SOME DYNAMICS OF A BREEDING COLONY OF LAYSAN ALBATROSSES

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The purpose of this paper is to present data gathered over a 13-year period (1960–73) on Eastern Island of Midway Atoll, North Pacific Ocean, on certain aspects of the biology of breeding Laysan Albatrosses, *Diomedea immutabilis*.

Special attention is given to the close attachment to the home colony, the age composition of the breeding colony, the ingress of new breeders, and the frequency and patterns of breeding. These are analyzed in the light of published and unpublished information on this species, but the scarcity of valid, comparable data for other procellariiform species makes it unprofitable to attempt much intra-ordinal comparison.

METHODS

Our techniques for capturing, marking, and banding albatrosses and for keeping detailed records on each bird are described in other publications and will not be repeated here. Only one aspect of our search for banded birds has not been noted. Early investigations showed that Laysans had a close affinity for the site of their first nest and, indeed, for the nest site where they had been hatched (Fisher and Fisher 1969; Fisher 1971b). But since this affinity was so important in studying breeding dynamics, we wanted to verify it specifically for the plot used in this study.

In 9 of the 12 seasons we checked twice a week for any of our birds that might have moved into a strip some 50 m wide that bordered our plot on the north, south, and west. The eastern border was paved runway unsuitable for nesting. In 3 seasons we also recaptured all breeding birds in the "triangle" (Fisher and Fisher 1969:218, Fig. 6) which represented all adjoining suitable habitat.

The banding of chicks which began in 1956 and continued thereafter, the banding of juveniles which were centering their activities in our study area, and the banding of all breeders each year, starting with the 1960–61 season, made us confident that we had identified virtually all Laysan Albatrosses using this part of Eastern Island. This was verified by the fact that after the 1963–64 season no more than 7 unknown breeding albatrosses were captured in any succeeding year.

The population studied thus consisted of birds whose ages: (1) were known; (2) could be calculated with a good degree of accuracy on the basis of their first entry into the breeding population; and (3) were unknown and could only be stated in minimal values.

When the exact age of a bird was not known, an age was assigned as follows: First-time breeders were assigned to year classes on the basis of the percentages of males and females known to initiate breeding at various known ages (Van Ryzin and H. I. Fisher, ms). Applying these percentages to the new breeders found in any season, 1963–64 for example, we assumed that certain percentages of them were hatched each year between 1952–53 and 1957–58. All breeders banded in the plot between 1959–60

and 1962–63 seasons were assigned a minimum age of 8 years, since the mean and modal ages for both sexes at first breeding are between 8 and 9 years. However, this group was believed to include disproportionately large numbers of birds 12 or fewer years of age and of birds 20 or more years old. Dates of egg deposition (Fisher 1969) added credence to this view.

The greatest fallibility in these assignments of age may lie in the assumption that there was no significant annual variation in mortality, in the ages at which young birds first began to breed, or in the production of young which later became breeders. We know such variations exist, but there was no certain way to assess their magnitude in each of the 13 seasons of observations or in the years earlier when chicks were hatched that later became part of our study. However, the "cyclic" recurrence of these variations, the length of the study and the sizes of the samples mitigate against significant, cumulative errors.

RESULTS

Attachment to site.—Of the 49 non-breeders of unknown age that frequented the plot each season between 1962 and 1965, 20 males first bred a mean distance of 15 m (1 to 46) from the site of first capture and banding, and the 22 females 18 m (2 to 46). Only 6 of the first-nesting sites (4 of females and 2 of males) were outside the plot; they were within the 50 m border. Seven birds were never caught again.

Of the 1288 plot breeders of 1960 to 1963, only 3 males and 7 females were discovered breeding outside the plot. The males were 2 to 3 m outside, and 2 of them were with new mates. All 7 females had new mates; 6 were on nests a mean 14 m (5 to 32) from the nearest plot border, and the seventh female was incubating some 90 m from her former nest site.

Just 2 males and 1 female of 1078 fledged in the plot and of an age to breed were found nesting beyond its borders—the males 6 and 13 m outside and the female 7 m away. Fifty-six males were incubating a mean distance of 19 m and 49 females 26 m from their natal nests. One plot fledgling of 1960 was temporarily on a nest on Kure Island on 8 January 1969, but we could not be certain it was truly breeding there. Vernon Kleen, who found it, also reported 2 additional 1960 chicks of ours from Midway, but not from the plot, nesting on Kure that same year. These 2 were verified by me as actual breeders on 1 February 1969.

Age composition of the breeding colony.—I wish to emphasize again that many of the ages used are minimal, calculated on the basis of presumed age at first breeding. To minimize possible errors, data in Table 1 are presented in 5-year spans of ages, except in the instances of the 8- and 9-year-old birds. Many of these were of known age, and the estimated ages of others probably varied from true ages by no more than a year or so.

Birds 8 or fewer years of age constituted approximately 10% of the breeders each year (Tables 1 and 2). Nine-year-olds made up a mean 6.3% (2.5 to

TABLE 1

MEAN AGE DISTRIBUTION OF LAYSAN ALBATROSSES BREEDING IN THE PLOT, 1963 TO 1972, INCLUSIVE

Years	n	Age				
		8 or less	9	10–14	15–19	20 or more
1963	1392	8.5%	2.5%	44.1%	45.3%	
1964	722	14.5	2.8	40.0	43.3	
1965	1445	9.5	9.5	50.2	30.0	
1966	1243	9.3	5.7	54.9	29.4	
1967	1332	12.0	5.0	56.5	27.5	
1968	939	11.5	9.8	41.6	33.1	3.5
1969	1455	9.3	8.5	20.7	51.2	10.6
1970	1383	9.7	8.5	22.2	42.6	16.0
1971	1660	8.4	5.0	24.0	35.0	28.0
1972	2208	9.3	5.8	23.6	30.0	31.5

9.8) of the breeding population. Birds 10 to 14 years of age averaged 37.9% of the breeders each year, but the range was great—20.7 to 56.5%.

Data on breeders judged to be a minimum of 15 years old are combined until 1967; we started the study in 1959–60 with many birds of unknown age—birds which did not reach the more reliably ascertained 15- to 19-year group until 1968. However, birds of a minimum of 15 years of age constituted from 27.5 to 45.3% of the population prior to 1968 and from 30.0 to 51.2% after that. The 20- or more-year-olds made up 3.5 to 31.5% of the breeders between 1968 and 1972.

