NESTING PATTERNS OF LEACH'S STORM-PETRELS ON MATINICUS ROCK, MAINE

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INTRODUCTION

Leach's Storm-Petrels (*Oceanodroma leucorhoa*) are colonial seabirds of the northern oceans that dig nesting burrows in the earth on islands where the danger of terrestrial predators is low or absent. They first appear on their nesting colonies in the Gulf of Maine in late April or early May (C. E. Huntington, pers. comm.), and their single offspring fledges between September and November (Gross, 1935; Wilbur, 1969). Their longevity, their extended breeding season, and the relatively easy accessibility of many nests make these birds attractive subjects for studies of nesting success, nest-site fidelity, and mate fidelity. Although the breeding biology of small procellariiform birds has been the subject of several studies, almost all published work of this type upon Leach's Storm-Petrels in the western Atlantic Ocean is based upon work performed at Kent Is., New Brunswick (W. Gross, 1935; A. Gross, 1947; Huntington, *in* Palmer, 1962; Huntington, 1963; Wilbur, 1969).

Matinicus Rock, Knox Co., Maine, the site of the present study, lies approximately 180 km southwest of Kent Is. The population of breeding petrels here is much smaller than that on Kent Is.: approximately 600 pairs nested there in 1976 (Buchheister, unpubl. data), whereas 15,000 pairs are estimated to breed on Kent Is. (Wilbur, 1969). Furthermore, the colony on Matinicus Rock lies almost at the southern and western extremity of this species' breeding range in the western Atlantic, with the few colonies beyond it consisting of no more than a few pairs each (Drury, 1973). The colonies in this part of the petrel's range fluctuate drastically, most (although probably not the one on Matinicus Rock) decreasing strikingly over the past 75 years (Drury, 1973). Therefore, comparison with the much larger colony on Kent Is., which lies closer to the center of this species' breeding range in Newfoundland (Huntington, 1963), is of inherent interest, as is an assessment of current conditions in the present area of apparent flux, for future comparison.

In this paper we present information on several aspects of nesting success, nest fidelity, and mate fidelity, and compare the results where possible with those from Kent Is. Morse is responsible for analyzing the results and preparing this report, and Buchheister is responsible for carrying out part of the fieldwork 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, Knox Co., Maine, and 8 km south of the nearest sizable island, Matinicus Is. It consists of a boulder-strewn meadow slightly over 3 ha in size surrounded by an extensive granitic shoreline. The meadow is covered by various forbs and grasses, of which the com-

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monest species are Purple-stemmed Angelica (*Angelica atropurpurea*), Seaside Angelica (*A. actaefolium*), Yarrow (*Achillea millifolium*), Witch-grass (*Agropyrum repens*), and Timothy (*Phleum pratense*). For the most part the island is undisturbed, although a lighthouse, foghorn, and accompanying buildings are maintained by personnel of the U.S. Coast Guard. This station has been occupied continuously since the early 1800's, and while livestock were maintained on the island during the periods when lightkeeping families lived there, no livestock have been kept there at least since 1934 (H. Buchheister, pers. comm.). The island does, however, support several abundant alien plants, as indicated above. The area is currently maintained cooperatively as a refuge of the U.S. Fish and Wildlife Service by that organization and by the U.S. Coast Guard.

METHODS

In 1974, 150 burrows were identified with numbered plastic markers. Contents of these nests were examined both in June and in August or September of 1974, 1975, and 1976. Most nests were visited at least twice in June and once in August or September. Many of the nesting birds in this study area had been marked during banding operations of previous years, thus permitting individual recognition.

Most burrows on Matinicus Rock can be reached by hand without damaging them, and only these were investigated. They permitted an assessment of fidelity to nest site and facilitated work upon overall success rates and mate fidelity. The 1974–1976 work is supplemented in some places by data from an earlier (1963–1964) unpublished field study on Matinicus Rock by H. R. Tyler, Jr.

