as evidenced by their frequently empty stomachs and retarded growth, were fed less frequently than normal chicks. Five chicks died of apparent starvation on 21 February, 23 and 28 March, 6 April, and 25 July. Only eight chicks survived. The one that appeared to have been fed regularly was last seen on 2 July and presumably fledged successfully. The other seven were still present on 25 July, well after the normal departure date; one of these was so emaciated that its early death was certain. It thus appears that a single adult is seldom able to supply a chick with sufficient nourishment for normal growth throughout the nestling period.

Time of Egg Laying

Egg laying averages about 10 days earlier in the Black-footed Albatross than in the Laysan Albatross.

In the 1957–1958 season we found the first Black-foot egg on 8 November. On one study plot where 118 nests were under daily observation, laying extended over a period of 18 days, from 13 to 30 November (Figure 11). The mean time of egg laying was 21:00 on 21 November (SE = 11 hr), with a standard deviation of 5.11 days. The median date was 20 November, the mode 21 November.

The first Laysan Albatross egg was found on 15 November. On a study plot where 115 nests were under twice-daily observation, laying extended over 27 days, from 20 November to 16 December (Figure 11). The mean

time of egg laying was 07:00 on 30 November (SE = 12 hr) with a standard deviation of 5.21 days. The mode and median date was 30 November.

Eggs are laid at any time of day. At 115 Laysan nests egg laying occurred during the 14 hours from dusk until dawn 50 times, and during the 10 daylight hours 65 times. At 10 Black-foot nests five eggs were laid at night, five during daylight.

Behavior of Female during Egg Laying

The act of egg laying by Laysan Albatrosses was observed three times—twice briefly, once in detail. In each instance the bird was standing over the nest at the moment the egg was dropped. Field notes on the one complete observation, made at a distance of less than two meters, starting at 17:03 on 4 December 1957, follow:

17:03—Female standing on nest; wings drooping. Cloaca alternately dilating and closing, so that the egg was visible in the cloaca when the latter was dilated. The interval between successive dilations was about seven seconds at first, later slowing to 10 and 11 seconds.

17:10—Cloaca open about 30 mm; egg continuously visible.

17:12:00—Female (still standing) leans back, raising breast, and lowering posterior end of body almost to surface of nest.

17:12:20—Egg drops. Female resumes previous normal standing position, bends head down, and looks at egg. Silent; does not touch egg with beak.

17:12:50—Female settles on egg and begins incubation.

The male was not present when this egg was laid. The female remained on the egg until the next day, when the male arrived. The male took over incubation sometime between 08:00 and 18:00 on 5 December.

INCUBATION

Length of Incubation Period

Ninety-five Laysan Albatross nests were observed twice daily from before egg laying until after hatching. The incubation period varied from 62.5 to 68.0 days (Table 6). The mean was 64.44 days (SD = 1.02; SE = 0.10). The mode was 64.0 days, the median 64.5 days.

Seventy-five nests of Black-footed Albatrosses were observed once daily beginning prior to egg laying and continuing until egg laying was completed, and again from prior to hatching until hatching was completed. The incubation period varied from 63 days to 68 days (Table 7). The mean was 65.57 days (SD = 1.18; SE = 0.14). The mode and median was 65 days.

The difference in the mean length of the incubation period of the two species is highly significant statistically ($P < 0.001$).

TABLE 6
LENGTH OF INCUBATION PERIOD OF 95 LAYSAN ALBATROSS EGGS

Number of days	*Number of eggs*	*Per cent*
62.5	4	4.2
63.0	3	3.2
63.5	14	14.7
64.0	23	24.2
64.5	22	23.1
65.0	14	14.7
65.5	6	6.3
66.0	2	2.1
66.5	5	5.3
67.0	0	
67.5	1	1.1
68.0	1	1.1

Participation of the Sexes

Both male and female albatrosses share in incubation. While one bird is setting, its mate remains at sea. The egg is incubated continually from laying until hatching and is never left unattended, even briefly, either during an incubation span or during nest relief. On 110 Laysan Albatross nests under regular twice-daily observation for a total of 7,319.0 nest days, the male was incubating 4,099.0 (56 per cent) days, the female 3,220.0 (44 per cent) days. On 35 Black-foot nests under observation for 1,925.5 nest days, the male was incubating 1,026.5 (53 per cent) days, the female 899.0 (47 per cent) days. The lesser amount of time spent incubating by the female is due primarily to the shortness of her first incubation span or shift.

Both sexes develop an incubation patch. In non-nesting birds it is partially or completely covered with short, gray down. The down is shed before the start of incubation, leaving an oval, slightly concave, bare area just large enough to accommodate the single egg.

Foreign objects such as rocks, coffee cups, and beer cans are readily accepted in lieu of the egg, and are incubated for the full term, even if the egg is in sight near the nest.

TABLE 7
LENGTH OF INCUBATION PERIOD OF 75 BLACK-FOOTED ALBATROSS EGGS

Number of days	*Number of eggs*	*Per cent*
63	1	1.3
64	13	17.3
65	25	33.3
66	20	26.7
67	10	13.3
68	6	8.0

TABLE 8
LENGTH OF INCUBATION SPANS OF LAYSAN ALBATROSSES

Span number	*Sex*	*N*	*Number of days*			
			M	*SD*	*95% confidence interval*	*Range*
1	♀	110	2.53	3.59	1.85– 3.21	<0.5–17.0
2	♂	110	22.58	4.41	21.74–23.41	1.5–32.0
3	♀	110	21.69	4.11	20.91–22.47	13.5–38.0
4	♂	101	14.80	3.63	14.09–15.52	6.0–23.5
5	♀	75	7.32	2.86	6.66– 7.98	2.5–18.0
6	♂	17	7.09	2.48	5.82– 8.36	4.0–12.5
7	♀	2	5.50			4.0– 7.0
Last[1]	♂ or ♀	95	8.32	4.23	7.45– 9.18	2.5–26.5

[1] Span during which egg hatched, regardless of number (includes, in part, spans 3 to 7).

When an albatross returns to relieve its mate at incubation, the setting bird is reluctant to leave the nest. The pair may remain together at the nest for several hours, indulging in Mouthing and giving the Double-call. Finally, the newly arrived bird manages to displace its mate from the nest. Once displaced, the previously incubating bird does not attempt to get back on the nest; it shortly leaves and heads out to sea.

Of 385 recorded changeovers of Laysan Albatrosses, 108 (28 per cent) took place during the 14 hours from dusk until dawn, 277 (72 per cent) during the 10 hours of full daylight. Of 165 changeovers by Black-foots, 61 (37 per cent) took place at night, 103 (63 per cent) during daylight. Most of the changeovers recorded as having occurred during the night probably took place between 18:00 and darkness, or between dawn and 08:00. During the hours of darkness, albatrosses are seldom seen in flight over land and are generally inactive.

Incubation Spans

Incubation spans by individual birds are prolonged. Laysan Albatrosses incubate for significantly longer spans than do Black-foots. Statistical data on the length of the incubation spans of 110 pairs of Laysans and 33 pairs of Black-foots are presented in Tables 8 and 9, and are shown graphically in Figure 12. The length of incubation spans is determined, of course, not by the setting bird, but by the length of time its mate remains at sea.

The females of both species remain on the egg for only a short period after laying. The female is normally relieved by the male within three or four days.

The second span (the first by the male) is much longer than the first, and is usually the longest span of the entire incubation period. In the Laysan Albatross, it averages 22.58 days, and may last as long as 32.0 days. In the Black-foot, the second span averages 18.16 days, with a maximum of 34.0 days.