The observable trends lend some credence to the validity of the method of assigning ages. There is less variation in the percentages involving birds of the 2 younger categories, and at least some of the variations are explicable. Note that the low percentages of birds 9 or fewer years old in the first 2 years are reflected in the higher percentages of 10- to 14-year birds in 1965–67 and in the increased percentages of 15- to 19-year birds in 1969–70 and, still further, in the larger percentages of birds more than 20 years old in the period of 1969 to 1972.

Seventeen to 20% of the breeders were fewer than 9 years old in 1964 and 1965, and 19 to 22% were of this age in 1968 and 1969; these percentages were higher than those in any other years. The 1964–65 season showed a drop of 5% in the 10- to 14-year-old class, and in 1965–66 there was a 10% increase. This same age group showed a major drop in relative numbers between the 1967 and 1968 seasons and remained at the lower level for the remainder of the study. Although the numbers in the 15- to 19-year class increased dramatically between 1968 and 1969, they declined thereafter. Birds

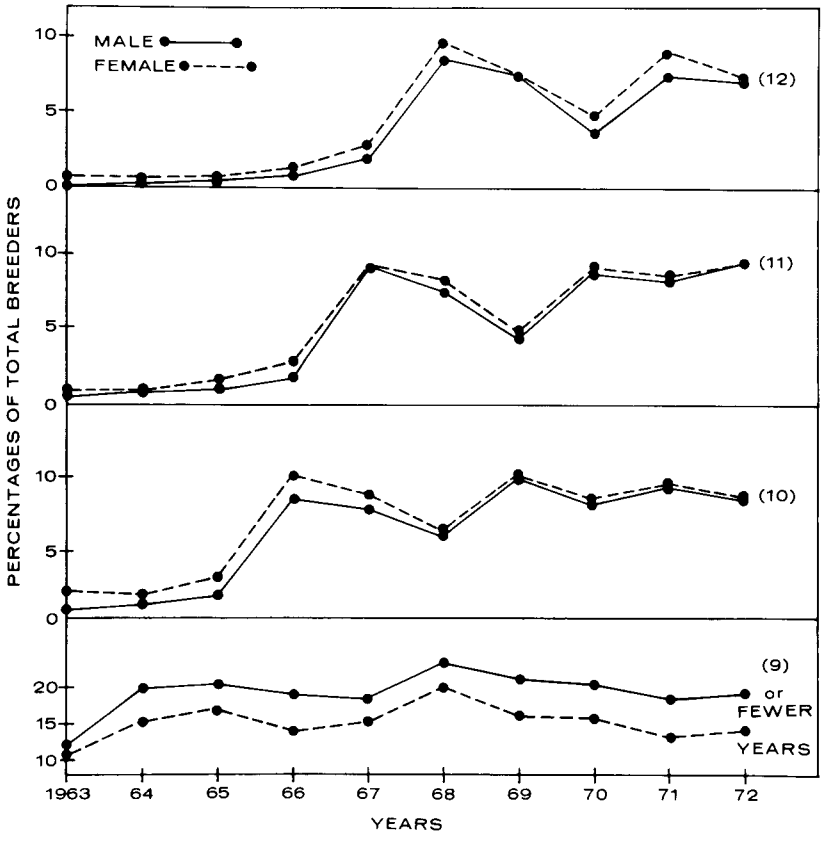

FIG. 1. Percentages of young breeders in a Laysan Albatross colony during a 10-year period.

identifiable as at least 20 years of age were relatively few in 1968, as compared to 1969 when their numbers began to increase.

The changes in the relative numbers of breeders to age 12 are illustrated in Fig. 1. Despite some significant, annual variations in the numbers of birds 9 or fewer years of age, many of them in their first breeding, this age group constituted a fairly uniform 15 to 17% of the breeding population during the 10-year period. The relative numbers of 10-year-olds rose greatly in 1966, and this showed up as increases in 11-year-olds and 12-year-olds in following years.

The drop in numbers of 10-year-olds in 1968 was reflected in fewer 11-year birds in 1969 and in fewer 12-year-olds in 1970. Once the numbers of each of these 3 age classes recovered from the decreases, they stabilized until

TABLE 2

MEAN AGE COMPOSITION, BY SEX, OF 13,849 LAYSAN ALBATROSSES BREEDING IN THE PLOT, 1963 TO 1972, INCLUSIVE

Age (years)	Males			Females		
	n	Mean	Range	n	Mean	Range
6	63	0.9%	0.4– 1.5	21	0.3%	0.1– 0.4
7	223	3.2	1.7– 5.7	152	2.2	1.6– 3.7
8	486	7.0	3.9–12.6	373	5.4	3.7– 9.0
9	438	6.3	2.5– 9.8	421	6.1	2.8– 9.5
10	438	6.3	1.2–10.1	489	7.1	2.2–10.3
11	362	5.2	0.5– 9.6	379	5.5	0.8– 9.4
12	264	3.8	0.2– 8.7	304	4.4	0.3– 9.8
13	195	2.8	0.1– 7.6	234	3.4	0.2– 8.9
more than 13	4485	64.5%		4422	65.6%	

the end of observation in the 1972–73 season—the 10-year and 11-year birds at approximately 9% of the breeders, and the 12-year-olds at 7 or 8%.

There was also sexual variation associated with the age variation in composition. Figure 1 and data in Table 2 indicate the greater percentages of males of ages through 9 years. Considering all birds 10 or fewer years old in the breeding population (Fig. 2), males predominated by 2 to 4% from

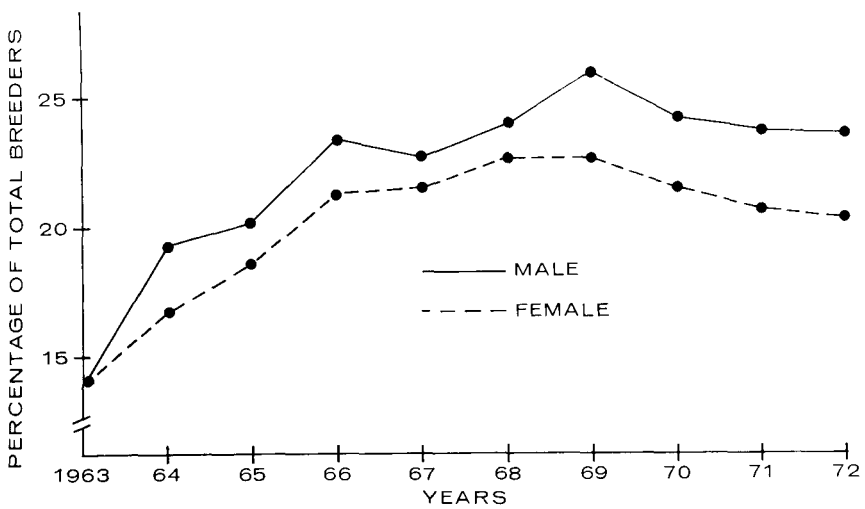

FIG. 2. Sexual variation in the numbers of breeding Laysan Albatrosses 10 or fewer years old.

