THE AUK
A QUARTERLY JOURNAL OF
ORNITHOLOGY

VOL. 92 JULY 1975 No. 3

THE RELATIONSHIP BETWEEN DEFERRED BREEDING AND MORTALITY IN THE LAYSAN ALBATROSS

HARVEY I. FISHER

IN discussing the fact that long-lived seabirds often do not begin to breed until they are several years of age, Lack (1966: 275) suggested that "in such species, breeding is difficult and individuals which try to breed when younger than the normal age leave, on the average, fewer not more surviving young than those which start later." He noted that this view depended upon the hypotheses, first, that "young parents are less efficient at raising young than older parents" and, second, that "breeding somewhat lowers the chances of survival of young adults."

These views were in contrast with those of Wynne-Edwards (1955) who held that delayed breeding had evolved through group selection to reduce the number of offspring produced and thus prevent overpopulation. Lack (1966) observed that there was no real evidence for either set of ideas.

The observation that some species do not breed until the individuals are several years old has led, not necessarily correctly, to the concept of deferred maturity. The term delayed breeding is preferable for we still have no evidence that such birds are sexually immature prior to their first attempts at breeding.

Correlated with Lack's views is the suggestion that young breeders often begin to nest later in the season and are thus most often the parents of the late offspring that suffer greater than average mortality. If this mortality is related to the time of year the young fledge, as well as to the inexperience of young pairs—and we think it is in many species—then natural selection might be expected to have produced a narrowly limited reproductive season and a situation in which experienced breeders, forced, for whatever reason, toward late breeding in a season, would not even attempt reproduction, as for example Tuck (1960: 112) noted in murres.

The belief most frequently suggested as a basis for this age-related

differential in nesting success and in mortality is that the younger breeders in some way cannot compete as well. Richdale (1949: 14) was one of the first modern students to express this. He reported that experienced breeders among Yellow-eyed Penguins, *Megadyptes antipodes,* produced more young that survived to return to the colony. Although he did not venture an explanation, he did recognize that these experienced parents were most valuable for the species.

Fretwell (1969) attributed the greater mortality of late-reared chicks to their presumed subdominant position in their cohort. He also suggested that young breeders may be subdominant, unable to secure suitable nesting sites, and thus the parents of subdominant offspring, without which the colony would be better off. Neither of these ideas appears applicable to Laysans, as will be seen later.

Orians (1969) believed that lesser foraging efficiency in young Brown Pelicans, *Pelecanus occidentalis,* might cause delayed breeding. He found that hunting success improved with age. Ashmole and Tovar (1968) theorized that prolonged parental care might be associated with specialized feeding methods that require a prolonged learning process. Carrick and Ingham (1967) thought that the Wandering Albatross, *Diomedea exulans,* might need a decade to perfect its food-getting skill sufficiently to support a chick and that premature attempts would increase the hazards. They also established, to their own satisfaction at least, that socially induced deferment of maturity in the Royal Penguin, *Eudyptes chrysolophus,* "is due to competition for feeding status at sea and not for nest-site or breeding status ashore." Robertson (1969) considered that the greatest stress for young breeding Sooty Terns, *Sterna fuscata,* occurred when they arrived late in the season and had to compete for nest sites with already established breeders. He surmised (p. 634) that the individual "may ultimately leave more progeny if it delays return until better able to compete and until a greater probability of vacant and suitable sites exists," a view comparable to Fretwell's.

These few examples from the many papers that touch upon the subject highlight, I think, the belief of many students that delayed breeding by the individual does enhance the success of the species. The hard evidence to support this belief is generally meager and unsatisfactory. It contributes little to suggest "experience" or "highly skilled" foraging techniques when no one can define, from the avian viewpoint, the degrees of experience, skill, or social status requisite for individual survival or for successful reproduction.

