

AGE AND SURVIVAL OF BREEDING LEACH'S STORM-PETRELS IN MAINE

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Although procellariiform birds have been the subject of several long-term studies (e.g., Richdale, 1963; Richdale and Warham, 1973; Fisher, 1976), Beck and Brown's (1972) account of Wilson's Storm-Petrels (*Oceanites oceanicus*) is the only published work documenting in detail the population structure of small, burrow-nesting storm-petrels (*Hydrobatidae*). Therefore, the present data on age and survival of Leach's Storm-Petrels (*Oceanodroma leucorhoa*) assume particular interest.

Leach's Storm-Petrels share many characteristics with other pelagic birds: late initial reproduction, small clutch size, prolonged incubation and time to fledging, and low adult mortality rates (Gross, 1935; Huntington in Palmer, 1962). However, the mortality patterns of this species have for the most part been inferred from the other characteristics listed here, although Gross (1947) showed that some birds banded as breeding birds lived as long as 12 additional years, and Huntington has subsequently reported one bird estimated to be 24 years of age (Kennard, 1975).

Several hundred pairs of Leach's Storm-Petrels nest on Matinicus Rock, Knox Co., Maine, and over 3,000 individuals have been banded over the last 20 years. This effort, the result of several workers, particularly the junior author and assistants since 1968, makes it possible to report upon the age distribution of breeding individuals in this population and the minimal survival patterns of established breeders. Morse is responsible for analyzing the results and preparing this report, and supervising the rest of it.

THE STUDY AREA

Matinicus Rock lies about 30 km south of the nearest mainland in the vicinity of Rockland Co., Maine, and about 8 km south of the nearest sizable island, Matinicus Is. Matinicus Rock has a lighthouse, foghorn, and accompanying buildings. No grazing animals have been kept on the island for at least 40 years (H. Buchheister, pers. comm.), and for the present purposes it can be considered undisturbed. A rock-strewn meadow of slightly over three ha, punctuated with frequent outcroppings of granite ledge, lies in the middle, skirted by an extensive granitic coastline. The petrels nest in the well-drained parts of the meadow, usually in burrows excavated by them. This island is described more fully elsewhere (Morse and Buchheister, Ms). The area is currently maintained cooperatively as a refuge by the U.S. Fish and Wildlife Service and the U.S. Coast Guard.

THE POPULATION

The Matinicus Rock population of Leach's Storm-Petrels has apparently been considerably more stable than most other populations of this species along the Maine coast; this relative stability is attributable to the absence of large numbers of gulls and live-

stock in the past (Drury, 1973). Unfortunately, we cannot state unequivocally whether or not the petrel population on Matinicus Rock has been completely stable during the period of study (1955-1975). Buchheister has increased his estimate to 600 burrows from the 300-400 that he reported in 1968 (*in* Drury, 1973), but this change results in large part from additional field work on the island. Tyler's banding and burrow-marking efforts in 1963 and 1964 are consistent with a population similar in size to the present one (H. R. Tyler, unpublished data). The most reasonable conclusion thus is that the numbers of breeding petrels have remained relatively constant during the period of the study, and probably previous to that as well.

METHODS

Most of the birds reported in this paper (both breeders and chicks) were removed from their nests in order to read their bands (or band them if necessary) and then returned. A few of their burrows were so long that it was impossible to reach them. The nests in 10 of 150 burrows (7.5%) monitored regularly for a companion study in this colony (Morse and Buchheister, Ms) could not be reached. During a given year we visited approximately one third to one half of the accessible burrows. Smaller numbers of birds were captured in mist nets at night in 1963, 1964, and 1970.

Individuals captured in a burrow with an egg or small chick were considered to be breeders. We assumed petrels first caught as breeders to be four years of age, that is, in their fifth summer (Huntington and Burt *in* Grubb, 1973). This is a conservative estimate, because many individuals apparently do not begin to breed by this time, and where banding effort is light older breeders will be inadvertently added to this category. Petrels first captured in nets (18.7% of fledged birds) were assumed to be two years of age, following Huntington's (*in* Wilbur, 1969) estimate that most such visiting birds commence to appear about nesting sites when two years of age. Again, this estimate is conservative, because older birds might be captured in this sample also. Thus, only individuals banded as chicks can be aged precisely.

The recapture effort was sporadic over much of the period covered here, thus preventing making a direct estimate of maximal survival rates or age structure from this sample. However, by calculating the relative frequency of return by different-aged birds (last return of each individual) when a comparable proportion of all age classes is marked, one may establish a preliminary minimal estimate of survival rate.