TABLE 9

LENGTH OF INCUBATION SPANS OF BLACK-FOOTED ALBATROSSES

Span number	*Sex*	*N*	*Number of days*			
			M	*SD*	*95% confidence interval*	*Range*
1	♀	12	3.62	3.92	1.16– 6.09	<0.5–11.5
2	♂	19	18.16	7.24	14.69–21.69	8.0–34.0
3	♀	33	15.77	4.41	14.21–17.33	7.0–23.0
4	♂	31	17.02	6.04	14.80–19.23	7.0–39.0
5	♀	30	9.95	3.83	8.52–11.38	3.0–17.5
6	♂	16	8.84	3.91	6.77–10.91	3.5–18.0
7	♀	7	4.50			0.5– 9.5
8	♂	4	2.50			1.5– 5.0
9	♀	1	2.00			
10	♂	1	1.00			
11	♀	1	3.50			
12	♂	1	1.50			
Last[1]	♂ or ♀	26	7.15	4.25	5.44– 8.87	1.5–14.5

[1] Span during which egg hatched, regardless of number (includes, in part, spans 5 to 8, and 12).

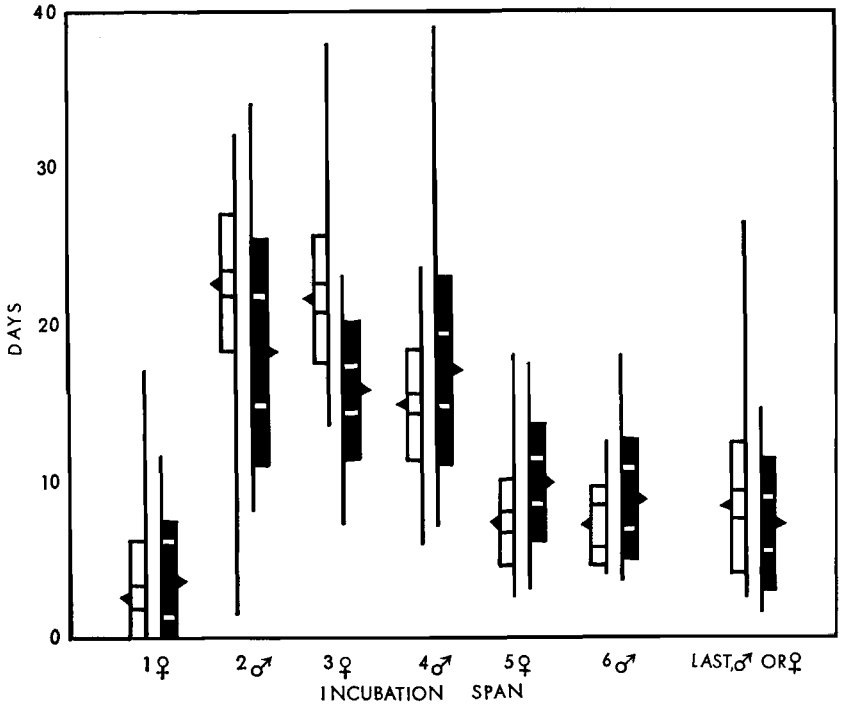


Figure 12. Length of incubation spans of Laysan Albatrosses (white bars) and Black-footed Albatrosses (black bars). Vertical line indicates the range; triangle, the mean; vertical bar, one standard deviation above and below the mean; crosslines inside bar, the 95 per cent confidence interval.

TABLE 10
SPAN DURING WHICH HATCHING OCCURRED AT 94 LAYSAN ALBATROSS NESTS AND 26 BLACK-FOOTED ALBATROSS NESTS

Number of spans	*Laysan Albatross*		*Black-footed Albatross*	
	No.	*Per cent*	*No.*	*Per cent*
3	1	1.0		
4	22	23.4		
5	54	57.4	11	42.3
6	15	16.0	8	30.8
7	2	2.1	3	11.5
8			3	11.5
9				
10				
11				
12			1	3.8

In the Laysan Albatross the third span (the second by the female) is only slightly shorter than the second. The fourth span (the male's second) is significantly shortened to a mean of 14.80 days. The fifth and subsequent spans are further shortened to a mean of less than eight days. In the Black-footed Albatross the third and fourth spans are only slightly shorter than the second. There is a marked reduction to a mean of 9.95 days during the fifth span, and each succeeding span is progressively shorter.

At 94 Laysan Albatross nests the egg hatched during the third to the seventh span (Table 10); the majority hatched during the fifth span (M = 4.95; SD = 0.725; SE = 0.075). At 26 Black-foot nests the egg hatched during the fifth to the eighth spans, except for one that hatched during the twelfth (Table 10); the mode was the fifth span (M = 6.15; SD = 1.567; SE = 0.308).

The mean length of the span during which hatching occurred (regardless of number) was 8.32 days in the Laysan, 7.15 days in the Black-foots (Tables 8 and 9).

The longest normal (relieved) spans recorded during this study were 38.0 days in the Laysan Albatross, 39.0 days in the Black-foot. Incubating albatrosses that are not relieved, due to desertion by or death of their mates, remain on their nests longer than normal. Maximum spans were 42.0 and 52.0 days by two female Laysans, and 41.5 and 49.0 days by two female Black-foots.

Incubating birds lose considerable weight during the long incubation spans; no food is ingested while they are incubating, and they drink only a few drops of rain, which they avidly attempt to catch with open upstretched beak. We weighed 17 incubating Laysans at four- to six-day intervals over four- to 23-day incubation spans. In Table 11 the initial and final weights of these birds are presented. Weight loss may exceed 20 per

TABLE 11
WEIGHT LOSS OF LAYSAN ALBATROSSES DURING INCUBATION[1]

Number days incubating	*Weight (kg)*		*Loss*	
	At start	*At end*	*kg*	*Per cent*
4	3.12	3.01	0.11	3.5
5	2.38	2.32	0.06	2.5
5	2.55	2.44	0.11	4.3
6	3.29	3.12	0.17	5.2
9	2.61	2.44	0.17	6.5
9	3.06	2.78	0.28	9.1
10	3.46	2.87	0.59	17.1
11	3.69	3.17	0.52	14.1
11	2.78	2.61	0.17	6.1
11	2.61	2.38	0.23	8.8
11	2.83	2.44	0.39	13.8
11	2.89	2.66	0.23	7.9
12	3.69	3.29	0.40	10.8
16	3.35	2.61	0.74	22.1
16	3.23	2.66	0.57	17.6
17	2.78	2.32	0.46	16.5
23	2.61	2.04	0.57	21.8

[1] Sex of birds not determined.

cent during a long span. Weight loss is most rapid during the first few days. In general, the heavier birds lose weight more rapidly than do the lighter ones, probably because initial weight loss results from food digestion, while subsequently it is due to the utilization of fat reserves.

Long incubation spans permit the birds to range widely between spans. Homing experiments (Kenyon and Rice, 1958) have revealed that albatrosses can cover more than 5,000 km in 10 days. Thus they could travel to any part of their North Pacific range and return during a normal 20- to 25-day period between incubation spans. One banded Laysan Albatross (U.S. 587–51729) incubating on 3 December 1956 was captured 22 days later 3,700 km away at 42°30′ N, 144°00′ E, off Hokkaido, Japan.

In length of incubation spans albatrosses exceed most other sea birds, and are equaled or exceeded only by certain species of penguins. The trend is carried to the extreme by the Emperor Penguin (*Aptenodytes forsteri*) of Antarctica, in which the male takes charge of the egg immediately after laying, and incubates continuously for the entire 62- to 64-day period (Stonehouse, 1960).

