The Visits of Laysan Albatrosses to the Breeding Colony

Harvey I. FISHER and Mildred L. FISHER

Department of Zoology, Southern Illinois University, Carbondale, Illinois

Introduction

Most of the knowledge available on the breeding biology of the Laysan Albatross (*Diomedea immutabilis*) has been gained in the last 10 years. This period has been one of rather intensive investigation by a number of different individuals and organizations, stimulated in large part by the conflicting use of Midway Atoll by birds and men. Earlier papers (among them, Dill, 1916; Dill and Bryan, 1912; Hadden, 1941; H. I. Fisher and Baldwin, 1946; H. I. Fisher, 1949) provided useful but fragmentary information. It was not until the reports by DuMont and Neff (1955), Kenyon and Rice (1958), Kenyon, Rice, Robbins, and Aldrich (1958), Rice (1959), Robbins (1960a, b), Aldrich, Robbins, and Dykstra (1961), and particularly Rice and Kenyon (1962a, b) that the basic pattern of the life cycle of this albatross became known.

The latter studies benefited from the excellent pioneering studies of southern hemisphere albatrosses by Richdale (1939, 1942, 1949a, b, 1950, 1952), Rowan (1951) and Sorenson (1950a, b); and they formed a comprehensive foundation for subsequent continuing studies which examined certain aspects of the biology of the Laysan Albatross in considerable depth. Among these may be mentioned those by Howell and Bartholomew (1961), Bartholomew and Howell (1964), H. I. Fisher (1966a, b, c, 1967, and 1968), Brown and H. I. Fisher (1966), and Hamlet and H. I. Fisher (1967).

None-the-less many features of the life of the Laysan Albatross remained virtually unknown. There existed, still, no answers to such fundamental questions as: 1) What proportion of the annual cycle is spent on land? 2) What is the chronology of the birds' visits to the breeding colony, and how is this influenced by their age, sex, and breeding status? 3) Do juveniles return to the place of their natality to visit, and there later to breed? And at what age do they nest for the first time? 4) In what manner do nestlings move from the colony to the beaches and thence to the sea and what determines the direction they take? And 5) Do adults or juveniles visit islands other than the ones where they were hatched?

The purpose of this paper is to provide answers to these and related questions.

Methods: Between the 1956 and 1960 seasons the United States Fish and Wildlife Service banded several thousand nestlings on Eastern Island. We in our

Micronesica 5 (1): 173-221. 1969 (July).

turn banded more than 35,000 fledglings on this island between 1960 and 1965. In our permanent study plot, the young have been banded each year since 1956, with the exception of 1958 and 1964. It is from the recapture of these birds of known age that we gleaned the primary information presented in this paper.

Although scattered recaptures of juvenile birds have been made throughout the last 10 years, a systematic search for banded birds was not conducted on a regular and continuous basis until recently, from October, 1964, to June, 1965. In this period we made 11,889 recaptures involving 5,426 albatrosses, of which 3,908 were juveniles of known age, and 1,518 were experienced breeding birds. In November-December of 1965, 1,505 "walkers" (see below for definitions) were recaptured and 2,429 albatrosses were retaken during the egg-laying season in 1966.

Laysan Albatrosses on the nest are unafraid and may simply be picked up, but other age groups, especially the juveniles, are often wary and retreat on foot or fly away. We found it advantageous to capture them at night, using a spotlight. All recaptures of non-breeding birds since October 1964 have been by this method which, of course, presumes little or no diurnal variation in occurrence on land, a reckoning verified by several spot checks.

A regular route on Eastern Island was followed on each of three nights per week in the 1964–65 season when banded walkers were being retaken. The strip we traversed measured roughly 100 yards wide and extended along the shore from the southeast corner of the island (Fig. 6) west to "SW Tip" and northeast through the area labeled "S. Pier." Each banded bird was recorded, but birds of unknown age were not included in the final calculations. That we succeeded in taking most of the juveniles is indicated by the number of repeats late in the season. By late May only a third of the recaptures represented birds not taken earlier, and these were mostly 2- and 3-year-olds. Some juveniles by this time had been recorded six times. Further, the total number of recaptures dropped from an average of more than 200 per night in April and March to less than 30 in the last two weeks of May.

Some loss of bands does occur, but we know of no way to compensate for this in our calculations.

Definitions: Although Richdale (1949a), Carrick and Dunnet (1954), and Warham (1963) have proposed definitions, no one of their systems is fully applicable, we think, to the biology of Laysan Albatrosses. We use some of their individual terms, but for purposes of clarity these words, too, are here defined:

Breeder: Bird currently nesting.

Former breeder: Bird known to have nested in past years but not currently nesting.

Failed breeder: Bird known to have initiated nesting, in the current season, but for any reason unsuccessful in rearing young.

Adult: Any current, former or failed breeder.

Juvenile: Bird that has gone to sea but has never bred.

Fledgling: Young at the time of departure from the breeding colony and the

island.

Associated twosome: Two birds found together constantly—the "keeping company" of Richdale (1949a) and the "sweethearting" of J. Fisher and Lockley (1954).

Walker: Any bird walking in the breeding colony. The term "unemployed" of other students, sometimes used for these birds, has the connotation of "not being employed," which is erroneous. These walkers are going to and from nests, selecting territories, mates, etc.; they are certainly "employed" at tasks vital to the success of the species.

Arrival of Adults

Breeding Birds

Season of arrival: Since 1961 the number of adults has been counted at dusk every day or so between the time of arrival of the first Laysan Albatrosses and the cessation of egg-laying in three differently sized plots in the interior of Sand Island. The two smaller plots are among stands of 65-year-old ironwood trees (*Casuarina*); approximately 200 to 300 pairs nest there each year, depending upon the year. About 1200–1500 pairs use the largest plot, which is an open, mowed field.

It is estimated that these plots normally accommodate 5 to 10% of the total breeding population on Sand Island. They thus constitute an adequate sample of the breeding birds, which is also used in estimating the total population on Midway.

In the 1964–65 season the counts of adults were continued throughout the season in these plots, in the permanent plot on Eastern Island, and, for comparison, in the main colony of Black-footed Albatrosses on the south beach of Sand Island.

The yearly data for the November-December period in 1961, 1962, 1963, and 1964 showed the same relative changes, although the absolute numbers of albatrosses varied. Further, during 1964–65 the counts of birds in the different plots on Sand Island exhibited the same seasonal changes. Consequently, in Figure 1 are combined all counts of Laysan Albatrosses on Sand Island in 1964–65. Since no observations were made after June 2 in 1965, data from the 1962–63 season, reduced to proportionate levels, have been interpolated. The 1964–65 data from the plot on Eastern Island and from the colony of Black-footed Albatrosses on Sand Island are graphed in Figure 2.

The first few Laysan Albatrosses usually arrive early in the first week of November, although several in past years have been reported during the last week of October (Frings and Frings, 1959, 1961). By November 10 these stragglers have become a flood of birds that usually reaches an average maximum or "stability" in the last 10 days of November. This stability in numbers, it must be remembered, is of the colony as a whole, not of its members which come and go constantly. There must be some variation between years, for according to Rice and Kenyon (1962b: 523) the numerical stability of the birds was attained on November 20 in 1956 (or 1957), while Hadden (1941:211) reported only 60% of the albatrosses as being

present by this date. Frings and Frings thought a plateau in numbers was apparent "about November 25" in 1958, and we found it on December 1 in 1964 on Sand Island, where both the earlier studies were made. However, in 1965 the stability began on November 25.

Because of differences in time of arrival of different age groups, which will be discussed later, and year-to-year variations in the age composition of the colony, annual variations in arrival of the whole colony of breeders would be expected. All workers are agreed that 95% of these arrivals in November come in a 10- to 12-day period. Frings and Frings (1959) reported that the arrival came in bursts and was not a gradual accretion. The jagged peaks on the November part of the curves in Figures 1 and 2 tend to support this view.

Our nesting records show that by the end of the first week in December essentially all of the experienced, potential breeders of the year are in the colony; birds breeding for the first time often are not present until after December 1. The first-time breeders join the colony and nest progressively earlier in subsequent years, until as aged birds they are the first to arrive and the first to nest.

The period, December 1 to 9, is critical in any analysis of the arrival of breeding albatrosses and of colony composition; we have used several types of information to try to establish the facts.

Analysis of ages of birds killed by antennas (H. I. Fisher, 1966b, and Table 1) indicates that less than 4% of the birds present in November are juveniles. A number of factors make even this low observed percentage higher than it actually is. Nearly five times as many juveniles as adults have been banded on Eastern Island, and it is probable that some of the seven-year-olds, recorded as juveniles, were first-time breeders but had not yet been recaptured on an egg.

Further evidence that prior to the end of November the birds in the breeding colony are almost entirely experienced breeders is given in Table 2. In 1964 we recaptured 514 banded albatrosses at random on December 6, 7, and 8 and 763 birds on December 11, 12, and 13 in the same area in 1965. No birds were taken off nests, but this did not preclude the fact that many of them could have been

Table 1. Different age groups present as shown by deaths of banded Laysan Albatrosses at antennas on Eastern Island.[1]

	Banded dead	Per cent juveniles[2]
November	80	3.8
December	72	4.2
January	56	5.4
February	19	5.3
March	67	44.8
April	27	59.3
May	10	30.0

1. Data may be used only in a general way for totals of living, banded juveniles and adults are unknown.

2. Seven or fewer years of age.

Table 2. Recaptures of banded Laysan Albatrosses in the breeding colony during the first and second weeks of December, 1964 and 1965.

	Total recaptures	Per cent of total recaptures			
		No data[1]	Known breeders	At least 8 yrs. old	Less than 8 yrs. old[2]
Dec. 6–8, 1964	514	5	70	23	2
Dec. 11–13, 1965	763	7	64	5	24

1. Information not available from U.S. Fish and Wildlife Service.
2. With the exception of one 4-year-old chick, these were 6- and 7-year-olds.

breeding currently; later recaptures showed this to be true.

Birds younger than the expected initial breeding age of 8 years constituted only 2% of the colony by December 8; 2 of the 9 birds making up those 2% were first-time breeders, and the others may also have been birds breeding at an earlier than usual age. After December 8 this group of young birds made up 24% of the birds in the colony.

If we combine the data in a different way—birds old enough to breed versus those usually considered too young to breed—we find that on or about December 8, at least 93% of the colony's birds are of breeding age, versus 69% in the following week.

We think the birds in the non-breeding category will attempt nesting within the next two years. Between December 5 and 31, 1962, we banded 260 birds in the plot, birds known not to have bred that year. Egg-laying was 85% complete by December 5 and we identified 588 pairs at the 626 nests with eggs that year. Banding in the plot since 1960 was thought to have included almost all of the living albatrosses of breeding age that could have been expected to nest there. Consequently, we are confident that, except for birds which may have lost bands, the 260 were juveniles. Our data on these birds in the 1963–64, 1964–65, and 1965–66 seasons show the following: 1) 109 first returned to breed in 1963, 31 in 1964, and 25 in 1965. Thus, 42% bred the first season after being in the colony in late December, 54% within 2 years, and 63% within 3 years; 2) 49 or 18% returned as birds not known to breed; 3) 44 or 17% have never since been seen; and 4) 7 or 2% are known to be dead.

Another group of non-breeders, consisting of 58 walkers, was banded in the colony during November and December of 1964; of this group which we banded before December 15, 54% bred in the plot the following season, and 60% a year later. Only one-fourth of 44 walkers banded in the last half of December nested the following year, and only an additional 10% bred the second season.

In both these samples the percentages of walkers subsequently found breeding in the plot are misleadingly low. Although these albatrosses tended to frequent the same area each year, they did not necessarily "belong to" the plot area. Many were found nesting outside the borders of the plot, and it is likely that some breeders were not found.

Some 1,505 walkers were recaptured in November-December 1965 in two time

periods—November 25 to December 8 and December 10 to 14. The first span represents the height of the egg-laying season and the latter the interval when the last 2 or 3% of the eggs are laid. (In the 1961 to 1967 seasons, exactly 97% of the eggs were laid each year by December 9).

Our knowledge of the past history of these walkers is shown by the fact that we had records extending back 5 years for 28% of them, 4 years for 33%, 3 years for 21%, 2 years for 7%, and 1 year for 11%. In November-December 1966 we attempted to determine the subsequent status of these birds and obtained the information summarized in Table 3. It is evident that before December 9 the colony consisted essentially of breeding birds. In the following week, however, the proportion of breeders to non-breeders radically changed, with only 57% being breeders. However, of the non-breeders present, nearly 20% will breed the following year. It should be specially noted that before December 9, the colony included few birds that had failed to breed in 1965 or 1966, while, of birds recaptured after December 9, 18% were not known to breed in either year.

Table 3. Analysis of the recaptures of 1,505 "walker" Laysan Albatrosses in November-December 1965, 1966.

	Nov. 25–Dec. 8	Dec. 10–14
Number of birds	707	796
Breeding:		
in 1965	85.7%	56.5%
in 1966, not known in 1965	4.1	18.5
Not known to breed in either year	1.0	18.0
Status unknown or not recaptured in 1966	9.2	7.2
	100.0	100.2

Further pertinent information comes from an analysis of egg dates of 202 aged females (in their sixth year of nesting) and of 205 females laying for the first time. The old females laid 85% of their eggs prior to December 1 and 99% prior to December 9. Young females mated to older or younger males laid half their eggs by December 1 and 99% by December 9. Only 8% of the young females mated to males of the same year class laid before December 1; they laid 77% of their eggs between December 1 and 9.

The conclusion drawn from these several kinds of observations is that before December 1 perhaps 90% of all birds in the colony are experienced breeders and that after that date there is an influx of: 1) birds breeding for the first time (3–8%); 2) birds that will nest the next year for the first time (3–8%); and 3) birds (1–3%) perhaps 2 years from their first breeding. However, the circumstantial nature of our evidence should be noted; none of these walkers were of known age. Then too, there is the probability we included a small contingent (approximately 2–4%, based upon other of our studies) of single surviving members of pairs of former breeders.

Figures 1, 2, and 4 illustrate the precipitous arrival of the experienced breeders

and its similarity on the two islands. However, the breeders in this particular season on Eastern Island were nearly a week behind the Sand Island population in reaching their peak numbers. The pattern of arrival is basically the same as for the Black-footed Albatross, but the gain in the latter's numbers is not so rapid.

Time of day: Between November 6 and 20, 1964, the period during which the arrival of breeding Laysans is most concentrated, counts on the plots were made at dawn, noon, and just before dark in attempts to see if the albatrosses favored a particular time of day for their arrival. The results, though generally inconclusive, indicated that the albatrosses did not move onto or off the island during darkness; there was close agreement between the counts at dusk and at the following dawn. Noon counts were always lower, often by 10 to 20%, reflecting the departure of birds in the morning hours and a subsequent buildup of numbers in the afternoon and evening. This did not mean that birds did not arrive in the morning; we saw many come in. The only possible conclusion is that more departed than arrived.