This figure is somewhat of an underestimate because of possible obliteration of band numbers or loss of bands. At present that problem largely concerns the oldest birds in the population, a result of the light capture effort put forth between 1965 and 1969. Since 1970, when an intensified effort was commenced, eight birds with partially illegible bands have been recaptured. Fortunately, enough legible numbers remained on five of these individuals to assign them to a banding year, or at the very least, to within one year of their actual year. No such birds have been captured since

1973. Another 20 birds have had one or two numbers worn to the point of being illegible or nearly illegible, but adequate numbers on the bands remained to establish their identity. It is further possible that actual band loss was taking place between 1965 and 1969, although in only one instance did we find a band so thin that it could be easily removed by hand, as opposed to the 28 birds reported above with partially obliterated numbers. Subsequently, with a program emphasizing constant rebanding, the number of illegible or partially illegible bands has dropped virtually to zero, so we are confident that in the part of the colony being worked intensively error due to band loss at present is virtually nil.

RESULTS

Age Distribution of Breeding Birds.—Figure 1 presents the age distribution of adult *Matinicus* Rock petrels captured in burrows, based upon longest return period from each of the 444 different birds banded from 1959 through 1975 and recaptured through 1976. Birds younger than five years of age are rare in the sample because of the infrequent appearance of prebreeding individuals in the burrows. Since prebreeders can readily be captured in nets on the island, these low figures should not be considered an estimate of the number of these birds present about the colony or the size of the year class. The rest of the distribution approximates a constant rate of loss of individuals over time.

Since banding effort differed considerably from year to year (Table 1), creating the possibility that certain year-groups might be represented out of proportion to their actual abundance, we adjusted the data. We took the year of maximum banding effort for each category (breeders = 1964, birds captured in nets = 1963, chicks = 1963) as 1 and multiplied the results of each other year by an appropriate factor greater than 1. The magnitude of this factor was determined in the following way: Factor = year of maximum effort/year for which factor was to be calculated ($F = Y_{\max}/Y_o = 1/Y_o$). In order not to assign unrealistically large values to single returns we adopted an *a priori* rule-of-thumb that yearly samples would be included only if the banding effort of the year in question exceeded 10 percent of the year of maximum effort ($F < 10$). The largest factor within these confines actually turned out to be considerably smaller than 10, $F = 6.4$ (15.6% of maximum effort). In performing this adjustment, it was only necessary to discard 3 of the initial 444 birds.

The resulting plot (Fig. 1) does not differ greatly from the unadjusted plot discussed in the preceding section, although the three youngest classes of breeders (5, 6, 7 years) average over 10 percent lower than the results of the unadjusted plot.

Survival.—Calculation of the age distribution of established breeders makes it possible to estimate the minimal survival of individuals in this cumulative sample over a considerable part of their life span (Fig. 2). Mean survival for these adults is 78.9% in the adjusted sample.

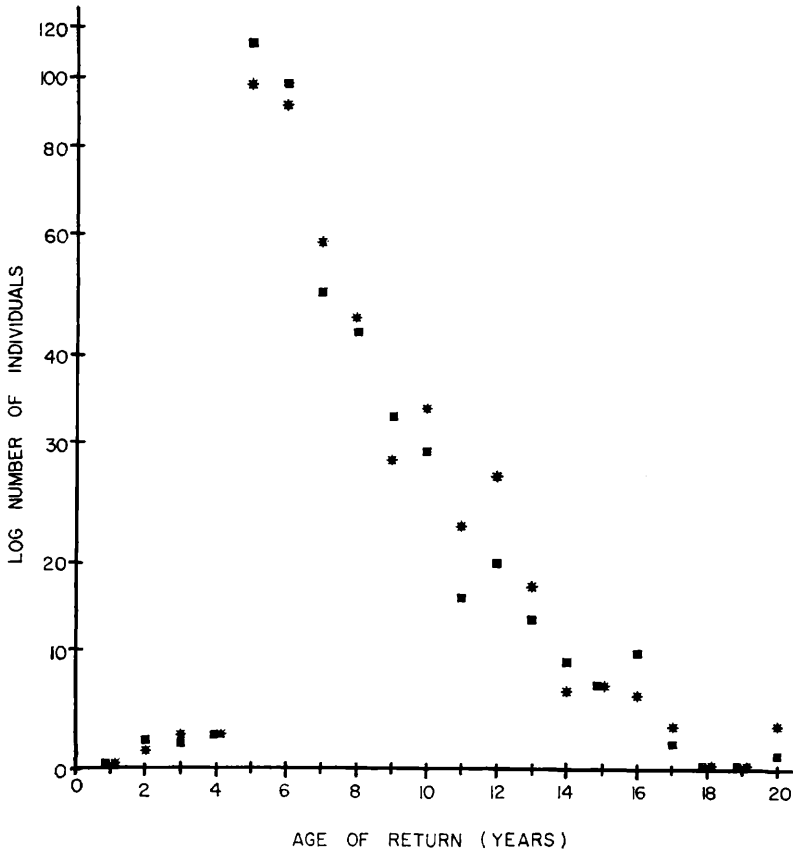


FIGURE 1. Age distribution of Leach's Storm-Petrels captured in burrows. ■ = raw data, * = adjusted data (see text).