HATCHING

Hatching dates of 85 Black-footed Albatross eggs extended over a period of 24 days, from 15 January until 7 February (Figure 13). The mean time of hatching was 04:00 on 25 January (SE = 14 hr), with a standard deviation of 5.31 days. The modal dates were 25 and 26 January, the median 25 January.

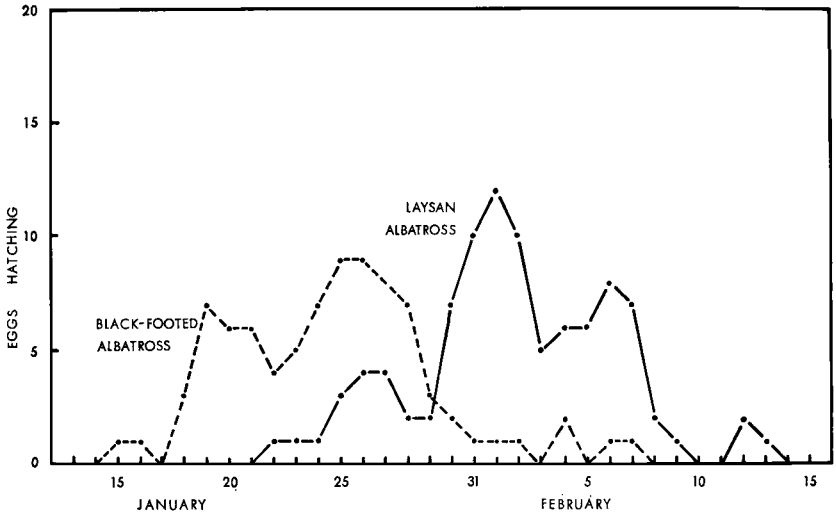


Figure 13. Hatching dates of 95 Laysan Albatross eggs and 85 Black-footed Albatross eggs at Midway Atoll in 1958.

The eggs of 95 Laysan Albatrosses hatched over a period of 23 days, extending from 22 January to 13 February (Figure 13). The mean time of hatching was 11:00 on 2 February (SE = 13 hr). The modal date was 1 February, the median 2 February.

The process of hatching is prolonged, as in other species among the lower orders, and requires from about 48 to 132 hours for completion. A typical example follows: The first tiny crack appeared on the surface near the large end of a Laysan Albatross egg on 27 January 1957 at 14:00; 19 hours later the bill protruded through a hole 10 × 3 mm; at 24 hours the hole measured 10 × 10 mm; at 51 hours, 20 × 50 mm; at 66 hours, 60 × 30 mm; and at 71 hours the shell had broken apart and the chick was working free of the membrane and shell fragments.

The eggs of 95 Laysan Albatrosses, examined twice daily, were pipped 59.0 to 65.0 days after laying (Table 12). The mean was 61.22 days (SD = 1.54; SE = 0.16). The mode and median was 61 days. Seventy-four Black-footed Albatross eggs, examined once daily, were pipped at 60 to 65 days after laying (Table 13). The mean was 62.57 (SD = 1.18; SE = 0.14). The mode and median was 62 days.

At 95 Laysan Albatross nests the chick was free of the shell 2.0 to 5.5 days after pipping (Table 14). The mean was 3.23 days (SD = 0.65; SE = 0.07). The mode and median was 3.0 days. At 82 Black-foot nests the eggs hatched one to five days after pipping (Table 15). The mean was 3.01 days (SD = 0.68; SE = 0.08). The mode and median was 3.0 days.

TABLE 12
INTERVAL BETWEEN LAYING AND PIPPING OF 95 LAYSAN ALBATROSS EGGS

Number of days	*Number of eggs*	*Per cent*
59.0	1	1.1
59.5	4	4.2
60.0	12	12.6
60.5	18	18.9
61.0	22	23.1
61.5	15	15.8
62.0	8	8.4
62.5	4	4.2
63.0	5	5.3
63.5	4	4.2
64.0		
64.5	1	1.1
65.0	1	1.1

PARENTAL CARE

Brooding and Attending

The nest life of an albatross chick is divided into two stages: the guard stage and the post-guard stage (Richdale, 1952). The guard stage is that period following hatching during which one parent remains at the nest with the chick.

For the first few days, while the chick is small and inactive, it is brooded by the parents. It grows rapidly, however, and soon becomes too large to be brooded comfortably. It also becomes more alert, and is not content to remain under the parent. Its head frequently protrudes from under the parent's breast, wing, or tail. When it gets too large to be brooded, one of the parents sits beside the nest and guards it. Or, if the parent is reluctant to leave the nest, the chick may build its own miniature nest beside the original nest.

The male and female share equally in guarding the chick. At 93 Laysan Albatross nests under regular observation for a total of 1,311.0 nest days from hatching until the chick was first left unattended, the male was guarding the chick 651.5 (49.69 per cent) days, the female 659.5 (50.31

TABLE 13
INTERVAL BETWEEN LAYING AND PIPPING OF 74 BLACK-FOOTED ALBATROSS EGGS

Number of days	*Number of eggs*	*Per cent*
60	1	1.4
61	12	16.2
62	27	36.5
63	17	23.0
64	12	16.2
65	5	6.8

TABLE 14
INTERVAL BETWEEN PIPPING AND HATCHING OF 95 LAYSAN ALBATROSS EGGS

Number of days	*Number of eggs*	*Per cent*
2.0	6	6.3
2.5	12	12.6
3.0	35	36.8
3.5	24	25.3
4.0	13	13.7
4.5	3	3.1
5.0	1	1.1
5.5	1	1.1

per cent) days. At 25 Black-foot nests under observation for 409.0 nest days, the male was on guard 211.0 (51.59 per cent) days, the female 198.0 (48.41 per cent) days. Therefore, we have not segregated by sex the data on length of guard spans (Tables 16 and 17).

Guard spans are much shorter than incubation spans. In both species, the first span following hatching averages less than three days. The longest recorded guard span was six days. There is a gradual but slight decrease in subsequent spans, to a mean of less than two days by the seventh span.

Laysan Albatross chicks were guarded continuously for three to 10 spans (M = 6.00; SD = 1.302; SE = 0.135) (Table 18); Black-foot chicks were guarded for five to 12 spans (M = 7.58; SD = 1.612; SE = 0.329) (Table 18).

Ninety-four Laysan chicks were first left unattended at 12.0 to 24.5 days of age (M = 17.18; SD = 2.47; SE = 0.26). Twenty-four Black-foot chicks were first left unattended at 12.5 to 24.5 days of age (M = 19.12; SD = 2.65; SE = 0.54).

Among 93 Laysan nests the male was the first to leave the chick unattended at 45 (48.4 per cent) nests, the female the first at 48 (51.6 per cent) nests. Among 24 Black-foot nests the male was first to leave at 14 (58.3 per cent) nests, the female at 10 (41.7 per cent) nests.

