THE AGE OF LAYSAN ALBATROSSES, DIOMEDEA IMMUTABILIS, AT FIRST BREEDING

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Knowledge of the breeding biology of the Laysan Albatross (*Diomedea immutabilis*), a pelagic species of the North Pacific Ocean, has increased greatly in the last dozen years (for example, Rice and Kenyon 1962a, b, Fisher 1967, 1969, 1971a, b, 1972, Fisher and Fisher 1972, and Fisher and Fisher 1969). Still, many fundamental questions remain unanswered.

Although it is common among long-lived seabirds, such as the Laysan Albatross, to defer breeding (Fisher 1975), the age at which breeding begins in this species, has not been studied thoroughly. This paper extends the preliminary report of Fisher and Fisher (1969: 190–191) and explores the age at which these albatrosses begin to breed and some of the factors that may influence this age.

Among procellariiform birds, petrels apparently initiate breeding at the earliest age. Lack (1966:261) reported that Richdale found diving petrels breeding at age 2, and Gross (1947:123–124) recorded one Leach's Petrel (*Oceanodroma leucorrhoa*) with an egg at age 3. Warham (1962:141) suggested that the Giant Petrel (*Macronectes giganteus*) does not breed until at least 5 years of age. Serventy (in Lack 1966) reported that: 1) most Manx Shearwaters (*Puffinus puffinus*) first bred at 5 years, although some individuals bred at 3 and 4 years; 2) female Short-tailed Shearwaters (*Puffinus tenuirostris*) from 5 to 7 years and males from 5 to 8; and 3) Sooty Shearwaters (*Puffinus griseus*) at approximately 6 years. Pinder (1966:30) noted that 4 years may be the earliest a Cape Pigeon (*Daption capensis*) breeds although most may not breed until the fifth year.

The smaller albatrosses apparently begin to breed earlier than the large ones. Harris (1973:502) reported that the majority of Waved Albatrosses (*Diomedea irrorata*) first bred in their fifth and sixth years. However, some started at 4 years and others not until the eighth year or later. One female Light-mantled Sooty Albatross (*Phoebetria palpebrata*) was recorded by Kerry and Colback (1972:62) as starting at age 7. The Laysan Albatross may breed first at 7 years (Rice and Kenyon 1962b:521), and Fisher and Fisher (1969:190) found a mean age of 8 years among 207 individuals.

Studies of the Royal Albatross (*D. epomophora*), a large species, indicated a later age at first nesting: 1) Richdale (1952:124) recorded one female first laying at 9 and two males breeding at 8 and 11 years; 2) Westerskov (1960:46) thought they initiated breeding at 8 and 9 years; and 3) Robertson (1972: 48) believed these albatrosses were capable of laying eggs at 8 and 9 years but usually did not produce fertile eggs until the ninth and tenth years.

Most of these investigations contained no discussion of age determination. We repeat here the ages as published although there may be a year's variance from those determined by the method we describe later.

METHODS AND SAMPLES

A permanent study plot was established by the junior author in 1961 on Eastern Island, Midway Atoll, North Pacific Ocean. The United States Fish and Wildlife Service banded Laysan Albatrosses here in 1956–1960. About 99% of the birds currently using this plot are believed to have been banded before the 1964–65 season.

The numbered nests were checked every morning during each egg-laying season (mid-November to mid-December) from 1961 through 1972. The band number and sex, determined by cloacal examination, of the incubating bird were recorded with the nest number, and the bird's head was marked with a small paint spot. As both sexes share incubation duties and seldom rest even momentarily on a nest not their own, an unmarked bird found subsequently on a marked nest was assumed, temporarily, to be the mate of the bird previously found on that nest. Multiple records on individual birds made it possible to verify the sex determinations and the pairings in each of several subsequent years.

We assumed that an incubating bird was an inexperienced breeder if we had no previous record of its breeding because: 1) young Laysan Albatrosses return to the close vicinity of their birth place to begin breeding (Fisher and Fisher 1969:195–197); 2) males return consistently year after year to the same territory; 3) females, once paired, return to their mate's territory as long as the pair-bond is intact; 4) the plot was searched daily and we recorded all new birds every day; and 5) a 50-foot-wide strip of land just outside the borders of the plot was

TABLE 1. Age at first breeding in Laysan Albatrosses in the plot.