Most samples in the following analyses do not total to 150. Several of the burrows were empty. They were possibly deficient in some way or other, because in three cases the nest in question was vacant for the first two years of the study or for all three years. Some burrows became too deep to be reached, others were inadvertently missed during one or more censuses, and a few could not be found subsequent to marking because of the tall, dense grass cover developing by July and August. In certain cases birds were captured in burrows without eggs or young and were not subsequently found in these burrows.

RESULTS

Rates of Nesting Success

Two-thirds to four-fifths of the nests containing eggs in June produced young. Nesting success (percentage of eggs resulting in live young at last visit) in 1963 and 1976 was significantly higher than in 1974 and 1975 (Table 1) ($P < 0.05$ in both cases in χ^2 tests upon original data). Success in 1963 may be somewhat higher because of the late date of the first visit (thus missing some early losses); however, this difference cannot explain the 1976 results.

TABLE 1.
Occupancy and success of Leach's Storm-Petrel burrows.

Year	Total burrows	Number with adult and egg	Number of successes[1]	Number of failures	Egg present at last check	Adult but no egg (only in June)	Empty in June and August	Not visited[2]
1963[3]	167	88 (7 July)	67 (81.7%)	15 (18.3%)	6 (14–17 Aug.)	1	13	65[4]
1974	150	125 (11–27 June)	81 (65.9%)	42 (34.1%)	2 (9–18 Aug.)[5]	11	4	10
1975	150	102 (11–18 June)	59 (68.6%)	27 (31.4%)	16 (1–9 Aug.)	3	12	33
1976	150	109 (6–11 June)	86 (79.6%)	22 (20.4%)	1 (9–10 Sept.)	1	10	30

[1] Young in nest at last visit.
[2] Could not be reached, inadvertently missed, or could not be found.
[3] Records contributed by H. R. Tyler, Jr. 167 burrows.
[4] 59 of these burrows were visited only in July.
[5] 8 of the 1974 nests were checked in September or October.

TABLE 2.
Activities at burrows after birds abandoned first clutch.

Year	Adults disappeared	New egg laid	Adult captured without egg
1963	14	6	1
1974	36	5	3
1975	25	13	5
1976	22	1	0

In a technical sense the measure used is not a fledging success, because these records are for birds not yet out of the nest. However, since only one dead chick was found in the burrows during the 1974–1976 period (0.4% of total chicks), it may be considered a close approximation of fledging success. The inspection schedule of the nests (June, August–September) did not permit calculation of separate hatching and post-hatching successes.

In only a minority of unsuccessful burrows did birds lay a second egg (Table 2). In no case did the pattern of checking the nests make it possible to establish unequivocally that both members of the original pair were involved in the second nesting effort. The tendency for new eggs to be laid, regardless of their ownership, differs somewhat from year to year. This effort in 1975 was significantly higher than those of 1974 and 1976 ($P < 0.05$ in χ^2 tests). Care should be taken in interpreting these differences, however, since dates of investigating these burrows differ (Table 1).

The Role of Previous Success

Burrows containing previously-known nesters were compared with those containing birds for which we had no past history (Table 3). Many of the "previous nesters," and all of the sample from 1974, were birds banded in years preceding the marking of the burrows. This comparison

TABLE 3.
Relative success of known previous breeders and birds of unknown history.

	Previously unknown birds			Previous breeders		
Year	Successful	Unsuccessful[1]	%	Successful	Unsuccessful[1]	%
1974	48	26 (1)	64.9	33	18 (1)	64.8
1975	13	12 (3)	52.0	46	31 (13)	59.7
1976	15	5 (0)	75.0	70	19 (1)	78.7

[1] Birds last observed with eggs in August are assumed to be unsuccessful (see Table 1), but are indicated in parentheses.

TABLE 4.
Success of individuals in the same burrow during preceding year.

Year	Group	Successful in preceding year	% success	Unsuccessful in preceding year	% success
1975	Successful	22 (0)[1]	71.0	12 (1)[1]	54.5
	Unsuccessful	9 (0)		10 (0)	
1976	Successful	27 (5)	90.0	10 (1)	55.6
	Unsuccessful	3 (1)		8 (1)	

[1] Figures in parentheses represent the number of known pairs included in the group.

might provide a rough estimate of the success of birds that had previously bred and those that had not.