After the chicks are left unattended for the first time, they are guarded intermittently during another 10 days or so. Ninety-two Laysan chicks were guarded for the last time at 17.5 to 40.0 days of age (M = 27.29;

TABLE 15
INTERVAL BETWEEN PIPPING AND HATCHING OF 82 BLACK-FOOTED ALBATROSS EGGS

Number of days	*Number of eggs*	*Per cent*
1	1	1.2
2	13	15.9
3	53	64.6
4	14	17.1
5	1	1.2

TABLE 16
LENGTH OF GUARD SPANS OF LAYSAN ALBATROSSES[1]

Span number	*N*	*Number of days*			
		M	*SD*	*95% confidence interval*	*Range*
1	93	2.66	0.84	2.49–2.83	0.5–5.0
2	93	2.28	0.64	2.15–2.41	1.0–4.0
3	93	2.48	0.71	2.33–2.63	1.5–5.5
4	92	2.40	0.81	2.23–2.57	1.0–5.0
5	80	2.53	0.82	2.35–2.71	1.0–5.5
6	62	2.02	0.91	1.79–2.25	0.5–4.0
7	31	1.71	0.63	1.48–1.94	1.0–3.0
8	11	1.41	0.62	0.99–1.83	0.5–2.5
9	2	1.25			1.0–1.5
10	1	0.50			
Last[2]	93	1.94	1.16	1.70–2.18	0.5–5.5

[1] Does not include the intermittent spans subsequent to the time the chick is first left unattended.
[2] Span following which chick was first left unattended, regardless of number (includes, in part, spans 3 to 10).

SD = 4.67; SE = 0.49). The 24 Black-foot chicks were last guarded at an age of 21.5 to 42.5 days (M = 29.79; SD = 6.93; SE = 1.41).

During the post-guard period the parent birds visit the chick only briefly to feed it.

Feeding

The chick is fed by regurgitation, which is stimulated in the parent when the hungry chick pecks or "nibbles" at its bill. The chick inserts its bill

TABLE 17
LENGTH OF GUARD SPANS OF BLACK-FOOTED ALBATROSSES[1]

Span number	*N*	*Number of days*			
		M	*SD*	*95% confidence interval*	*Range*
1	24	2.83	1.29	2.29–3.37	0.5–5.5
2	24	2.50	0.72	2.20–2.80	1.0–4.5
3	24	2.15	0.71	1.85–2.45	0.5–3.5
4	24	1.98	0.77	1.65–2.31	0.5–3.0
5	24	2.00	0.98	1.59–2.41	0.5–4.5
6	23	2.54	1.23	2.01–3.07	0.5–6.0
7	19	1.84	0.96	1.38–2.30	0.5–4.0
8	8	2.31	0.92	1.56–3.06	1.5–4.0
9	7	1.93			0.5–4.0
10	3	1.83			0.5–4.0
11	1	2.50			
12	1	0.50			
Last[2]	24	1.98	1.54	1.33–2.63	0.5–6.0

[1] Does not include the intermittent spans subsequent to the time the chick is first left unattended.
[2] Span following which chick was first left unattended, regardless of number (includes, in part, spans 5 to 12).

TABLE 18

NUMBER OF GUARD SPANS FROM FIRST CHANGEOVER FOLLOWING HATCHING UNTIL CHICK WAS FIRST LEFT UNATTENDED

Number of spans	*Laysan Albatross*		*Black-footed Albatross*	
	No.	*Per cent*	*No.*	*Per cent*
3	1	1.1		
4	12	12.9		
5	18	19.4	1	4.2
6	31	33.3	4	16.7
7	20	21.5	11	45.8
8	9	9.7	1	4.2
9	1	1.1	4	16.7
10	1	1.1	2	8.3
11				
12			1	4.2

crosswise between the parent's mandibles, allowing the oil and partially digested stomach contents (which spurt as if from a hose nozzle) to pour into the distended throat (Figure 14). During a single feeding visit, which, after the guard stage, may last from 15 to 25 minutes, the parent may feed the chick three or four times.

While its parents are absent, a chick may wander over an area up to 30 meters in diameter and build a number of nests for itself, but it is always fed by returning parents at or near the original nest site.

Figure 14. The parent albatross is stimulated to regurgitate when the chick nibbles and pecks at its bill as illustrated here. KWK 995.

The following incident illustrates a typical feeding visit by a Laysan Albatross: On 18 June 1957 a marked chick rested in a nest it had constructed about 25 meters from its home nest. At 07:15 one of its parents returned from a feeding expedition at sea. At this stage in the breeding period, several days may elapse between feedings, and, in this case, the chick appeared quite hungry and anxious to be fed. It was directly in the path of the returning parent; as the parent approached, giving the Double-call, the chick answered and assumed begging posture. The parent, however, completely ignored the chick, hurried past it, and proceeded directly to the nest where it assumed the Yapping posture while uttering the Double-call. The chick, which had followed giving the begging '*peep-peep*' call, was recognized and subsequently fed by the parent only after it had taken position on the old nest. After feeding, the parent departed at 07:28.

After feeding their own chicks parents of both the Laysan and Black-footed albatrosses often rush to the nearest neighboring nest and attack the unattended young. While running to the attack a high-pitched shriek is uttered, the head is lowered and the neck extended. The chick being attacked exhibits Facing-away behavior, exposing the back of its neck to the attacking adult, which grasps the neck, shaking and pinching it vigorously for five to 10 seconds. Certain adults are more violent in their attacks than others. Young repeatedly attacked by such an adult may be bare of down and bloody on the back of the head and neck. Death sometimes occurs in such cases. In general, the attacks of Black-foots are more violent than those of Laysans. Submissive behavior is among the first behaviorisms expressed by the newly hatched chicks. Perhaps because the attack behavior is more violently expressed in the Black-foot than in the Laysan, submissive behavior is expressed earlier and with greater frequency in the newly hatched Black-foot than in the Laysan. Unfortunately, no quantitative behavior data were recorded.

The frequency of feeding was determined for 12 Laysan and five Black-foot chicks by weighing them twice daily during the first 30–40 days of life. If the chicks had been fed during the previous half day, an increase in weight was apparent. Weight records for two of these chicks have been graphed in Figures 15 and 16, which illustrate the relation between feeding frequency and the presence of the parents.

During the first two weeks or so following hatching, while the parents continually brood or guard the chick, they feed the chick frequently. During 186.0 nest days of observation of Laysan chicks, feeding was recorded 211 times, for an average interval of 0.88 days between feedings. During 71.0 nest days of observation of Black-foots, feeding was recorded 68 times, for an average interval of 1.04 days.

During the latter phase of the guard stage, when the parents guard the

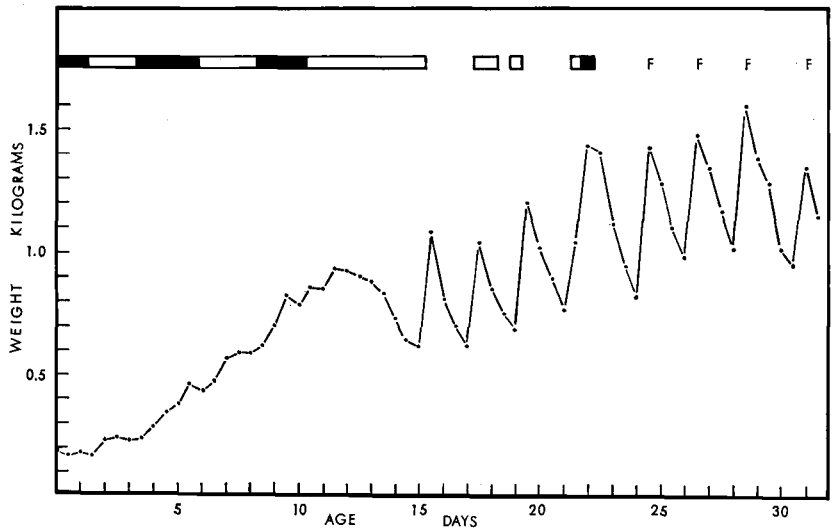


Figure 15. Parental care and weight of Laysan Albatross chick No. 99. Black bar=male guarding; white bar=female guarding; F=feeding visit.

chick only intermittently, feeding of Laysan chicks was recorded 56 times during 79.5 nest days of observation, for an average interval of 1.42 days. Feeding of Black-foot chicks was recorded 15 times during 29.5 nest days, an average interval of 1.97 days.

