EGGS AND EGG-LAYING IN THE LAYSAN ALBATROSS, *DIOMEDEA IMMUTABILIS*

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The purpose of this study was to determine the chronology of the cyclic deposition of eggs by Laysan Albatrosses (*Diomedea immutabilis*) as a colony and as individuals. A prime concern was the frequency and regularity with which individuals of this species laid eggs during a span of years. Further, an attempt was made to determine the effects of the age of the female and of the age of her mate on the time of egg-laying.

The detailed nature of this study was made possible by our establishment in 1961 of a long-range investigation in a marked plot on Eastern Island, Midway Atoll, Pacific Ocean. More than 99 per cent of the breeding birds using this plot are banded, as are most of the non-breeders that frequent it. Some of the chicks were banded as long ago as 1956–57 and some breeding birds in 1960–61 by the U.S. Fish and Wildlife Service. The plot has been worked throughout the egg-laying period each year since 1960. Complete biographical data on each bird are maintained on individual McBee Keysort cards.

THE EGG-LAYING SEASON

In the six breeding seasons (1961–62 through 1966–67) the dates of the laying of 3540 eggs in our study plot have been recorded. The extreme dates are 20 November and 24 December. In four of the six seasons laying began 20 November but in only two did it continue beyond 15 December. Only eight of 3540 eggs were laid after this date. We conclude, as shown in figure 1, that the expected and normal period is 21 November to 15 December, although some few eggs may be deposited a day or so beyond these limits as indicated by Rice and Kenyon (1962:540). It is notable that, in each of the six years, 97 per cent of the eggs were laid by 10 December, despite yearly variations of as much as 100 per cent in the number of birds in the breeding population. Further, both the median and modal dates varied only between 29 November and 1 December, except in 1964–65 when the modal date was 27 November. Rice and Kenyon reported 30 November as the modal and median date. The breeding population in 1964–65 was half as large as in the season preceding or following it, and the high percentage of older birds is thought to be responsible for the earlier egg-laying, as will be discussed later.

Hadden (1941) reported that by 5 December "most of the eggs" have been laid, as did Rice and Kenyon (1962:540). The reference to egg-laying "in December and January" (H. I. Fisher 1951) is an error and should have read "in November and December."

The egg-laying period in the Laysan Albatross is as regular as in the Fulmar, *Fulmarus glacialis* (J. Fisher 1952:374), and the Slender-billed Shearwater, *Puffinus tenuirostris* (Marshall and Serventy 1956; Serventy 1963), but not as abbreviated. Only 50 per cent of the albatross eggs, but 85 per cent of the shearwater eggs, for example, appear in the three days on either side of the mean date.

Based upon only two years of my own observations and the report of Rice and Kenyon (1962), egg-laying in the Black-footed Albatross (*Diomedia nigripes*) begins, and reaches its zenith, a week or ten days earlier than in the Laysan, but may continue over a longer time. Buller's Mollymawk (*Diomedea bulleri*) lays over a period of seven weeks (Richdale 1949a), but the same author reported only 13 days of egg-laying for his small group of Royal Albatrosses. Rowan (1951:148) indicated that the season at Tristan da Cunha "covers a period of three weeks at the very least."

EFFECT OF ACTUAL AND RELATIVE AGE OF FEMALE ON DATE OF EGG-LAYING

The proportion of aged females (those known to have bred for at least six seasons) to young females may affect the rate and length of egg-laying by the colony as a whole. In figure 2C it may be observed that the curve of egg dates for all females in the colony is attenuated to the right, to 15 December when it seems it might well end at about 7 December. From figure 2B it is evident that aged females virtually cease laying by the end of the first

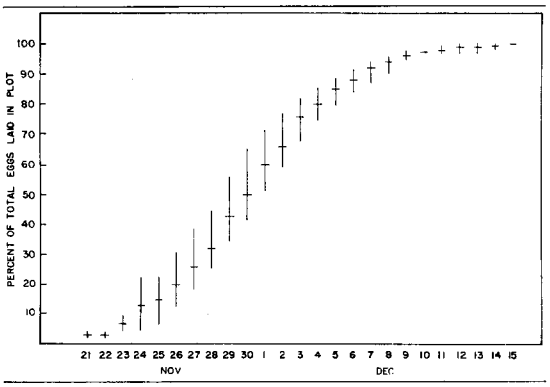

FIGURE 1. The dates of egg-laying by a colony of Laysan Albatrosses, expressed as per cent of total number laid in each year (1961–1966) which varied from 350 to 750.

week in December and that their major contribution to total egg production in the colony comes between 24 and 30 November (median date, 27 November). It is the females laying for the first time (fig. 2A) that prolong the season beyond the first week in December (median date, 4 December). By 1 December, 82 per cent of the aged birds and only 20 per cent of the first-time breeders have laid, compared to approximately 60 per cent of all females that will lay in the colony. By 4 December more than 90 per cent of the aged females and only half of all young females have deposited eggs.