Rate of Recapture and an Independent Estimate of Survival.—Rates of recapture appear in Table 2. They vary strikingly among the categories, with each category being significantly different from all the others.

Numbers of recaptures per breeding individual appear in Figure 3. By calculating a regression it was possible to extrapolate the number of individuals that should have returned, but which were not captured in the process of the incomplete censusing efforts. This technique suggests a much higher mean annual survival (93.7%) than that calculated from the rates of return of different-aged individuals (Fig. 2). The extremely high value for $r^2 (= 0.9994)$ in the regression equation suggests that this estimate is realistic.

Mean Life Expectancy Subsequent to Entering the Breeding Pool.—Life expectancy as a breeder was calculated using the equation $\bar{L} =$

TABLE 1
 Numbers of Leach's Storm-Petrels banded on Matinicus Rock, 1955-1975. These birds form the basis for the calculations.

Year	Breeders in burrows	Birds netted	Nestlings
1955	1	— ¹	2
1956	33	—	28
1957	54	—	46
1958	0	—	26
1959	6	—	6
1960	39	—	10
1961	39	—	10
1962	51	—	0
1963	143	156	213
1964	211	129	154
1965	36	—	49
1966	0	—	0
1967	0	—	0
1968	33	—	7
1969	0	—	91
1970	193	54	136
1971	151	—	84
1972	173	—	1
1973	61	—	114
1974	120	—	150
1975	124	—	165
Total	1,477	339	1,292

¹Dashes (—) refer to years when no netting took place.

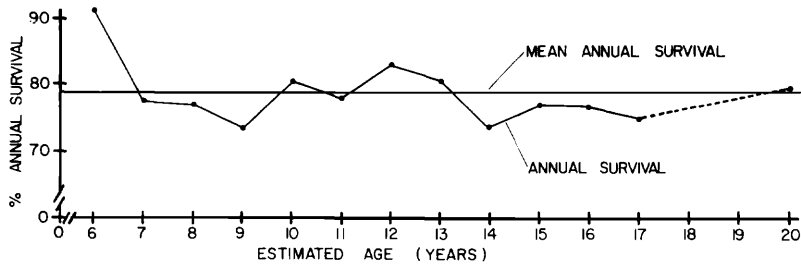


FIGURE 2. Annual survival of Leach's Storm-Petrels banded as breeders (from adjusted sample).

TABLE 2.

Numbers of Leach's Storm-Petrels banded on Matinicus Rock, 1955-1975, and recaptures through 1976.

Category	Number banded	Number of individuals recaptured through 1976	% recapture	Level of significance ¹
Breeders in burrows	1,477	392	26.5	0.001
Birds > 1 year in nets	339	26	7.7	0.001
Nestlings banded from 1955 through 1972	863	25	2.9	0.01
Nestlings banded from 1973 through 1975 ²	429	1	0.02	

¹ χ^2 tests upon the original data.

²Since birds are now recaptured in the burrows only, the nestlings banded during 1973-1975, probably being prebreeders, do not yet have a probability of recapture equal to that of nestlings banded in preceding years; therefore, the two groups are separated here.

$2-m/2m$ (Richdale, 1957), where m = the percentage of annual mortality. With $m = 21.1\%$ ($100 - 78.9$ (mean survival)), mean breeding life expectancy (\bar{L}) was 4.2 years. At the other extreme of m ($100 - 93.7$), $\bar{L} = 15.4$ years.

Causes of Mortality.—This study produced little information that would specifically account for mortality of individuals subsequent to their leaving their birthplace. Dead petrels were occasionally found about the breeding colony, the likely prey of Herring Gulls (*Larus argentatus*), but they were not tallied unless already banded, and indeed, it was not possible to determine whether or not they were taken while alive.

Predation by fish, seals, and cetaceans represents a possible source of mortality when these birds are at the water's surface. A small percentage of these birds had injuries to their feet, ranging from parts of a foot to an entire foot missing. Of 1,254 fledged birds handled between 1963 and 1976, only 7 (0.6%) had either an entire foot or part of a foot missing.