No significant differences occurred between the two categories in any of the years ($P > 0.05$ in χ^2 tests). This result does not, however, unequivocally prove that birds breeding in earlier years are no more successful than new breeders, since some of the first-caught individuals undoubtedly were experienced breeders that had not been captured before. However, if birds breeding a second time (or more) enjoy enhanced success, as is often the case among birds (Lack, 1966, 1968), their improvement is not great enough to show in this rather insensitive analysis.

High sustained banding efforts in long-lived populations such as this one should progressively lower the number of relatively old birds mistaken as first breeders. Thus, the 1976 sample should be the most sensitive sample in Table 3, yet it does not differ from the results of 1974 and 1975. Successful breeding in the same burrow during the preceding year (Table 4) did not significantly affect the success of birds in 1975 ($P > 0.05$), but it did have such an effect in 1976 ($P < 0.02$).

Success of Old Birds

A small sample of birds banded as adults and chicks in 1963, 1964, and 1965 provided a group of individuals 11 years of age or older. This age is calculated on the assumption that breeding birds are at least four years old (Huntington and Burtt, 1972). Records available suggest that the mean age of first-time breeders at Matinicus is well over four years (Morse and Buchheister, 1977).

The results (Table 5) do not differ significantly from the majority of the population (remaining data for years 1974–1976 in Table 1) ($P > 0.05$ in a χ^2 test); in fact, the two subgroups are virtually identical (71.4% for old birds, 71.3% for others). That the old categories do not decline in reproductive success is further suggested by the fact that the oldest birds, at least 16 and 17 years old (four individuals, five breeding records), were even more successful than the others in Table 5.

TABLE 5.
Nesting success of birds banded in 1963, 1964, and 1965.[1]

Age	Nests producing chicks	Nests not producing chicks
11	1	0
11+[2]	2	1
12	2	1
13	3	1
14	5	3
15	2	2
16	3	0
17	2	0
Total	20	8

[1] One to three breeding records for each individual. Results obtained from 17 individuals, banded either as nestlings or adults.
[2] Birds with old, partially illegible bands presumed to have been banded during this period.

Importance of Nesting Time to Nesting Success and Subsequent Nesting Efforts

A minority of individuals still had eggs in their nests when the burrows were investigated in August 1974 and August 1975. Subsequent visits to several of these burrows in September and October 1974 by W. H. Drury, Jr., and P. Smith indicated that success rate was significantly lower than that of early-nesting birds (80 successful and 35 unsuccessful nestings (69.6%) for early breeders vs. one successful and seven unsuccessful nestings (12.5%) for late-breeding birds; $P = 0.003$ in a one-tailed Fisher Exact Probability Test). However, this sample is small, and the conclusion needs further verification to determine whether 1974 was a typical year.

Additionally, individuals that nested late in the season were recaptured the following season (in 1975 and 1976) at only about half the frequency of the earlier-nesting individuals (Table 6). Whereas the rel-

TABLE 6.
Recapture rates of early[1] and late-nesting[1] birds in succeeding season.

	Recaptured in burrow during next season	Not recaptured in burrow during next season	%
Early nesters—1974	65	63	50.8
Late nesters—1974	3	10	23.1
Early nesters—1975	70	86	44.9
Late nesters—1975	10	28	26.3

[1] Early-nesting birds had hatched young at last visit in August, late-nesting birds had eggs at this time.

TABLE 7.

Rates of return of marked breeding birds in study area.

Number nesting[1]		Number captured		Number recaptured		Estimated returns in following year[2]	
Year	Number	Year	Number	Year	Number	Number	%
1974	282	1974	141 (47, 94)[3]	1975	68 (23, 45)[4]	93 (31, 62)[4]	66.0 (66.0, 66.0)
1975	266	1975	194 (111, 83)	1976	80 (48, 32)	145 (87, 58)	74.7 (78.3, 68.9)

[1] Burrows with nesting activity × 2.