The purpose of this paper is to examine the concept of deferred breeding as it may apply to one species, the Laysan Albatross, *Diomedea immutabilis.* This is feasible because of the detailed records we have

TABLE 1

AGE AT WHICH LAYSAN ALBATROSSES BEGIN TO BREED[1]

	Number	Mean	Mode	Median	Range (years)
Males	474	8.4	8	8	6–16
Females	379	8.9	8	9	5–15

[1] Birds banded as chicks; from Van Ryzin and Fisher (MS).

on individuals of known age and sex and because of the scope of information available on the species' biology.

The Laysan Albatross exhibits well several aspects of deferred breeding. Males do not begin to breed in significant numbers before the age of 7 years (mean 8.4), or females before 8 years (mean 8.9) (Table 1). Chicks that become ready for departure late in the season, especially in the last 2 weeks of the post-hatching period in the colony, suffer heavy mortality. I showed (Fisher 1969) that the young females are the last to lay eggs in any season, and these eggs do produce the late chicks just mentioned. I further noted (p. 106) that the female tends to lay a little earlier in each subsequent season, until her egg is dropped near the median date for all eggs (27 November). Of the experienced females 80% lay within 3 days of this date. These patterns of egg-laying produce a much restricted egg-laying period for the colony (21 November to 15 December), with 97% of the eggs deposited by 10 December, and this is reflected in the 1-month period the following summer when most successful chicks leave the colony.

Experienced breeders that return late in the season and below normal in weight do not attempt to breed (Fisher 1967). This is in line with Tuck's observations on murres and, in general, is supportive of Lack's opinion (1966: 259–260) that food supplies just before egg-laying time may influence the seasonality of egg deposition or, as in this instance, prevent laying. The failure of these albatrosses to attempt late nesting had two results of apparent benefit to the species. The absence of reproductive stresses in a year of adversity permitted greater survival (the mortality rate was no higher than in the previous or the following year), and no late, generally unsuccessful chicks were produced.

As Laysan Albatrosses exhibit a range of several years in the ages at which different individuals first breed, it was possible to test the hypothesis that birds that start breeding at the usual age of 8 to 9 years have higher survival rates. We have no data on the physiological maturity or readiness to breed of any of these albatrosses, and we thus had to concern ourselves only with observations on mortality associated with observed ages of first breeding.

TABLE 2

MORTALITY OF YOUNG, BREEDING LAYSAN ALBATROSSES IN THE PLOT

Sex	Original number	Percent[1] during breeding year									Mean
		1	2	3	4	5	6	7	8	9	
Males	531	2.1	4.0	6.8	5.5	5.6	5.4	1.3	2.7	2.7	4.0
		2.1	4.0	7.2	6.3	6.9	7.2	1.9	3.8	4.0	4.8
Females	429	2.6	3.7	4.0	3.7	6.0	4.9	2.0	3.9	2.8	3.7
		2.6	3.8	4.2	4.2	7.0	6.1	2.8	5.4	4.1	4.5

[1] Percent is calculated in two ways: the first line is percent of original sample, the second is percent of birds alive at beginning of risk period.

METHODS

The methods and techniques used to obtain the data on Midway Atoll may be found in Fisher and Fisher (1969) and Fisher (1971). Of the two basic samples, one was of chicks banded in the study plot between 1956 and 1963, inclusive, and found breeding there between 1961 and 1972. Sexing at the time of recapture showed 531 males and 429 females. The second sample contained 1068 birds of the 1960- to 1963-year classes, that first bred between 1966 and 1972. Available assistance did not permit sexing these birds.

The interpretation and other use of the data on mortality require a word of caution. The Midway Atoll colony of Laysan Albatrosses has grown greatly in numbers since the turn of the century, and breeding numbers have approximately doubled in the last 15 years (Fisher MS). Consequently all the observed mortality rates may be atypically low for the species as a whole, but this possibility should not affect the validity of comparisons between rates observed for various cohorts within the same span of years—the use made of them in this study.