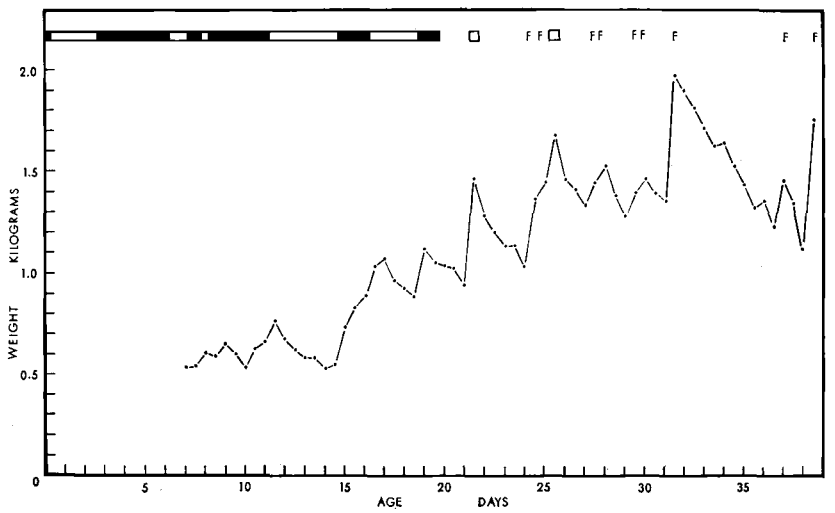


Figure 16. Parental care and weight of Black-footed Albatross chick No. 33. Black bar=male guarding; white bar=female guarding; F=feeding visit.

Following the end of the guard stage, the chicks are fed much less frequently. Observations of Laysan Albatross chicks totaling 66.5 nest days revealed only 27 feeding visits by the parents, or one every 2.46 days. Black-foot chicks, during 57.5 nest days, were fed 20 times, or once every 2.87 days.

General observations suggest that feeding visits become somewhat less frequent as the chick grows larger, but we have insufficient data to demonstrate this.

The chick is more often fed during daylight hours. Of 294 recorded feedings of Laysan chicks, 185 occurred during the 10 daylight hours, and 109 occurred during the 14 hours from dusk until dawn. Of 103 feedings of Black-foot chicks, 58 occurred during daylight, and 45 during darkness. Most of the "night" feedings probably occurred during the twilight or dawn hours.

Function of Stomach Oil

The origin and function of the stomach oil of procellariiform birds has been the subject of much controversy. Matthews (1949) has demonstrated that it is a secretion of the proventriculus, and he has reviewed all the hypotheses regarding its function, some of which appear quite imaginative. Our observations of albatrosses and several petrels and shearwaters demonstrate beyond question that the oil serves primarily as a food for the chick, and is thus analogous to pigeon milk; in some species (but not in albatrosses) it is secondarily utilized as a defense mechanism. In support of this theory we present the following facts:

1. Stomach oil is produced in quantity only by breeding albatrosses; it first appears near the end of the incubation period. Unemployed birds, and breeding birds during early stages of incubation, when roughly handled, may vomit mostly greenish bile or digestive fluids, or partially digested food, with no more than a trace of stomach oil.

2. Newly hatched chicks are fed exclusively with stomach oil for the first few days; the oil forms a large proportion of the diet of older chicks.

3. Albatrosses do not deliberately eject the oil for defensive purposes. When highly excited they may vomit up large quantities, but it is not directed at an intruder. (Some species of petrels apparently eject oil through the nostrils as a defensive action; albatrosses never eject the oil through their nostrils.)

4. The oil is definitely not used for preening. The plumage of albatrosses has a characteristic sweetish, rather pleasant, somewhat cowlike odor. Their stomach oil has a penetrating, nauseating, "fishy" odor, completely unlike that of the plumage, and it would be easily noticed if it were applied to the plumage.

Experiments should be conducted to determine the exact chemical composition of the oil, and its function in the nutrition of the chick.

Recognition between Parents and Young

Residents at Midway frequently move newly hatched, orphaned chicks to nests of pairs whose own egg or chick was destroyed; the foster chicks are readily accepted and cared for. Two quantitative studies were undertaken which indicated that up to about 10 days of age, at least, parents do not recognize their own chicks. By the time chicks have reached the age of six to seven weeks, most parents recognize their own young and will not feed a strange chick which has been exchanged for their own. (See Tinbergen, 1958: 145, regarding parental recognition among the Laridae.)

1. *Interspecific exchange of newly hatched chicks.* In an area where Black-footed and Laysan albatrosses nested in a mixed colony, young birds or eggs from five nests of each species were exchanged with eggs or chicks of comparable age of the other species. The exchanges were made on 5 February 1957 as follows: (1) Two pairs of nests—eggs exchanged; (2) two pairs of nests—newly hatched young exchanged; (3) one pair of nests—young about 10 days old exchanged. Sixteen observations were made at intervals of two to four days, the last on 8 April, 63 days after the exchange.

All eggs and young were apparently accepted by their foster parents. However, two Black-foot chicks, newly hatched when exchanged, died, apparently of starvation, one on the 6th day after the exchange and the other on the 49th day. When observations were terminated, all remaining young appeared to be in excellent condition.

It was observed in several instances that when a Laysan parent was feeding a Black-foot chick, the feeding foster parent appeared disturbed by the chick's behavior, which is more aggressive and "rough" than in the Laysan chick. The fact that no Laysan chicks given to Black-foot foster parents died, while two Black-foot chicks given to Laysan foster parents did die, may indicate that, in individual cases, the difference in behavior of the Black-foot chicks disturbed the foster parent Laysan Albatrosses to the extent that feeding was inhibited. Other Laysan foster parents, however, appeared to become well adapted to the behavior of their foster young, which they reared in excellent health. The experiment, however, was conducted on such a small scale that a positive conclusion could not be drawn.

The observations were discontinued primarily because time was needed for other studies. The chicks, at about the age of two months, often wandered 10 to 20 meters from their nests and sought shelter under

Scaevola bushes, so that much time was required to find them and read their leg bands.

One Black-foot chick that was raised by Laysan foster parents on the Post Office lawn during the 1958 season was an exceptionally healthy individual, and was successfully fledged.

2. *Intraspecific exchange of older chicks.* On 20 March two plots about 25 meters apart were selected on Eastern Island. Ten young Laysan Albatrosses, about six to seven weeks old, from one plot were exchanged for 10 young of comparable size and age from the other. The birds were each marked with regulation leg bands and red dye. Each of the 20 nests was marked with a numbered stake. An hour after being placed in the strange nests, 10 of the young had moved out of them, several as far as two meters. All were replaced in their foster nests, and most remained in or near them until the study was discontinued on 23 May. After the nest exchange on 20 March, only one chick returned to its original nest, and it was returned to its foster nest on 23 March. The young were first weighed on 23 March and were subsequently weighed on 14 occasions.