Sex	N	Percentage beginning at age (years)											
		5	6	7	8	9	10	11	12	13	14	15	16
Both	847	0.1	3.5	16.5	32.5	23.6	14.8	5.9	2.0	0.6	0.2	0.1	0.1
♂♂	471	0.0	5.3	18.3	36.1	22.3	10.6	5.1	1.5	0.4	0.2	0.0	0.2
♀♀	376	0.3	1.3	14.4	27.9	25.3	19.9	6.9	2.7	0.8	0.3	0.3	0.0

searched each year to discover any of our birds that might have established territories or nests there.

Time did not permit us to maintain such records for albatrosses in the South of Pier sample or to make such intensive efforts at recapture. The birds, banded as fledglings in the summers of 1960, 1961 and 1962, were searched out two or three times a week during the egg-laying seasons from 1964–65 to 1972–73, inclusive. In 1964–65, 1968–69 and 1972–73 the search continued through the incubation period. Some birds may have been missed, but the rapid decline in the number of recaptures of new birds toward the end of each search period indicated that their numbers were relatively few.

Although all birds used in this study were banded as chicks, the designation of their ages must be explained. We considered a chick hatched in February, 1961, from an egg laid in November, 1960, to be a 1960 chick. In November, 1968, this chick would have been 8 years old.

The following categories of birds are referred to: 1) plot chicks were birds hatched from eggs laid in the plot; 2) South of Pier chicks were birds hatched from eggs laid in the South of Pier area; 3) Walkers were any birds walking in the breeding colonies during the incubation period after all the current breeding birds had been identified (for the most part, they were juveniles 1 or 2 years from first breeding); 4) inexperienced breeders or birds were birds for which we had no previous record of breeding; and 5) experienced breeders or birds were those known to have bred previously.

A composite sample of 847 birds (471 males and 376 females), used to demonstrate the age of first breeding in the plot, included chicks from the 1956 through the 1964 age-classes. Chicks banded after 1964–65 were not included because the oldest would have been only 7 years old by the 1972–73 season, when the field study was ended, and their inclusion might have biased the data toward a falsely younger age of initiation. The sexual difference in numbers in the sample reflects the fact that males return more closely than females to their natal nest sites and thus are more apt to be recaptured in the vicinity; it does not indicate any sexual difference in mortality.

Within our sample, 428 albatrosses were paired; thus, 214 pairs were composed of a known-age, inexperienced male and a known-age, inexperienced female. Of the remaining birds: 1) 30 known-age, inexperienced males were paired with known-age, experienced females; 2) 26 known-age, inexperienced females were paired with known-age, experienced males; 3) 227 known-age, inexperienced males were paired with females of unknown age and unknown breeding experience; and 4) 136 known-age, inexperienced females were paired with males of unknown age and unknown breeding experience.

Mates of these 847 first-time breeders were first classified by age categories of older, younger, same-age, or age unknown; and experience categories of experienced, inexperienced, or experience unknown. Most of the mates of unknown age and experience were first banded as walkers, and many were recaptured several times in the years prior to the first record of their breeding with one of our inexperienced birds. We assumed that these walkers were also inexperienced, although it is possible that a few experienced, unbanded females moved into the plot after being widowed in areas we did not search.

These mates of unknown age and experience (136 males and 227 females) were assigned to various age and experience categories according to the percentages observed among the mates of known age and experience. We thus formed a sample in which all mates were "known" by age, relative to the other member of the pair, and by experience in breeding.

Further validity was given this procedure by an analysis of an additional sample of 73 known-age, inexperienced chicks belonging to the 1965 and 1966 age-classes. There was close agreement between the percentages in the various age and experience categories.

The three year-classes represented in the South of Pier sample (580 unsexed birds) were treated individually to demonstrate the relative numbers in each class initiating breeding at different ages.

We often relied upon comparisons of what observed percentages of albatrosses did, and upon modes and medians more than upon means as indicators of the true biological situation in the population. First, the means may have been unduly influenced, especially in the smaller samples, by inclusion of birds at the ends of the observed ranges, of whose status we could not be certain. Second, since breeding occurs for only a limited time once a year, a fractional-year difference between observed means may signify as much as a calendar year's difference in behavior.