TABLE 3

INGRESS OF FIRST-TIME BREEDERS INTO A LAYSAN ALBATROSS COLONY, EXPRESSED AS PERCENT OF TOTAL BREEDERS EACH YEAR

Age (years)*	1963	64	65	66	67	68	69	70	71	72
8 or less	8	14	10	9	12	12	10	10	8	9
9 or less	11	17	19	15	17	21	19	18	14	15

* See table 1 for sample sizes.

1964 onward, and by a constant 3% from 1969. By age 10 and thereafter, at least to age 13, the number of females was greater in each age class (Table 2). Birds 13 or fewer years old were equal in sex representation and constituted a mean one-third of all breeders.

Ingress of first-time breeders.—First-time breeders (8 or fewer years old) made up a mean, annual 10% (8 to 14) of the total breeding population during a 10-year period, 1963 to 1972 (Table 3). If the 9-year-old birds observed breeding for the first time are included, the mean, annual percentage of new breeders is 17 (14 to 21). Male breeders 9 or fewer years old consistently made up 2 to 5% more of the breeding population than did females of these ages, but this sexual difference was not present in the older age groups (Fig. 1).

Frequency of breeding.—The frequency of breeding by experienced birds in 212 constant pair bonds is shown in Table 4. Eighty-two pairs known from the 1960–61 to the 1972–73 season bred a mean 91% (43 to 100) of the time. Comparable data on 64 pairs known from 1961 to 1972 were a mean 84% (47 to 100), on 36 pairs known from 1962 to 1972 a mean 79% (47 to 100), and a mean 80% (40 to 100) for 30 pairs known from 1963 to 1972.

TABLE 4

PERCENT OF PAIRS* OF LAYSAN ALBATROSSES BREEDING EACH YEAR OF 10- TO 13-YEAR SPANS

Banded as breeders in:	No. pairs	Percent breeding in: 1960	61	62	63	64	65	66	67	68	69	70	71	72
1960	82	100	100	99	95	43	94	79	85	55	85	78	84	100
1961	64	—	100	100	91	47	97	72	84	59	87	77	88	100
1962	36	—	—	100	75	47	94	89	78	56	78	69	78	100
1963	30	—	—	—	100	40	97	67	93	57	83	87	80	100
Averages				96		44		86		57		81		

* Constant pair bond for period indicated; age unknown.

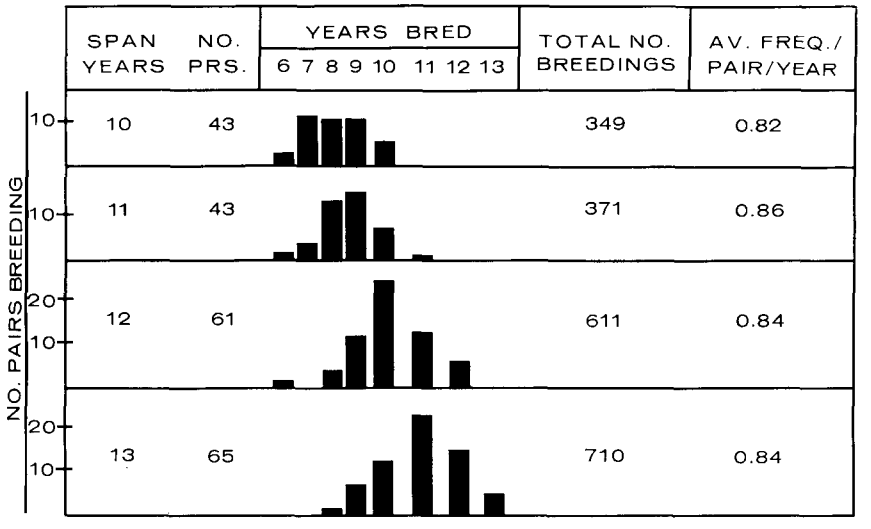

FIG. 3. Frequency of breeding by 212 constant pairs of Laysan Albatrosses during 10- to 13-year periods.

In each instance the lowest percentage occurred in the 1964–65 season and the next lowest in 1968–69, the "poor seasons" mentioned previously. The mean percentage of all 212 pairs that bred in these 2 seasons was 44 and 57, respectively (Table 4). Note also that 95 and 94% of the 1960 sample, 91 and 97% of the 1961 birds, 75 and 94% of the 1962 pairs, and 100 and 97% of the birds banded in 1963 nested in the season before and the season after 1964–65. The same relationships exist for the 1968–69 season, although the percentages are lower.

A mean 96% of these 212 pairs bred in the 1960–61 to 1963–64 seasons, inclusive, 86% during the 1965–66 to 1967–68 seasons, and 81% bred from 1969–70 to 1972–73.

All 82 pairs banded as breeders in 1960 also bred in 1961, and all 64 pairs banded in 1961 bred in 1962.

Figure 3 shows that the 212 constant pairs of unknown age contributed 2041 nestings during these years. The mean frequency of breeding per pair per year ranged from 0.82 to 0.86. The pairs in the 11-, 12-, and 13-year samples exhibited a more or less normal distribution in the total number of times they bred.