Among the 20 chicks given to foster parents, 12 were never fed, and starved to death. The mean survival time was about 22 days, with extremes of eight and 36 days. The other eight chicks were fed regularly, presumably by the adults in whose nests they were placed. The mean gain in weight in 68 days was 0.72 kg; the minimum gain was 0.36 kg, and the maximum gain was 1.42 kg. One individual, although fed on several occasions, showed a net loss of 0.25 kg at the end of the study period. Although still in apparently good health when the study terminated, there appeared little chance that it, and even others showing some weight gain, would ultimately survive. To be conclusive this experiment should have been carried on until all young had left or died. It is probable that some young, being fed by only one foster parent, would have survived until the feeding cycle of the attending adult terminated, and then would have died because of retarded development.

It is concluded that at this age, recognition of chicks by their parents has become established to the extent that over half of the parents failed to feed a strange chick substituted for their own.

The parents definitely recognize their chick when it is older, and strange chicks are attacked (see Feeding).

Older chicks also recognize their parents. When a parent bird returns from the sea and alights near the nest, the chick, which may be 30 meters away, immediately rushes up to the parent and begins begging. Other adults it ignores. Starving chicks, however, will beg from any adult passing nearby.

Nest Sanitation

When defecating, nestling albatrosses raise the posterior part of the body and eject the feces in a forceful stream a meter or more beyond the nest. Thus the nest is kept clean. This behaviorism is present in the chick at hatching. The small quantity of feces emitted by both incubating and young albatrosses is surprising when compared in general with that of other marine birds.

Nest Defense

During the guard stage, as during incubation, adult albatrosses will snap at and attempt to bite intruders—whether they be men, dogs, or other albatrosses. (All dogs on Midway soon learn to ignore albatrosses, both adults and chicks.) Albatross chicks are much more aggressive than are their parents. They keep up a rapid, continuous snapping of the beak when approached closely. While Snapping, Black-foot chicks usually utter a snorting nasal grunt, which corresponds to the Yammer of the adult, but Laysan chicks are usually silent.

DEVELOPMENT OF YOUNG

Newly hatched albatrosses are altricial, nidicolous, and ptilopaedic.

Growth

The bill, wing, tarsus, and middle toe of 10 Laysan and five Black-footed albatross chicks were measured at five-day intervals from hatching until age 75 days, by which time they had nearly attained adult weight (Figure 17). The rate of weight increase of these chicks is illustrated in Figure 18. Other duties prevented the continuation of these observations until the chicks were fledged.

Plumages

The plumages and plumage sequence of Laysan and Black-footed albatross chicks appear almost identical. The only obvious difference is the lighter coloration of the Black-foot chicks, due to more extensive white tips on the down. The bill of the newly hatched Laysan chick is blue-gray, that of the Black-foot is black.

The gray, white-tipped natal down is moderately long, loose, and ragged, with a distinct peppercorn appearance (Figure 19). Almost immediately after hatching, the mesoptiles begin to grow, the protoptiles remaining attached to their tips. By the end of the guard stage, the chick is covered with the long and very dense coat of secondary down, still retaining the peppercorn appearance.

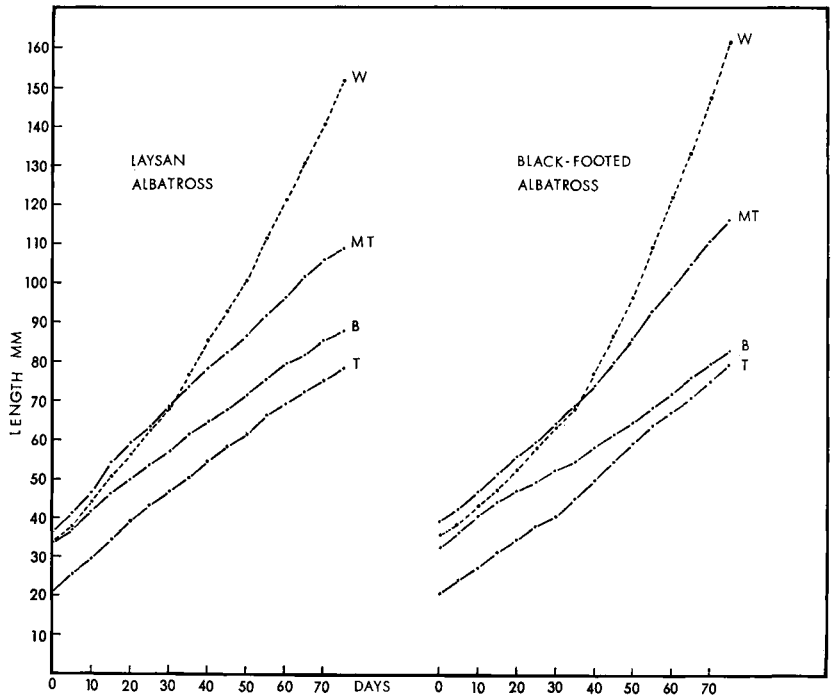


Figure 17. Mean growth curves of 10 Laysan and five Black-footed albatross chicks from hatching to age 75 days. W=wing, MT=middle toe, B=bill (culmen), T=tarsus.

The primaries begin to sprout at about 35 days of age. By March the growing teleoptiles are well developed on the breast, but are evident only when the down is parted. The mesoptiles remain firmly attached until late April or early May. The down is first lost from the back and the sides, then from the belly. The upper breast, neck, and head are the last areas to lose the down (Figure 20). In general, the molt works upward in this area, and the head may retain some down at fledging.

The plumages of the fledglings are almost identical to those of the adults. Fledgling Laysans may have a few grayish feathers on the upper thighs, and gray flecks on the crown; their bills are gray, rather than orange as in the adults. Fledgling Black-foots never show the white rump markings, which are characteristic of most adults.

Temperature Regulation

An experiment was conducted to determine the age at which albatross chicks attain the ability to maintain a relatively constant body temperature. A series of 19 young Black-footed Albatrosses of known age,

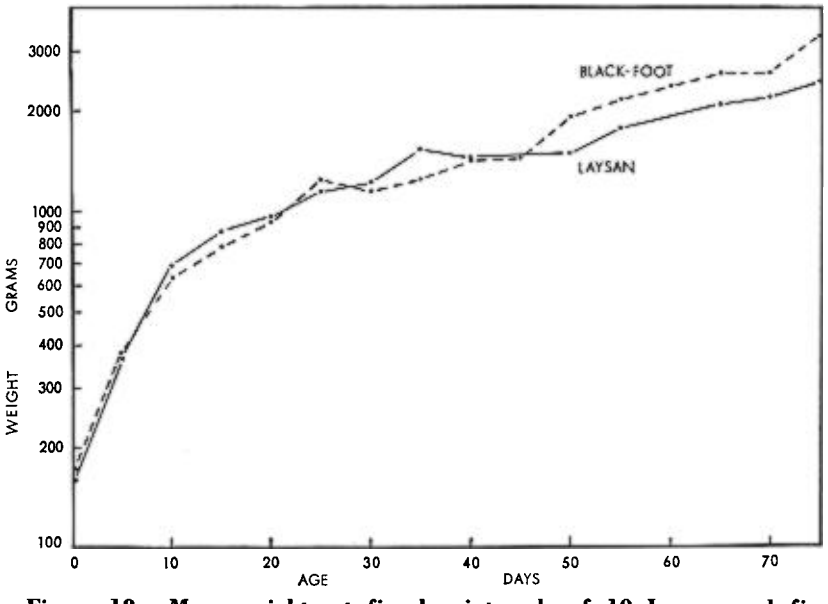


Figure 18. Mean weights at five-day intervals of 10 Laysan and five Black-footed albatross chicks from hatching to age 75 days.