RESULTS

AGE AT FIRST BREEDING

The percentages of 847 plot birds that initiated breeding at various ages are shown in table 1. The mode for the combined sexes was 8 years (median 8, mean 8.6, and range 5 to 16). The mode for 471 males was 8 years (median 8, mean 8.4, and range 6 to 16). The mode for 376 females was 8 years (median 9, mean 8.9, and range 5 to 15). Between ages 7 and 10, inclusive, 87.3% of the males and 87.5% of the females began to breed. However, 59.7% of the males but only 43.9% of the females began by age 8. Essentially all males

TABLE 2. Age at first breeding in Laysan Albatrosses in the plot, when mate was inexperienced.

Sex	N	Percentage beginning at age (years)						
		6	7	8	9	10	11	12
Both	428	2.6	15.4	37.6	24.3	14.5	4.0	1.6
♂ ♂	214	4.2	16.8	43.5	21.5	9.3	3.7	1.0
♀ ♀	214	1.0	14.0	31.8	27.1	19.6	4.2	2.3

began to breed by age 12 and all females by age 13.

EFFECT OF EXPERIENCE OF MATE ON AGE AT FIRST BREEDING

The percentages of 214 pairs, both members inexperienced, that initiated breeding at various ages are shown in table 2. The mode for the combined sexes was 8 years (median 8, mean 8.5 and range 6 to 12). When the sample was considered by sex, the only variation from the data obtained on all 847 birds was in the means—8.3 years for males and 8.7 years for females. Between the ages of 7 and 10, inclusive, 91.1% of the males and 92.5% of the females initiated breeding. However, 64.5% of the males, but only 46.8% of the females, began breeding by age 8. By age 9, 86.0% of the males and 73.9% of the females had started. Virtually all these albatrosses nested by age 12.

The percentages of 75 birds that initiated breeding with experienced mates at various ages are shown in table 3. The mode for the combined sexes was 9 years (median 9, mean 9.3, and range 5 to 12). The mode for the 45 males was 9 years (median 9, mean 9.3, and range 7 to 12). The mode for the 30 females was 10 years (median 10, mean 9.4, and range 5 to 12). Between the ages of 7 to 10, inclusive, 88.9% of the males and 70.0% of the females bred for the first time. Only 20.0% of the males and 26.6% of the females initiated breeding by age 8. By the ninth year 62.2% of the males, but only 46.6% of the females, had started. We found only one instance of a 5-year-old breeding, a female paired with an experienced bird.

EFFECT OF AGE OF MATE ON AGE AT FIRST BREEDING

The percentages of inexperienced males and females of various ages first breeding with younger, same-age, and older mates are shown in tables 4 and 5. All males initiating breeding at 6 years were paired with older females. Nearly 80% of those starting at age 7 were with older females, and slightly more than 20% were paired with females their own age. Only among those males that started reproduction at age 8 or later were some with younger females; even at this age, more than half were paired with older females. Thereafter, as the age at which males began breeding increased the percentage of older and same-age mates decreased and, obviously, the percentages of younger mates increased.

All females beginning to breed at ages 5 or 6 had older mates. At age 7, half of the mates of the inexperienced females were older, a fourth were younger, and a fourth were the same age. Among mates of females beginning to breed at 8 years, slightly more than 40% were the same age as the females, 33% were older and 25% were younger. At older ages of initiation (to 11 years at least), the percentage of mates older than or the same age as their inexperienced females declined, and the percentages of younger male mates increased correspondingly.

Despite this trend in both sexes for older mates when initiating reproduction at an early

TABLE 3. Age at first breeding in Laysan Albatrosses in the plot, when mate was experienced.

Sex	N	Percentage beginning at age (years)							
		5	6	7	8	9	10	11	12
Both	75	1.3	0.0	6.7	14.7	33.3	26.7	12.0	5.3
♂ ♂	45	0.0	0.0	4.4	15.6	42.2	26.7	8.9	2.2
♀ ♀	30	3.3	0.0	10.0	13.3	20.0	26.7	16.7	10.0

TABLE 4. Percent of male Laysan Albatrosses initiating breeding at various ages (in years), when mate was younger, same age or older.