Sexual variations: The fact that "males come in first" is well established (see Hadden, 1941, for example); however, sex ratios for successive dates during the arrival period were not reported and, most importantly, it had not been established whether males preceded their mates.

Frings and Frings (1961:306) recorded a "striking preponderance" of males between November 1 and 15, with "approximately equal numbers" being present by November 20. They did not, however, report the sex of their sample of birds accidentally killed. Their data accordingly may be biased because males are both more sedentary and more restricted to their home stations than females at this season; thus males are less prone to wander where they might be killed by vehicles.

Frings and Frings (*op. cit.*) oddly enough did not find a sex difference in time of arrival of Black-footed Albatrosses; if such a difference truly is absent, the species is unique among the albatrosses studied by Richdale (1950) and Murphy (1936) and the lariiform birds by J. Fisher and Lockley (1954).

Murphy (1936) reported that male Wandering Albatrosses constitute "most of the early arrivals" and that "For some time, therefore, the early female albatrosses are outnumbered four or five to one." Rice and Kenyon (1962b:519), who found no female Laysan albatrosses until November 10, stated that females tended to arrive "a few days later" than males.

Our data on sex ratios of arriving Laysans of breeding age are given inTable 4; these birds resided in a relatively undisturbed colony and had been banded as breeders four or more years earlier. Of the birds not on nests, males proved to be always more numerous, albeit decreasingly so during the egg-laying period. The greater proportion of males after the maximum number of birds has been reached in the colony is a result of the differential behavior of the sexes with the advance of the breeding season. As the season progresses and more of the females lay their eggs and depart; their males move onto these eggs. But throughout the period some males of breeding age wait for mates that are late or dead (see later), and a few of these mature males apparently never have had mates. Further, males

Table 4. Sex ratios of Laysan Albatrosses of breeding age[1] in November and December of 1962 and 1963.

	Birds not on nests			All birds		
	Males	Females	Ratio (♂:♀)	Males	Females	Ratio (♂:♀)
Nov. 12	81	19	4:1	81	19	4:1
19	76	24	3:1	77	23	3:1
24	71	29	2.4:1	83	19	4.4:1
Dec. 1	79	32	2.5:1	105	14	7.5:1
2	69	32	2.2:1	115	15	7.7:1
5	67	33	2:1	113	14	8.1:1
9	69	41	1.7:1	106	6	17.7:1

1. All birds in their fourth season of breeding.

waiting for females are more constantly in their territory than are females waiting for mates; thus males are more often included in the sample.

The data on sex ratios of all birds in the colony (Table 4) provide further evidence of the decreasing preponderance of males before egg-laying started and demonstrate the colony's subsequent increasingly male complexion, which continued until the females returned for their second span of incubation. The ratio of 18 males to 1 female in the colony on December 9, 1963, seemed very high. Therefore, on December 9, 1965, we counted the sexes in our plot where the heads of males were painted red and the females' blue or black. The ratio was again high, 17.7:1 (726 males, 41 females).

In 1964–65 we painted distinctive marks on the white breasts of the first 20 Laysans to arrive on their stations and observed them at two-hour intervals during the daylight hours until almost all their mates had appeared (Table 5). Eighteen of these first 20 birds (90%) were males, only two being females, each of which preceded its mate by 8 days. Mates of 5 of the 18 males never appeared and one male was never seen again; the five males stayed on station an average of 15 days (5–28), but number 4 male was observed on station again on January 2, 1965. That 5 of 18 males never met their females may furnish another reason for the relatively high proportion of males among the former breeders, but one would expect non-appearance of male mates just as frequently. Perhaps the more valid reason is found in the facts that females wait only 8 days for their mates and males 11 days and that while waiting the females are on station fewer days; that is, they return to sea more frequently than males. Ten males waited for their females an average of 11 days (range, 6–16; median, 10); in two other instances the time of arrival of the female was not determined.

Former Breeders

Former breeders show two periods of massive arrival—the middle weeks of November, and the weeks between late December and late January. Approximately 45% arrive in each of these intervals. The 1964–65 season proved a "low" for breeding, the number of former breeders being thus proportionately greater.

Table 5. Pre-egg chronology of twenty Laysan Albatrosses in 1964.

Bird	Sex	Arrived	Mate arrived	Both departed	Returned	Egg Laid
1.	♂	Nov. 2	Nov. 17	Nov. 18	Nov. 28	Nov. 28
2.	♂	2	—— [1]	——	——	——
3.	♂	3	19	——	29	29
4.	♂	3	—— [1]	——	——	——
5.	♀	5	13	14	19	20
6.	♂	5	14	15	28	29
7.	♂	5	15	15	Dec. 2	Dec. 3
8.	♂	4	13	16	Nov. 21	Nov. 23
9.	♂	5[2]	——	——	——	——
10.	♂	5	21	22	Dec. 3	Dec. 3
11.	♂	3	—— [1]	——	——	——
12.	♂	4	—— [1]	——	——	——
13.	♂	4	—— [1]	——	——	——
14.	♂	6	13	14	Nov. 23	Nov. 24
15.	♀	7	15	16	18	19
16.	♂	5	——	——	Dec. 7	Dec. 7
17.	♂	5	21	22	——	Dec. 1
18.	♂	5	11	12	——	Nov. 29
19.	♂	4	?	[3]	——	Nov. 24
20.	♂	4	10	10	23	—— [4]

1. Mate never arrived.
2. Bird never seen again.
3. He was there each time; if he left it was for less than a 2-hour period.
4. No egg laid.

No satisfactory explanation can be made at this time for the late November to late December plateau in numbers (Fig. 4). One might think the first wave of arrivals was made up of members of broken pairs—that is, of birds ready to breed, yet lacking a mate—and that the second wave chiefly included birds not in breeding condition (H. I. Fisher, 1967) or birds slower to respond to seasonal stimuli. This series of inferences furnishes a plausible explanation for the second wave but not for the first wave. Mortality of aged breeding birds under normal conditions approximates 5 to 10% per year (H. I. Fisher, *in litt.*). High communications antennae near the study area in some years may impose an additional 1 to 3% death rate on these particular birds (H. I. Fisher, 1966b). Thus, not more than 90 (15% of 600) of the 250 former breeders present by December 1 should have lacked mates. Unfortunately most of these former breeders, banded as breeders in 1960 and 1961, were of unknown age.

Movements to and from the Sea Between First Arrival and Egg-Laying

While waiting for the return of mates of previous years, the females, as pointed out above, not only go to sea more frequently than do the waiting males; they wait

a shorter time. We refer again to the 20 birds in Table 5: the 2 females were away a total of 3 times and stayed away for an average of 2.5 of the 8 days; 7 of the 10 males that awaited and regained their mates were never once absent to our knowledge; 2 of the others left for one day each, and one male was away 4 days in the middle of his 16-day stay. Two males whose mates never came waited continuously for 15 and 16 days, respectively.

We frequently have noted that copulation normally occurs within hours of the reunion of mates in the breeding colony, and that both birds usually leave within 36 hours. Seldom do three days pass before the departure of the pair, as in the case of male No. 8 in Table 5.

One or both members of a pair ordinarily return after about 10 days (av. of 34 recorded instances; range 2 to 17 days). Failure of a male or female to leave for the "honeymoon" at sea after copulation was noted only once (bird No. 19, Table 5). In 29 of 34 instances (85%) the females returned at least 12 hours earlier than their partners, and both members of five pairs came in within an hour of each other; the female always arrived first, however. In 15 instances (50%) the female was still alone at the time of egg laying. Egg laying usually occurred within 24 hours of a female's return.

Travel During Incubation

The data on time spent at sea by breeding birds of all ages are summarized in Table 6. Derived from studies of incubation spans, these data make no allowance for the time spent on land during the exchanges at the nest. Such ceremonies, which normally take no more than 12 to 24 hours and include the post-exchange tarrying of the relieved bird, thus do not introduce a possible error of more than a day in any one period or four days during the entire incubation season.

A sample of 75 young males, on the average, returned from sea to start their first incubation duty within 3 days after the egg was laid (median, 2 days; range, 0–32); 593 experienced males came back in 1.7 days on the average (median, less

Table 6. Days spent at sea by Laysan Albatrosses during the incubation period

	Number birds	Days at sea		
		Mean	Median	Range
Males				
Post-laying	686	2.1	<1	0–32
Trip 1	451	20.3	21	6–38
2	109	7.0	7	1–24
3	2	1.5	—	1–2
Females				
Trip 1	166	24.1	24	9–58
2	269	14.2	14	1–32
3	36	4.8	5	1–11

than 1 day; range, 0–14).

According to Rice and Kenyon (1962b) there are 8 spans of incubation during which one member of the pair is absent, but our studies of 626 nests in the 1962–63 season revealed no more than 7. Of these, only six are initiated after egg-laying, three by each sex; the post-laying absence of the male is part of the "honeymoon period."

Using the median days in Table 6 we find that males are away 29 days and females 43 and that successive trips of each sex become progressively abbreviated. (That the combined days of absence for both sexes produce a greater total of days than the average length of the incubation period (65 days) is a statistical anomaly which arises from averaging the data on the incubation spans of many different birds.)

Post-Hatching Movements of Adults

It is impossible to make a neat distinction between guard and post-guard phases because adults at all seasons frequently rest briefly by the chick after feeding it. But, in general, the guard phase ends rather abruptly for each chick, and in our records we used as its culmination the first time the chick was observed alone.

Guard Phase

During the guard phase of the cycle in 1964–65 we obtained records of the sex on guard, of the lengths of time which each bird spent guarding and of the total period of guarding which the two birds between them contributed. The length of the guard phase in 131 instances averaged 14 days (range 7 to 21). Both parents were present in only 79 of 3012 observations, an indication that 95% of the time one or the other parent was at sea.

The parents share guard duties equally, as noted by Rice and Kenyon (1962b: 548). No sexual difference in length of guarding spans (av., 2 + days; range, 1–4) was discovered; nor did length of span change as the period progressed.

Weather effects movement off, but not onto, the island at this time. Rain and wind on Midway tend to delay the departure of "off-duty" parents by as much as a day, but should the storm continue the birds move out anyway. The number of birds returning remains constant, and the delayed departure of mates results in more pairs being found with the chicks.

An adult in this stage of the cycle, we may conclude, makes three trips to sea, spending about three days there.

Post-Guard Phase

By mid-February most chicks are past the guard phase and their parents have begun to spend an increasing amount of time on the ocean. Chicks are fed by one parent or another at intervals of up to 48 hours in length until mid-May, when the intervals occasionally extend to 3 days. However, despite the fact that many chicks may survive the longer intervals (Rice and Kenyon, 1962b:554, reported 2.5 days) our studies of 25 chicks in early May, 1964, show the median interval to be approx-

imately one day (range, 0.3–5.0). Longer intervals may increase the mortality of the chicks. On June 25–27, 1962, we maintained a continous 72-hour watch on 317 chicks; 239 were not fed at all and of these we know 13 died later. But of 78 which were fed at 20-hour intervals only 2 died. In 1961, an identical watch was kept on 154 chicks from July 12–14. Ninety-four of these were not fed; 5 later died. Among the 60 chicks fed at 24-hour intervals only one died.

It is possible that the primary factor affecting frequency of feeding at this season is age of the young; the range of age difference of the chicks in the colony was approximately one month, and the ones which we saw being fed each day may have been the younger chicks. Unfortunately, having not been present to observe the hatching of the chicks in the sample observed, we did not know their ages.

Seldom do both parents attend the chick at the same time, but both may feed it on the same day in this post-guard phase. In general we may state that each parent contributes about half the number of two successive feedings (the parents feed the young alternately in the remainder); in fewer than half of the instances, both parents feed the chick during the same day. This pattern shows but little seasonal change, and to date it has not been possible to determine whether the differences are due to constant individual behavior patterns or to the vagaries of weather and/or abundance of food.

It is thus evident that from mid-February to mid-May the parents are seldom as much as a day's travel from Midway and that in this 90-day period they make perhaps 50 or 60 roundtrips between the colony and the sea. Further, since the adults normally leave Midway less than 2 hours after a feeding, most of them probably spend fewer than 150 hours, or less than 4% of their time, on land.

As the chicks mature in June and July, adults frequent the land even less often and for shorter periods of time. In the 60-day interval of mid-May to mid-July (when a number of the older young have already gone) each parent probably visits the island at intervals of about 3 or 4 days, as indicated by the frequency of the feeding of the young and by the alternation of the parents in this duty. In other words, the parents may make 15 roundtrips after mid-May and spend perhaps 3% of the time in the colony.

Departure of Adults for the Season

Successful Breeders

These birds start to leave in mid-June, and by the first of August few of them may be seen in the colony. Counts of known breeders, with chicks in our plot on June 15, were made at 8 a.m. daily for the remainder of the season in 1962–63. The greatest number was on July 7 when 23 were found (10% of 229 nestlings still present). The next largest numbers of parents were present on July 9 (11) and July 1 (10), but for most days in these last 6 weeks of the season only 1 to 5 parents were found. These low counts are in large part the result of the briefness of the visits to feed the chicks, but they do show as well the declining numbers of adults

in the breeding colony. After August 7 adults of any category are seldom observed on Midway. In most instances the stimulus for departure seems to be the failure to find the chick which has already gone, but we have observed that a few of our marked birds returned a second time (usually 2–5 days later). About one per cent of the chicks are abandoned after August 1. Most of the latter are young of first-time breeders.

Failed Breeders

After destruction of an egg either parent may remain at the nest as long as 3 or 4 days, but seldom more than 2 days. They may return as individuals during the next month or so and remain for as long as a day. Occasionally the pair is together at the nest site, but after late January we do not usually find them in the colony. However, it is difficult to follow the chronology of these birds and our records are few.

Loss of a chick or desertion results in a similar pattern of irregular visits, but in all these instances of failure at breeding the frequency of return and the duration of each visit decline as the season progresses.

Death of a mate during the early part of the breeding cycle causes the survivor to return to the breeding site at infrequent intervals until March or April. It may then be seen rather continuously. A male is on its home station enticing females just as are juvenile males. A female shows no such attraction to the restricted area of the station, although she may return to it briefly and occasionally as she visits males in an area at least 100 yards in diameter.

Thus, failure to breed through loss of egg or chick produces a series of returns to the colony that are unlike those of birds whose failure at breeding came from the loss of a mate.

Former Breeders

Just as in the case of failed breeders, the possession of a mate is the critical factor in determining the number, length, and timing of the returns to the breeding colony. Pairs of experienced breeders not currently nesting most often begin to leave the colony by mid-December and by late January most of them have gone, although some pairs are known to return as late as May.

Unpaired birds of this category, however, remain throughout the season, except for brief sojourns at sea, or until they find a mate. Males of course restrict their activities to their home stations and females wander from male to male in the vicinity of their former nest sites.

It is evident in all categories of adult albatrosses that the station of the male is the focal point, the wheel hub, where all pathways of the male and the female join. It is the meeting place where members of the pair unite, where bereaved birds first return, the male to wait for another mate, the female to radiate out short distances in search of an unmated male, and where chick and parent meet.