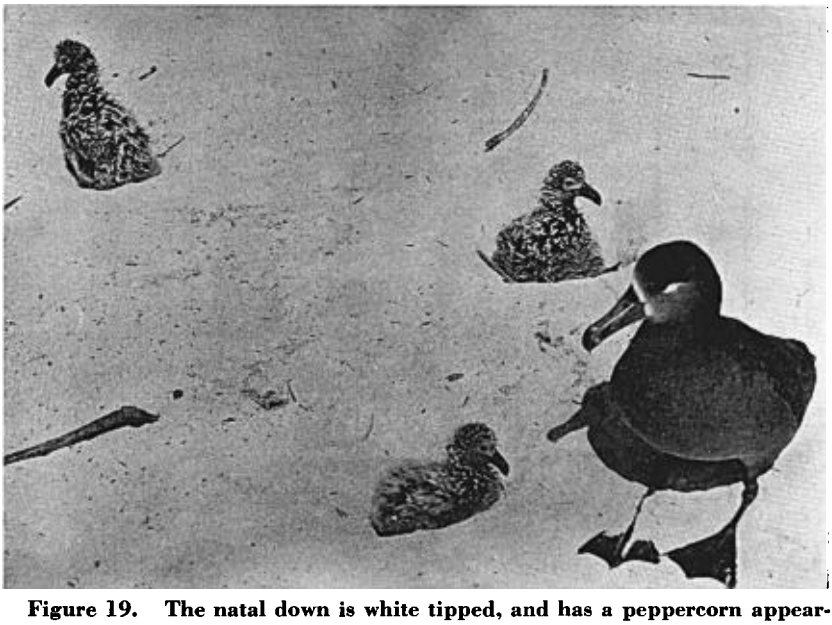


Figure 19. The natal down is white tipped, and has a peppercorn appearance. These Black-footed Albatross chicks rest in excavations which they form by frequently kicking sand backwards. Streaks of excrement may be seen on the sand near the nests. KWK 991.

Figure 20. A fledgling Laysan Albatross illustrates the last stages of molt shortly before departure from the nesting ground. DWR 1001.

varying from 0 to 22 days, was selected. The rectal temperature of each was recorded, and they were then removed from their nests and placed in the shade of nearby *Scaevola* bushes. At the time the air temperature in the shade was 20.6° C, and the ground temperature was 17.8° C. After 30 minutes, the rectal temperature of each bird was again recorded, and a notation made as to whether or not it was shivering. Each bird was then returned to its nest.

The body temperature of the younger birds dropped slightly more than that of the older birds (Table 19). Chicks 0 to 11 days old dropped a mean of 2.0° C, while chicks 12 to 22 days old dropped a mean of 1.3° C. The chicks up to about 18 days old, which were still being brooded by one of their parents, shivered when placed in the shade. The older chicks, which were no longer being brooded, did not shiver. The drop in the body

TABLE 19

RECTAL TEMPERATURES OF BLACK-FOOTED ALBATROSS CHICKS DURING EXPERIMENT IN THERMOREGULATION

Age (days)	*Brooded*	*Rectal temperature (°C)*			
		At start	*After 30 min in shade*	*Change*	*Shivering*
0	yes	37.4	34.5	−2.9	yes
2	yes	38.2	35.6	−2.6	yes
4	yes	38.2	36.5	−1.7	yes
6	yes	37.7	35.8	−1.9	yes
7	yes	37.8	36.5	−1.3	yes
8	yes	37.7	37.0	−0.7	yes
9	yes	38.8	36.0	−2.8	yes
10	yes	39.3	37.3	−2.0	yes
11	yes	38.0	35.7	−2.3	yes
12	yes	37.7	36.5	−1.2	yes
13	yes	38.2	37.7	−0.5	no
14	yes	37.8	37.7	−0.1	yes
15	yes	39.0	36.5	−2.5	yes
16	yes	38.4	36.5	−1.9	yes
17	yes	38.2	36.5	−1.7	yes
18	no	38.7[1]	36.7	−2.0	yes
19	no	39.1[1]	37.4	−1.7	no
21	yes	38.1	37.7	−0.4	no
22	no	38.8[1]	38.4	−0.4	no

[1] Nest site in direct sunlight.

temperature of the older unbrooded chicks may be explained by the fact that the nest sites from which they were removed were in direct sunlight.

It thus appears that Black-footed Albatross chicks attain the ability to maintain a normal body temperature without shivering at an age of about 18 to 20 days, at the time the parents cease to brood them.

As the chicks grow older and the weather grows hotter, they are faced with the problem of keeping cool. This is facilitated by three behavioral adaptations:

1. *Seeking shade.* During hot afternoons albatross chicks often seek the shade of bushes, if any are nearby. They will go as far as 25 meters from the nest site. They always return to the nest site toward sundown.

2. *Panting.* Albatross chicks pant vigorously in hot weather. The beak is held open, and the gular region is distended and pulsates, resulting in evaporative cooling in the throat.

3. *Raising the feet.* During clear weather the sand or coral rock and rubble becomes very hot due to the absorption of radiant heat from the sun. To avoid conduction of this heat through the large area of webbing on ther feet, young albatrosses assume a characteristic posture. They rest on their heels (tibio-tarsal joints) and raise their feet about 3 to 10 cm above the surface of the ground. If there is a breeze blowing, this may also permit evaporative cooling on the surfaces of the web.

The body (rectal) temperatures of 20 adult albatrosses of each species

TABLE 20
RECTAL TEMPERATURES (°C) OF ADULT ALBATROSSES

Species and status	*Mean*	*Range*
Laysan Albatross (10 incubating)	37.6	36.9–38.6
" " (10 unemployed)	39.4	37.7–40.2
Black-footed Albatross (10 incubating)	39.0	38.6–39.7
" " " (10 unemployed)	39.0	37.7–40.2

were taken. Ten individuals of each species were incubating or brooding; the other 10 were unemployed. The results are presented in Table 20.

The markedly lower temperature of the incubating Laysan Albatrosses is perhaps due to the fact that their nests were built in the shade on moist organic soils, whereas the incubating Black-foots were in direct sunlight on dry coral sand.

Since the above was written, Howell and Bartholomew (1961) have published the results of a more detailed study of thermoregulation in Midway Island albatrosses.

FLEDGING

Length of Nestling Stage

The mean length of the nestling stage, calculated from hatching dates and departure dates (see below), is 165 days in the Laysan Albatross, and about 140 days in the Black-footed Albatross. Unfortunately, we have no data on the exact age of individual birds at fledging.

The "Starvation Period"

Richdale (1954) has marshaled convincing evidence that refutes the theory of the "starvation period," insofar as it applies to the Royal Albatross and the Wandering Albatross (*D. exulans*). (There is apparently a true starvation period prior to fledging in several species of the family Procellariidae.) We found that there is normally no starvation period in Laysan and Black-footed albatrosses. Most of the chicks were fed until they were able to fly and to leave the island.

During June and July, however, many emaciated chicks were found along the beaches. These were chicks that had left their nest sites before they were able to fly efficiently, and were no longer fed by their parents. The majority of these chicks died. Some of them had considerable amounts of down attached to their feathers; when they made feeble efforts to fly away, they floundered in the lagoon, became waterlogged, and drowned; many were washed ashore. Others simply remained on the beaches and starved to death.