There were 3094 nestings by 366 birds involved in 2 or more pair bonds (Table 5). These birds had a mean frequency of breeding per year of 0.71 (0.64 to 0.78). The mean frequency was 0.64 (0.55 to 0.70) for birds with

TABLE 5

FREQUENCY OF BREEDING BY LAYSAN ALBATROSSES WHICH HAD TWO OR MORE MATES DURING 10- TO 13-YEAR SPANS

Span of years	No. birds	Total no. breedings in variable no. pair bonds				Mean frequency per bird per year in variable no. pair bonds			
		2	3	4	5	2	3	4	5
Ten:									
males	24	156	—	—	—	0.65	—	—	—
	1	—	7	—	—	—	0.70	—	—
females	30	194	—	—	—	0.65	—	—	—
	2	—	11	—	—	—	0.55	—	—
Eleven:									
males	27	214	—	—	—	0.72	—	—	—
	8	—	58	—	—	—	0.66	—	—
females	29	205	—	—	—	0.64	—	—	—
	5	—	34	—	—	—	0.62	—	—
	2	—	—	13	—	—	—	0.59	—
Twelve:									
males	50	453	—	—	—	0.76	—	—	—
	11	—	86	—	—	—	0.65	—	—
females	39	346	—	—	—	0.74	—	—	—
	4	—	31	—	—	—	0.65	—	—
	1	—	—	6	—	—	—	0.50	—
Thirteen:									
males	55	561	—	—	—	0.78	—	—	—
	18	—	163	—	—	—	0.70	—	—
	4	—	—	39	—	—	—	0.75	—
females	46	445	—	—	—	0.74	—	—	—
	7	—	53	—	—	—	0.58	—	—
	1	—	—	6	—	—	—	0.46	—
	1	—	—	—	7	—	—	—	0.54
Means	—	—	—	—	—	0.71	0.64	0.57	0.54
Totals	366	2574	443	70	7	—	—	—	—

3 different mates, and 0.57 (0.46 to 0.75) for 9 albatrosses with 4 successive mates. Only one bird was known to have 5 mates in 13 years, and it bred only half the time.

Males with 2 successive mates bred a mean 68% of the seasons and females only 60%.

Data on the number of breedings per pair bond are presented in 3 ways

TABLE 6

THE NUMBER OF BREEDINGS PER PAIR BOND IN LAYSAN ALBATROSSES

	Minimal Number of Breedings During Bond, All Ages, 13-Year Span[1]												
No. birds	1	2	3	4	5	6	7	8	9	10	11	12	13
12,396	1,363	2,167	1,051	494	326	216	144	106	101	102	76	42	10
Percent of bonds	22	34	16	8	6	4	2	2	2	2	—	—	—

	Number of Breedings During Bonds, All Ages, 9-Year Span[2]								
No. birds	1	2	3	4	5	6	7	8	9
1,968	335	275	173	99	58	32	8	4	0
Percent of bonds	34	28	18	10	6	3	1	—	—

	Minimal Number of Breedings During First Five Years of First Bond				
No. birds	1	2	3	4	5
128	12	9	14	18	9
Percent of bonds	19	14	24	28	14

[1] Minimal because bond was present at beginning of study or still intact at end of study, or both.
[2] Bond consummated and broken during study.

(Table 6). The top part of the table shows that 56% of the 12,396 breeders whose bonds were in force at the beginning or at the end of the study, or at both times, had a minimum of 1 or 2 matings with a mate and that 80% had 4 or fewer. This is very gross information, but the data in the middle of Table 6, on 1968 birds whose lengths of pair bond (or bonds) were known definitely, revealed similar percentages—62% had 1 or 2 breedings with a mate and 90% had 4 or fewer.

The mean frequency of breeding in their first 5 years by 64 pairs made up of 2 inexperienced birds was 0.59 per year, 189 attempts in 320 pair-years (Table 6, bottom). Nineteen percent of the pairs disappeared after their first attempt, but 9 pairs (14%) bred in each of these 5 years. However, in a sample of 27 inexperienced females and 18 inexperienced males paired with experienced birds of various ages, there was a mean frequency of breeding per bird per year of 0.80 for both sexes. One inexperienced female began breeding at age 5 with an experienced male and laid an egg each season for 4 more years.

Seventy-five percent of the 619 breeding pairs of 1961–62 also bred in 1962–63. Sixty-eight percent of the 417 pairs which fledged chicks in the summer of 1962 returned to breed that winter, and 81% of 202 pairs which failed to rear a chick in the 1961–62 season bred the next year.

Patterns of breeding.—The only "patterns" of breeding by 65 constant

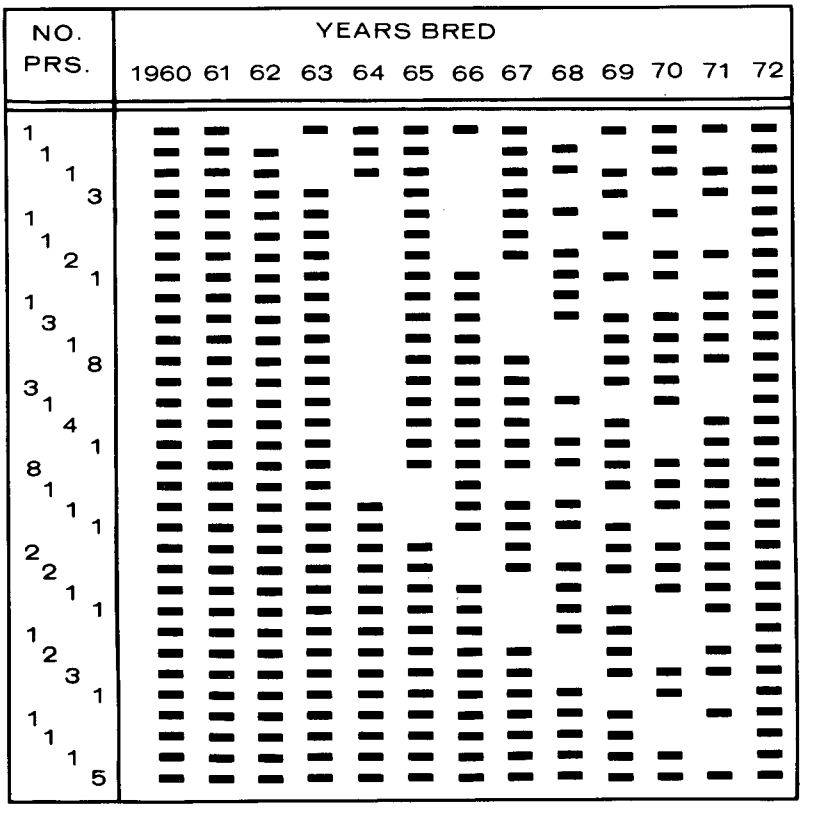

FIG. 4. The breeding patterns of 65 constant pairs of Laysan Albatrosses during a 13-year period.

pairs of experienced breeding birds of unknown age is that, generally, they bred every year (Fig. 4). In 1964 and 1968 many failed to breed, as indicated earlier. Twenty-six pairs bred each year, with the exception of one or both of these seasons. There were 60 instances of pairs breeding 4 successive years, 7 instances of 5 successive years, 7 of 6 years, 3 of 7 years, 13 of 8 successive years, 1 of 9 years, 2 of 10 years, 1 of 11 years, and 5 pairs bred in each of these 13 years. In only 7 instances did a pair fail to breed in as many as 2 successive seasons.