[2] Based upon correction for capture effort:

$$\% \text{ returning} = \frac{\text{No. recaptured in Yr N + 1} \times \text{No. returning in Yr N + 1}}{\text{No. captured in Yr N} \times \text{No. captured in Yr N + 1}}.$$

[3] Data in parentheses refer to birds previously captured as breeding adults, birds not previously captured as breeding adults.

[4] Data in parentheses refer respectively to birds captured as breeders both in previous year and in some earlier year ("old breeders"), birds captured as breeders only in previous year ("new breeders").

atively small yearly samples only approached statistical significance (0.1 ($0.10 > P > 0.05$ both years in χ^2 tests), the combined sample is highly significant ($P < 0.001$), suggesting strongly that they nested at a much lower frequency in the season following a late nesting.

Estimated Rate of Return during Following Year

Individuals breeding one year were recaptured with high frequency during the next breeding season (Table 7). These raw data were converted to estimated numbers of returns (Table 7) in order to account for incomplete success in trapping all nesting adults. Estimated frequency of return of birds breeding the preceding year was higher in 1976 than in 1975, the difference approaching statistical significance ($0.10 > P > 0.05$ in χ^2 test).

An attempt was made to assess the frequency of return by individuals that had nested in an area only once and by more established breeders that had nested twice or more in a location (Table 7). No significant difference occurred between the two categories, either for individuals nesting in 1974 and returning in 1975 or for those nesting in 1975 and returning in 1976 ($P > 0.05$ in χ^2 tests). A sizable number of previously unmarked established breeders could mask a real difference, so it is premature to assume that no difference exists between the two categories.

Fidelity to Burrow

The vast majority of known captured individuals returned to the burrow that they used during the preceding summer (Table 8). Of the few individuals that changed burrows, in each case the burrow involved was an adjacent one, in five of seven known instances the nearest one. In

TABLE 8.
Fidelity to burrow.

Years	In same burrow	In different burrow	% in same burrow
1963, 1964	12	1	92.3
1974, 1975	65	3	95.6
1975, 1976	76	4	95.0
1974, 1975, 1976[1]	35	0	100.0
1974 and 1976[2]	12	2	85.7

[1] Included within sums for 1974, 1975; 1975, 1976.
[2] Not captured in 1975.

two cases birds moved from their 1974 burrow to a different burrow in 1975, only to return to their previous (1974) burrow in 1976. However, these were not pairs.

Fidelity to Mate

Over two thirds (13 of 19) of the individuals recaptured at the same nest site in two consecutive years as pairs (1974–1975, 1975–1976) retained the same mate. In only one of the six cases in which individuals took new mates was the previous mate captured (at a nearby burrow with a different mate); however, since the probability of capturing a given individual was considerably <1, the possibility remains that some of the five individuals in question still survived.

Thus, whereas the frequency of remating at a given burrow site is high, unequivocal evidence of mate switching at a given burrow site exists (one case), and in other instances either this has occurred or one partner died or deserted, with the remaining member of the pair remating. On the other hand, in none of the five cases where birds switched burrows and their mates were known did they retain their mate. One of the previous mates of these birds was recaptured, providing further evidence that pair bonds are not inviolate while both birds are still present. The difference between the tendency to retain a mate when remaining at a given burrow and when moving is significant ($P = 0.01$ in a Fisher Exact Probability Test).

Fidelity to mate (68.4%) is significantly lower than fidelity to nest site (95.0%: Table 8) ($P < 0.001$ in a χ^2 test), which suggests that the primary bond is to a nest site rather than to a mate per se.

Desertion of Nests

It seems inevitable that some desertion might occur as a result of monitoring the nests. Although disturbance in the present study was minimal, attempts to capture both adults typically resulted in two or even three visits in June, and each burrow was generally visited once in August.

TABLE 9.
Production of chicks in burrows subjected to varying amount of disturbance.