Age of the female is not the only factor involved in determining the date of egg deposition. Analysis of the double peak curve for aged females (fig. 2B) revealed that a majority of the females contributing to the first peak were mated to males of similar experience and most had been mated with the same male for at least six years. Females of the second peak were, for the most part, mated with younger males or had remated in the six-year period.

The effect of age and experience of the mate on females laying for the first time is illustrated in figure 3. A young female paired with a male of a different age (fig. 3B and C) lays her egg earlier in the season than if she is paired with a male of her own age class (fig. 3A). Although the number of pairs in the sample is small, it appears that the process is hastened when she is older (median date 30 November versus 2 December). This might well be expected, for the cycle of egg development in the female starts before she returns to the island and rejoins her mate for the season.

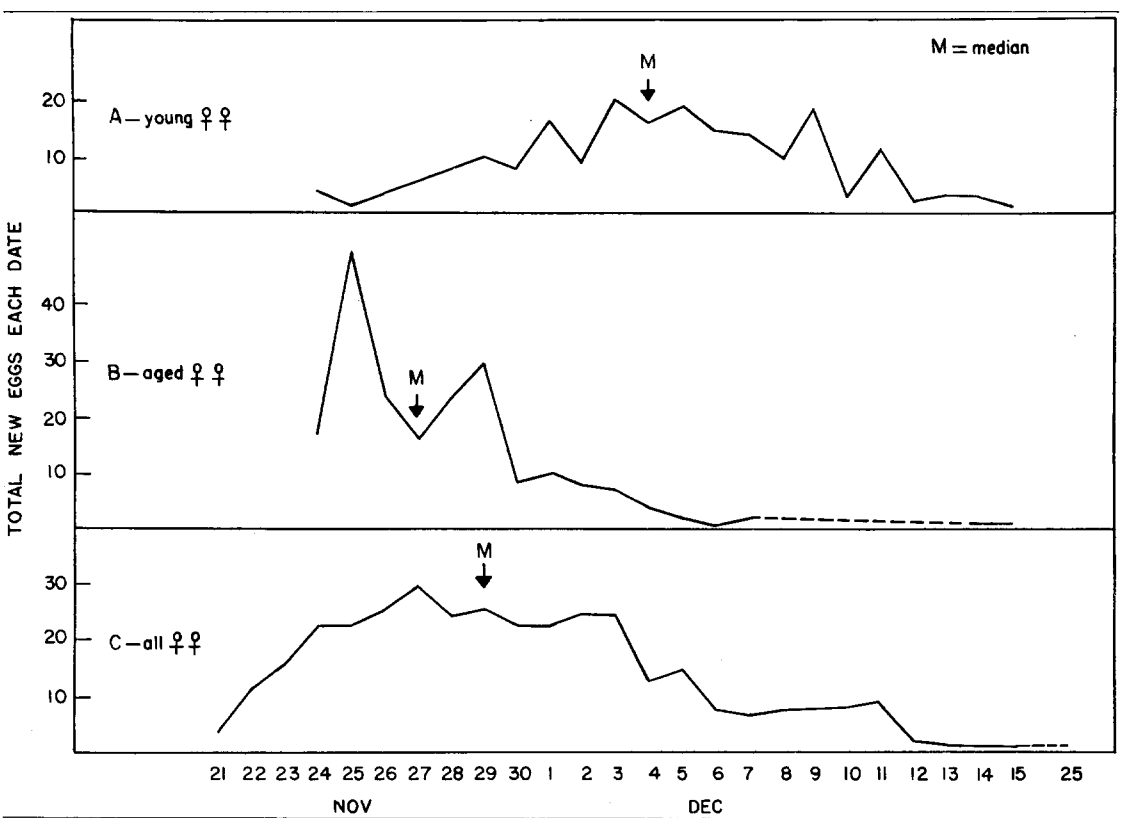

FIGURE 2. The effect of age and experience of the female Laysan Albatross on date egg is laid.