Sixty-four pairs of inexperienced birds (Table 6) whose exact ages were known exhibited no discernible patterns in breeding after the first 2 years of a 5-year span. Thirty-five pairs (55%) failed to breed the season after the first attempt, and 2 pairs skipped the second and third years as well before resuming breeding. Eight pairs bred in the first and second years and then

TABLE 7

BREEDING SEASONS LOST BY LAYSAN ALBATROSSES BECAUSE OF THE LOSS OF A MATE

No. seasons lost	Males (168)		Females (124)	
	Number	Percent	Number	Percent
0	3	2	0	0
1	112	67	59	48
2	37	22	39	31
3	12	7	13	10
4	4	2	9	7
5	0	0	4	3
Mean seasons lost	1.4		1.9	

missed one or more seasons. Only 5 pairs bred in 3 consecutive years before missing a season. One pair bred the first 4 years, and 9 pairs bred in each of the 5 seasons of this phase of our investigations.

I found no evidence that age of mate or age at which breeding commenced affected either the pattern or the frequency with which these young breeders attempted to nest.

Studies of the pattern of breeding among 366 birds involved with 2 or more mates (Table 5) revealed that 363 (99%) failed to breed the season after their mates disappeared. These results were confirmed by, and other information gleaned from, an additional 292 birds which formed more than one pair bond during the study (Table 7). Only 1% bred the season following the mate's disappearance. Two-thirds of the males and half of the females failed to breed only in the first season after the mate was lost. An additional fifth of the males and a third of the females did not nest in the first or second seasons. Ten percent of the males and 20% of the females failed to breed for 3 to 5 years after the disappearance of their mates. Females lost a mean of 1.9 seasons and males a mean of 1.4 seasons during the 5 seasons after the original pairs were first identified.

DISCUSSION

Attachment to site.—Laysan Albatrosses are firmly attached to their home island, colony and nest site, and with few exceptions they return there regularly (Fisher and Fisher 1969; Fisher 1971b). Data from this study substantiate these findings for the birds in the study plot and elaborate on the distances that exceptional birds may move.

The Fishers (1969:197) found that 16% of 986 juveniles visiting an area eventually nested within 100 m of the site of first banding. The present data on more closely observed juveniles revealed that 85% later bred in the plot.

Fewer than 1% of 1288 established breeders moved their nests significantly in later years, and then only when there was a change of mates. There was sexual difference in this movement. The 3 males that moved short distances are thought to have shifted within their original territories primarily in response to different nest sites selected by subsequent mates. The 7 widowed females moved significant distances as a result of pairing with different territorial males.

The data on location of first nests of breeders fledged in the plot are identical to those I gave earlier (1971b:394, Table 2) and support the preliminary views expressed by Fisher and Fisher (1969:197). Males settle to breed a mean of some 15 m from their nests of origin, and females locate about 26 m away. The sexual difference comes about because it is the males that establish territories; they can exert considerable influence on their location. Females, on the other hand, are dependent upon finding a suitable, unpaired male on a territory.

We undoubtedly did not discover all of the more distant nesting sites of our birds, but the one 1960 plot chick at least temporarily incubating on Kure Island and the 2 other Midway chicks actually nesting there are the only acceptable records we have of any of our chicks nesting on other islands. Despite these instances it is evident that both sexes of Laysan Albatrosses make an attempt to locate permanently near their natal nests.

One result of such close affinity for a site would be intense inbreeding within an island's population or within colonies isolated on an island. There is, apparently, very little genetic exchange between island populations of these birds. Fisher and Fisher (1969:197–201) discussed the available records of inter-island movements and concluded that most were of juveniles banded as they island hopped to their home colonies. They most likely did not represent chicks reared on one island and breeding on another. The banding of miscellaneous juveniles or of birds in migration, as done all too frequently, has obscured the true picture of the degree of breeding isolation of this and other species.

With a high degree of inbreeding, one might expect divergence among the colonies of birds nesting on the series of small islands used by this species, and even among colonies on the same island. Intense inbreeding, even within different parts of the same, large colony, may have produced the "subcolony associations" we found earlier (1969) in the time of egg-laying, the feeding of chicks, and the grouping of chicks at first departure from the colony. Further evidence may be the groups of "dwarfs" found among Laysan fledglings in the same areas in successive years (Fisher 1967:381).

The effect of rigorous site attachment on genetic isolation of the Laysan Albatross merits detailed investigation.

Age composition of the breeding colony.—Previously, I have alluded in general terms to the atypical nature of Midway's Laysan colonies, but some specific, historical facts are pertinent here. Few albatrosses could possibly have bred in the study plot between 1940 and 1946. There were few chicks when I first visited the area in May of 1945 (Fisher and Baldwin 1946) and few nests were found during my visit in the winter of 1946 (Fisher 1949). The blacktop paving and wooden, rock-covered bunkers probably prevented much reproduction until at least 1948.

Therefore, by 1960 when the current, detailed investigation began, the breeders must have consisted largely of birds hatched prior to 1940, and thus at least 20 years old, and of birds hatched in 1948 or later years, and thus 12 or fewer years of age. The data in Table 1 tend to support this hypothesis, but, unfortunately, there was no way even to estimate the sizes of these components of the breeding colony.

The percentage of breeding birds 8 or fewer years of age is not highly variable from year to year. If one omits the percentages for 1964 and 1968, which were inflated because of major decreases in the actual numbers of older birds, the mean percentage is 9.6 (8.4–12.0). Much the same can be said for the 9-year-old group—a mean 6.3% (2.5–9.5) of the breeding population. The lower number of 9-year birds, compared to 8-year-olds, is because the majority of Laysans begin to breed at 8 years and many of these do not attempt to breed in their ninth year.

As increased numbers of young produced in the mid-1950s entered the breeding colony, there was a shift toward an older average age among the breeders, demonstrated first by the 10- to 14-year classes from 1965 to 1967, a few years later by the 15- to 19-year group, and, finally, by the relative numbers of birds 20 or more years of age after about 1969.

Recognizing that breeders 9 or fewer years of age tend to be a fairly constant proportion of all breeders, it appears that breeders belonging to the 10- to 14-year class had dropped by 1972 to perhaps half their 1963 numbers (Table 1). They made up a nearly constant 21 to 24% of all breeders in the last 4 years, indicating that their relative numbers may have stabilized. The detailed analysis of breeders in the 10- to 12-year-old classes demonstrated that their relative numbers stabilized between 1970 and 1972 (Fig. 1).