Departure of Fledglings

From The Colony

Nestlings begin to leave the colony about June 20 (Fig. 3) and those that survive are essentially gone by August 2 or 3. Of the three curves for these departures the one for 1962–63 is the most accurate; the young belonging to our study area were color-marked to avoid the inclusion of chicks that moved in from other areas. The result of this movement of chicks into the study area shows in the anomalous increases in numbers in 1960–61, in 1961–62, and apparently in the graph of Rice and Kenyon (1962b:563).

Our data are in general agreement with the findings of these workers, but many of our nestling birds were gone before July 1, the date on which Rice and Kenyon showed the first ones leaving. In 1961, 10% left before July 1, in 1962, 9%, and in 1963, 26%. The period of most rapid departure was July 5 to 25, but 50% of the young albatrosses were gone by: July 15 in 1961; July 16 in 1962; and by July 9 in 1963. Some annual variation in the time of departure of fledglings could be expected as a result of differential loss of eggs laid at different times and of variable mortality of chicks hatched over a three-week period. It is also possible that the rate of development of the chick is somewhat dependent upon the energy supply (food supplied by parent) and the energy loss (weather); both may be variable from year to year, but no data are presently available.

Assuming that the older chicks leave first, we may determine the fledging period as the time between laying of 50% of the eggs and the departure of 50% of the young. In the 7 years for which we have complete data on egg-laying, 50% of the eggs have been deposited by November 29 to December 1, inclusive. Thus, the period of parental care, including the 65 days of incubation, is approximately 220 to 230 days or a post-hatching period of 160 days (165 days, Rice and Kenyon, 1962b:562), compared to 231–252 for young Royal Albatrosses (Richdale, 1954: 247).

The movement of young from one part of the island to another in the last week of June and the first two weeks in July is considerable. On June 24 and 25, 1961, we banded all the chicks (672) in an area limited on all sides by blacktopped roads. Only 61% were still there on July 15, but some 269 unbanded chicks were then present.

Movement to the Beaches

Departure from the natal site must not be confused with departure from the island; the birds may be gone from their home colony as much as a week before leaving the island.

To study their movements in this time we attempted to band "all" chicks on Eastern Island early in the summer of 1963; later, random samples indicated we had banded about 80% of them. The island was divided into eight areas (Fig. 6) and bands were applied consecutively in each. Young birds in the study plot were conspicuously painted. From July 3 through July 30, the time of most de-

partures, we walked the island's beaches each morning, catching banded young and counting young (dead or alive) on the beaches which were divided into six sectors (Fig. 6). Birds swimming within 100 yards of these sectors were totaled separately; young and adults could not always be identified at this distance, but other data on the composition of the population at this time caused us to estimate that more than 95% of the birds in the water were young of the year.

The data from these beach tallies are in Table 7; 24% of the young banded that summer were recaptured on the beaches. However, because the young may temporarily move some distance from the nest site in July, and thus be banded in an area other than the home colony, we included in the analyses only those 9,073 chicks banded prior to July 3.

Table 7. Counts of fledgling Laysan Albatrosses on the beach areas of Eastern Island, July 3–30, 1963

	Northwest beach		East beach		South beach	
	N. Pier	S. Pier	North	South	East	West
Dead	16	16	8	51	226	91
Live-beach	103	216	195	490	1837	252
-swimming	39	43	87	154	527	141
Totals	158	275	290	695	2590	484
Per cent	3.5	6.1	6.5	15.5	57.7	10.8

To understand the direction of movements by fledglings between the nest site and the beach it is necessary to explain the sectors. The lagoon side of Eastern Island faces northwest and has a pier near the middle of its length; hence, "north" and "south" of pier. The south edge of the island faces the ocean across the reef which is no more than 150 yards from the beach: "south beach" was the eastern half, "southwest beach" the western half. The east side of this basically triangular island was divided into "north half, east beach" and "south half, east beach;" the reef is as much as half a mile from this eastern beach (Fig. 6).

Many of the young in the colonies along the lagoon-side of the island could see the water, for the land there is flat and clear of obstructions. No birds in the interior and few of those on the east and south could sight the ocean because of intervening vegetation and revetments remaining from World War II.

It is also fundamental to know that the prevailing wind in the summer is from the eastnortheast but sometimes goes eastsoutheast and that the sound of waves on the reef and on the south and east beaches carries to the middle of the island but not to the lagoon half of the land, as judged by human ears.

The breeding colonies that year (1963) were well distributed over the island, as is indicated by the number of young banded in each sector. The "south edge" had a heavy population, but "east edge" was low; hence, in the analyses the two areas counterbalance each other, and we think no particular bias is included.

The direction the fledglings go as they leave the breeding colonies is well il-

lustrated by the data in Table 7. Only 10% go to the beaches facing the lagoon; 90% move toward the open sea. That these latter move more southeast by east is shown by the facts that: 1) more than twice as many went to the south half as to the north half of east beach; and 2) five times more went to the east half of south beach than went to the west half. Further, analysis of the banding site-recovery site data on these young birds showed that the east-southeast movement contained birds from all over the island (Fig. 7).

The validity of these conclusions is also supported by a detailed summary of recovery of young albatrosses banded in the triangle on Eastern Island. Six hundred thirty were identified on the beaches; 13% went lagoonward, 87% toward the open sea; 72% were found on the south half of east beach and the east half of south beach; three times as many were on the south half of east beach as on the north half, and six times as many young frequented the east half of south beach as the west half of this shore.

Since our daily records of young on the beaches also included wind direction, and a general annotation of wind force, it was possible to correlate numbers of fledglings on a particular beach with the daily direction of significant winds. One example should suffice: from July 12 to 15 the wind was "fair to strong" from the south; on July 16 it changed to a "strong" northeast wind. Two observations of the effects of this shift, typical of wind changes in this month, may be made: 1) more birds were on the beaches when the wind was from the south; and 2) with the wind shift from south to northeast, the number of young on the south beach dropped by 40% and increased 250% on the northeast beaches.

We believe it is evident that the young move east-southeast against the prevailing wind as they travel to the beaches preparatory to departure. For the determination of the stimulus involved it is unfortunate that both the wind and the sounds of the nearest reef come from the southeast, but the difference in numbers recovered in the east and west stretches of the south beach where the reef is almost parallel to the shore leads us to suggest that wind is the major factor. Moreover, observations of the first flights of the young show that all of them take off upwind, that turns across the wind and flights downwind are difficult for the inexperienced birds, and that such trial flights frequently end quickly and unsuccessfully. Thus, no matter how many flights are required, the direction of progression toward the beach is usually upwind.

On small islands this behavioral pattern has no adverse effect on the success of young in reaching the sea and may actually cause them to travel in a more direct line to the sea, but on larger land masses it might so delay the arrival on the ocean feeding grounds as to be fatal. Vallentin (1924:298) *In* Boysen (1924) reported that many young Black-browed Albatrosses flew into the interior of the Falkland Islands and perished, unable to take off because of the flat terrain and absence of wind. The advantages to albatrosses of nesting on windward shores where bad weather and strong winds are more constant have been emphasized also by Murphy (1936: 550–551) who included many observations by earlier workers.

Although we have emphasized movement from the nest site to the beach, it should be understood that many of the young albatrosses do not stop on the shores; their first major flights carry them to water, but a high percentage of these return to the beach by drifting, swimming or flying. We think a majority of the departing fledglings spend some time on the beaches.

Time Spent on the Beaches

Our successive recapture of the same young birds on the beaches in the summer of 1963 provided information on the length of this stay. Of 152 twice-recaptured birds that survived to leave: 53% were caught on the beach on 2 successive days and then seen no more; an additional 43% were caught within a 6-day period; 3 birds were taken after 12, 13 ,and 14 days, but we think these must have been to sea and returned. The median time is between one and two days.

Seventy-eight birds were recaptured once and subsequently found dead on the beach; most of these had been in the water as evidenced by wet plumage. Sixty-three per cent of these 78 were dead within 3 days and 90% within a week; one survived for 16 days and another for 24. The median survival time was between two and three days. Twenty-eight young were recaptured twice on the beaches and subsequently died there; median survival from first recapture was between three and four days.

We conclude that most surviving fledglings leave the island for the year within 48 hours of first reaching the shore, that 4 or 5 days represent the maximum length of survival during continuous presence on the beach, and that the 1 or 2% recaptured a second time after an interval of a week represent birds that have fed at sea and returned or have retraced their steps to shoreside colonies and been fed by the parents.

Another aspect of the departure of the young is worthy of note. Groups of young (6 to 10) reared near each other in the colony are often found near each other at the same time on the beaches; it appears that they may have moved there more or less as a group. The frequency of this observation is too great to be accounted for by chance; although the young from a colony tend to go to the same beach, depending upon wind direction, one would not expect to find consecutively banded young together at the same time. We have also noted this phenomenon in the colony; closely associated groups of fledglings tend to disappear on the same day. Moreover, this "subcolony association" shows up in the close approximation of dates of egg-laying by groups of pairs physically near each other in the colony and in that these same groups of adults tend to return at the same hour on the same days to feed their young. These "flurries" of feedings in restricted parts of our study plot were quite obvious in the summers of 1961, 1962, and 1963 when we had the area under nearly constant surveillance.

Direction taken from the Beaches

Evidence for the direction of travel away from the island is scant, but it indicates a westerly movement. In the summer of 1961, 1,980 nestlings were banded on

Sand Island and 2,476 on Eastern Island. Subsequent checks that summer of banded young on the two islands revealed eight Eastern birds on Sand Island, but no young from the latter island were found on Eastern Island.

Records of banded juveniles at sea in the few months after departure are very few, but they indicate a slow movement of young albatrosses west and northwest toward Japan.

Age of Return for First Nesting

The only evidence we have to indicate physiological readiness to breed is egg-laying and, more narrowly even, the presence of a bird on an egg. Not too often is a bird actually observed in the act of depositing the egg. Ownership of the egg is inferred, but in the instance of young birds there must be repeated observations of the same bird on the same egg; many young birds due to breed for the first time in the following year often adopt abandoned eggs and incubate them for two or more weeks, and a few birds two years away from their first nesting may take over such eggs for a few days. There is also loss of some mates during the required two-year engagement period, and consequent delay in breeding, despite perhaps physiological readiness. The extent of this loss is unknown, but 7 instances were noted among the 207 birds whose records are being reported.

A final caution in determining the age of sexual maturity lies in the considerable yearly variation in the numbers of breeding birds in the colony, even in the numbers of experienced birds. The same unknown factors may influence not only the percentage of young that return to breed in any one year, but also the age at which they lay their first egg.

The data must be evaluated then in the light of these disruptive elements. Age as used here is from breeding season of hatching to year of egg-laying; a chick hatched in February 1960, from an egg laid in December 1959, is considered to be 7 years old in 1966.

There is no essential difference in the age-pattern of first nesting by males and females (Table 8), unless it be that the female is more variable in reaching sexual maturity. More females than males first nest in their fifth and tenth years, but the data are too few for assurance. Most birds of each sex breed for the first time in their eighth year (mode and median are at eight plus years). Two-thirds nest first in the eighth and ninth years, and more than 80% from the seventh to ninth years which would, therefore, seem to be the normally expected span of ages.

Table 8. Age of return of Laysan Albatrosses for their first breeding.

	Age (years)					
	5	6	7	8	9	10
Males-118	1.7%	5.1%	14.4%	43.2%	26.3%	9.3%
Females-89	3.4	1.1	21.3	36.0	25.8	12.4
Both sexes-207	2.4	3.4	17.4	40.1	26.1	10.6

At least 10% return for the initial breeding after the ninth year; it is likely that some are delayed until the eleventh year or even longer, but our study is not yet old enough to encompass this age group. The most plausible explanation for this prolonged, pre-nesting period is loss of mates, as indicated previously.

Breeding at the age of 5 or 6 years is seemingly even more unusual. Rice and Kenyon (1962b:521) suggested eight (8) years as the earliest, as indicated by the fact that less than 7% of their birds laid the first egg then. Only 5 (2 males and 3 females) of our 207 birds bred in the fifth year; all 3 females were mated to older males, but mates of the 2 males were not known. Six males and one female first nested in their sixth years, and two of the males were known to be paired with older females, one with a female of the same age class, and three with unrecorded females. Thus, of 12 birds that bred in the fifth and sixth years, nearly 50% were known to be mated with older birds, but only 14.5% of the sample of 207 were so paired. It appears that pairing with an older bird speeds up the maturation process and permits breeding in an earlier year, or it may be that a significant number of the young are physiologically but not behaviorally mature at age 5. (See H. I. Fisher, 1968, for a discussion of the influence of the age of the mate on the date of egg deposition.)

Return of the Juveniles

We have already presented evidence (p. 170) to show that the majority of birds just emerging from the juvenile status, whatever their age in years may be, and preparing to breed for the first time, come to the colony during the last week of November and the first week in December. Most of the Laysan Albatrosses arriving in the last two weeks of December are former breeders or those juveniles that will first breed in the next two seasons. The latter are probably seven or more years of age; see Figure 4.

In this section then, we are interested for the most part in birds younger than 7 years, but since many of the 7- and 8-year-olds are still not breeding, we include these age groups. Most particularly we wish to determine, for the Laysan Albatross, the basis for and the implications of the statement of Rice and Kenyon (1962b:520) that ". . . the innubile individuals tend to reach the breeding grounds relatively late in the season, the number of returns increasing as the season advances," the view of Jameson (1961:208) that "New birds [Wandering Albatrosses] are continually arriving at the nesting site from the sea, the youngest not coming ashore until February or March. . . .," and of Murphy (1936:552), also referring to the Wandering Albatross ". . . younger birds which had certainly not been anywhere near the breeding grounds until several weeks after the bulk of the mature albatrosses had arrived."

The data and our interpretations will be presented separately for each group; Figure 4 shows the cumulative arrival of birds of all ages, and in Figure 5 may be found the absolute numbers of each age group captured on each date after the

incubation period. To prevent the necessity of explaining for each group the anomalous drop in numbers in mid-March and mid-April (corrected by dotted lines in Figure 5) we note here that on both occasions a full moon made recapturing very difficult and relatively few juveniles of any age were recorded.

Recaptures within a 5-day period were considered representative of a continuous stay, a single trip to the colony, in the instance of all juveniles.

It is not possible to report at this time on any sexual differences in the times of arrivals of juveniles for sexing is uncertain except at the egg-laying season.

In this discussion consideration of the few records of recaptures at unexpected seasons will be avoided since we are interested in the usual chronology. Eventually if records were kept long and accurately enough, there probably would be at least one report of each age group for each month of the year. To mention a few, we note: two 5-year-olds in November; two 4-year-olds in January; and two 2-year-old birds on September 2 and one on November 22.

Eight-year-olds (1956–57 chicks):

Forty-eight of the 321 recaptured (15%) were breeding in 1964–65; 35 were apparently breeding for the first time and 13 were known to be in their second season. (Variations in data between Table 8 and the discussions of 7- and 8-year-old birds, based largely on Table 4, come about because Table 8 includes only the plot birds of the total sample.)