		Male						
	Age	6	7	8	9	10	11	12
Female	N	25	86	170	105	50	24	7
Younger		0.0	0.0	17.1	28.6	34.0	62.5	85.7
Same age		0.0	22.1	31.8	30.5	32.0	12.5	0.0
Older		100.0	77.9	51.1	41.0	34.0	25.0	14.3

age and for younger mates when initiating at a later age, male first-time breeders predominantly had older mates and female first-time breeders had younger mates. Slightly more than 50% of the inexperienced males breeding for the first time had older mates, about 25% had mates of the same age, and about 20% had younger mates. The reverse situation occurred with inexperienced females; approximately 25% of the mates were older, about 25% were the same age, and slightly less than 50% were younger.

EFFECT OF SEASON ON AGE AT FIRST BREEDING

We found great annual variation in the age of first breeding in the three year-classes for which we had adequate samples (table 6). No 6-year-olds of the 1960 class bred, but 18.2% of the 1962 sample bred at this age. Only 6.4% of the 1960 group, but 58.8% of the 1961 class, first bred at 7 years. Only 4.1% of the chicks of 1961, but 64.3% of the chicks of 1960, first bred at age 8. Other age groups showed similar diversity. Only in the instances of the 8- and 9-year-olds of the 1962 sample, the 10-year-olds of the 1961 class, and the 11-year-olds of the 1960 chicks was there essential agreement with the weighted means for all three years. The mean percentages that initiated breeding in the sixth, tenth or later years were significantly different from the means for these ages in the years 1956 through 1964.

DISCUSSION

AGE AT FIRST BREEDING

The composite sample of 8 year-classes of chicks (table 1) shows that Laysan Albatrosses most often begin to breed in their eighth and ninth years, although they may begin at 6 years or as late as 15 or 16 years. This span encompasses completely the ages of first breeding suggested for other albatrosses.

All measures of central tendency for the age of first breeding in the Laysan Albatross are found around 8 and 9 years (56.1% of all albatrosses), and 87% of these birds start breeding in years 7 to 10, inclusive. Only 4% begin earlier and 9% later.

Although Fisher and Fisher (1969:190) were not able to demonstrate sexual difference in the age at first breeding, our data show that females lag approximately one year in beginning to breed. The Fishers noted their "data are too few for assurance," and any possible sexual difference was partly masked in their study because they could not include data on birds older than 9 years; the percentages for the early years were thus higher than usual.

The older age at which females begin breeding is shown in all our samples by: 1) their greater mean age (although the differences between the means for the two sexes were not always statistically significant, even a fractional year difference suggests a full season's difference); 2) their greater median age at initiation; 3) their predominant pairing

TABLE 5. Percent of female Laysan Albatrosses initiating breeding at various ages (in years), when mate was younger, same age, or older.

		Female							
	Age	5	6	7	8	9	10	11	12
Male	N	1	5	54	105	95	75	26	10
Younger		0.0	0.0	22.2	23.8	59.0	66.6	73.1	70.0
Same age		0.0	0.0	25.9	42.9	26.3	17.3	15.4	0.0
Older		100.0	100.0	51.9	33.3	14.7	16.0	11.5	30.0

TABLE 6. Annual variations in age (in years) at first breeding in Laysan Albatrosses using the South of Pier area.

Year	Number known to breed	Percent initiating breeding at age						
		6	7	8	9	10	11	12
1960	171	0.0	6.4	64.3	21.6	3.7	3.6	0.0
1961	146	2.7	58.8	4.1	15.7	8.9	9.6	?
1962	263	18.2	13.3	36.4	19.7	12.5	?	?
Averages (weighted for)								
Sample size		8.9	22.7	36.5	19.1	9.1	3.4	?
Year		7.0	26.2	34.9	19.0	8.4	?	?
1956–1964	847[a]	3.6	16.5	32.5	23.6	14.8	5.9	3.0

[a] Does not include the 580 from 1960–62.

with younger males; and 4) the fact that 16% fewer females than males began breeding by age 8 and 13% fewer by age 9.