The primary continuing changes in age composition among the breeders are in the 2 groups 15 or more years old. Together, they made up 61.8% of all breeders in 1969 and approximately the same percentage in all years since. As the 15- to 19-year-olds declined in relative numbers, the older component among the breeders increased in size. It appears that the changes are slowing, however, and, considering the information available on mortality and longevity, they may be expected to cease in the next 2 or 3 years.

For purposes of discussion, I consider the age composition of the breeding colony essentially stabilized in 1972. This population of Laysan Albatrosses may be said to consist of: (1) a group of learners, birds 9 or fewer years old and breeding for the first or second time but making little significant reproductive contribution, and forming 15% of the breeding colony; (2) the prime, reproductive birds, aged 10 to 19 years, upon which the maintenance of the species may really depend and which constitute 54% of all breeding birds; and (3) birds of 20 or more years, composing 31% of the breeders, which are in the last third of their expected 16 to 20 reproductive years (H. I. Fisher, ms). This last component, birds experienced in survival and reproduction, probably makes an important contribution, for in a study still in progress I find that three-fourths of the birds more than 30 years of age are still reproductively active.

There is sexual variation within the age variation in the composition of the breeding colony. Males predominate within the 6- to 9-year classes, and the females are more numerous among breeders age 10 through 13 years. However, because of the preponderance of males in the early years, they still are more numerous among all breeders 10 or fewer years old. These differences in sexual representation come about because females generally initiate breeding a year later.

Ingress of first-time breeders.—The true percentage of naive, young breeders entering the breeding population in an "average" year probably is greater than the 10% observed for birds 8 or fewer years old. However, it is equally inappropriate to accept without question the observed 17% ingress of new breeders, based upon the inclusion of 9-year-olds.

We know that 47% of the young Laysans do not begin to breed until at least the ninth year (Van Ryzin and H. I. Fisher, ms); more females than males delay until this time. Also established are the facts that: (1) 18% of the males and 14% of the females first breed at 7 years; (2) relatively few inexperienced birds complete incubation of their first egg; and (3) approximately half of them do not attempt to breed the following year. Considering all these, it is probable that some birds initiating at 7 years were undetected then because they deserted before capture, and they could not be recaptured in their eighth year because they did not come to the colony during the egg season. They were thus first observed breeding in the ninth year. My best estimate of their numbers is about 2 or 3% of all breeders.

Consequently, if these are added to the 10% first found breeding at 8 or fewer years, approximately 13% of the breeders are new each year. The 3% must also be subtracted from the observed 17% for all birds 9 or fewer years old. The resulting 14% includes the above 13%, plus the approximate 1% of the breeders which begin to breed at age 9.

An annual recruitment of 14% is surprisingly high, considering the 5 to 6% annual mortality among breeding birds and expected 16 to 20 years of reproductive life.

Not all of the indicated increase in the breeding population on Midway can be attributed to this rate of recruitment. The growth of the colony is probably not typical of undisturbed Laysan Albatross colonies. Rice and Kenyon (1962) discussed the history of the Midway colony and the factors influencing its numbers up to 1957. The trend has been generally upward since 1903, largely, they thought, because of increased protective vegetation on Sand Island, but with some depressions in the years of World War II. Part of the post-war increase on Eastern Island (sometimes called Green Island in early accounts) may be attributed to the war-time opening up of the vegetation which may have been too dense for maximum use by Laysans. However, the virtual cessation of human disturbance must be a primary factor in the continuing "explosion" in numbers on both islands since the early 1960s. The resulting decrease in mortality makes possible increased life expectancies for aged, breeding birds and increased survival of juveniles to be recruited into the breeding population. Since these recruits were raised in the Midway colony and did not originate from other colonies, as Robertson (1973) believed may have happened with the Royal Albatross colony on Tairoroa Head, New Zealand, the impact of the increased survival of juveniles is more evident.

Frequency and patterns of breeding.—The evidence presented here and in other studies of procellariiformes indicates that these birds are physiologically capable of breeding each year. That is, the basic reproductive cycle is an annual one, and it is important in this discussion to keep in mind the difference between observed frequencies of breeding and potential capabilities for reproduction. Murphy (1936:664) seemingly did not when he suggested that longer than annual reproductive cycling of the individual procellariiform may have developed to permit multiple use of the very limited space in the colony. We know now, at least for the Laysan Albatross, that experienced birds not currently breeding return to the colony frequently enough to maintain their territories and to prevent their use by other pairs. It also seems improbable that space is a limiting factor in most albatross colonies.

Most individuals of some procellariiform species breed in successive seasons (Laysan, Rice and Kenyon 1962, and this study; Black-browed, *D. melanophris*, Tickell and Pinder 1967; Waved, *D. irrorata*, Harris 1973; and Black-footed albatrosses, *D. nigripes*, Rice and Kenyon 1962; and the Fulmar *F. glacialis*, J. Fisher 1952). However, the Wandering (*D. exulans*), Royal (*D. epomophora*), and Gray-headed (*D. chrysostoma*) (Tickell and Pinder

op. cit.) and the Yellow-nosed albatross (*D. chlororhynchus*) (Elliott 1970) are regarded as biennial breeders. These views have been developed from gross information on the colony-wide return to breed in successive years and, in general, without consideration of the possible effects of several, major, biological factors—namely, mortality, food supply, nature of the formation of the pair bond (and its constancy), and influence of the age and experience of the members of the pair upon their patterns or frequencies of breeding.

The factors usually discussed are body size and the energy required for the successful rearing of a chick; the biennial cycle in some species is attributed to the long period of parental care which may be correlated in part with larger body size. The deviations from the annual reproduction expected in other species are often said to result from the exigencies of fledging a chick.

For example, Rice (1959:6) observed that 33% of the nesting Laysans failed to breed the next season and, more specifically, that only 63% of the successful breeders nested the next year, and that 87% which lost the egg early in incubation bred the following season. Rice and Kenyon (1962:521) reiterated these conclusions and further indicated that 87% of the pairs with "sterile" eggs bred the year following. This latter is puzzling because Laysans do not abandon sterile eggs. Indeed, a Laysan may incubate such an egg for weeks past its expected hatching date (Fisher 1971a:51). They are not released from the energy requirements of incubation, and one would expect the percentages of such pairs that returned to breed the next year to approximate the 75 to 79% Rice and Kenyon gave for pairs losing the egg late in incubation or the chick during the guard phase.