The curve for accumulated presence on the island (Fig. 4) is nearly a straight line, and the plotting of numbers recaptured (Fig. 5) shows relatively even numbers after the incubation season except for a major influx in mid-February. The relative uniformity of the curves is probably due to increasing maturity and response to stimuli as well as to the fact that a number of albatrosses of this age are included in the curve for experienced breeders.

The slight peak in numbers in mid-February in this group as well as in the 7-year-olds is real, we think, and is related to the end of the guard-phase. Birds of these age groups already have strongly developed parental instincts and are attracted to the hatchlings of the species, which, it is likely, most are seeing for the first time. Frequently they remain in the colony for several days, watch the exposed chicks, and even nestle down close to them.

Most returning juveniles of this age are in "associated twosomes," pairs, and they revisit the island several times during the season. They may be captured repeatedly near the same bush, bare spot, tuft of grass, or old nest. In other words, they are on station, and they remain as many as five days without leaving.

A typical pattern of recapture is: Dec. 15, 23, Jan. 6, 9, 22, Feb. 5, 17, March 12, 13, 14, April 17, 19, 26, and May 1 and 16. A curious trait of all recapture patterns of individuals is that the birds are not retaken during at least one period of a month; in this instance it was March 15 to April 16.

Seven-year-olds (1957–58 chicks):

Two of the 507 recaptured were breeding, but birds of this groups are essentially juvenile birds. They begin to straggle in in mid-December. Associated twosomes

are most in evidence in late December, January and February, but may be found at any time between mid-December and late May. We estimate that half to two-thirds of the recaptures are of associated pairs, indicating that at least that percentage of the birds have formed pairs.

It is noteworthy that 50% of the returning birds have not appeared until the first week in March, compared to 50% of the 8-year-olds by the second week of February.

A resurge in the number of recaptures occurs in the last week of May; it also takes place in 6- and 5-year-olds but not in the younger classes (Fig. 5). We cannot correlate it with any particular event in the breeding cycle.

Perhaps 75% of these albatrosses make repeated visits to the colony (Table 9); usually, but not so consistently as the 8-year-olds, they are recaptured in the same places. Their visits to the colony are similar in individual duration (3 ± days), but not so frequent. An example of a typical set of recaptures is Feb. 7, March 1, 20, April 17, 22, and May 12.

Table 9. Frequency of visits in 1964–65 of color-marked, non-breeding Laysan Albatrosses

Age (yrs.)	Sex[1]	Range of dates	Total visits all birds			Known lengths of visits (days)
			Pair	Male	Female	
8	4 prs. + 1 ♂	Jan. 30 —May 12	5	4	4	1–4
7	4 prs. + 2 ♀	Feb. 2 —May 24	4	5	4	1–5
5	3 prs. + 2 ♂	Mar. 12 —May 28	2	6	3	1–3
4	6 ♂ + 6 ♀	Mar. 12 —May 14	0	4	1	1–3
3	8[2]	Mar. 20 —May 6		8		1
2	5[2]	April 6 —24		5		1

1. "Pair" means male and female associated.
2. Sex could not be determined.

Six-year-olds (1958–59 chicks):

The number of recaptures (53) is too small for any positive statements, but the first birds of this age are retaken in the first week of February, and they are found in small numbers throughout the season; peak abundance is in April. By the last week in March 50% have been recorded (Fig. 4). In this same figure one may see that the curve for this group is out of the orderly sequence of years; perhaps the small sample is responsible.

More than 50% of these albatrosses are observed in associated twosomes. Twenty-two of the 53 were recaptured at least twice; 8 were taken three times, 5 four times, and one was recaptured March 22, April 6, 26, 28, and May 1.

Five-year-olds (1959–60 chicks):

The first real movement onto the island begins early in February (Fig. 5), and 50% of the birds are recaptured by the third week of March or 2 weeks later than the same percentage of the 7-year-olds (Fig. 4). Their peak numbers come in

the middle of April and almost immediately decline abruptly, only to resurge in the first week of May and again in the last week of May (Fig. 5).

Few of the birds are first seen in associated twosomes; twosomes of birds of this age begin to appear in late April and recaptures thereafter are perhaps at least 25% of "pairs" rather than of individuals. We have the impression from somewhat casual, yet repeated observations, rather than from quantified data, that birds in twosomes stay longer each visit and return more frequently.

Four-year-olds (1960–61 chicks):

A very small percentage return in late January and early February. Significant numbers are first recaptured in mid-March and they reach their greatest abundance in mid-April. Not until the first week of April are 50% of them recorded, nearly 2 weeks later than the recapture of 50% of the 5-year-olds (Fig. 4).

In one area where 407 chicks were banded in the summer of 1961 we kept careful records of repeated captures. Of 207 birds recaptured: 89 were reported two or more times; 24 three times over periods of 22, 32, and 42 days, respectively; 4 recorded four times; and one caught five times between April 4 and May 28.

The longest spread of time from first to last recapture was 82 days; the next longest was 61 days. Most birds visited just once, but some are known to have made three different stays of one to three days within a 50-day period. The usual interval between trips or stays, as contrasted with time between recaptures, was 16 to 25 days.

In 1964–65 we recaptured nearly 50% of a sample of 407 birds of this age class, nestlings banded in June and July, 1961. Considering probable but still unknown mortalities in the span of four years, it appears that most Laysan Albatrosses return at least once to the colony in their fourth year.

Three-year-olds (1961–62 chicks):

Robbins (1960a) found less than 1% of 3,200 chicks banded in 1957 on Sand Island. Of 390 nestlings we banded in one test plot in June and July of 1962, 124 (32%) were recorded in the colony during the spring of 1965. The lower recapture rate, as compared to 4-year-olds, signifies, we believe, a lesser tendency to return in the third year and not a lesser survival. If, as seems likely, the 50% recapture of 4-year-olds means return of most survivors, and if mortality is the same in the two age groups, then a 32% recapture of 3-year-olds indicates a return to the colony of 2 of every 3 living birds.

Few birds three years old are found before the end of the first week in March or after the middle of May (Figs. 4, 5). Peak numbers occur in the third week of April, and 50% of these birds have arrived by the end of the first week in April; both events are a week later than in the case of 4-year-old albatrosses. As a group the birds are in the colony over a shorter period than are any of the older birds.

Thirty-six birds of a sample of 124 were recaptured two or more times—2 were taken four times over spans of 22 and 49 days, respectively, and 2 were recorded five times with 11- and 49-day spans, respectively. The frequency of recapture, considering recaptures within 5 days as indicative of a single visit to the colony,

indicates that 25 birds made two trips, 3 visited three times, and none are known to have returned four or more times. Further, they remained for a shorter time on each visit, compared to older birds (Table 9), and the intervals between visits were longer. Typical records of recapture of birds believed to have returned on three separate occasions are: April 6, 24 ,and May 6; March 22, April 18, 24; and April 21, May 5, and 11.

None of this age group are found in associated twosomes and they tend to wander more, to be recaptured at different places within the general area as Kenyon, *et al.* (1958) indicated. This movement on land may have been a factor in the lesser recovery rate of known 3-year-olds.

Two-year-olds (1962–63 chicks):

Although an occasional bird of this age may be in the colony at any time in the breeding season, records before April 1 or after the first week in May are rare; the span of their presence in significant numbers is thus much more restricted than that of any other group that returns. Maximum numbers occur in the third week of April and 50% have returned by the second week of that month, nearly a week later than birds a year older (Figs. 4, 5).

Very few of them return to the island. Only 181 (6%) of 3,087 nestlings banded were taken in areas we searched, and in our study plot just 8 (2%) of 445 were recaptured. Only 8 of the 189 birds were recaptured twice in 1964–65.

Some part of the low recovery rate may be because the birds are obviously warier, are presumably not yet so firmly affixed to one area of the island, and do not remain for long, but the essential picture for 2-year-olds is that perhaps one in 10 makes one brief return in a late and restricted part of the breeding season. Sorenson (1950b) also noted that the earliest return of Light-mantled Sooty Albatrosses was at the end of the second year.

One-year-olds (1963–64 chicks):

We recaptured none of 2,930 banded in the areas searched in 1964–65, and none of this age were recaptured by Rice and Kenyon (1962b:520). It is perhaps pertinent and interesting that Sladen, *et al.* (1966) found no yearling Adelie Penguins, *Pygocelis adeliae*, in the colony, despite the presence of 2-, 3-, and 4-year-olds.

The data on return of 2- and 1-year-olds in part substantiates the comment of Rice and Kenyon (1962a:383) that "... no appreciable number of innubile birds return until at least the third season following hatching. . . .", but our recapture of significant numbers of 3-year-olds (their 2-year-olds, we believe) does not.

Return of juveniles to the same area

The questions to be resolved here are whether the juveniles first return to the natal area, how closely they do so, and whether they come back to this area on subsequent visits in the same season and in following years? If so, are these visits preparatory to pairing and nesting in the same area?

Our study is too young and the data thus far too few to justify conclusions, but we may make some preliminary statements which amplify such comments as that by Robbins (1960a) that 3-year-olds are found in the same general part of the

island where they were raised.

The juveniles in subsequent years are found in the areas where they were hatched. The evidence is from a variety of observations. For three summers (1961–63) we banded all nestlings in a test-swath on Eastern Island; the area was 100 yards wide, 200 yards long, and near the shore. Bands were applied in continuous sequence each summer to make easier the later identification of the area of origin. None of the yearlings (of 1963) returned, but in Table 10 are data showing that 94% of the 3-year-olds that visited the colony and 99+% of the 4-year-olds recaptured were taken where they were banded. Data for our study area (Table 10) indicate that 55% of the birds 3 years old and 90% of those 4 years old returned to the natal area. Another aspect of these data is that significantly more of the older birds were captured in the home area; this may be a result of more of them visiting the area and/or of their remaining for longer times.

Table 10. Return of three- and four-year-old juvenile Laysan Albatrosses to the place of their own natality.

	Banded		Recaptured		Per cent of recaptures			
					Area where banded		Other areas	
	3 yrs.	4 yrs.	3 yrs.	4 yrs.	3 yrs.	4 yrs.	3 yrs.	4 yrs.
Swath	767	407	210	205	93.8	99.5	6.2	0.5
Plot	485	298	108	135	54.6	89.6	55.4	10.4

The apparent differences between the data on recaptures of 3-year-old birds in the plot and in the swath are rather easily explained, we think. Returning young birds often land first on the shore and then move to the interior of the island. Since the swath was on the shore, any bird belonging to the area and landing there was immediately recorded as a "recapture at banding site," but the plot was in the interior and a plot bird captured on the shore area was not recorded as recaptured at banding site. A contributing factor may have been the wariness of the 3-year-olds; a plot bird taken on the shore may have been frightened away to sea without ever going to the plot. Evidence for this latter view lies in the lower total recapture rate of 3-year-old plot birds (22.3%) versus 27.4% for birds belonging to the swath.

Repeatedly in our recaptures of banded birds we have taken, in successive catches, albatrosses bearing consecutive numbers or separated by only a few digits. Since the bands were applied in sequence to nestlings often only a few feet apart, their frequent juxtaposition several years later can only mean that the birds are returning to fairly restricted areas.

Another measure of the attachment of a bird to a specific part of the island is how often it visits there in a single season. In one group of 124 recaptures of 3-year-old albatrosses, 36 were taken two or more times in the same place (2 taken four times and 2 taken five times). Further, in this same group, 3 birds are known to have made at least 3 trips from the sea to that place, and 25 made at least 2 separate journeys. In one sample of 197 recaptures of 4-year-old albatrosses, 118

were taken two or more times in the same place (89 twice; 24 three times; 4 four times; and 1 five times), and approximately 60% of the 118 birds are known to have made at least two roundtrips between the sea and the natal place.

To eliminate as much as possible the factor of fright in reducing the number or duration of visits in 1964–65 of a selected group of juveniles, we color-coded their breasts and searched for them each time we were near the site of their first recapture. These data (Table 9) indicate that older birds revisit this site oftener, longer each time, and over a greater part of the season. Especially is this true of paired birds.

Other data on return of juveniles to the original banding site in successive years are limited, but evidence from recaptures of three groups of young albatrosses in our study plot also indicate successive return to the same place.

The group of 260 older juveniles, banded in late December, 1962 and discussed previously, showed in 3 years a 63% return to nest in the plot; and 18% were recorded as non-breeders in later years. Thus, 81% of these birds did come back to this acre-plus plot.

In March of 1964, Mr. Chandler Robbins banded 185 "walkers" in our plot. Their younger juvenile status was substantiated in late 1964 when we recaptured 50% in the study area after December 9, and found only 2 birds (2%) breeding. In 1965 we could only be in the colony from November 25 to December 15, a time too early to expect many of these birds to be present, but 18% of the 185 were recaptured and 12% were breeding. In the two breeding seasons since 1965, 63% of the 185 are known to have returned at least once. When the probable mortality since 1962 is considered, the percentage of return approximates 90. Therefore, we suggest that younger birds (probably 5- to 7-year-olds in this instance) are already strongly attached to an area.

Referring once again to the visiting juveniles of all ages banded in the study area in 1964–65, the fact that 16% of 986 birds were found in the next 2 years nesting within a 100-yard radius of the site of banding indicates a proclivity of older juveniles to return to the same site. That 60% of those captured in the plot before December 15 bred in the plot within two years is further evidence.

And finally, four of our 1960–61 group of chicks have settled down to breed; for each of these the natal site is known. Their breeding sites are 22, 20, 47, and 106 feet away.

Interisland Movement

Kure to Midway

During the 1964–65 breeding season, members of the Smithsonian Institution's Pacific Project staff painted the heads and/or breasts of the birds they captured on Kure Island. The obvious nature of these color marks made it easy for us to see these birds on Midway, and we made every effort to recapture them.

A total of 188 different, newly banded individuals were taken; 45 of these were captured 2 or more times between February 6 and June 2, 1965. Four juveniles

banded on Eastern Island in previous years visited Kure in this time period and were retaken later in the season by us on Eastern. But among the nearly 12,000 recaptures we made on Midway in that season we found no birds banded on Kure Island before the fall of 1964.

Of the 45 individuals taken two or more times, 29 were caught twice, 13 three times, and 3 birds four times. Based on our studies of juveniles known to belong to Midway we think the usual visit of a juvenile lasts no more than 4 or 5 days, but some may stay continuously for as long as a week. Although we could not be certain of the continuity of presence of the Kure Island birds, the frequency of their recapture in the same part of the island indicated the 45 "belonged to Midway;" in 15 instances they were recaptured in less than a week.

In addition to these 45 birds recaptured on two or more different dates, 21 other birds repeated on the same date but at different locations on Eastern Island; one bird was taken three times during one night at places along the shore separated by as much as three-fourths of a mile. Despite the fact that capture undoubtedly excited the birds, and might have resulted in their moving, we found few such same-day-different-place repeats among the thousands of juveniles known to have been raised on Midway. When we did it was usual to find the bird first near the shore and then in its natal colony in the interior of the island. The wariness of some of these Kure to Eastern birds was also a factor in our conclusion that they were strangers on Midway.