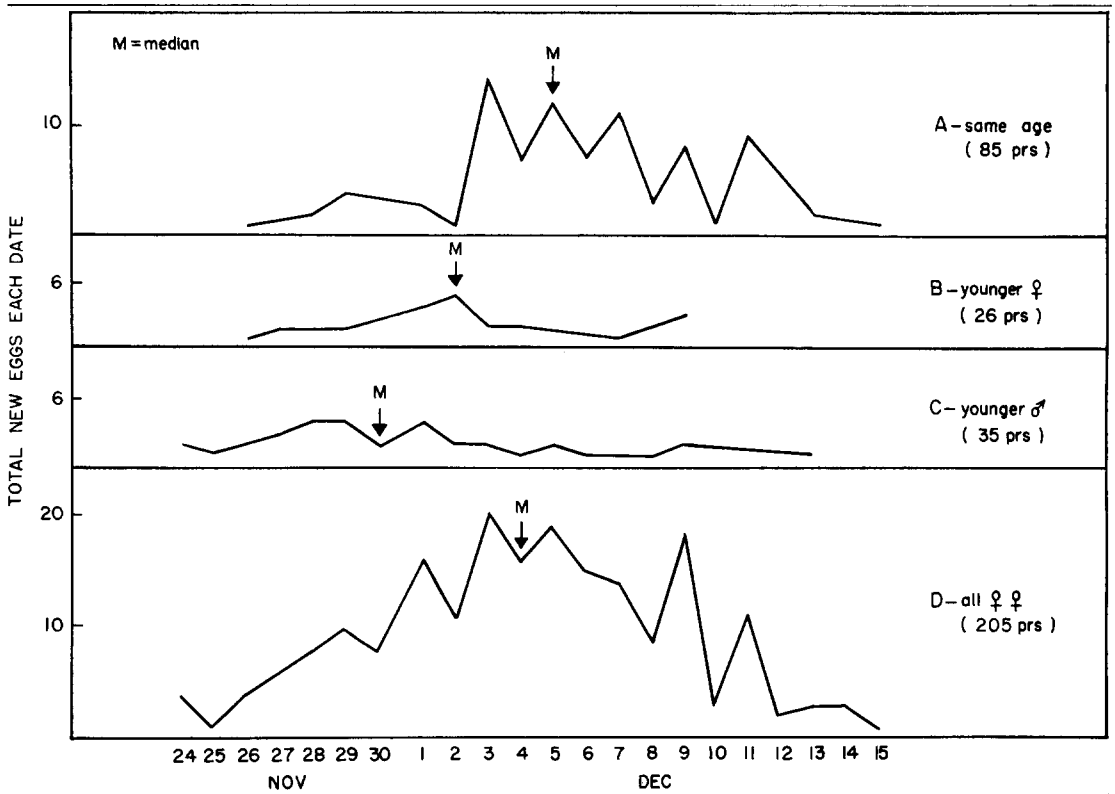

FIGURE 3. The effect of age of mate of the female Laysan Albatross on date egg is laid.

There may be related behavioral factors modified by age of the female, since she is the permissive member in copulation. Her older age may lead to earlier copulation and perhaps even to more rapid development of the egg. However, the egg-laying season for females of all pairs of dissimilar age is drawn out, indicating perhaps less uniformity in reaching the requisite behavioral and physiological conditions for laying. When the members of the pair are of the same age (fig. 3A) the onset of egg-laying is more abrupt, as is its cessation. However, the median date is delayed as much as a week, compared to the date for young females with mates of different age, and as much as a day compared to all females laying for the first time (fig. 3D). Of all eggs produced in a season by first-time females, 60 per cent of those eggs present before 1 December are laid by females mated to males of a different age.

In this regard it is interesting to note the similarities in the curves of egg-laying by aged females and by females mated with males of the same age. The onset in each instance is sudden, and the period of most egg-laying is confined to a week or 10 days. When these two curves are plotted together (fig. 4) and the curve for egg-laying by all females in the colony is superimposed, three facts become evident: 1) aged females and pairs whose members are of the same age class and are breeding for the first time have nearly discrete egg-laying periods, with significant overlap only from 29 November to 3 December; 2) it is the pairs whose members were hatched in the same year which are responsible for most of the extension of the period to the middle of December; and 3) the individual female must lay earlier in successive years as her age and experience increase; otherwise, the egg-laying period for the colony as a whole would occur progressively later.

Since egg dates for all females assume a more or less normal curve of distribution and since it has been shown that the curves for aged and for first-time females mated with males of the same age form a bimodal distribution, there must be an explanation of that portion of egg dates falling between these two peaks. Partly responsible are females which have remated and those which have older or younger males as mates, but age of the female has a clinal effect.

A number of studies have indicated that young female birds of various species may nest later, but to my knowledge this phenomenon has not been studied in much detail with

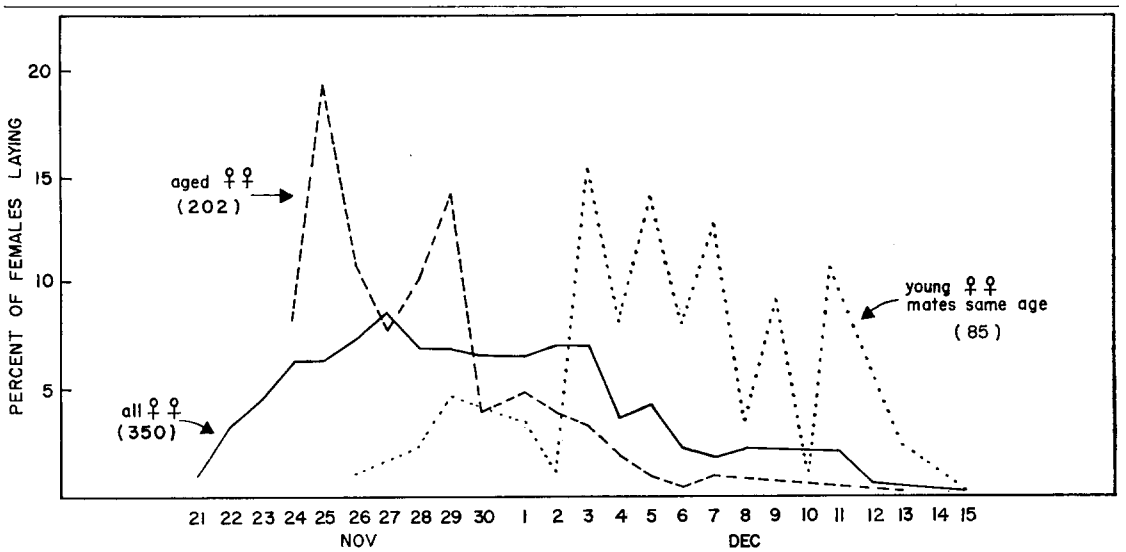

FIGURE 4. A comparison of egg-dates of aged female Laysan Albatrosses and first-time breeders, 1964–65.