	Burrows visited in June and August			Burrows visited in August only		
Year	Chick produced	No chick produced[1]	%	Chick produced	No chick produced[1]	%
1963	66	33	66.7	159	117	57.6
1974	70	61	53.4	66	34	66.0
1975	77	56	57.9	86	46	65.2

[1] Includes empty burrows and ones containing eggs or adults without eggs or chicks. This is not a direct estimate of breeding success, since several burrows in the June–August samples were empty, and this was assumed to be the case in the August sample as well. However, since inactive burrows could not be separated from those in which an unsuccessful nesting took place, it was necessary to use this measure to estimate effects of nest disturbance.

During some years efforts were made in August to band young birds at sites in addition to the burrows forming the basis of this study. These burrows, visited only in August, provide the basis for an assessment of the effect of disturbance caused by the visits in June. Comparison rests upon the assumption that both sets of nests are of equal quality and that they are populated by equally competent parents.

The comparisons (Table 9) are based on burrows occupied by chicks and ones that were demonstrably empty, contained eggs, or adults without eggs. Eggs and adults are included in the second category because their presence in August may result from earlier failure. Furthermore, attempted late nesting may be extremely unsuccessful (see above). The results of these comparisons are equivocal. The sample in 1963 shows that production of chicks in the more-visited nests was higher than it was in the burrows visited only in August, although this difference is not signficant ($P > 0.05$ in a χ^2 test). However, in both the samples in 1974 and 1975 the less-visited nests produced more young than did the more regularly visited nests, although in neither case is the result statistically significant ($P > 0.05$).

In several cases eggs were found near the entrance to a nest or broken, conditions associated with disturbance of the nest by Gross (1935). These remains were tallied in August 1974 at nests visited in June and August, and in those first visited in August. No significant difference ($P > 0.05$ in a χ^2 test) was found in the frequency of misplaced or broken eggs in the two samples (seven such eggs at 149 burrows visited in both June and August (4.7%) vs. four eggs at 96 burrows visited only in August (4.2%)).

The data for 1974 and 1975 thus suggest a desertion rate of approximately 10% associated with visits to the burrows in June, but do not yet clearly demonstrate this difference. It is unclear why Tyler's data differ fundamentally.

DISCUSSION

Nesting Success

The nesting success of these birds (66–82%) is similar to the 62–75% reported for another species of the temperate zone, the European Storm-Petrel (*Hydrobates pelagicus*; Davis, 1957). They indicate that most loss occurs during incubation and that relatively little loss occurs among chicks, at least after the first few days, a trend found in several other procellariiforms as well (e.g., Warham, 1962; Mougin, 1975).

The production of chicks per burrow was significantly higher each year in this study (Table 9) than in Wilbur's (1969) study of Leach's Storm-Petrels (194 chicks in 454 burrows = 42.7%; $P < 0.0001$ in χ^2 tests). The greatest part of this difference (122 out of the 260 burrows not containing young in August, 26.9% of all burrows) in Wilbur's study resulted from burrows with "signs of prebreeder activity" (fresh nests with green vegetation, signs of fresh digging, one or two adults without eggs or chicks). Such burrows made up only 7.2% of the total in 1963, 7.3% in 1974, and 4.0% in 1975 on Matinicus Rock. Signs of fresh digging were not prominent in August on Matinicus Rock, as they were in Wilbur's study. The burrows used for comparison with Wilbur's were not visited in a previous year, thus permitting direct comparison with his results.

The fundamental difference between the two sites in this regard could be that the study area on Matinicus Rock was already largely or totally saturated with active burrows, whereas the one on Kent Is. was not. Wilbur (1969) noted that Kent Is. was not saturated with burrows, although that statement might not necessarily hold for his study site. It has often been suggested that much of the burrowing activity late in the season is performed by young birds that have never bred (e.g., Wilbur, 1969), which often occur in great numbers about colonies. Large numbers of these birds also appear at Matinicus Rock (Buchheister, unpubl. observ.), so it is unlikely that this apparent difference results from a shortage of prebreeding birds.