RESULTS

Mean annual mortality (percent of original sample) was 4.0% (1.3 to 6.8%) for young males in their first nine breeding seasons and 3.7% (2.0 to 6.0%) for females (Table 2). In an unpublished study I have demonstrated that the mean annual rates for birds of all breeding ages in two colonies were 5.3 and 6.3%, varying annually between 1.9 and 8.5% and showing no significant sexual variation during the 13-year period. If mortality is expressed as percent of birds exposed to risk in each year (Table 2), the mean annual rate for young breeding males was 4.8% (1.9 to 7.2%) and 4.5% for females (2.6 to 7.0%).

Both expressions of mortality revealed that breeding birds of both sexes were much more vulnerable from the third to the sixth breeding years, inclusive. Annual mortality in breeding years 1 and 2 and 7, 8, and 9 averaged approximately half that during years 3 to 6.

As males begin breeding essentially one season earlier than females, the survival rates in Table 3 must be offset one year for comparison. The rates of survival of 9-year-old males and 10-year-old females show

TABLE 3

SURVIVAL OF YOUNG, BREEDING ALBATROSSES IN THE PLOT

	No. birds	Percent never recaptured	Percent survived to age (years)								
			9	10	11	12	13	14	15	16	17
Males	531	2.1	97.9	93.9	87.1	81.6	76.0	71.6	70.3	67.6	64.9
Females	429	2.6	100	96.3	92.3	88.6	82.6	77.7	75.7	71.8	69.0

close agreement, for example. Some three-fourths of both sexes survived through five breeding seasons (males to age 13 and females to 14).

Data on differential survival among birds beginning to breed at different ages were gathered in the plot and in the South of Pier areas. The results varied only insignificantly between the two locations, and I have chosen to present the South of Pier sample for discussion. Two aspects of this sample need clarification. First these birds, using 8-year-olds as a typical group, exhibited only 65% survival to age 13, in contrast with the somewhat greater than 75% shown by plot birds (Table 3). The difference had three causes: (1) The plot was searched once each day, and the South of Pier area only two or three times per week. (2) We had detailed pair bond information on the plot birds, which often enabled us to know of the survival of a mate even though we did not actually recapture the bird. Such records were not available for South of Pier albatrosses. (3) Mean annual mortality in a South of Pier sample of breeders of unknown age averaged 1% per year higher during a 9-year period, perhaps because of human disturbance. If a similarly elevated rate occurred among the known-age first-time breeders, it alone could account for the lower survival rate.

The second item of seeming discrepancy is that I found only 38% survival to 12 years of age among 7000 chicks (including those in Table 4)

TABLE 4

SURVIVAL OF LAYSAN ALBATROSSES INITIATING BREEDING AT DIFFERENT AGES[1]

At first breeding		Percent[2] survived through age (years)			
Age	No. birds	9	10	11	12
6	64	75.0	71.1	68.0	50.1
7	271	91.7	83.3	76.4	55.0
8	483	86.0	81.6	75.0	65.0
9	217	—	80.3	75.0	54.0
10	27	—	—	85.0	71.3
11	6	—	—	—	83.4

[1] Chicks of the 1960-, 1961-, and 1962-classes in South of Pier area.
[2] Percentages represent weighted averages because numbers of birds in the three year-classes varied.

banded in this area. It is easily cleared up. The 8-year-olds in Table 4 represent a weighted mean of 53% that survived to breeding age. Thus 65% of 53% is 34%, which is near the 38% survival found among all the chicks originally banded. The data in Table 4 may be compared in two ways: (1) survival to a specified age, and (2) survival for varying years after initiating breeding.

Birds that began breeding at age 6 showed the lowest survival, and those beginning to breed at 7 years had the highest rates for survival to ages 9, 10, and 11 years. Only in survival to 12 years was the 7-year-old group seemingly less successful than the 8-year-old. Birds that began to breed at 9 years survived to 10 and 11 years as well as the 8-year-olds, but their survival to 12 years was approximately 10% less than that for the 8-year-olds.