banded birds. For example, Coulson and White (1960) noted that old female Kittiwakes (*Rissa tridactyla*) laid about 10 days before first-time layers and Perrins (1965) observed that even Great Tits (*Parus major*) laying for the first time did so "a few days later than experienced birds." But Richdale (1949b:92) concluded that it was "obvious that age had no influence whatsoever" in the Yellow-eyed Penguin (*Megadyptes antipodes*). The female Pigeon Guillemot (*Cepphus columba*) tends to lay on dates in successive years which have the same relationship to the mean date for the entire colony, according to Drent (1965), who concluded that age was not a factor.

Previous information on albatrosses is even more meager. Murphy (1936) offered little more than that birds at their first nesting came in "fully eight weeks" after the first eggs were laid by old birds. Richdale (1952:20) who worked with a few pairs of Royal Albatrosses (*Diomedia epomophora*) for a number of years, stated that "Individual albatrosses tend to lay in the same order each season. . . ." This much of his statement could be consistent with the findings of my work on the Laysan Albatross; there is an orderly and consistent yearly progression of egg dates of individual females. But individual Laysan Albatrosses are not "consistently early-layers, medium-layers, and late-layers." With age, all eventually become "early-layers."

Egg dates of albatrosses whose histories are known from first-egg date to one or more subsequent egg dates are shown in table 1. Median egg date for the first laying was 5 December; for the second, it was between 2 December and 3 December, and for the third egg it was 5 December. It is believed, however, that the sample for the third year was too small and that the actual median date was prior to 2 December. Support for this view comes from another analysis.

In 1960 several hundred female Laysan Albatrosses on eggs were banded in the area that was to become our study plot. This group undoubtedly included breeding birds of all ages, from first nesting on, but if we follow the egg dates of this group from the 1961–62

TABLE 1. Egg dates of female Laysan Albatrosses in their first three seasons.

	Laying season		
	First	Second	Third
Nov. 25	–	1	–
26	–	–	1
27	–	2	–
28	1	2	–
29	–	4	–
30	1	3	1
Dec. 1	3	7	1
2	4	1-med.	1
3	6	2	3
4	3	6	–
5	5-med.	4	5-med.
6	–	1	1
7	2	–	3
8	4	1	–
9	6	4	–
10	–	1	–
11	5	–	–
12	–	–	–
13	–	–	–
14	–	1	–
Total	40	40	16

TABLE 2. Span of egg-laying dates of Laysan Albatrosses after a minimum of three previous breeding seasons.

	Days									
Seasons	1	2	3	4	5	6	7	8	9	10+
4th to 6th	2	9	13	6*	4	5	2	4	4	4
4th to 7th	3	18	19	13	22*	13	20	5	6	8

* Median span.

through the 1966–67 season we discover the following: the 1961 median date was 2 December; in 1962 we had too few records; in 1963 the median date was 29 November, and in the next three years it vacillated between 27 and 28 November. These latter dates agree well with the median date of 27 November discussed earlier. Thus, stability in individual egg dates may not be reached until or after the fourth year of breeding. Data on individual birds also indicate the validity of this schedule and show that it is not a statistical creation resulting from inclusion of extreme dates.

It is evident, then, when one considers the span of days over which a female lays eggs in successive seasons, that the sample must be selective not only for age but for breeding experience as well, and that the data from remated females must be excluded. A homogeneous sample that avoided these variables in Laysan Albatross could include only data on constantly-paired females after the fourth year of breeding. Such a group is provided by females whose breeding histories are known for the last seven years (table 2).

The median span for 53 females over three seasons is four days. Sixty per cent of the spans lie between two and five days, inclusive, and 74 per cent between two and seven days, inclusive. In the instance of the four-season sample of 127 birds the median span is five days; 57 per cent of the spans are between two and five days, inclusive, and 83 per cent between two and seven days, inclusive.

It may be concluded that the first-time layer deposits the egg between 2 and 11 December, and usually close to 5 December. Her second egg, the next year, is two to four days earlier, near 1 or 2 December. In her third year the egg is laid approximately four days sooner; in subsequent years the median date of her laying will be 27 or 28 November, and 80 per cent of the eggs from these females will drop on this date, plus or minus three days.

The span for the individual females in successive years is nearly comparable to that for the Slender-billed Shearwater which has been considered by Serventy (1963) to be uncommonly restricted. In view of the effect of age and experience on the egg date in the Laysan Albatross, more homogeneous samples of this shearwater might reveal considerable shorter spans than reported.