Nesting success fluctuated from year to year, but the basis for these differences is unclear. Since these birds feed at relatively slow rates upon the surface of the water, variation in weather patterns and consequent changes in food availability could account for differences (see Huntington, 1963). However, we have not explored this possibility further. Elsewhere, success rates may fluctuate markedly from year to year in procellariiforms, a function of climatic variation (Beck and Brown, 1972; Mougin, 1975).

Success as a breeder in the previous year was the only factor investigated that predicted the probability of success of a nesting individual. However, several of the other analyses were not highly sensitive tests of the factors associated with nest success, because at present it is difficult to age the birds precisely (see below) or to determine whether they have nested previously. A more critical test will occur when birds banded as nestlings (only banded in large numbers from 1969 onwards) begin to nest. Only two of these birds had appeared as breeders in the marked burrows by the summer of 1976. Birds banded as nestlings by Tyler in 1963–1964 have been recovered regularly as breeding birds; unfortunately, a systematic recapture effort had not commenced by the time these individuals probably first commenced to breed. Both Davis (1957) and Harris (1969) reported higher rates of return for successful nesting storm-petrels than for unsuccessful ones (European Storm-Petrel and Harcourt's Storm-Petrel (*Oceanodroma castro*), respectively).

The data for late breeding birds suggest strongly that if a nest fails it is not advantageous to renest that year, even if it were physiologically possible. This result is in line with success rates of early and late chicks in other procellariiforms (e.g., Manx Shearwater (*Puffinus puffinus*), Perrins, 1966; Harcourt's Storm-Petrel, Allan, 1962; Harris, 1969). If these data are typical, this may explain why the majority of individuals that deserted apparently did not attempt to renest (Table 2). Wilbur (1969), on the other hand, was impressed by the frequency of apparent renesting efforts of Leach's Storm-Petrels at Kent Is., although his studies were terminated too early to determine their degree of success. The rates of possible renesting in his study were slightly, although not significantly ($P > 0.05$ in a χ^2 test), higher than those in this study (Table 2).

In general, procellariiforms show limited tendencies to renest early in the breeding season or no tendency at all (e.g., Fisher and Lockley, 1954; Lack, 1966; Mougin, 1975). Furthermore, it can seldom be proven beyond doubt that a single female has actually laid a second egg that may appear (Beck and Brown, 1972; Mougin, 1975). We must reemphasize at this point that in no case could we unequivocally demonstrate that renestings in this study involved the same pair of birds. Lack has argued that it is difficult for an adult to produce a second large egg, and if this is so, one might expect to find year-to-year differences in the frequency with which replacement eggs were laid. This hypothesis is consistent with the data presented in this study, although they do not prove the point. Individuals' "decisions" whether to renest or not could thus be simply a response to their nutritional condition. The possible relatively high tendency of the Leach's Storm-Petrel to lay a replacement clutch may be related to the fact that they lay a somewhat smaller egg than do other hydrobatids (Lack, 1968; Harris, 1969; Beck and Brown, 1972), even though the size is still a prodigious 20% of body weight. Consistent with this argument is the fact that the Giant Petrel (*Macronectes giganteus*), which lays a considerably smaller egg than most other procellariiforms of its size (Lack, 1968), is one of the few species in this order known to produce a clutch of two eggs occasionally (Warham, 1962; Mougin, 1975).

The failure to find decreased reproductive success among the older birds is not surprising in light of the general failure to obtain this relationship in other procellariiforms (Richdale and Warham, 1963). Furthermore, few of the birds in the study area may be approaching physiological senility, because the oldest individual known in this sample is a bird, banded as an adult, that is estimated to be 17 years old. Elsewhere in the Matinicus Rock colony the oldest individual currently known is estimated to be 20 years old (Morse and Buchheister, 1977). Unfortunately, prior to 1963 the banding effort on Matinicus Rock was light and sporadic, so the probability of capturing older known individuals is slight. Furthermore, among birds of this age not yet captured excessive band wear will become a significant factor. The oldest reported Leach's Storm-Petrel apparently is one of at least 28 years, banded by Huntington on Kent Is. as a breeding adult (C. E. Huntington, pers. comm.).