Birds that began to breed at 6 years of age did not survive for as many subsequent breeding seasons—75% for 3 years and 71% for 4 years, compared to 83% and 76% survival for comparable periods by 7-year-old first-time breeders. But 92% of the latter survived for two seasons after first breeding (versus 82% for 8-year-olds), 83% for 3 years (75% for 8-year-olds), and 76% for 4 more years (versus 65% for 8-year-olds). Nine-year-old first-time breeders showed significantly lower survival rates than did 8-year-olds for the 2- and 3-year spans.

The data on the birds that first began breeding at 10 and 11 years may show marginally lower survival rates than those for birds that first began to breed at 8 years, but they are less reliable because of the small samples and the fewer years they could be observed.

DISCUSSION

We may conclude that in Laysan Albatrosses, except among birds starting to breed at 6 years of age, the initiation of breeding before the usual age of 8 or 9 years does not result in increased mortality. There may be lesser survival among birds that begin to breed at older than usual ages. Laysans seem to survive best if they begin to breed at 7 years of age. If this is true, one would expect a greater percentage of them to begin breeding at 7 years, unless the shift to a younger breeding age is still in process.

Several facets of the life cycle of the species may bear on this question. Seven years provide a relatively long period of training or experience for self-survival, perhaps sufficient also to prepare the bird for the added demands of reproduction. The period of association before the first pair bond is consummated extends over two seasons usually, and the loss of an intended sexual partner during this time delays the initiation of breeding by at least an additional year. We do not know

the extent of this early loss of mates, but annual mortality during these associative years is approximately 2%.

The associative years are of significance in other ways. The association between a novice male and the female that eventually becomes his mate begins only after his territory is firmly established. As she nests within his territory and is not involved in nest-site defense until the first year of breeding (Fisher 1971: 51), neither member of the pair expends much energy on territoriality in the year or so before they first breed. Thus I cannot believe that the last year or two of delay before breeding is begun by the Laysan can be ascribed to the need for increased competitiveness for nest sites, as Robertson (1969) and Fretwell (1969) proposed for other species.

As it is known that the male and female Laysans that eventually become a pair, whether in the first or subsequent bonds, are together at least one breeding season, and often two, before they attempt reproduction, it seems justifiable to attribute a minimum of 1 year of the delayed breeding to the formation of a firm pair bond. The development of a life-long, monogamous bond in a species whose courtship is so complex and stereotyped, could well require longer than expected periods. The time needed for the reduction of individuality and aggression to the point where the male and female can associate and for the subsequent process of physiological and behavioral coordination necessary between them for successful reproduction may well be responsible for 2 years of delay.

The low mortality shown by all Laysans in their first breeding year occurs because relatively few complete even the incubation portion of the reproductive cycle. I noted (1971: 30) that only 50% of the eggs of all inexperienced females hatched, compared to 75% of the eggs of experienced birds, and that nest success declined as eggs were laid later in the season. Young breeders were also much less successful in fledging the few chicks they did manage to hatch.

The lesser reproductive stresses that may permit this lower mortality in the first year often continue into the next season, if the young birds try to breed, but my study of the breeding patterns of known age birds revealed that many young birds do not attempt nesting in the following season, which relieves them entirely of whatever rigors reproduction might add. Thus because the young breeders have not yet really undergone the full gamut of reproductive requirements, mortality continues at about the same rate as during the associative years (Table 2).

Not until the third season, when the young birds finally settle down to annual reproduction, are the Laysans subjected in consecutive years to the further behavioral and energy requirements of rearing a chick,

and the mortality rate increases accordingly. In the young male's third to sixth breeding seasons, inclusive, the mean rate is 5.8%, compared to approximately 5.4% among all breeding males and to a 3.0% average in his first 2 years as a member of the breeding population. Although the female's rate also rises from a mean of 3.2% in the first 2 years to 4.7% in the 4 following years, the latter observed rate is still below the mean for breeding females of all ages.