The specific factors responsible for the close synchrony of egg-laying by the albatross colony as a whole and for the near-constancy of egg dates for individual females in successive years are not known. The evidence would seem to point toward inherent rhythms in the female modified to a certain extent by the age and experience of her mate. The very brief periods in which the members of the pair are together (H. I. Fisher, unpublished) decrease the probability of major influence by the male over any extended time in the months or weeks just prior to the deposition of the egg.

Similarly, it appears that the effect of interpair stimulation in the colony or at sea is minimal, at least on experienced breeding birds. The members of the pair meet on the territory and, with little or no courtship display, copulate and return to the sea where the male or both remain until 24 or fewer hours before egg-laying. There is no readily discernible stimulation of the whole colony as first envisioned by Darling in 1938 or "local synchrony" as reported for the Galapagos Swallow-tailed Gull by Hailman (1964). However, within a single colony there appear "subcolony" groupings in which the activities of reproduction are more closely synchronized than for the colony as a whole. Further, this synchrony is evident in the pre-breeding activities of the juveniles produced by such a group.

BREEDING IN SUCCESSIVE SEASONS

The females banded on eggs in the 1960–61 season form the basic sample for this analysis. Data in table 3 show the percentage of this same group laying eggs in the six succeeding seasons. It must be pointed out that for an unknown reason the 1964–65 season was a poor one. Breeding colony size was down 50

TABLE 3. Per cent of 392 (1960–61) female Laysan Albatrosses laying eggs in successive years.

1960–61	61–62	62–63	63–64	64–65	65–66	66–67
100	71.0	55.4	55.5	23.0	41.5	31.1

TABLE 4. Lengths of lapses in the breeding of 392 female Laysan Albatrosses of all ages.

	Years					
	1	2	3	4	5	6
N	292	80	72	37	28	9
%	56.4	15.4	13.9	7.1	5.4	1.7

per cent but not because of deaths of birds in this group (41.5 per cent returned to breed in 1965–66). Consequently, the data for 1964–65 must be considered with this in mind. A second caution is necessary; data of this type can not be used for studies of year-to-year mortality in Laysan Albatrosses. Experienced breeding birds often skip one or more seasons because of the loss of a mate or for other and unknown reasons. Missed breeding seasons during 2744 breeding-bird years are listed in table 4. Disregarding mortality, we note that these 392 females skipped 19 per cent of the breeding seasons (518/2744) and 28 per cent bred each year for two or more years before disappearing. Slightly more than half of the failures to breed occurred as single years with egg-laying in the previous and the following seasons. Twenty-nine per cent of the seasons in which females failed to lay were in groups of two or three years; 14 per cent of the birds failed to lay eggs for as many as four to six years before resuming breeding. It is this phenomenon of interrupted sequences of breeding that makes such data so unsatisfactory for computing short-range mortality or for estimating populations. For example, Rice and Kenyon (1962:381) reported 77 per cent of their adults returning the following year. This fits in well with the 71 per cent in 1961–62 (table 3), but note that 55 per cent of aged females in this study returned to lay in 1962–63 and in 1963–64 and that nearly twice as many of this group laid in 1965–66 as in 1964–65.

Another method of analysis is to determine the number of consecutive years in which a female laid an egg (table 5). It must be mentioned that the 1964–65 season caused many egg-laying series to be broken after four years. In fact, this year is so important in this regard

TABLE 5. The longest series of consecutive egg-laying in a seven-year period by 392 female Laysan Albatrosses of all ages.

	Years						
	1	2	3	4	5	6	7
N	46	98	51	134	20	17	26
%	11.7	25.0	13.0	34.2	5.1	4.3	6.6

TABLE 6. The effect of one bad season (1964–65) on consecutive egg-laying by a group of Laysan Albatrosses of all ages.

	Series stopped after: [a]		Series interrupted: [b]		
Years	3	4	5	6	7
N	13	39	23	12	59
%	8.9	26.7	15.8	8.2	40.4

[a] Birds alive but failed to breed in next three years.
[b] Interrupted only by failure to breed in 1964–65.

that its effect on successive egg-layings is shown in table 6. The effect was greatest on the seven-year series. Were it not for this year, 25 per cent of the females might be presumed to have laid in six consecutive years and an additional one-fourth of them in seven consecutive years.

The last analysis of the group of mature females designed to show the frequency of egg-laying is to be found in table 7. More than half tended to lay each year (those laying four to seven times), and the figure may be raised to three-fourths if one wishes to compensate for the 1964–65 season. Although only 6.6 per cent of the females of all ages laid eggs for seven consecutive years (table 7), a sample of 180 aged females (known to be alive from 1960 to 1966 inclusive) showed 14.4 per cent nesting in all seven years. This may indicate a tendency for the more experienced breeders to nest more frequently. If this is true, it is of major significance to the survival of the species. It imparts to the species more of the genetic characteristics which in part have enabled these mature birds to survive and to reproduce each year.