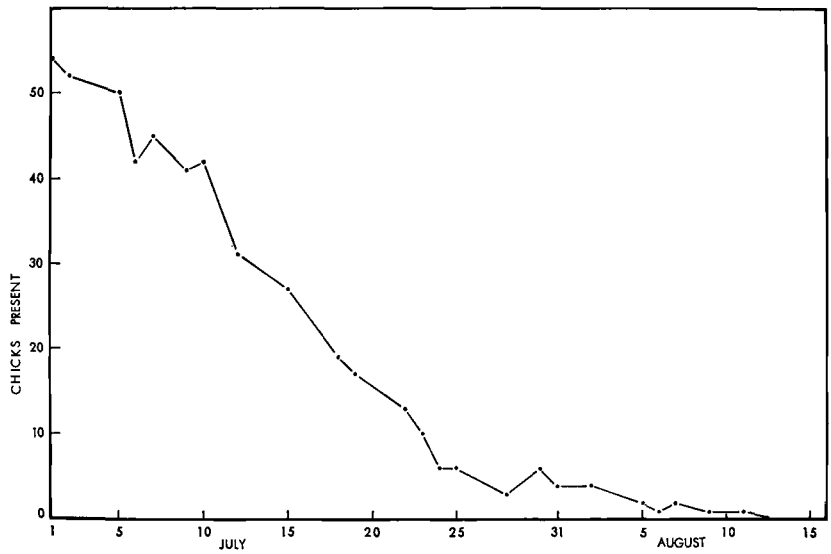


Figure 21. Departure of young Laysan Albatrosses from study plot at Midway Atoll, 1957.

Departure from the Island

Prior to departure, the young birds strengthen their wings for several weeks by spreading them in the breeze, flapping them, and making short, exploratory flights of a few meters. Before final departure the young birds may make several brief flights during which they may alight on the lagoon before returning again to the beach.

The dates of departure of 54 young Laysan Albatrosses from a sample plot are shown in Figure 21. Young Black-foots depart on the average about 30 days ahead of the Laysans. The adults cease to visit the breeding grounds at the time the chicks are fledged.

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SUMMARY

Laysan Albatrosses (*Diomedea immutabilis*) and Black-footed Albatrosses (*D. nigripes*) were studied throughout two successive nesting

seasons at Midway Atoll in the Leeward Chain of the Hawaiian Islands.

Both species may first return to the breeding grounds at an age of three (rarely two) years. They may breed when they are seven years old but most apparently do not nest until they are older. Adults normally breed annually.

Black-footed Albatrosses begin to arrive on the breeding grounds about 18 October, Laysan Albatrosses about 1 November. Females arrive, on the average, about five days later than males.

Unmated pairs "keep company" for a year or more before the pair bond is consummated. The pair bond normally remains intact year after year unless broken by the death or disappearance of one of the partners.

Laysans and Black-foots use homologous vocalizations, but the calls of the latter species are lower pitched, louder, and have a nasal quality. Vocalizations of the adult include the Whinny, Whine, Moo, Double-call, and Yammer. Likewise, the ritualized display postures of the two species are homologous, with minor differences. These include (using Richdale's terminology where applicable) Bowing, Gawky-look, Billing, Mouthing, Yapping, Snapping, Clappering, Whinnying, Head-shake-and-whine, Sky-call, Head-up-and-whine, Scapular-action, and Head-up-and-clap.

The Dance is a mutual gamosematic and epigamic display indulged in by breeding pairs prior to nest building, and by unemployed birds throughout the breeding season. The Dance consists, in varying sequence, of Clappering, Whinnying, the Scapular-action, the Head-up-and-clap, and, less frequently, the Head-shake-and-whine, the Sky-call, and the Head-up-and-whine.

Territory is confined to the immediate vicinity of the nest and is used only for mating and nesting. Birds normally return to the atoll on which they were reared, but not to their exact hatching site, to establish nesting territory. Once established, a territory is held for life. Attachment to a site is so strong that birds deserted their nests and eggs or chicks when these were experimentally displaced more than two meters.

Both sexes build the nest, beginning one to three days before the egg is laid. The nest is of the directly adaptive type, consisting of a depression in the substratum surrounded by a raised rim.

Only one egg is laid each year; if destroyed, it is not replaced. Experiments showed that birds cannot successfully incubate two eggs; pairs are unable to raise two chicks; neither can a single adult successfully rear a chick. The mean date for egg laying by Black-foots was 21 November (range: 8 to 30 November); the mean date for Laysans was 30 November (range: 15 November to 16 December).

The incubation period is 64.4 days in the Laysan, 65.6 days in the Black-foot; the difference is statistically significant ($P < 0.001$). Both

sexes incubate. Incubation is continual. The female is usually relieved within three or four days after egg laying. The first span by the male averages 22.6 days in the Laysan, 18.2 days in the Black-foot. Subsequent spans are successively shorter; the last span averages 8.3 days in the Laysan, 7.2 days in the Black-foot. The mean number of spans required to complete incubation is 5.0 in the Laysan, 6.2 in the Black-foot.

The mean hatching date for Black-foots was 25 January (range: 15 January to 7 February); for Laysans, 2 February (range: 22 January to 13 February). The interval between pipping and hatching is 48 to 132 hours.

Laysan chicks are guarded continually by one parent until they reach a mean age of 17.2 days (range: 12.0 to 24.5 days), and then intermittently until the age of 27.3 days (range 17.5 to 40.0 days). Black-foot chicks are guarded continually until the age of 19.1 days (range: 12.5 to 24.5 days), intermittently until the age of 29.8 days (range: 21.5 to 42.5 days). The parents alternate in guarding the chick; the first and last guard spans, respectively, average 2.7 and 1.9 days in the Laysan, 2.8 and 2.0 in the Black-foot.

Chicks are fed by regurgitation. Stomach oil is their sole food for the first few days. During the early part of the guard stage, they are fed at least once every day; during the early post-guard stage, they are fed on the average of once every 2.5 days (Laysans) or 2.9 days (Black-foots). Experiments revealed that until the chicks are about 10 days old they are not recognized by their parents, who up to then readily accept foster chicks. As the chicks grow older, there is mutual recognition between parents and young; parents will feed only their own chick, and chicks normally beg only from their parents.

At hatching chicks are altricial, nidicolous, and ptilopaedic. They weigh an average of 0.16 kg; they grow rapidly, and by 75 days of age, Laysans average 2.23 kg, Black-foots 3.33 kg. The protoptiles are replaced by the mesoptiles soon after hatching. The primaries sprout at about 35 days. By 75 days the growing teleoptiles are evident under the down, which begins to be shed at about 120 days, starting on the breast. At fledging (140 to 165 days) some down may still cling to the head and upper neck.

At about 18 days of age unbrooded chicks can maintain a normal body temperature without shivering. Older chicks keep cool during hot weather by seeking shade, panting, and raising their feet off the ground.

The mean length of the nestling stage is about 165 days in the Laysan, about 140 days in the Black-foot. There is no "starvation period"; chicks are normally fed until they are fledged; those that are not almost always starve to death. Chicks make short practice flights before final departure,

which averages about the middle of June for Black-foots, a month later for Laysans.

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SUPPLEMENTARY NOTE

Chandler S. Robbins has informed us (*in litt.*, 9 August 1962) that during the 1961–1962 season he found four five-year-old Black-footed Albatrosses nesting. These were birds that we had color banded as nestlings on Eastern Island, Midway Atoll, in the 1956–1957 season; he found two nesting at Midway Atoll (one on Eastern Island, one on Sand Island) and two at Kure Atoll, about 100 km northwest of Midway. Many other members of this year class also returned to Midway during the 1961–1962 season, but did not nest.

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