DISCUSSION

The results are consistent with other studies of both storm-petrels (Beck and Brown, 1972) and other procellariiform birds (e.g., Mougin, 1975) by indicating that some birds live to an extremely old age (Fig. 1). If mean annual survival is calculated in the conventional way, the present data do not, however, indicate a survival rate as great as that found for most other procellariiforms. Almost without exception yearly survival of breeders is 90% or greater in these birds, including the Wilson's Storm-Petrel, the only hydrobatid thus far intensively investigated from this viewpoint (Beck and Brown, 1972). The present results fall just below 80%, but this figure probably is an underestimate resulting pri-

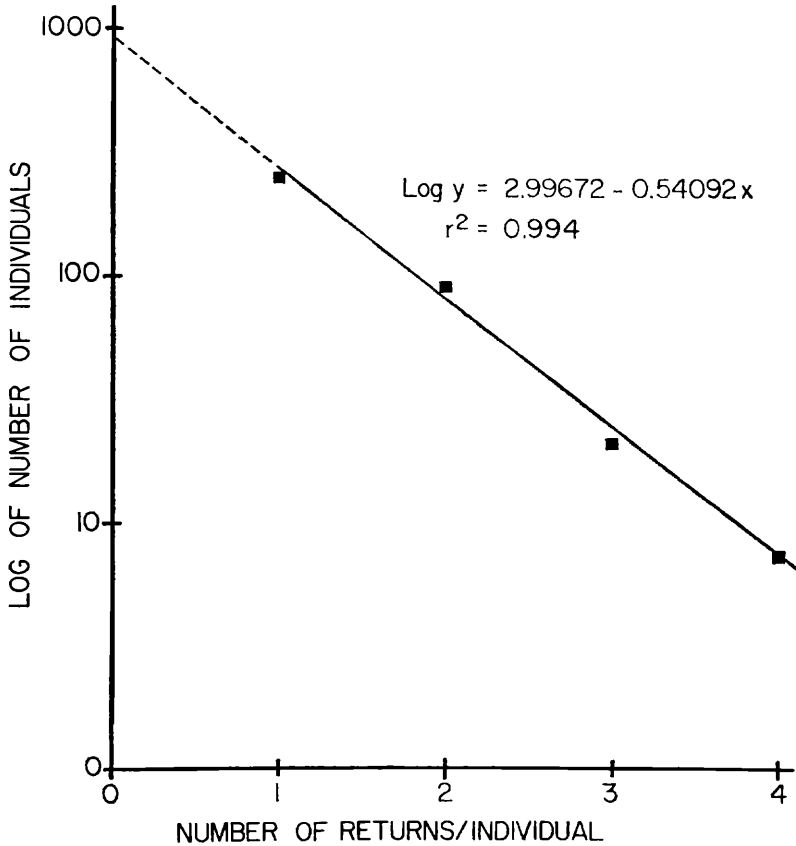


FIGURE 3. Number of returns per breeding individual.

marily from the low recapture effort made on this population. The estimate of 93.7% survival based upon the number of birds recaptured 0. . . . 4 times resembles results from other procellariiforms more closely than does the first one. If the latter estimate is accurate, survival rates of Leach's Storm-Petrels are comparable to the maximum survival rates of procellariiforms (reviewed by Beck and Brown, 1972) and only inferior to those of large albatrosses (Lack, 1954; Tickell, 1968). This estimate also slightly exceeds the rate of 90.8% obtained for Wilson's Storm-Petrels by Beck and Brown (1972).

With the data available it is only possible to state that the average Leach's Storm-Petrel breeds several times upon reaching maturity. The calculations of life expectancy differ greatly, depending upon which of the two calculated mortality rates is accepted.

Although dead birds were occasionally found about the colony, most mortality must take place at sea, similarly to other procel-

lariiforms (e.g., Mougín, 1975). Information from other studies on storm-petrels (e.g., Harris, 1969; Beck and Brown, 1972) suggests that the majority of dead birds found about the colonies are prebreeders, captured by gulls and other predators.

The frequency of damaged feet serves as a possible indicator of predatory pressure upon these birds away from the breeding grounds. Level of damage to the Matinicus Rock birds was considerably lower than that reported for the closely related Harcourt's Storm-Petrel (*O. castro*). Allan (1962) found that 3.5% of the birds that he examined on Ascension Is. had such damage to their feet, whereas Harris (1969) had a figure of 7.0% for a Galapagos population of the same species. However, these figures are open to alternate interpretation, for it could be argued that a high percentage of maimed feet indicates high escape rates and consequent greater success in eluding predators than the low percentage found in this study.

SUMMARY

Several hundred pairs of Leach's Storm-Petrels breed on Matinicus Rock, Maine, and over 1,500 nesting birds were banded there from 1955 through 1975. This population contains many relatively old individuals, with breeders having a mean annual survival of at least 78.9%, and a mean life expectancy subsequent to breeding of at least 4.2 years. Arguments are made that both variables probably considerably exceed these minimum levels. Only 0.6% of the fledged birds were missing a foot or substantial parts of a foot, a possible indicator of predatory pressure away from the breeding colony.

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