It is evident that older Laysan Albatrosses are capable of laying, and frequently do lay, each year. Even young females frequently lay in their first and second years of breeding. Not until the third year do as many as 50 per cent fail to lay (table 1); but in the fourth year (1966–67) this sample of 40 young females was represented in the colony by only three laying females. It has frequently been suggested that raising a chick successfully is such an arduous and time-consuming task that breeders who do so may fail to lay an egg the following season.

H. I. Fisher (1967) has indicated that weight

TABLE 7. Number of times 392 female Laysan Albatrosses (of all breeding ages in 1960) laid eggs from the 1960–61 to the 1966–67 seasons, inclusive.

	1	2	3	4	5	6	7
N	8	43	63	82	85	85	26
%	2.0	11.0	16.1	20.9	21.7	21.7	6.6

losses in nesting Laysan Albatrosses during the breeding season are not greater than in formerly breeding birds or even in sexually immature juveniles. This casts some doubt on the supposedly great energy drain of rearing a chick and its subsequent deleterious effect on the potential for breeding the next season. Moreover, our studies over several years have shown that 66 to 73 per cent of the successful breeders may nest in the following season. Since no more than 81 per cent of the pairs which fail to fledge a chick return to breed in the next season, it is doubtful that success in reproduction is a significant factor in determining breeding in the next season.

TIME OF DAY OF EGG-LAYING

Egg-laying normally starts as soon as the nest basin is "ready" and, infrequently, before, for some eggs are laid on flat ground with no evidence of nest construction. Females are at sea and at varying distances from the colony at the time of the post-copulatory journey and arrive on the island at all daylight hours. No particular stage of readiness of the nest scrape is a prerequisite for laying as completion of egg development is primarily a function of post-copulatory time, with copulation taking place at any hour. Therefore, egg laying tends to be spread over all the daylight hours.

One might expect proportionally as many eggs to be laid at night as well, considering the factors just mentioned. We did not find this to be true in our plot on Eastern Island, although Rice and Kenyon (1962:541) reported that nearly half the eggs were laid "from dusk to dawn." Laying of eggs from dark in the evening until the early-morning hours was rare in our observations. In one sample of 78 eggs, nearly 30 per cent were dropped between 05:00 and 06:00 when a flashlight was still necessary to examine nests. By 10:00 slightly more than 65 per cent were laid, and by noon approximately 75 per cent were in the nests. This left but 25 per cent deposited in the last eight or nine hours of daylight. One possible explanation for the variance between our findings and those of Rice and Kenyon, if it is not simply in the definition of "dawn," is that our study plot is away from the lights of the inhabited portions of Midway, and lights may affect the behavior of these albatrosses which are so restricted in their activities by darkness on land.

Richdale (1952:22) believed that eggs of the Royal Albatross (*Diomedea epomophora sanfordi*) were "laid at any time of the day," but he was absent in the early morning and perhaps attributed "dawn eggs" to the hours of darkness. Sorenson (1950a) noted that the Royal Albatross "laid during daytime."

PROCESS OF EGG-LAYING

The female is alone at the time of deposition in approximately 50 per cent of the instances. When the male is present, he usually stands quietly and watches until the egg is dropped; on occasion he "*eh ehs*" (double-call) to the female and "sky-moans" ("*moo*") softly. Only rarely is the "whinny" emitted. Richdale (1950:49) wrote "In the Royal Albatross, Buller's Mollymawk, and the Laysan Albatross (Hadden 1941:210), the male *tends to absent himself* [italics mine] when the egg is about to be laid," and "He usually leaves the breeding area temporarily. . . ." The implication is that only the male leaves. I am unable to verify Richdale's rephrasing of Hadden who clearly stated (p. 23, repaginated reprint) that "after mating they often go to sea again for a short time (about two weeks) before starting nest building and egg laying." Both members of the pair leave, nearly simultaneously, for the sea. We have never observed even one member remaining in the territory of the pair. From my field notes is a typical example of egg-laying:

"Female at a 60° angle, tail raised slightly, feet flat and legs halfway flexed. Wings dropped slightly; quivered as she strained. Male standing alongside. She made the usual straining motions and looked down beneath her at intervals of 4 or 5 seconds, between contractions. Between looks her bill pointed down and forward at 45° and her eyes were partly closed. The male almost motionless, but watching. When the egg dropped, after about 5 minutes, the female touched it with her bill and the male moved up to nest, looked, touched and tried to move onto egg, but female squatted on it without getting it in incubation pouch. She raised up again and both birds looked at mucous-covered shiny egg. She then simply flattened out on it and remained resting, eyes partly closed and seemingly exhausted."

It is difficult to judge the time required to expel the egg, but we watched five females from the time they first started the nest scrape until the egg dropped. Completion of the scrape and beginning of the ejection was judged to be when the female stopped working with the bill and stood up. Time for laying varied from 11–73 min.

A female who has just laid is easily distinguished from other females by her appearance on the nest. Her lower back and rump are more depressed, sometimes to the extent of forming a shallow depression, perhaps as a result of the loss from her body of the large volume of the egg. Her internal organs do

TABLE 8. Dimensions of newly-laid Laysan and Black-footed Albatross eggs.