Most probably we did not record each Kure Island bird each time it was present, but the median interval between 45 visits was 28 days (range = 5 to 68 days), and it is evident in the pattern of return of the 16 birds recaptured 3 or more times that they came in at approximately one-month intervals.

Total numbers of birds banded on Kure and recaptured on Midway were as follows: February, 11; March, 58; April, 100; May, 61; and June, 2 birds. Since the seasonal pattern of numbers captured is similar to the pattern established for known juveniles and quite unlike that for the breeding birds, it is a safe assumption that most of these were non-breeding juveniles who stopped only briefly on Kure. Sixteen birds were on Midway within 48 hours of their first, known presence on Kure.

Midway to Kure

The analysis of recaptures on Kure Island of birds banded on Midway presents quite a different picture. Because so many more Laysan Albatrosses of all ages have been banded on Midway than on Kure one might expect, if there is an equal percentage of albatross travel in both directions, more Midway birds on Kure. Although our Eastern Island albatrosses were color-marked on the head and thus easily noted by the Smithsonian group which worked constantly and diligently on Kure Island, only one of 3,000 recaptures they made in February, 1965, involved a Midway bird, and between November, 1963, and May, 1965, they recorded only 109 birds first banded on Midway; 98 were of known age (Table 11). More than half of the birds may be presumed to have been of breeding age, and one was a

Table 11. Ages of Midway Laysan Albatrosses recaptured on Kure Island

	Age (years)							
	3	*4*	*5*	*6*	*7*	*8*	Unknown	Breeder
Number of birds	3	9	17	2	56	11	10	1

known nester on Midway.

Further, the pattern of the time of the visits fits older age groups of birds. Ten were recorded in November, 20 in December, 14 in January, 74 in February, and 17 in March; none were recaptured in April or later (see also Fig. 4). If the time of a bird's presence on Kure is plotted against its age (Table 12), we find that the different age groups returned approximately as on Midway (Figs. 4 and 5), the two 5-year-olds in November being the major departure from the expected. However, the arrival of the juveniles appears to be somewhat earlier than on Midway, if these few birds are representative.

Table 12. Age of bird and time of recapture of Midway Laysan Albatrosses on Kure Island

Age (yrs.)	November	December	January	February	March
3				2	1
4			2	5	
5	2			13	1
6			1		1
7	7	13	9	39	10
8	1	5	2	4	3

Twenty-four of the 109 birds were captured on Kure more than once. One 8-year-old Laysan was found on Kure once in each of 3 seasons: March, 1964; February, 1965; and November, 1965. Two 8-year-olds were taken twice at intervals of a year, and one 8-year-old was recorded in 1963 and 1965. Thirteen 7-year-olds were captured in 1964 and again in 1965, and two were reported in 1963 and in 1965. Only five birds (all 7-year-olds) were taken twice in the same breeding season; four were caught twice in February and one was recorded in November and March of the same season. Thus, although Midway birds that landed on Kure tended to visit there again in percentages about equal to those of Kure birds found on Midway (24%) there is a difference of major import. Only 5% of the Kure-reported Midway birds revisited in the same year, compared to 24% of the Midway-reported Kure albatrosses.

This is not unexpected, for Kure Island is the most northwest land of the breeding area and the closest to the presumed feeding range of the younger birds. In fact we think it likely that some breeding Laysan Albatrosses and others, which will breed in future years farther southeast in the Hawaiian Archipelago, "island hop" as they first return each year from the northwest Pacific. That they are not so inclined as they go back to sea is indicated by the absence of Midway birds on

Kure after March, and by the relatively fewer recaptures of Midway birds on Kure at any season.

Only a great number of future recaptures will verify this hypothesis that many juveniles banded on Kure and Midway islands in late winter will eventually be found nesting on islands to the southeast—Pearl and Hermes, Lisianski and Laysan—from which the birds came in the first place.

Between Sand and Eastern Islands of Midway Atoll

The data presented here are from the 1964–65 breeding season when, for other purposes, we made the most intensive and widespread attempt to recapture banded birds. However, the design of the observations intended for other experiments led to our searching the beaches and shore areas of Eastern Island and only the interior of Sand Island. Since we know that Laysan Albatrosses on a strange island tend to frequent the shore areas more than the interiors of the land, no valid comparisons may be made of the direction of movement between the two islands.

One might expect considerable movement between islands within sight of each other and that this travel would be demonstrated by the considerable number of birds we have banded—approximately 5,000 nestlings on Sand Island and 30,000 nestlings and nearly 5,000 adults or juveniles on Eastern Island. But such is not the case; there appears to be even less interisland movement than between Kure and Midway!

Only 37 juveniles and no adults banded on Sand were found on Eastern, and only 2 birds from Eastern (a 3-year-old juvenile and a bird of unknown age) were recaptured on Sand Island.

None of the recaptures involved breeding birds; in fact, in our experience of the last six years no breeders are known to have been found on other than their own of these islands constituting Midway Atoll.

Of the Sand Island birds found on Eastern: 8 were 4-year-olds; 24 were 3-year-olds; and 5 were 2 years old. Aside from the capture of a 2-year-old on February 26, the interisland movements took place between mid-March and the first week of May—8 in March, 24 in April, and 4 in May—and were similar to those from Kure to Midway in time, extent, and probable age of birds involved.

Between Sand, Eastern, and Lisianski Islands

Another insight to albatross movement between islands may be had from our attempts to transplant fledglings in July, 1961 and 1962. Of 934 birds transplanted from Sand to Eastern, 45 were found in 1964–65 on Eastern and 95 on Sand Island. One of the latter turned up on Kure Island January 25, 1964, and was on Sand Island May 17, 1965. One was on Sand Island March 2, 1965, and on Eastern Island April 24, 1965; another was recaptured on Eastern May 1, 1965, and the next day was on Sand. One moved from Sand Island to Eastern Island between April 15 and 24, 1965.

In 1962, 2021 nestlings were moved from Sand Island to Lisianski Island; 1847 survived the rough trip but we could not remain there long enough to determine survival at departure time. In 1964–65 we recaptured 13 at their home site on Sand

and 33 on Eastern; 2 were taken on Kure Island the first week in February, 1966. Four of the 48 were recorded in February, 24 in April, 8 in March, and 6 in May, 1965.

Transfer of 112 nestlings from Sand Island to Kure Island was accomplished in July, 1961. One died immediately and only one has since been recaptured on Kure (March 26, 1965); one was taken on Eastern Island on April 8, 1965, and 19 were recaptured at the home area on Sand Island.

Although the greater inter-island movement of these 2,950 transplanted juveniles may probably be attributed to navigational confusion resulting from the translocation, it does provide further evidence of the mobility of juvenile albatrosses of known age. It also indicates that the predominant movement occurs in March and April.

Summary and Discussion

This analysis of the movements of Laysan Albatrosses on and off Midway Atoll in the North Pacific is based upon more than 25,000 recaptures of banded birds. These were birds banded over a period of 10 years, albatrosses of all ages and in all phases of the life cycle. For more than 3,000 of the birds we have rather detailed biographies of their lives for the past 6 years, and the ages of an additional 4,000 were known.

Contributing greatly to our analysis is the fact that we have lived among the albatrosses for nearly 50 man-months extending from 1945 to the present and, we hope, the future. Most intensive study has centered in the past six years, however.

We draw the follow conclusions, some tentative, relative to the movement of Laysan Albatrosses to and from their breeding grounds on Midway.

Breeding Birds

1. Experienced birds arrive in the colony between November 1 and December 1. Their arrival is precipitous in the second and third weeks of November. Not only do males in general precede the females to the colony; in most instances they precede their mates.
2. Birds breeding for the first time usually arrive in the last week of November and the first week of December; exceptions are young males or females mated to older birds. The later arrival of young pairs has been shown to be typical for a wide variety of pelagic seabirds, as for example, *Sula bassana* by Robertson (1964).
3. First-time breeders nest, for the most part, in their eighth and ninth years. Nearly 25% first nest from their fifth to seventh years, some perhaps as a result of pairing with older birds. At least 10% do not breed until after the ninth year; for some birds, the delay is occasioned by the loss of a mate during the 2-year engagement period.
4. Successful breeders begin to depart in mid-June, when the oldest fledglings leave the colony, and most are gone by the last week of July. After August

1, they are rarely observed. The presumed stimulus is absence of the nestling at the nest site.

5. Failed breeders depart within three or four days of loss of egg or chick, but may return to the colony, and more specifically to the nest site, several times before mid-May. They usually are not found there after this time. Birds unsuccessful in rearing a chick because of the loss of the mate exhibit a somewhat different pattern. Disappearance of the mate during incubation leads to an inordinately prolonged span on the egg, followed by nearly weekly visits to the nest site until February. In March and April bereaved males are rather continuously on territory, and the single females just as often wander through the colony. If loss of mate occurs after hatching, the remaining member of the pair, male or female, continues feeding the chick until the chick dies.
6. For all these birds, as well as for the associated twosomes, the territory of the male is thought to be the meeting place for members of the pair and is known to be the focal point of their activities.

The regularity of the return and departure of the colony as a whole, the progressive earliness of arrival of aging adults and juveniles in successive years precludes the postulation of any single external stimulus immediate either in time or place.

Whatever the stimuli may be, all ages (save one-year-olds) do respond. The stimuli are definite and seasonally oriented, as indicated by the specific times of arrival for different age groups, and the abrupt arrival of experienced breeding birds which evidently respond more quickly and uniformly. We may theorize that the cline of arrival times results from increasing physiological maturity coming with age, from summation of stimuli in previous seasons, or from summation in a single season. We can not relate the stimuli to daylength; all breeding birds arrive with shortening days, and essentially all the juveniles during times of lengthening days. Temperatures are decreasing when breeders arrive, and increasing when the two- to five-year-olds come in. The possible stimuli for departure may be more easily suggested. Temperature is increasing when all ages leave for the season, and daylength is increasing at least until the exodus of fledglings and breeders begins.

It is not impossible, of course, that Laysan Albatrosses respond to some astronomical factor, as suggested by Marshall and Serventy (1956) and Serventy and Marshall (1959) for *Puffinus tenuirostris* and Jameson (1961:99) for albatrosses. This would in no way explain the differential arrival of the age groups, unless we further assumed that they reacted to different, seasonal celestial patterns, and it would necessitate a slow correction by all groups, over the years, to compensate for shifts in celestial configurations.

Breeding birds are presumably widely scattered over the North Pacific in the non-breeding season and must travel distances that vary considerably and cover many degrees of latitude and longitude. However, the Laysan Albatross is strong and swift in flight, as the experiments of Kenyon and Rice (1958) showed, and within

the range of the normal period for arrival for its age or status group it could fly from any part of the North Pacific. Hence, consideration of local conditions may be useless unless these albatrosses congregate off shore before the breeding season as some other species of seabirds do (Manx Shearwaters, for example, as reported by J. Fisher and Lockley, 1954:187) and move onto land more or less *en masse*. If this happens, and congregations of several hundred Laysan Albatrosses have been reported at this season within 50 to 100 miles of Midway by pilots of Midway's air-sea rescue group, local weather or moon stages might influence by a few days the arrival on land.

Long-time human residents of the atoll believe that the majority of the birds return with the full-moon in November, and in 1964 the moon was waxing during the time of maximum influx of breeding birds. We have no evidence that local storms influence the return of these breeding birds. Midway's location is such that winds may blow from all four cardinal directions in a single day, and seldom at this season is the wind constant from one direction for more than a day or so. In the fall of 1964 there were major increases in the number of birds in the colony during winds from the SSE, NNW, NE, S, ESE, NW and SW. Local weather later in the year does have an effect on the numbers of albatrosses present on the island, but the breeding birds first come in response to some internal stimulus whose schedule has perhaps remained unchanged, even by a long-ago shift from southern to northern hemispheres. The primary factor in this retention of the ancestral time schedule may be that it produces chicks after many of the winter storms are past and permits their first departure during mild summer weather when the trade-winds aid in moving them westward toward their oceanic "nursery grounds" east of Japan.

To obtain a concise overview of the periodicity of the movements of breeding Laysan Albatrosses to and from the colony we show a typical pattern for each sex in Table 13. One is impressed immediately with the truly oceanic life of this species. Each breeding bird visits the colony a maximum of perhaps 75 times each breeding season, and despite a season which continues for 8.5 months it manages to be on land for a total of only 2 months!

Remarkable also is the very little time the male and female spend together on land. We estimate the average time as 5 to 10 days of the 230-day breeding season, aside from the infrequent and chance meetings during incubation and feeding of the chick.

The movements of the two sexes are nearly identical. The only difference in the number of trips to the breeding colony is that the male makes an additional one while waiting for his mate. The sex difference in total annual time on land (male, 18%, female, 12) or sea comes from the male's wait on land for his mate and his considerably greater share of incubation duties.

A number of factors of breeding behavior contribute to the potential ability of each bird to return to the colony so infrequently and, aside from the incubation period, to remain there so briefly: 1) as indicated above, the sharing of all duties;

Table 13. Typical, annual periods on land and sea of an experienced, breeding Laysan Albatross

Stage	Number of trips to Midway	Duration (days)		
		Total	On land	On sea
Off-season		115		
Males	0		0	115
Females	0		0	115
Reunion[1]		11		
Males	2		10	1
Females	1		1	10
Honeymoon		10		
Males	1		0	10
Females	1		1	8
Egg-laying		1		
Males	0		0	0
Females	1		1	0
Incubation		65		
Males	4		43	30[2]
Females	3		30	43[2]
Guard		14		
Each sex	3		7	7
Post-guard		(150)		
Mid-Feb. to Mid-May		90		
Each sex	50		3	87
Mid-May to Mid-July		60		
Each sex	15		2	58
Totals				
Males	75	366	65	308[2]
Females	74	366	45	328[2]

1. Based on male preceding female to Midway.

2. Inconsistency of eight days in incubation period results from averaging periods of many birds and causes inconsistency in total days in year.

2) the almost immediate copulation after the reunion, and the quick return to the sea; 3) the quick deposition of the egg; 4) the oftentimes quick exchange at the nest, followed by immediate departure; 5) the capacity of a single adult to guard and feed the newly-hatched chick for several days without relief; 6) the general practice of alternate feeding of the chick by the parents; 7) the short guard period; and 8) the ability of the parent to carry to the nestling on each feeding trip sufficient food for as long as two or three days and, of course, the capacity of the chick to receive these amounts. Related to these are a number of physiological attributes, among them the ability to forego food and water for extended periods and to withstand tremendous losses in body weight.

Perhaps the most unusual of all these contributing elements, and it is really a combination of several, is the infrequency of the trips to the colony and the economy of energy that results. To rear a chick successfully during a period of 230 days requires only 160 trips to the colony by the parents, fewer by far than many pas-

serines make to the nest in a single day.