Later initiation of nesting is also found in female Red-billed Gulls (*Larus novaehollandiae scopulinus*) (Mills 1973:150). However, females breed earlier than males in several other long-lived aquatic species. For example, female Black-legged Kittiwakes (*Rissa tridactyla*) breed at 3 and 4 years, males at 4 and 5 years (Coulson 1966:270), female Short-tailed Shearwaters first breed at a mean of 5.3 years and males at 6.6 (Serventy 1967:180), and nearly half of the female Yellow-eyed Penguins (*Megadyptes antipodes*) start at age 2 and essentially all by the third year, while most males do not start until age 3 or 4 (Richdale 1957:106). According to Lack (1954, 1966) birds do not initiate breeding until they are at an age when they can raise young successfully without undue risk to themselves. Egg-laying places an extra, rapid energy requirement on the female, and a female Laysan Albatross may require an additional season to prepare for this stress. The physiological preparation is coupled with an additional behavioral development for securing the extra energy to form the egg. Although a male albatross expends considerable energy in securing a territory and a mate, these activities take place a year or two before first breeding and at a much slower pace than the development of the three-quarter-pound egg (Fisher 1971b:41–42).

A few Laysan Albatrosses are very late in beginning to breed. We are relatively certain that the four males not found breeding until their 13th or later years were actually first-time breeders. Males are not known to change location once they have established a territory, and they cannot secure a mate without this permanent territory (Fisher ms). We cannot be so sure about the five, late-breeding females. It is possible, although not probable, considering the nature and size of the plot and our searches of the surrounding areas, that they first bred outside the plot and later moved to a new male's territory on the plot when their first mate died.

This unusual delay may be the result of several factors. Some individuals may not mature sexually until later, but we made no gonadal examinations. Some birds may not be able to secure a mate in the earlier years, despite the apparent abundance of potential mates among the eligible, young birds that invade the colony from February to April. Although this seems improbable, despite the expected differential in physiological and behavioral development, it is not impossible. Further delays in pairing might place a bird among albatrosses so different in age or experience or both that pairings would be more difficult. The primary factor in these long-delayed breedings, we believe, is loss of mate before breeding is ever started. Fisher and Fisher (1969:190) noted seven such instances among the 207 birds of their study, and these birds are included here. Since the prebreeding association or courtship period encompasses at least one and often two breeding seasons, the loss of a mate during this time would prevent the survivor's breeding for an additional 2 years. Loss of two successive mates might well result in a delay of 3 to 4 years.

EFFECT OF EXPERIENCE OF MATE ON AGE AT FIRST BREEDING

When both members of a pair are inexperienced, they begin to breed at mean ages comparable to those found in the entire colony. Fisher and Fisher (1969:191) suggested that an experienced partner might hasten the maturation of an inexperienced mate during the long courtship period, especially if the immaturity was primarily behavioral rather than physiological. Our study does not support this hypothesis. The initiation of reproduction by

inexperienced albatrosses, paired with older, experienced birds, was frequently delayed for approximately 1 year beyond the usual age (table 3).

Evidence that novice males paired with experienced females are further delayed includes: 1) mean age of 9.3 years in these males versus 8.3 years when they are paired with inexperienced females, 2) modal age of 9 years versus 8, 3) median age of 9 years versus 8, and 4) 44.5% more males fail to begin breeding by the usual age of 8 years.

That novice females with experienced males also undergo further delay is shown by: 1) their mean age of 9.4 years at first breeding versus 8.7 years when they are with inexperienced males, 2) modal age of 10 years versus 8, 3) median of 10 years versus 9, and 4) 27.3% more females fail to breed by the usual age of 9 years. These data, especially the means and the percentages that begin at various ages, also demonstrate that more males than females are delayed beyond the years expected in the delayed breeding characteristic of the species, when their mates are experienced breeders.

Since pairings of an inexperienced bird with an experienced one cause additional delays and since these albatrosses are physically capable of breeding at an earlier age, the effect of the "experience" probably lies in acquired behavior. The "problems" causing additional delays most likely occur in the stereotype aspects of territoriality and of the courtship display in the prebreeding association.