	$\bar{X} \pm SE$	N	Range	V[a]
Length (mm):				
Laysan	108 ± 0.9	28	100–121	4.4
Black-footed	108 ± 0.3	172	93–120	3.5
Diameter (mm):				
Laysan	67.1 ± 0.4	28	62.1–71.6	3.1
Black-footed	70.0 ± 0.2	172	64.2–74.0	3.3
Ratio of diameter to length:				
Laysan	62.5 ± 0.6	28	54.8–67.9	5.2
Black-footed	65.0 ± 0.2	172	55.4–72.2	4.2
Weight (g):				
Laysan	278 ± 4.6	26	218–317	8.3
Black-footed	304 ± 3.4	24	275–333	5.4
Ratio of egg weight to body weight:				
Laysan	11.9 ± 0.26	8	10.9–12.8	5.8
Black-footed	9.7 ± 0.39	10	8.3–11.5	12.1

[a] Coefficient of variability.

not immediately fill the space formerly occupied by the egg, and the rear of her body sinks lower than usual.

DESCRIPTION OF THE EGG

Ridgway (1900:50), in characterizing the egg of members of the family Diomedeidae, stated "Egg single, ovate, or elliptical ovate, white, sometimes speckled or sprinkled on larger end with reddish brown." Since that time a number of observers, among them Murphy (1936), Sorenson (1950), Hagen (1952), J. Fisher (1952), Downes et al. (1959), Frings (1961), and Jameson (1961), have referred to these red-brown spots in various species of procellariiform birds.

The spots of color have also been ascribed to the egg of the Laysan Albatross (Rothschild 1893), but as Frings and Frings (1959) pointed out, and we have verified, the color is derived from blood. The blood spots may arise from rupture of capillaries caused by distension of the membranes of the oviduct at egg-laying (Frings and Frings 1959) or, as Kinnear (*in* J. Fisher 1952) suggested in the case of the Fulmar, the blood spots may come from the activities of parasites in the lower oviduct, cloaca, or the incubation patch. The latter site is the most likely, for many newly-laid Laysan eggs are not spotted.

At first the egg is shiny white and smooth because of the thin, wet mucous covering, but within an hour or so the surface is dry and dull. As incubation progresses the shell surface becomes chalky white and rough. At times, if the egg is rubbed briskly with the hand, a white dust is left on the fingers.

Individual eggs of Laysan and Black-footed Albatrosses cannot be distinguished on the basis of color, shape, or measurements. There are relatively few reliable measurements reported for albatross eggs and even fewer weights. Data in C. Frings (1961) and table 8 are evidence of the similarity in length of the egg in the Laysan and Black-footed Albatrossess, and of the greater diameter of the latter's egg. The coefficients of variability indicate that the dimensions exhibit a degree of variability comparable to most biological measurements. The Black-footed's egg is also significantly heavier, although it is not as heavy in relation to the body weight of the female. Comparison of these data with those in the literature may be misleading because of the loss of weight of the egg during incubation (to be discussed later) and the absence of information on when the eggs were weighed.

Judging by the data at hand, the eggs of the Laysan and Black-footed Albatrosses fall in the middle of the range of size for eggs of albatrosses. The smallest egg is that of the Yellow-nosed Albatross, *Diomedea chlororhynchos* (97 by 63 mm, Murphy 1936:520; 94 by 63 mm, Rowan 1951:148; and 96 by 62 mm, Hagen 1952). The eggs of Buller's Mollymawk, *D. bulleri* (102 by 60 mm, Richdale 1949a), of the Light-mantled Sooty Albatross, *Phoebetria palpebrata* (102 by 64 mm, Sorenson 1950b; 103 by 66 mm, Murphy 1936:499), and of the Sooty Albatross, *Phoebetria fusca* (102 by 67 mm, Verrill *in* Murphy 1936:494) form the next largest group. Eggs of the Wandering Albatross, *D. exulans* (126–140 by 74–86 mm, various authors *in* Murphy 1936:539; and 127 by 81 mm, Hagen 1952) and the Royal Albatross, *D. epomophora* (127 by 79 mm, Sorenson 1950a) are the largest.

With regard to egg weight the situation is apparently much the same, although the data are fewer. Murphy (1936:539) and Heinroth (1922) reported weights of 467 and 470 g for fresh eggs of *D. exulans*. For the same species, Hagen (1952) stated that two "half-incubated eggs" weighed 375 and 410 g. Sorenson (1950a) indicated 426 g for *D. epomophora*, Richdale (1949a) 250 g for *D. bulleri*, and Sorenson (1950b) stated that eggs of *D. palpebrata* weighed 216 g. Heinroth (1922) provided the only comparative data on the relationship between the weight of the egg and the body weight of the laying female, 6.25 per cent in one instance in *D. exulans*. If this is truly representative, the egg of the Laysan Albatross is relatively much larger (11.9 per cent in eight instances), but not so large as in *Puffinus puffinus* (14–15 percent in five instances; Harris 1966:19).