Former Breeders

1. Former breeders begin to arrive early in November, along with the breeders, but only 50% have been in the colony by December 1. Many of these pairs are gone by mid-January. It is known that some (10 ± %) of these early arrivals have lost a mate and hence do not breed. No explanation can be offered for the others. Former breeders without mates reappear in the colony at frequent intervals throughout the season, or until they begin to associate with another bird.
2. A second wave of arrivals begins in mid-December and continues to mid-January; approximately 40% of the former breeders are first recaptured then. Presumably these are birds which for one reason or another are not physiologically ready for breeding.
3. Additional pairs and singles may be found in the colony until March, but former breeders are rare after April 1.

The manner and timing of visits by experienced breeders tend to bring them together at a time before most of the juveniles, paired or not, arrive in the colony. Adults which have lost mates the season before are first exposed to each other and this increases the proportion of rematings between older birds, which has a major benefit for the species and comes about in two ways.

Other of our studies (*in litt.*) show that these albatrosses do not normally breed the year after the pair bond is formed; this is virtually the rule for first pairings. But in the instance of re-pairings it seems that a greater percentage, though still small, of nestings occur in the year following the loss of a mate when both members of the new pair are experienced breeders. Thus the advantage for the species is the immediate prevention of a year's loss of the reproductive potential of some of these birds. Further, if birds of disparate ages pair there is more chance of a later disruption of the bond by death before the reproductive life of either individual is completed.

Pre-Egg Stage of Breeders

1. Males are on territory some 6 to 16 days before their females arrive.
2. Males are more constantly on territory during this time than are the relatively few females who precede their mates.
3. Copulation usually takes place within 24 hours of the reunion on land, and within 36 hours the pair disappears from the island.
4. It is the female that returns first, but the male usually follows within 24 hours.
5. Fifty per cent of the time the female is alone at egg-laying which occurs in less than 24 hours from the time of return, and usually within 12 hours.

Movement of Breeders During Incubation

1. Although Rice and Kenyon (1962b) indicated eight spans of incubation, during which one member of the pair is absent, we found only seven, and only six of these involve trips to sea not already discussed.

2. Males make 3 trips for a total of 29 days. Females make 3 trips for a total of 43 days, and for both sexes the stay at sea is progressively abbreviated with each trip.

Post-Hatching Movements of Breeders

1. Guard phase: During the average 14 days of this phase each member makes 3 trips to sea and stays there a cumulative total of 7 days, primarily in the first half of February.
2. Post-guard phase: In general the parents alternate trips to the nestling on a 48-hour basis so that the young is fed daily until mid-June. After this time, and until the chick leaves the nest site, each parent averages a feeding trip each three or four days.
3. During the post-hatching period the average adult makes 60 to 70 trips to sea, and spends only 3 or 4% of the total time on land.
4. Because of the schedule just indicated, it is evident that parents are seldom more than a day's flight from Midway during the time the nestling is being fed.

Departure of Fledglings

1. The span of time for leaving the colony is about June 20 to August 1 or 2, but the greatest exodus occurs from July 5 to 25.
2. Departure from the island may be as long as a week after the fledgling leaves the nest site, but most survivors disappear within four or five days, of which no more than two days are spent on or near the beach.
3. Test-flights conducted of necessity into the wind result in most fledglings moving south and east and, perhaps incidentally, toward the sounds of the reef and the closest deep water where they can find food.
4. It is suggested that the pathway to the beach, established by the fledgling on its first trip seaward, becomes the reverse route for its later return as a juvenile, that each return reenforces the stimulus to use the route, and that it is "traditional" by the time the bird is sexually mature.
5. Fledglings tend to move to the beach in units which are already discernible as subcolony associations in the breeding colony.

Return of the Juveniles

1. Birds still one or two years from their first breeding, birds for the most part at least seven or eight years old, begin to arrive in the first week of December. Eighty per cent have appeared by March 1.
2. Eight-year-olds, not known to be breeders, begin to arrive the second week of December and continue to appear in similar numbers until mid-May, although they congregate in the greatest numbers in early February and late March and April. Mostly they are in associated twosomes and on territory where they frequently remain for as long as five days on more than a dozen occasions during the breeding season.
3. Seven-year-olds also first appear in the second week of December, but not until late January have 10% of them come into the colony. Thereafter,

they arrive in gradual fashion to reach a peak abundance in late March and April. Half to two-thirds of their number are in associated twosomes, but these latter are most evident from late December through February. Not so frequently as the eight-year-olds are they recaptured in the colony, and their stays on territory each time may be shorter (3 ± days).

4. Six-year-olds first appeared in our samples in the first week of February and were present throughout April, which month was the time of greatest numbers. Fifty percent of the birds were in associated twosomes, and less than half visited the colony at least twice. However, the number of recaptures was too small for any conclusive statements about this age group.
5. Five-year-olds begin to move on to land in considerable numbers in mid-February, although some arrive as early as the third week of January. Fifty percent have been in the colony by the third week of March, and maximum numbers are present in the middle of April. A month later a near-maximum peak is attained, and another late in May. Some five-year-olds are present as late as mid-June. This age group appears to visit the colony in relatively greater numbers, and to stay longer on each visit, then any of the younger birds. Associated twosomes of this group normally do not appear until late April; from that time at least 25% of the birds are associating. As yet scanty evidence suggests that the twosomes are formed after arrival on land; unassociated males on territories entice passing females and seemingly one of the latter eventually stays to form a twosome with the male.
6. Four-year-olds do not appear in significant numbers until mid-March; the first few arrive in late January. By the first week of April, 50% have visited the colony, and all through April albatrosses of this age are most numerous. We saw no twosomes, but records of first breedings indicate that an occasional bird of this group must be paired. Their trips to the colony decline rapidly in late May, and soon this group is gone for the year. Apparently fewer than half visit the colony twice in a season, although we did observe that 10% visit 3 or more times at intervals of 16 to 25 days. Their stays are brief. We judge that most surviving 4-year-olds make at least one trip to Midway.
7. Three-year-olds return to the breeding colony in lesser numbers than 4-year-olds; perhaps 1 of 3 stays at sea in this third year. Some stragglers appear in the second week of February and after the middle of May, but April is the month of abundance for this age group. There are no twosomes, and two-thirds of the individuals make but one fleeting visit to the colony. Territories are not held by albatrosses of this age.
8. Two-year-olds are virtually restricted to visiting in the month of April, although 10 to 20% may appear in late March. These albatrosses are warier and less apt to be retaken in the same place in the colony than any

older group; they are mobile. Perhaps one in ten surviving 2-year-old makes one short trip to the colony.

9. One-year-olds, in our experience, do not come to the colony.

It is evident that our data do not agree completely with the findings of Kenyon *et al.* (1958:12), "Large numbers of unemployed birds are on and near Midway *throughout the nesting season*" [italics mine], and reiterated in Rice and Kenyon (1962b:520). The greatest number of juvenile Laysan Albatrosses occurs in the colony between mid-March and mid-May, and the peak is in the middle of April. However, the overall abundance is composed of a chronologically arranged series of maximum numbers of birds of different ages. As their age increases to six years the juveniles return a week or so earlier each year. In their seventh year most come back at least 2 weeks earlier, and a month earlier when they are 8 years old and still not breeding. These major advances in the season of return may be due to the fact that most 6- to 8-year old birds are paired. Eight-year-olds and a few of the 7-year-olds that will breed the following year come in 6 to 8 weeks earlier (late December). Birds breeding for the first time return during the last week of November and the first week in December.

The studies of Serventy and Marshall (1959), Serventy (1961, 1963), Tickell and Pinder (1966), and Richdale (1954) indicate that a similar situation may be widespread in procellariiform birds, although in no other species has the age pattern been fully established. Hitchcock (1963:25) indicated that the first recovery of a Wandering Albatross on its natal island was at age 4 years and 11 months and that young White-capped Albatrosses (*D. cauta*) are widely dispersed from the nesting area in the first 2 years. And it may be a common phenomenon, for Coulsen and White (1958) working with *Rissa tridactyla* noted that "old breeding birds" returned earlier than "young birds" and that the majority of the young birds that visited the colony for the first time did so when the breeders were feeding young.

Other age-related changes are frequency and duration of visits to the colony, and attachment to a particular station. Yearlings do not return, and two-year-olds are found relatively infrequently. By the time they are five or six years old, most individuals return several times each season and are recaptured in the same stations. Rice and Kenyon (1962a:382) indicated that "Most unemployed birds are firmly attached to a particular site as are nesting birds. . . .," but Kenyon *et al.* (1958) had observed wandering of birds from the area where they were marked. However, in the latter instances the authors noted the attachment of some birds to a limited area. All these apparently conflicting observations may be correct; the explanation lies in the age of these non-breeders. Paired juveniles are usually on home stations; unpaired ones are not. In the spring months (the 1958 observations) both age groups are in the colony, but the 1962 data came before early March, before many unpaired juveniles arrived.

The evolution of a pattern of return, and departure, which involves successively later visits to the breeding colony by successively younger juvenile birds is of major significance to the survival of the species. First of all, arrival by age groups in-

creases the probability of pairings between birds of similar, if not identical ages, and this reduces the probability of untimely disruption of the pair by death of an older mate. This is especially important in the Laysan Albatross in which death of a mate may not only mean loss of a current egg or chick but failure to breed the following season. Prevention of these events increases the reproductive potential of the pair and the species.

Secondly, arrival of juveniles too young to pair, subsequent to the return of those of suitable age, reduces the density of occupation and the confusion in the colony, which might be expected to interfere with the processes of territory-seeking and pairing. Thirdly, the early and essentially separate return of experienced breeders means that these individuals with presumably greater capabilities for successful reproduction may proceed unhampered with copulation, egg-laying, and incubation. As Sladen, *et al.* (1966) suggested for the Adelie Penguin, social interaction with younger birds may be deterimental to reproductive success. The absence of breeders in March and April except for brief returns to feed the nestlings reduces the crowding and strife in the colony at the time certain juveniles are establishing territories and finding mates. Further, presence in the colony gives an opportunity for these juveniles to "practice" at nesting, as suggested by J. Fisher and Lockley (1954).

One example may be given of the magnitude of this potential crowding. The study plot is slightly more than an acre in extent. In some years as many as 750 pairs nest there, and more than 3,000 other albatrosses are known to frequent it consistently. If all these were present at one time, each bird would have less than 12 square feet, and this for all the activities of a six- to eight-pound bird with a six-foot wingspread.

Local weather has little effect on the arrival of juveniles; heavy rain may cause greater numbers to remain on the island, and fewer albatrosses are ashore on hot, humid days of spring and summer as Kenyon, *et al.* (1958) reported. However, there are some coincidences of moon stages and numbers of juveniles. Note in Figure 5 that the curves of numbers of 3- to 5-year-old birds have essentially three peaks; in each instance the maximum in April occurred at full moon in 1964–65; in March the numbers built toward a peak as the moon waxed; the peak in May preceded the full moon but the numbers did increase as the moon filled. In all instances numbers declined as the moon waned.

These coincidences were not so evident in the 7- and 8-year-old albatrosses where the stimulus of physiological maturity might be expected to be strong. But even here the February peak came as the moon increased, and the May maximum declined as in younger groups. However, all this simply may mean that moonlight nights make satisfactory travel times for these otherwise diurnal albatrosses.

It is possible that explanations for these periods of maximum numbers will come when we know the sexes involved.

Return of Juveniles to the Place of Their Hatching

1. They do return to the home island, and to the colony where they were

raised.

2. Moreover, they may return more exactly to the particular part of the colony where they were hatched.
4. Thus far, only four nestlings whose natal sites were plotted have been found breeding. All four were on eggs within 106 feet of the natal site; two were only 20 feet from it.

Inter-Island Movement

1. Relatively seldom does a Laysan Albatross of any age land on an island other than its home island.
2. Birds of presumed breeding age only rarely visit other islands; most such instances occur in November and December as these birds move southeast from oceanic feeding grounds and land on the more northwestern atolls of the Leeward Chain of Hawaii. Apparently they do not visit other islands as often during the breeding season or at all on their way from the colony at the end of the season.
3. Considerably greater numbers of juveniles, though still relatively few, visit islands enroute to, but not from, their home island.

Acknowledgments

So many persons have contributed so much over so many years that any expression of gratitude seems inadequate. Birds have been banded over a period now of ten years and records of current status maintained. Thirteen trips to Midway and more than two years of living there have involved a multitude of persons; we cannot even list here all the names.

A composite, heartfelt thanks, then, to all who helped us on Midway and especially to John Atwell, George Johnson, James Priest, Lt.-Cmdr. Glenn (Red) Wilson, and Captain George W. Davis V.

We much appreciate the aid that Mr. Chandler Robbins, Mr. Dale Rice, and Mr. Karl Kenyon of the U.S. Fish and Wildlife Service provided by banding albatrosses between 1956 and 1960 and by giving their permission to include data on our recapture of these birds.

Dr. John Stotlar, James R. Fisher, Murray Hamlet, Earl Meseth, and Paul Gurn helped band nearly 35,000 nestlings in the summers of 1961, 1962, and 1963. Dr. Robert Klemm spent three months with the senior author on Midway in the egg-laying seasons of 1961 and 1962. Earl Meseth and Dr. O. S. Pettingill in 1963, Gary Kloek and Howard Freemeyer in 1965, and Donald Abb and David Denison in 1966 assisted in the recapture of breeding birds in the study plot.

Earl Meseth shared with us on Midway from October, 1964 to June, 1965 the brunt of the day-after-day task of recapturing birds.

It is obvious that the keeping of records is an integral and meticulous part of such a study, and this has been done at various times by Gary Kloek, Keith Thomas, Sue Ebersole, and Mildred L. Fisher. In addition to long hours of maintaining

detailed records of birds on individual statistical cards, the junior author tabulated many of the summaries of data upon which this paper is based.

We are indebted to Dr. William George of Southern Illinois University for a critical review of the manuscript.

Without the help of all these persons directly connected with the investigation, the work could not have been done in the limited time available.

A special word of appreciation goes to Curt and Vienna Yates who, though not participating in the research, did so much as residents of Midway between 1962 and 1965 to make more effective and pleasant our sojourns on the atoll.

Financial support over the years has been given generously by the Office of Naval Research (Contract 3479(00)) and by the Graduate School of Southern Illinois University.

Literature Cited

Aldrich, J. W., C. S. Robbins, and W. W. Dykstra. 1961. Bird hazard to aircraft. U. S. Fish and Wildl. Serv., Wildl. Leaflet No. 429, 10 pp.

Bartholomew, G. A., and T. R. Howell. 1964. Experiments on nesting behavior of Laysan and Black-footed albatrosses. An. Behav. 12:549–559.

Boysen, V. F. 1924. The Falkland Islands. Oxford: Clarendon Press, Pt. 4, pp. 285–335.

Brown, L. E., and H. I. Fisher. 1966. Electrophoretic study of blood proteins of some procellariiform birds. Auk 83:111–116.

Carrick, R., and G. M. Dunnet. 1954. Breeding of the Fulmar, *Fulmarus glacialis*. Ibis 96: 356–370.