In any speculation concerning the factors bringing about the delaying effect of experience, it must be recalled that the male Laysan Albatrosses, through territory-seeking, initiate reproductive behavior a year or so earlier than the females. Males tend to breed, on the average, one season earlier than females and they are the instigators, leaders, and dominant ones in courtship activities. Thus, we believe females do most of the adapting to their partners' patterns of dancing and whatever minor deviations they may exhibit from the stereotype of this species.

Earl Meseth (pers. comm.), who has studied the courtship behavior in depth, agreed that males are the dance leaders "setting the pace and bringing the female slowly into the more vigorous core of the dance." However, he felt that the female is not solely a blind follower in these activities. He pointed out that both sexes follow several general rules in dancing, and that either may adapt to the partner's deviations in performance to abide by these rules. However, Meseth did accept the possibility that a female may be influenced by or "fixed on" the dance peculiarities of a particular male.

We think it probable that an inexperienced male, already dominant and secure on his territory, develops his individual version of courtship inherent in the species by dancing with a number of different females before his permanent pair-bond is established. An inexperienced female, although she may perform brief dances with many males, finally perfects her individual patterns, again within the species type, by dancing mostly with the male that becomes her mate. Thus, in both sexes, the patterns are established and fixed by the time the first pair-bond is consummated. Consequently, it should be easier and quicker for two inexperienced birds "to learn together" and to form an effective pair-bond, leading to somewhat earlier attempts at actual reproduction.

Although experience in either member of a pair causes further delays in first breeding by a novice mate, the pair-bond between an experienced female and an inexperienced male may require a longer period of firming. First, the female must "unlearn" or adapt her established set of responses to his set. If she does not, she, in effect, attempts dominancy in the situation, and this apparently prevents the formation of a pair-bond. Second, Meseth (pers. comm.) suggested that the nest site of the experienced female in the former mate's territory, and the rest of his territory as well, are places of "non-aggression." He further hypothesized that the dance reduces or eliminates any last vestiges of aggression and makes it possible for the female to accept the site and remain there with the male. Thus, she is attached not only to a nest site but to a mate's peculiarities, and these attachments are reinforced each season she breeds with him.

When this experienced female is widowed, the formation of a new bond entails leaving the established site of non-aggression and accepting a strange site as well as a new mate. Perhaps this two-fold acceptance is associated with the further delayed breeding by her inexperienced mate. It appears that these problems of acceptance may be worked out in two or three seasons of prebreeding association, for there is a sudden increase between the ages 8 and 9 in the percentages of inexperienced males that initiate breeding with experienced females.

The bond between an experienced male and a novice female may occasion lesser delays be-

cause she can more easily adapt to or adopt the male's patterns. She has no previously fixed, individual behavior or any attachment to a previous nest site or territory that might conflict with acceptance of the male's individuality and his territory. This experienced male, already established and dominant on a territory, has only to lead his novice mate into the courtship activities and, perhaps, to make minor adjustments in his version of courtship, which seemingly do not require as much time as the major adjustments required of the experienced female.

EFFECT OF AGE OF MATE ON AGE AT FIRST BREEDING

We could not determine if there was any discrete effect of age of mate on the age of first breeding; we had too few inexperienced birds of either sex that were several years older than their mates. However, birds of both sexes that initiate breeding younger than the norm for their sex predominantly pair with older birds. The reason may be that juveniles who mature earlier than others in their age-class return to the colony at a younger age and sooner in the breeding season than other members of their cohorts. Since the usual pattern is for the older juveniles to come back sooner in the season to seek territories and to form pair-bonds, these early-maturing birds are thrown into contact with potential mates of greater age.

This is especially evident in the sexual difference in age at first breeding. The earlier breeding males consistently have older, inexperienced mates in the primary years of first breeding, and even in the later years they are found more frequently with older, inexperienced females than are females with older, inexperienced males.

These later years may reflect more the availability of albatrosses of certain ages during the months that an aged, inexperienced albatross usually seeks a mate, than they do the usual age relationship within a Laysan Albatross pair-bond. Since the time of seasonal return to the breeding colony is dependent upon age and maturity, not experience, birds of similar age and sexual maturity would normally be present together and could be expected to pair, as we found. However, unpaired, experienced breeders of both sexes arrive in the colony in November, before most or any of the inexperienced albatrosses; they could be expected to form bonds with other experienced birds. If this does not occur, the experienced bird next comes into contact with the oldest, inexperienced albatrosses made available by bonds broken before reproduction could occur. Most of the pair-bonds the experienced birds could form later in the season would have to be with inexperienced albatrosses of younger and younger ages.