Richdale's view, expressed in 1952, that successful pairs of Royal Albatrosses breed in alternate years and that early nest failures enable pairs to breed the next season has been accepted (Carrick et al. 1960) and extended by Tickell (1960, 1968) and Tickell and Pinder (1967). These papers also corroborated Mathew's observation (1929) that the Wandering Albatross can breed only every second year, if it is successful in fledging a chick. Further, Tickell and Gibson (1968) noted that 60% of the Wanderers breed each year, and Tickell (1968:12) wrote that 55% of them did. Tickell and Pinder (1967) recorded 76% of 50 pairs of Black-broweds breeding in 2 successive years. Harris (1973:497) indicated that 90% of the Waved Albatrosses that reared a chick and 87% that lost eggs bred the next season. He thought, however, that all surviving pairs bred both seasons.

Underlying these observations, except those of Harris, is the theme of "necessary rest" for the parents (Richdale 1954:251). The necessary rest presumably spans a period during which the annual molt occurs and the bird not only regains any weight lost in fledging a chick, but also adds the

usual pre-breeding fat. Most Laysans have a minimum of 3 months between the successful rearing of a chick and the beginning of the movement toward the breeding colonies for the next reproductive season. In most instances this seems to be ample time, especially since I showed (1967) that incubating Laysans can regain a 20% loss of weight in approximately 3 weeks at sea. Net losses after incubation are less than 20%. It is unfortunate that we know so little of the timing or energy requirements of the molt in the Laysan.

The Gray-headed Albatross is also small-bodied and has a rest period similar to that in the Laysan, but it is considered a biennial breeder by Tickell and Pinder (1967). If this is true, neither body size nor length of parental care can be considered the sole or perhaps even primary factor determining whether pairs of albatrosses breed in successive years.

A further analysis of the percentages of Laysan Albatrosses that breed in successive years emphasizes the possible effects of raising a chick. Although 75% of the 619 pairs that bred in 1961–62 also nested the following season, the simple observation is misleading, as it is in most published accounts. The 6% annual mortality of experienced breeders, the 2% mortality of young breeders, and the 14% constituency of young breeders in the population must be considered.

If mortality was evenly distributed among the pairs that did not return, and evenly between one or both members of a pair, there were only 568 viable pairs to return. However, 14% or 87 of the 619 breeding pairs were probably made up of first-time breeders, of which 60% (52 pairs) would not attempt reproduction the second year. Subtracting these 52 pairs, only 516 pairs could possibly have been available to breed. The second year 464 pairs (90%) did breed, which is in contrast with the observed 75%.

The 417 pairs which fledged chicks in the summer of 1962 probably included no more than 10 of the 87 young pairs. The 417 pairs then became 407 pairs available for the next season, but these were reduced to 377 pairs by mortality. The 284 pairs that did return thus represented 76%, versus the 68% originally stated.

There were 202 pairs of failed breeders in the 1961–62 season. We assumed that the remaining 77 pairs of first-time breeders were among them. Only 40% or 31 pairs of the latter might be expected to attempt reproduction in 1962–63, if the pairs consisted of 2 young birds. However, 45 of the 77 pairs probably consisted of a young bird and an experienced bird, and 80% of these mixed pairs do attempt reproduction in the season following their first. (All mixed pairs are included here, rather than with the successful breeders because seldom do they raise a chick in their first breeding attempts.) Therefore, 36 mixed pairs and 13 pairs consisting of 2 young birds might have nested. The 202 pairs of failed breeders were thus reduced to 174, and to

162 pairs when mortality was considered. Since 164 of the 202 pairs were observed breeding in the second season, it is obvious that the application of overall means to a specific sample produced a minor statistical anomaly. However, it is equally obvious that essentially all failed breeders of 1961–62, alive and eligible to breed in 1962–63, did attempt reproduction in the latter season. This is similar to Tickell's observation (1968:9) that the entire Wandering Albatross population may breed the season following a catastrophic destruction of all eggs.

Availability of food must be assumed to be a major factor influencing reproduction, but, because of our ignorance of oceanic food chains and of annual or seasonal variations in oceanic conditions, for the most part we can only speculate about its role. There is, however, considerable circumstantial evidence that the size of annual breeding populations of the Laysan Albatrosses on Midway Atoll, and on Kure as well, may be greatly influenced by "anomalies" in North Pacific Ocean conditions (H. I. Fisher, ms). Briefly, it appears possible to correlate the highs and lows in breeding numbers with shifts in major water masses, aberrancies in sea-surface temperatures, variations in salinities, and with several kinds of data on evaporation. All these variables may well influence the availability of food in the usual foraging areas, and data from Midway and Kure atolls in 1964–65 and 1968–69 indicated that the albatrosses and some other avian species were short of food.

Lack (1966:243) suggested that young females of several avian species may lay eggs later in the season than experienced females because of the need to accumulate energy reserves to form the egg. Since this pre-egg energy stress is short lived, and since Laysans can regain lost weight very rapidly, it appears that the critical food period, as far as affecting reproductive attempts is concerned, is the 2 or 3 weeks immediately preceding egg-laying. For most Laysan Albatrosses this is the last 3 weeks in November.

In the 1964–65 and 1968–69 seasons of presumed food scarcity, it was the experienced breeding birds that failed to attempt reproduction. The numbers of first-time breeders did not decline. The unanswerable question raised by these observations is whether experience is the only determining factor and, if so, in what way does it operate?

Major fluctuations in the breeding numbers of various high-latitude birds have been known for years, and Bertram et al. (1934:827) commented ". . . it is clear that periodic extensive non-breeding is not uncommon in the Arctic among certain birds." They believed one major reason was the variable food supply, and Johnsen as long ago as 1929 suggested that these "cycles" perhaps depended upon climatic "pulsations" which influenced the availability of food.

Harris (1969) chronicled some massive failures in breeding by the Waved

Albatross on the Galapagos Islands; in other instances this species did not attempt to breed in its usual numbers. He found a correlation between breeding failure and heavier than average rainfall, a condition that may well have affected or been associated with other events that affected the food supply adversely.