Occasionally extremely small eggs are found, virtually round and no more than 50 mm in diameter, as has been reported for the Yellow-nosed Albatross (Rowan 1951). Since these abnormal eggs are not known to hatch and since the production of such eggs seems, at least in the Laysan Albatross, to be a temporary condition (no female has been known to produce two), their major biological significance is the loss of one year's reproductive potential of the pair.

NUMBER OF EGGS LAID IN A SEASON

Despite the several reports (e.g., Richards 1909) that Laysan Albatrosses may lay more than once in a season and the many old references to second (or more) eggs in southern hemisphere albatrosses, it is concluded that female albatrosses in general and the Laysan Albatross in particular lay but one egg each season (Vallentin 1924, *in* Murphy 1936; Richdale 1942; Rowan 1951; Rice and Kenyon 1962; Westerskov 1963; Tickell and Pinder 1966; and H. I. Fisher 1968). Two eggs in one nest are the products of two females, at least in Laysan Albatrosses.

Not only is the clutch composed of but a single egg, but Laysan Albatrosses do not lay a second egg even when the first is destroyed within a week of its deposition (H. I. Fisher 1968). Rice and Kenyon (1962:539) reported no re-laying when eggs were destroyed late in the incubation period.

As H. I. Fisher (1968) indicated for the Laysan Albatross, and Huntington (1963) for Leach's Petrel (*Oceanodroma leucorhoa*), the laying of but one egg a year could be a severe restriction on the reproductive potential of the species. However, the effect is not so serious with long-lived individuals (Amadon 1964), and the species have reduced the number of eggs laid to their potential for feeding a chick successfully. Neither of these species can rear two chicks simultaneously.

Thus, the Laysan Albatross may support David Lack's view that clutch size depends on the number of young that a pair can raise. Whether the inability of this albatross to raise more than a single chick is caused by the depletion of nearby offshore food sources, as suggested by Ashmole (1963) for the Sooty Tern (*Sterna fuscata*) and extended to "most tropical seabirds" (Ashmole, 1965:316) is not known. However, it would seem less likely in the albatrosses which have such strong powers of flight, the ability to survive long periods without food (both chicks and adults), and which have remarkably adapted to the exigencies of their existence both the periodicity of feeding and the amount of food delivered to the chick.

LOSS OF WEIGHT BY THE EGG DURING INCUBATION

Twenty eggs were weighed at weekly intervals. The average loss was 15.2 per cent (13.0–18.7). The largest eggs had lesser percentage losses as might be expected from their lesser ratio of surface to volume. Absolute losses ranged from 36 to 48 g. In each of the first seven weeks the weight decreased 4 or 5 g, but the loss was 7 g in each of the last two weeks. The increased rate of loss was presumably the result of greater size and metabolic activity of the chick.

SUMMARY

This investigation was based upon data gathered from 1960 to 1966, inclusive, in a study plot on Eastern Island, Midway Atoll. The colony of Laysan Albatrosses (*Diomedea immutabilis*) was studied during most of the egg-laying period in each of these years. Each nest and essentially all of the breeding birds are marked, and ages of many of the birds are known.

The expected laying period of the colony is 21 November to 15 December. Ninety-seven per cent of the eggs are laid by 10 December, and the median date falls between 29 November and 1 December.

The age of the female has a marked effect on the date of egg-laying. Aged females (known to have bred for at least six years) have a median date of 27 November and 82 per cent have laid by 1 December. Females

laying for the first time have a median date of 4 December and make their major contribution to the total number of eggs in the colony after 1 December.

Age and experience of the male influence the egg-date of the female. Aged females paired with the same male for at least six years lay four to five days earlier than females paired with younger males or females who have remated because of the death of a mate. Young females, laying for the first time and paired with a younger or older male, lay earlier than when mated to a male of their own age class; especially is this evident when the female is older than the male. Females mated to males of a dissimilar age, as a group, have a more lengthy egg-laying period, with the onset of egg-laying far less abrupt than when members of the pair belong to the same age class.

As might be expected from the statements above, there is a progressively earlier date for females in successive years, until at least the fifth year of breeding. In seasons succeeding the third year of nesting, 80 per cent of the females deposit their eggs within a six-day period.

Laysan Albatrosses are capable of laying an egg and rearing a chick each year. Although 30 per cent of the birds known to breed in the past may not breed in any one year, more than 50 per cent of them tend to lay each year. Seventy per cent of the pairs successful in rearing a chick (81 per cent of the unsuccessful ones) have been known to lay the following season, but there is great annual variation in the percentages returning to breed.

Eggs are usually laid during daylight hours, 66 per cent before 10:00 and only 25 per cent between noon and the following dawn.

The egg of the Laysan Albatross measures 108 by 67 mm and weighs approximately 280 g (12 per cent of body weight in eight instances). In linear dimensions and weight it falls in the middle of the ranges for albatrosses in general. The egg loses 15 per cent of its weight during incubation.

Laysan Albatrosses lay no more than one egg per season.

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