Coulson, J. C., and E. White. 1960. The effect of age and density of breeding birds on the time of breeding of the Kittiwake, *Rissa tridactyla*. Ibis 102:71–86.

Dill, H. R. 1916. The albatross of Laysan. Wilson Bull. 28:172–175.

Dill, H. R., and W. A. Bryan. 1912. Report of an expedition to Laysan Island in 1911. U. S. Dept. Agric., Biol. Surv. Bull. No. 40, 30 pp.

DuMont, P. A., and J. A. Neff. 1955. Report on Midway Islands albatross study. Rept. U. S. Bur. Sport Fish. and Wildl., 27 pp.

Fisher, H. I. 1949. Populations of birds on Midway and the man-made factors affecting them. Pac. Sci. 3:103–110.

———. 1966a. Airplane-albatross collisions on Midway Atoll. Condor 68:229–242.

———. 1966b. Midway's deadly antennas. Audubon Mag., July-August, 4 pp.

———. 1966c. Aerial census of Laysan Albatrosses breeding on Midway Atoll in December, 1962. Auk 83:670–673.

———. 1967. Body weights in Laysan Albatrosses, *Diomedea immutabilis*. Ibis 109:373–382.

———. 1968. The "two-egg clutch" in the Laysan Albatross. Auk 85:134–136.

———. 1968. Eggs and egg-laying in the Laysan Albatross, *Diomedea immutabilis*. Condor 71:102–112.

Fisher, H. I., and P. H. Baldwin. 1946. War and the birds of Midway Atoll. Condor 48:3–15.

Fisher, J., and R. M. Lockley. 1954. Sea-Birds. Boston: Houghton-Mifflin Co., 320 pp.

Frings, H., and M. Frings. 1959. Problems of albatrosses and men on Midway Islands. Elepaio 20:6–9, 14–16, 23–25, 30–33.

———. 1961. Some biometric studies on the albatrosses of Midway Atoll. Condor 63:304–312.

Hadden, F. C. 1941. Midway Islands. Hawaiian Planter's Record 45:179–221.

Hamlet, M. P., and H. I. Fisher. 1967. Air sacs of respiratory origin in some procellariiform birds. Condor 69:586–595.

Hitchcock, W. B. 1963. Eighth annual report of the Australian bird-banding scheme. July 1961 to June 1962. C.S.I.R.O., Wildl. Res. Tech. Paper No. 5, 32 pp.

Howell, T. R., and G. A. Bartholomew. 1961. Temperature regulation in Laysan and Black-footed albatrosses. Condor 63:185–197.

Jameson, W. 1961. The Wandering Albatross. Rev. Ed. New York: Doubleday and Co., 131 pp.

Kenyon, K. W., and D. W. Rice. 1958. Homing of Laysan Albatrosses. Condor 60:3–6.

Kenyon, K. W., D. W. Rice, C. S. Robbins, and J. W. Aldrich. 1958. Birds and aircraft on Midway Island. November, 1956–June, 1957 investigations. U. S. Fish and Wildl. Serv., Spec. Sci. Rept. Wildl., No. 38, 51 pp.

Marshall, A. J., and D. L. Serventy. 1956. The breeding cycle of the Short-tailed Shearwater, *Puffinus tenuirostris* (Temminck), in relation to trans-equatorial migration and its environment. Proc. Zool. Soc. London 127:498–510.

Murphy, R. C. 1936. Oceanic birds of South America. New York: Macmillan Co., 1245 pp.

Rice, D. W. 1959. Birds and aircraft on Midway Islands. 1957–58 investigations. U. S. Fish and Wildl. Serv., Spec. Sci. Rept. Wildl., No. 44, 49 pp.

Rice, D. W., and K. W. Kenyon. 1962a. Breeding distribution, history, and populations of North Pacific albatrosses. Auk 79:365–386.

Rice, D. W. 1962b. Breeding cycles and behavior of Laysan and Black-footed albatrosses. Auk 79:517–567.

Richdale, L. E. 1939. A Royal Albatross nesting on the Otago Peninsula, New Zealand. Emu 38:467–488.

———. 1942. Supplementary notes on the Royal Albatross. Emu 41:169–184, 253–264.

———. 1949a. The pre-egg stage in Buller's Mollymawk. Biol. Monog. No. 2, Otago Daily Times and Witness Newspapers Co., Dunedin, 50 pp.

———. 1949b. Buller's Mollymawk: incubation data. Bird-Banding 20:127–141.

———. 1950. The pre-egg stage in the albatross family. Biol. Monog. No. 3, Otago Daily Times and Witness Newspapers Co., Dunedin, 92 pp.

———. 1952. Post-egg period in albatrosses. Biol. Monog. No. 4, Otago Daily Times and Witness Newspapers Co., Dunedin, 166 pp.

———. 1954. The starvation theory in albatrosses. Auk 71:239–252.

Robbins, C. S. 1960a. Albatross management investigations on Midway and Kure Atolls—1959–60. Rept. U. S. Bur. Sport Fish. and Wildl., 45 pp.

———. 1960b. Albatross management investigation on Midway and Kure Atolls—1960–61. Rept. U. S. Bur. Sport Fish. and Wildl., 26 pp.

Robertson, C. J. R. 1964. Observations of the Black-backed Gull predation at the Cape Kidnappers gannetries: 1959–1963. Notornis 10:393–403.

Rowan, M. K. 1951. The Yellow-nosed Albatross, *Diomedea chlororhynchos* Gmelin, at its breeding grounds in the Tristan da Cunha Group. Ostrich 22:135–139.

Serventy, D. L. 1961. The banding programme on *Puffinus tenuirostris* (Temminck). II. Second Report, 1956–1960. Commonwealth Sci. and Indust. Res. Org. Australia, Wildl. Res., 6:42–55.

———. 1963. Egg-laying timetable of the Slender-billed Shearwater. Proc. XIIIth Internat. Ornith. Congr., Ithaca, 1:338–343.

Serventy, D. L., and A. J. Marshall. 1959. Experimental demonstration of an internal rhythm of reproduction in a transequatorial migrant (the Short-tailed Shearwater *Puffinus tenuirostris*). Nature 184:1704–1705.

Sladen, W. J. L., R. C. Wood, and W. B. Emison. 1966. Antarctic avian population studies, 1965–1966. Antarctic J. U. S. 1:141–142.

Sorenson, J. H. 1950a. The Royal Albatross. Dept. Sci. and Indust. Res., Wellington, Cape Exped. Ser., Bull. No. 2, 39 pp.

———. 1950b. The Light-mantled Sooty Albatross at Campbell Island. Dept. Sci. and Indust. Res., Wellington, Cape Exped. Ser., Bull. No. 8, 30 pp.

Tickell, N. L. N., and R. Pinder. 1966. Two-egg clutches in albatrosses. Ibis 108:126–129.

Warham, J. 1963. The Rockhopper Penguin, *Eudyptes chrysocome*, at Macquarie Island. Auk 80:229–256.

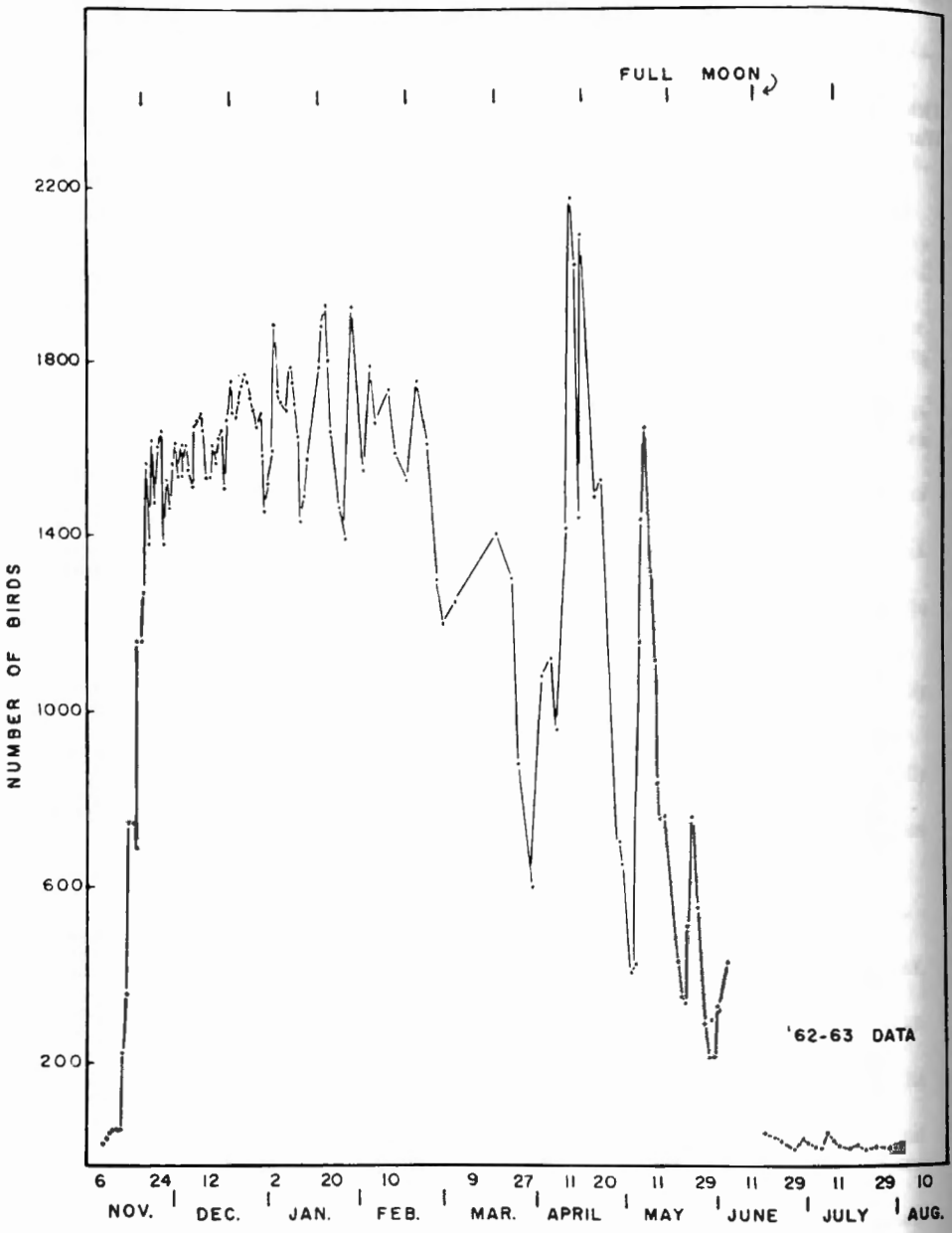


Fig. 1. Counts of adult and juvenile Laysan Albatrosses in three sample plots on Sand Island, Midway, during the 1964–65 breeding season.

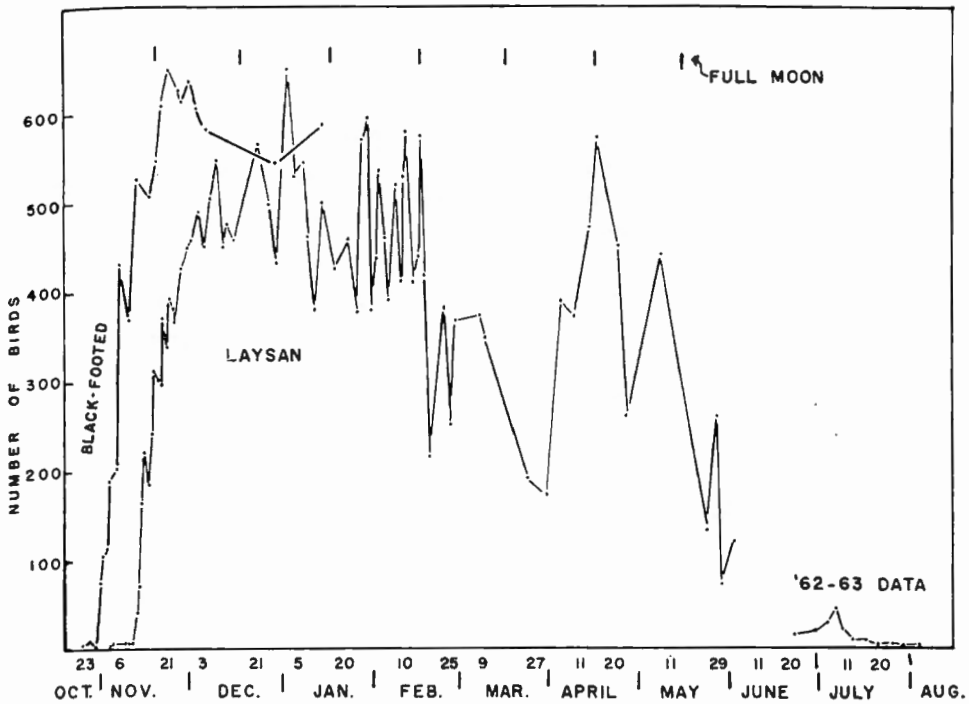


Fig. 2. Counts of adult and juvenile Black-footed Albatrosses in one sample plot on Sand Island and of Laysan Albatrosses in the permanent study plot on Eastern Island, Midway, during the 1964–65 breeding season.

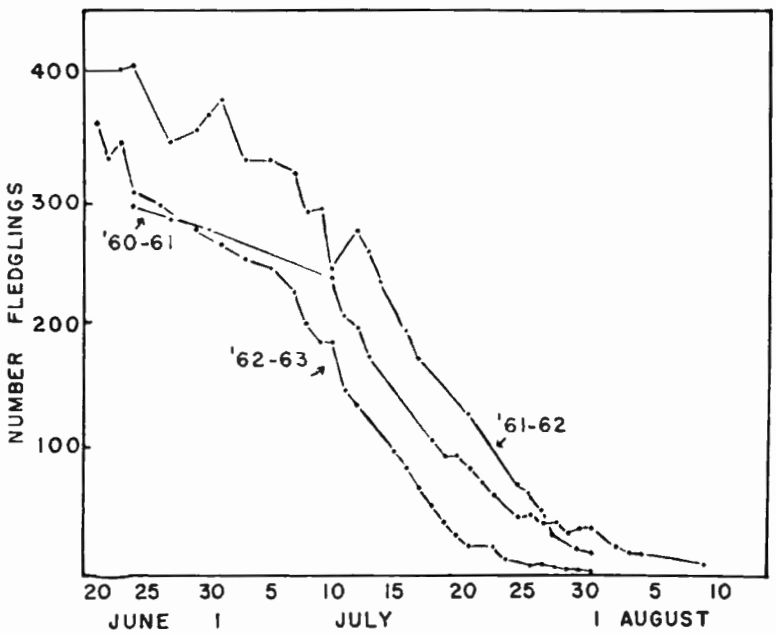


Fig. 3. Departure of fledgling Laysan Albatrosses from the permanent study plot on Eastern Island, Midway, in three summers.