As J. Fisher and Lockley (1954:124) stated, it is doubtful that climate ever completely prevented mature sea birds from breeding by direct action upon the birds' glands, but they also viewed the poor years as being simply due to ". . . bad weather closing down the food-supply." Although the Laysan Albatross does not support Wynne-Edward's (1939:127) view that irregular breeding may be characteristic of all deep-sea birds, his suggestion does have the intimation that major fluctuations in the breeding of birds are not limited to the Arctic. They do occur in albatrosses in the temperate and subtropical latitudes.

The frequency of reproduction by Laysan Albatrosses is dependent also upon several, more predictable circumstances. If the pair bond remains intact, the pair of young breeders may attempt breeding in 59% of their first 5 years and in from 82 to 86% of the years thereafter. More than half of these young pairs failed to breed in the season following their first attempt. Although age of mate and age at which breeding is first attempted apparently do not affect the frequency of reproduction in these early years, previous breeding experience in one member of the pair may raise the frequency, from 59% to 80%.

Birds with 2 mates during spans of 10 to 13 years have a mean frequency of breeding of 71%, those with 3 mates 64%, and Laysans with 4 mates may breed only 57% of the time. The trend is further indicated by one bird which had 5 mates and bred only 7 times. Of the birds which lose mates, 99% do not attempt to nest the following season. Females thereby lose 1.9 seasons in 5 and males 1.4 seasons.

These figures emphasize the importance of a continuous pair bond to the reproductive potential of the species. With each additional mate during the 10- to 13-year span of observations there was a decrease of from 7 to 11% in the years in which the bird attempted to breed. The loss in reproduction is a direct result of the one or more seasons required for the formation of each pair bond. The death of a paired, breeding bird eliminates not only its future reproductive capability but also approximately 5 to 10% of the lifetime potential contribution of the mate it left. And not to be forgotten, since both parents are necessary throughout the season for successful fledging of the chick, is the loss of the reproductive contribution during the season a mate dies.

In view of the significance of the continuous bond for the reproductive

potential of the species, it is surprising to find that perhaps 60% of the Laysans breed only once or twice with each mate and that 80 to 90% breed 4 or fewer times with each mate. Considering these facts, nest success, and mortality at various ages, it is apparent that the Laysan Albatross "needs" the 16 to 20 years of reproductive life I have suggested elsewhere.

SUMMARY

Attachment to site.—Chicks hatched in an area frequent that site for territory acquisition and pair formation in the 3 or 4 years immediately preceding first breeding. They attempt to establish themselves and to nest near the natal nest—males within perhaps 15 m and females less than 30 m distant. The young male has a greater influence on his location because he actively seeks a territory and establishes himself. The female can only search out an unattached male during her limited travels of the pre-pair bond period.

Breeding males do not change territories during their lifetimes, though they may accommodate to different nest sites of different mates within their territories. Females are just as consistently attached to their male's territory, but when the mate dies they may be forced to move significant distances to obtain a new mate.

Age composition of the breeding colony.—It is not certain that the colony of Laysan Albatrosses on Midway is typical for the species or that its age composition has yet completely stabilized. Human interference during World War II may have almost eliminated certain age groups. In 1960 the breeding population was believed to consist largely of experienced breeders a minimum of 20 years of age and of young breeders a maximum of 12 years old.

Despite major annual fluctuations in total breeding numbers and despite a doubling in breeding numbers between 1960 and 1972, the percentage of breeders 9 or fewer years old remained fairly constant at approximately 15%. After undergoing significant increases in the early years of the investigation, the group of breeders 10 to 14 years old settled down to a uniform 21 to 24% of total breeders in the last 5 years. The early increases in this group caused a major surge in the relative numbers of 15- to 19-year-old breeders midway in the study, which in turn is now reflected in increased percentages of breeders more than 20 years of age.

However, the changes in relative numbers of the older groups are slowing, and it is suggested that the following, stabilized population may be present: (1) 15% young breeders of no great current reproductive significance; (2) 54% prime, reproductive birds, 10 to 19 years old; and (3) 31% breeders 20 or more years of age.

Males predominate in each class through 9 years, females in age classes 10 through 13 years. By the latter ages the sexes are equally represented in the total numbers of these younger breeders. The differences in sexual representation are caused by males initiating reproduction a year sooner than females.

Ingress of first-time breeders.—In the rapidly growing population on Midway Atoll there is an approximate, mean 14% annual recruitment of new breeders. This is exceptionally high for a species which exhibits only 5 to 6% annual mortality during the 16 to 20 years of reproductive life. The historical and current conditions on Midway may have resulted in unnaturally high rates of recruitment. There has been a major decrease in human-induced mortality in the last 10 to 15 years.

Of particular note is the belief that all new breeders are recruited from the Midway colony itself, rather than from any other colonies.

Frequency and patterns of breeding.—The frequency with which the individual Laysan Albatross attempts to reproduce is influenced by: (1) the available food; (2) the strictly monogamous nature of the pair bond; (3) the number and length of the successive pair bonds formed over a period of time; (4) the time required to form each bond; (5) the age of the pair bond; (6) the mate's previous experience in breeding; (7) its success in fledging a chick; and (8) perhaps its sex.

Notwithstanding all these potential influences on the frequency of reproduction, the Laysan Albatross is physiologically and behaviorally capable of breeding each year after the second season of its reproductive life, and many do.

The mean, breeding frequency per pair per year ranges from 0.82 to 0.86 when the pair bond is maintained for 10 to 13 years. When an albatross has 2 mates during this span of years, the breeding frequency drops to 0.71, with 3 mates to 0.64, and with 4 mates to 0.57 times per year. Loss of a mate during the breeding season means the loss of the egg or chick of that year, as well as the loss of 1 or 2 breeding seasons by the survivor while it forms a new pair bond. Males which lose mates may form new bonds sooner than widowed females, indicated by a 68% frequency of breeding during 10 to 13 years by males with 2 mates, versus 60% for females which formed second bonds.

In the first 5 years of the bond between inexperienced birds, reproduction is attempted only in a mean 59% of the seasons. More than half of these young pairs do not attempt to breed the season after the first attempt. However, if the inexperienced bird pairs with an experienced one, the pair may attempt reproduction in 4 of the first 5 years.

A scarcity of food in the weeks immediately preceding egg-laying may prevent 50% of the mature, breeding population from even attempting to nest. In the years before and after such occasions 81 to 96% of the same pairs may breed.

When mortality and differential breeding patterns are considered in average or normal years, the colony-wide return of the eligible breeders of one season to breed the following season is 90%. Seventy-six percent of the breeders successful in fledging a chick return to attempt reproduction the following year, and all the failed breeders may nest the next season.

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