Rates of Return

Both Huntington (1963) and Wilbur (1969) reported return rates of adults banded the previous year at Kent Is. to be about 50% the following year. However, since Wilbur worked in a colony that had not been studied previously, his results should be higher, since Huntington (1963) has reported a 70% return rate for these birds in subsequent years. Wilbur's figures did not include an attempt to estimate birds that were not recaptured. When this is done, Wilbur's estimated return rate rises to 63.3%, a reasonable level for a combination of new and previous breeders, given Huntington's (1963) estimates for these two categories. This figure is not significantly different from the 1975 returns of our birds handled in 1974 ($P > 0.05$ in a χ^2 test), but it is markedly lower than the results from 1976 returns handled in 1975 ($P < 0.01$) (Table 7).

The Matinicus Rock population does not show the significant differences in return rates between first-caught and previous breeders reported by Huntington (1963). However, since relatively large numbers of unmarked old breeders may initially have been present in the sample treated as first-caught breeders, Huntington's conclusions may still turn out to be appropriate.

Fidelity to Burrow and to Mate

These birds exhibit a strong fidelity to burrow site (Table 8), and the switches recorded almost invariably involved adjacent or nearby nests. The rate of burrow fidelity for each pair of consecutive years (92–96%) far exceeds that of Wilbur (1969), who reported a fidelity rate of 68%, and the 70% rate reported by Huntington (1963). Each fidelity rate in this study differs highly significantly from Wilbur's ($P < 0.001$ in χ^2 tests). This difference may be a result of much easier digging conditions on Kent Is. (C. E. Huntington, pers. comm.).

On the other hand, the rate of mate fidelity of Matinicus Rock is considerably lower than that of nest fidelity. None of the few individuals that changed burrows were known to retain their mates. This evidence suggests that individuals do not establish a long-term pair bond, and that long-term pairs may simply be a consequence of high site tenacity. This relationship has also been hypothesized for the European Storm-Petrel (Davis, 1957) and Harcourt's Storm-Petrel (Allan, 1962; Harris, 1969). Given that Leach's Storm-Petrels in part orient to their burrow using olfactory cues (Grubb, 1974), this factor alone might suffice to sort out individuals if odors were retained from one season to the next. Since petrel odor is still pronounced, at least to human senses, a year after a burrow is last occupied (Palmer, 1962), this possibility seems reasonable.

Wilbur's (1969) data on mate fidelity are consistent with the hypothesis of site tenacity, although by no means as strongly suggestive of it as are those of this study. Wilbur found that a much higher proportion of individuals changing burrows mated with different birds than did ones retaining their burrows ($P < 0.01$ in a χ^2 test). Where burrow changes occurred, the differences between Wilbur's results and ours approached significance ($P = 0.07$ in a Fisher Test).

These possible differences between the two populations should be followed up to determine whether or not they represent more than an artifact of the techniques used. Wilbur (1969) felt that considerably higher rates of burrow fidelity and mate fidelity might have been obtained in his study, except for the disturbance created by the investigators. Still, his methods did not differ markedly from those of the present study, although the more intense rate of visitation characterizing his study might have made a difference. Even if this were so, however, it is unclear why the two variables of nest and mate fidelity should not have been biased in the same direction in the two studies.

SUMMARY

Success rates of nesting Leach's Storm-Petrels (*Oceanodroma leucorhoa*) on Matinicus Rock, Maine, ranged from 66 to 82% over a period of four summers. Possible attempts to renest were infrequent. No difference in success could be detected in different age groups. Late-nesting birds were less successful than the others. Late nesters were also captured less frequently than others in the subsequent nesting season. Estimated yearly rates of return for previously nesting adults varied between 66 and 75%. Returning birds showed an extremely high fidelity to their previous nesting burrows, which far exceeded mate fidelity, suggesting that remating is simply a function of nest fidelity. These data are compared with other studies on Leach's Storm-Petrels, other storm-petrels, and procellariiforms in general.

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