EFFECT OF SEASON ON AGE AT FIRST BREEDING

Fisher and Fisher (1969:190) cautioned that the season might have considerable effect on the age at which Laysan Albatrosses first bred. This was based upon their observation of major annual variations in breeding populations and not upon data bearing directly upon the question. Our data (table 6) are proof of a relationship between season and the age at which young albatrosses begin to breed.

Unusually high percentages of the 1962 sample bred as 6-year-olds; far more than expected of the 1961 cohort bred as 7-year-olds; and nearly twice the expected number of the 1960 class bred as 8-year-olds. All these high percentages of birds first breeding at an early age are representative of the same season, 1968–69. Further, these unusual numbers disrupt the normal distribution evident in the means in the last three lines of table 6. The 1968–69 season was notable for low breeding populations in the colonies and for the absence of many former breeders.

Despite the variability among the year-classes in the percentages that started to breed through age 9, it is important that: 1) 66 to 71% of the albatrosses in these three year-classes bred by their eighth year, compared to 53% in the composite 1956–64 sample; and 2) 81 to 92% of them bred by age 9, compared to 76% in the composite sample. Thus, any bias introduced by our inability to follow all these samples into their 11th and later years appears to be minimal by the 9th year. And, since the recapture methods were the same in these years, methods that produced equal numbers of males and females in other areas, we do not believe the annual variation was caused by the sexual difference in age at first breeding.

Thus, a season may be favorable for the initiation of breeding, but unfavorable for continued breeding by experienced albatrosses. There is no evidence, however, that an unfavorable season delays the initiation of breeding beyond the usual age of 8 or 9 years. Although we know almost nothing about possible oceanic conditions that might cause more young birds to breed in years when there were relatively few experienced birds breeding, we

do know that the absence of former breeders does not release territories or nest sites for use by first-time breeders. Their sites were determined a year or so earlier, and we must eliminate competition for them as an explanation for the breeding of greater numbers of novice birds.

The annual variation demonstrated for the 1960–62 period does not fault the overall picture shown by the 1956–64 sample of the age at which Laysan Albatrosses begin to breed. The greatest variations between the age-classes stemmed from conditions in a single season, and the 1956–64 sample included birds first breeding in an 11-year period which had several seasons of high and at least two seasons of low breeding numbers.

SUMMARY

This study involved 847 Laysan Albatrosses of known age and sex and 580 of known age but undetermined sex. All initiated breeding between the 1962–63 and 1972–73 seasons on Midway Atoll, North Pacific Ocean.

Males tended to initiate breeding one year earlier than females. The mean age in all males was 8.4 years (mode 8, median 8, range 6 to 16) and in all females it was 8.9 years (mode 8, median 9, range 5 to 15). Sixty percent of the males, but only 44% of the females, began to breed by their eighth year.

Among 428 inexperienced albatrosses paired together, the mean age for first breeding in males was 8.3 years and in females 8.7 years. Sixty-five percent of these males, but only 47% of the females, began to breed by age 8. Nearly all of these birds bred by age 12. Breeding experience in a mate caused a further delay of one year in the initiation of reproduction by the novice member of the pair. More novice males (45%) paired with experienced females than novice females (27%) paired with experienced males showed this further delay. The additional delay by greater numbers of inexperienced males paired with experienced females was related to her greater difficulty in forming a new pair-bond.

In both sexes there was a tendency for albatrosses first nesting earlier than the mean age to have older mates. They had younger mates when initiating after the mean age. Male, first-time breeders had predominantly older mates, and female, first-time breeders had younger mates. These differences between the ages of mates were related to sexual differences in age of maturity and to the seasonal differential in the availability of mates of different ages.

Unknown seasonal conditions influenced the age at which some year-classes of Laysan Albatrosses began to breed. Many individuals began to breed at unusually early ages in one season when a large percentage of experienced breeders failed to breed.

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