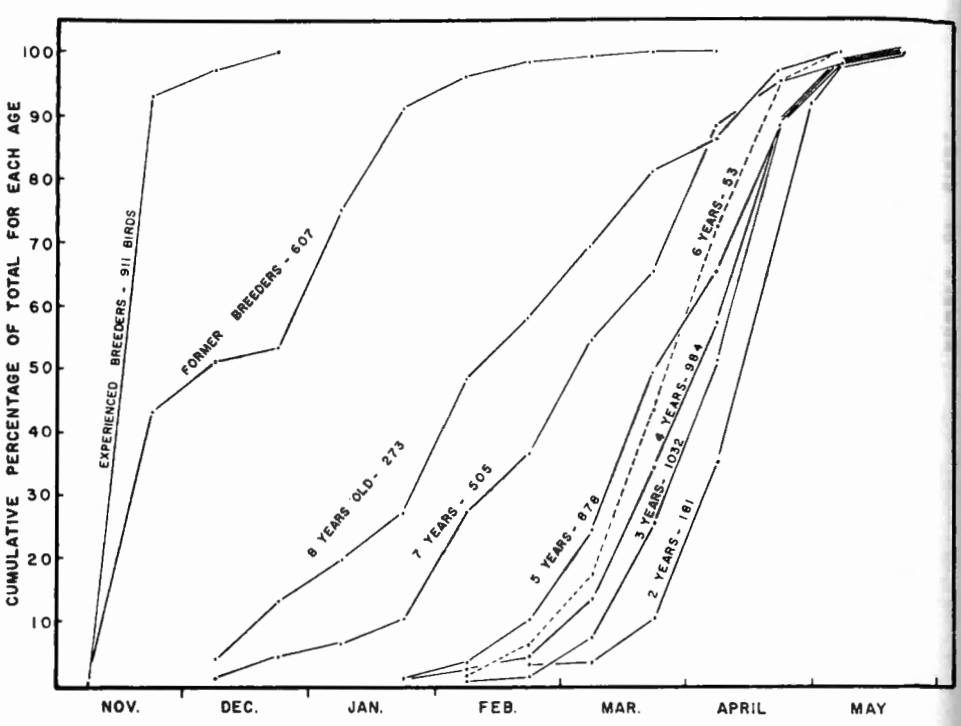


Fig. 4. Cumulative arrival of Laysan Albatrosses of different ages and categories on Eastern Island, Midway, in the 1964–65 season, computed as per cent of total recaptures in each group.

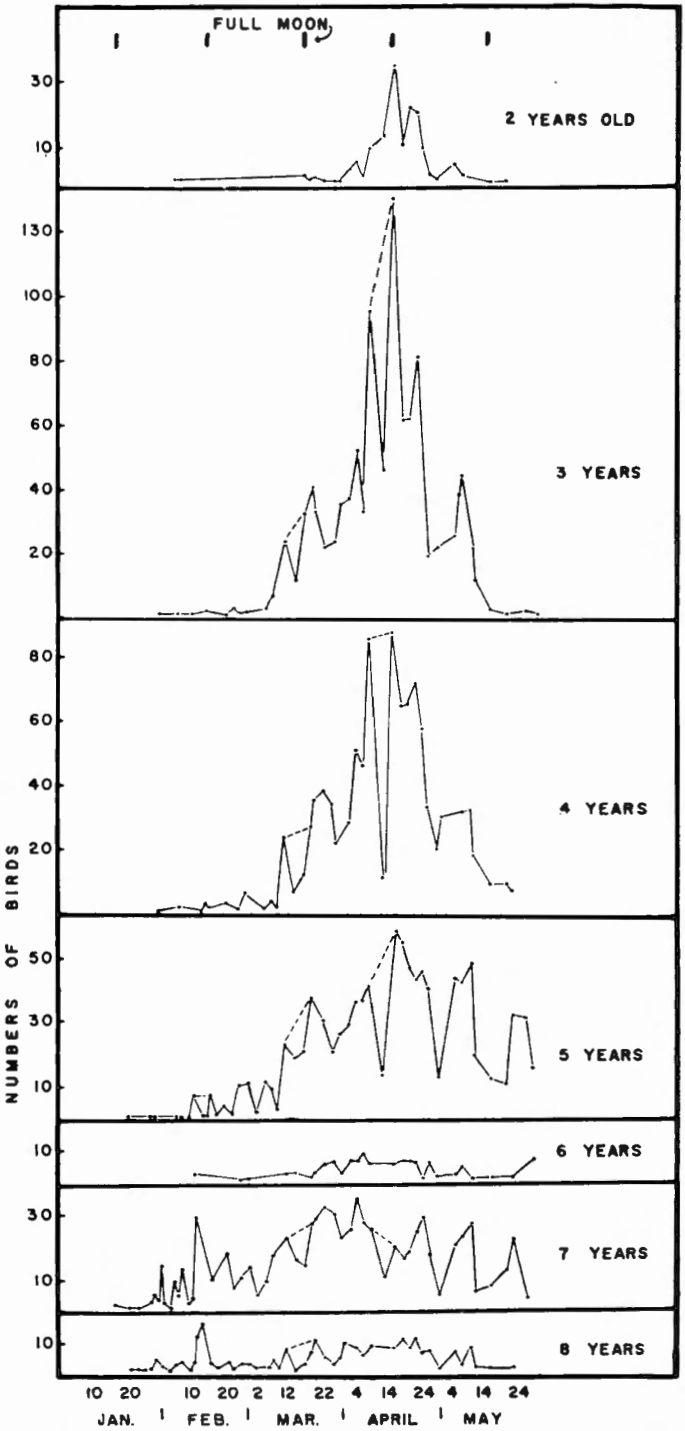


Fig. 5. Relative numbers of juvenile Laysan Albatrosses recaptured on Eastern Island, Midway, in 1965, by age and date.

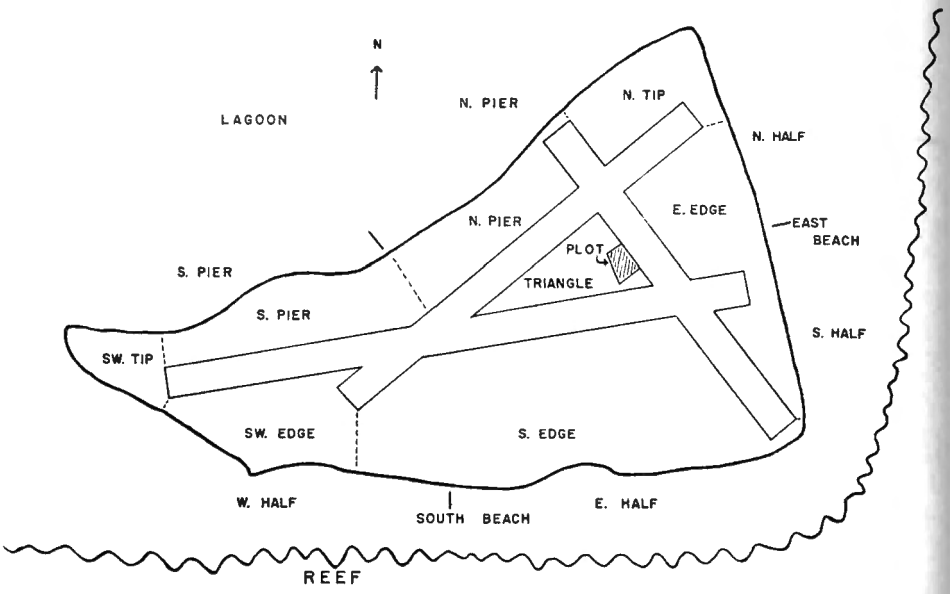


Fig. 6. Eastern Island, Midway, showing the location of the permanent study plot and the areas where Laysan Albatrosses were banded and recaptured.

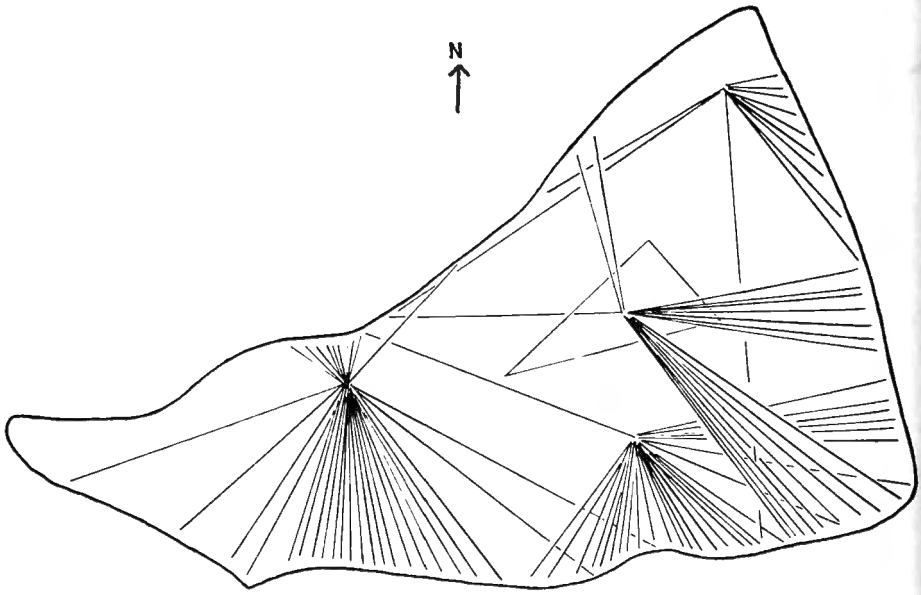
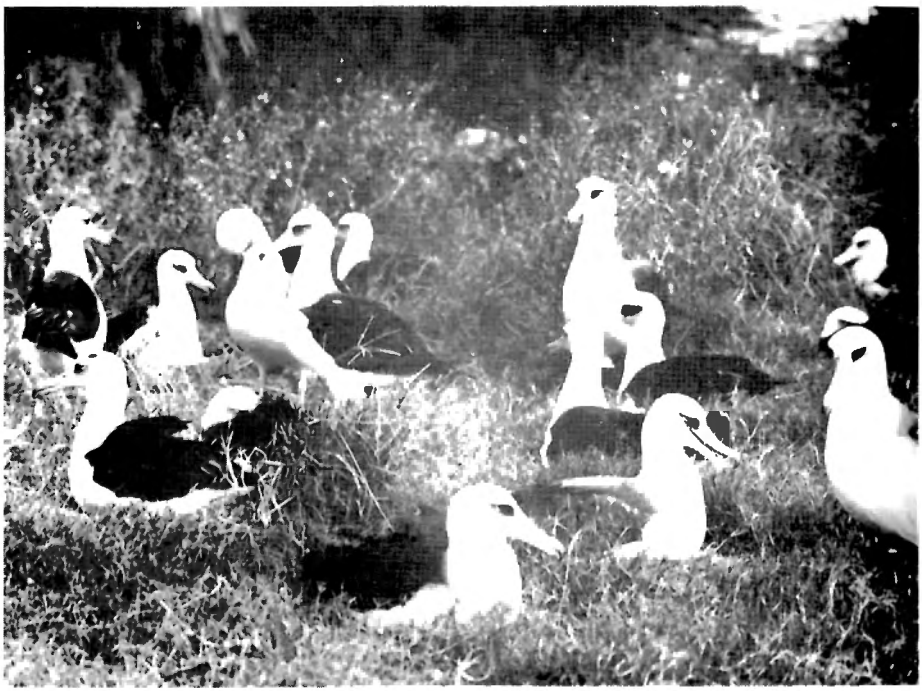


Fig. 7. Eastern Island, Midway, showing the direction of the movement of fledgling Laysan Albatrosses from the breeding colonies to the beaches in the summer of 1963.

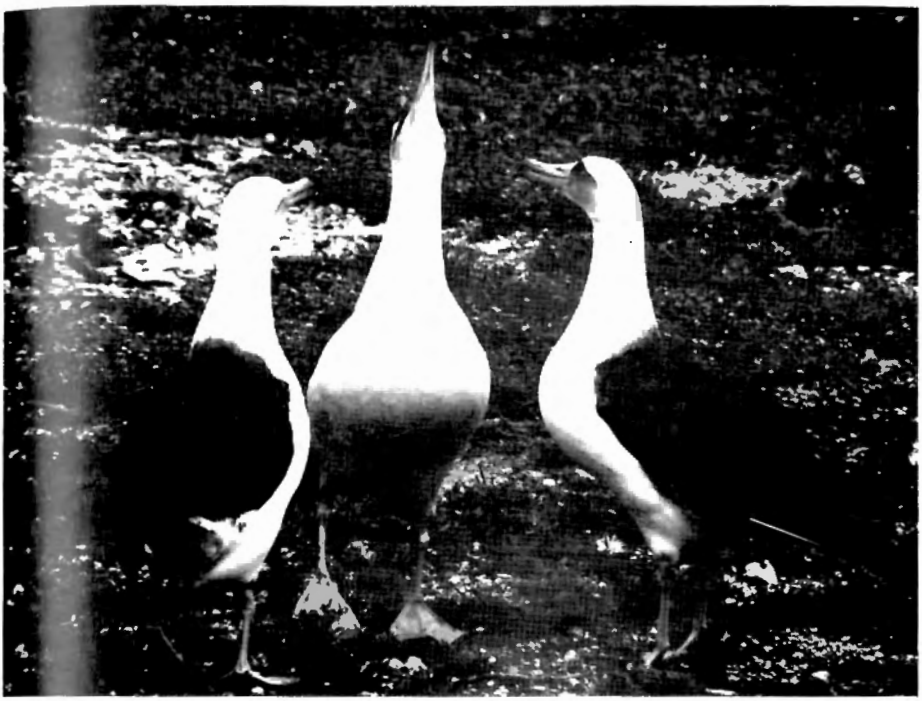
1. Adult Laysan Albatross in flight

2. The first male Laysan Albatross arrives on a lawn that soon will contain more than 30 males.

3. During the guard phase the adult Laysan Albatross may shield the chick from sun and rain.



4. Laysan Albatrosses socialize in groups in the springs of their third, fourth, and fifth years.



5. Five-year-old Laysan Albatrosses begin the process of mate selection; male in center, with two females.

VIEWS EXPRESSED BY THE AUTHORS ARE THEIR OWN AND DO NOT NECESSARILY REFLECT THOSE OF THE PUBLISHERS, EDITORS, PRINTERS, OR THE UNIVERSITY OF GUAM.

Authors are invited to contribute book reviews, review papers, shorter notes, letters, and news notes of scientific interest, as well as research reports.

SEND MANUSCRIPTS TO: Benjamin C. Stone, School of Biological Sciences, University of Malaya, Kuala Lumpur, Malaysia;

OR TO: Dr. L. G. Eldredge, Division of Biosciences and Marine Studies, University of Guam, Box EK, Agaña, Guam; OR TO any member of the Board of Editors, whichever is more convenient.

Printed by the International Academic Printing Co. Ltd.,
7–17, Fujimi 2-chome, Chiyoda-ku, Tokyo, Japan.