ACKNOWLEDGMENTS

Although a great many individuals and several institutions and agencies have contributed over the years to the culmination of this part of the study of the Laysan Albatross, space does not permit identifying them here. Nonetheless, I am grateful to all of them, and proper acknowledgment of their significant aid is made in other of my publications on this species.

SUMMARY

The dynamics of the Laysan Albatross show agreement with the concepts associated with delayed breeding in the following ways: (1) young birds do not first breed in significant numbers until the age of 8 or 9 years, (2) they nest later than experienced breeders in their first 2 or 3 years, (3) chicks hatched from eggs laid late in the season are subject to much greater mortality than those from earlier eggs laid by experienced breeders, and (4) young breeders fledge relatively few chicks in their first 2 years of breeding.

The generally increased mortality postulated as occurring when birds initiate breeding at ages younger than usual for the species is not found in the Laysan Albatross. Higher mortality rates occur only in the 3rd to 6th years of breeding, without sexual difference and without significant relationship to the age at which breeding began. Nonetheless, evidence shows that Laysans that initiate reproduction 2 years earlier or 1 or 2 years later than normal may not survive as long.

These observations, as a group, are related to, or perhaps partly explanatory of: (1) the much restricted egg-laying period; (2) the restricted period for departure from the colony of successful fledglings; (3) the failure of late-arriving, experienced breeders to attempt reproduction; (4) the single egg clutch; and (5) the failure of the Laysan to lay a replacement clutch.

Most Laysan Albatrosses have a prebreeding life of at least 8 years and an early breeding span of perhaps 2 years, or a total of 10 years, in which to acquire the experience, skills, or status requisite for successful reproduction.

As the increased mortality of young breeders does not begin to appear in Laysan Albatrosses until the second year after their first attempt at

nesting, it would seem that any consideration of the relationship evolved between deferred breeding, mortality, and success in other species should include especially the biology of the first years of breeding.

Literature Cited

Ashmole, N. P., and H. Tovar S. 1968. Prolonged parental care in Royal Terns and other birds. Auk 85: 90–100.

Carrick, R., and S. E. Ingham. 1967. Antarctic sea-birds as subjects for ecological research. Pp. 151–184 *in* Nihon nankyoku chiiki kansokutai, 1956–1962, Sci. Repts., Ser. B, Tokyo, Spec. Issue 1967.

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

Fisher, H. I. 1969. Eggs and egg-laying in the Laysan Albatross, *Diomedea immutabilis*. Condor 71: 102–112.

Fisher, H. I. 1971. The Laysan Albatross: its incubation, hatching, and associated behaviors. Living Bird 10: 19–78.

Fisher, H. I., and M. L. Fisher. 1969. The visits of Laysan Albatrosses to the breeding colony. Micronesica 5: 173–221.

Fretwell, S. D. 1969. The adjustment of birthrate to mortality in birds. Ibis 111: 624–627.

Lack, D. 1966. Population studies of birds. Oxford, Clarendon Press.

Orians, G. H. 1969. Age and hunting success in the Brown Pelican (*Pelecanus occidentalis*). Anim. Behav. 17: 316–319.

Richdale, L. E. 1949. A study of a group of penguins of known age. Biol. Monogr. No. 1, Dunedin, Otago Daily Times and Witness Newspapers.

Robertson, W. B., Jr. 1969. Transatlantic migration of juvenile Sooty Terns. Nature 223: 632–634.

Tuck, L. M. 1960. The Murres. Canadian Wildl. Serv. Monogr. No. 1.

Wynne-Edwards, V. C. 1955. Low reproductive rates in birds, especially sea-birds. Proc. 11th Intern. Ornithol. Congr. 2: 540–547.

Department of Zoology and School of Medicine, Southern Illinois University, Carbondale, Illinois 62901. Present address: Fenwood Toft, Triplett, Missouri 65286. Accepted 26 July 1974.