THE BREEDING BIOLOGY OF LEACH'S PETREL, *OCEANODROMA LEUCORHOA*

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THE Procellariiformes are the most pelagic of all seabirds. A delayed reproductive maturity, a reduced clutch size, a prolonged incubation and nestling period, and low mortality rates are consequences of their pelagic ecology. Lack (1954, 1966), Ashmole (1963), Serventy (1967), and others have discussed the evolution of this breeding strategy. These authors conclude that nesting on predator-free islands limits seabirds to small clutches by the need to search for widely dispersed or fluctuating food organisms. The age of first breeding is delayed because young, inexperienced birds cannot provide for the additional demands of reproduction and nestling care. The prolongation of the incubation and nestling periods is thought to be an adaptation to an irregular feeding schedule. The reduced reproduction rate, coupled with a density-dependent mechanism, necessitates the longevities characteristic of the group.

This paper adds to the life history of Leach's Petrel as described by Gross (1935), Ainslie and Atkinson (1937), Gross (1947), and Huntington (1962, 1963) and relates the renesting attempts of failed breeders to Lack's theory of the reproductive rates of birds. The observations reported in this paper were made during a study of the movements of Leach's Petrel, *Oceanodroma leucorhoa*, at the Bowdoin Scientific Station on Kent Island, Grand Manan, New Brunswick, Canada. Kent Island supports the southernmost large colony of Leach's Petrel in the Atlantic; an estimated 15,000 pairs breed on the island (Wilbur, MS). I spent 20 weeks on the island, from 3 June to 14 August 1965 and from 6 June to 17 August 1966.

METHODS

The study area was a section of the colony that had not been used previously for biological studies. Lattices of twigs were placed over all burrows in this section and were checked daily for at least a week after they were erected. When a lattice was found disturbed, the burrow was examined for the presence of nest material, an egg, or adult birds. Adults were removed from the burrows only during the day in an effort to minimize the number of egg desertions. In 1965 the study area contained about 140 burrows of which 86 contained eggs or chicks. In 64 of these burrows both adults were banded, in 22 burrows only one adult was banded. In 1966 the study area was enlarged to about 1.4 acres. We found 274 burrows of which 154 contained eggs or chicks. In 113 of these burrows both adults were banded, in 32 burrows only one adult was banded, and in the remaining 9 burrows neither adult was identified. These data do not necessarily reflect a change in the breeding population of the colony. From 8 to 13 August 1966, 444 previously undisturbed petrel burrows adjacent to the study area were examined.

The total breeding population of the colony was estimated by dividing the island into 43 communities distinguished by the changes in the color and texture of their

TABLE 1
MATE AND BURROW FIDELITY IN LEACH'S PETREL

	Males	Females	Unknown[1] sex	Total
Adults associated with a burrow in 1965	24	30	96	150
Recaptured in 1966	24	20	34	78
Not associated with a burrow in 1966	1	7	2	10
Associated with a burrow in 1966	23	13	32	68
Nesting with 1965 mate	7	9	13	29
Nesting with a new mate	3	3	8	14
Mate fidelity unknown[2]	13	1	11	25
Using 1965 burrow in 1966	15	9	22	46
Renesting with 1965 mate	5	7	11	23
Nesting with a new mate	1	1	2	4
Mate fidelity unknown[2]	9	1	9	19
Changed burrows in 1966	8	4	10	22
Renesting with 1965 mate	2	2	2	6
Nesting with a new mate	2	2	6	10
Mate fidelity unknown[2]	4	0	2	6
Not known to have nested in 1965, nesting in 1966	5	6	18	29
Not known to have nested but captured both years	1	2	15	18

[1] Females were sexed by the condition of the vent (Serventy, 1956). Males were sexed by their association with a known female.
[2] Mate fidelity could not be determined unless a petrel was associated with a mate in both years.

ecotones in aerial kodachrome photographs. The surface area of each community was calculated from the photographs and each community was assigned a burrow density based on its similarity to one of five sample areas of known density.

LIFE CYCLE

The first adult petrels arrive on Kent Island about the second week of May. Gross (1947) reports that the first digging of burrows in 1945 was noted on 11 May. My findings agree with Huntington's (1963) estimate that about 50 per cent of the birds banded while nesting return the year after their first capture. The data on burrow and mate fidelity (Table 1) suggest that about two-thirds of the adults use the previous year's burrows and about two-thirds of the adults retain their previous mates. A change in burrow is likely to involve a change in mate. Neither mate fidelity nor burrow reuse appear to be a function of sex. These figures are most certainly underestimates of the natural frequency of burrow and mate fidelity as disturbance to the birds in 1965 probably contributed to the changed nesting relationships in 1966.

Gross (1935) notes that only the males excavate burrows and that they spend about three nights digging. I believe that considerably more time may be spent constructing the burrow, and further disagree with Gross that mating necessarily occurs on the third night when the burrow

TABLE 2
STATUS OF UNDISTURBED PETREL BURROWS, 8–13 AUGUST 1966

Status	Age (days)[1]	Frequency
Number of burrows examined		461
Nest cavity could not be reached		7
Nest cavity empty or tunnel blocked		110
Burrows with signs of prebreeder activity		122
Fresh nests (green vegetation in the nest material)		58
Recent digging		60
Two adults in the burrow during the day		3
One adult in the burrow during the day		1
Active nests		222
Cold eggs		3
Adults incubating an egg		25
Chicks		194
Chick brooded by an adult	0– 2	17
Mesoptile plumage not visible under the skin	2– 4	10
Axillar mesoptile plumage visible	5– 8	15
Mesoptile plumage emergent	8–15	73
Primaries emergent but sheathed	15–25	62
Rectrices visible beyond mesoptile plumage	25–40	17

[1] Aging criteria developed by Barbara Denniston (pers. comm.).

is completed. In many instances fresh diggings appeared at burrow entrances intermittently over several weeks. To my knowledge no one has ever seen Leach's Petrel copulate. Gross (1935) states, without supporting evidence, that the purr call (transcribed by Ainslie and Atkinson (1937) as ". . . r-r-r-r-r-r-r-ooee-churr-r-r-r-r-r-r-r-ooee-churr, etc.") is given only during copulation and only on a single night. Huntington (1962) reports purring from the same burrow on successive nights. We heard purring from incomplete burrows, some only a few inches deep. On two occasions both parents purred in the presence of their chick.

We found freshly dug burrows throughout the summer. In the early August sample (Table 2) we found 60 instances of fresh digging and 58 fresh nests. Fresh digging is evidenced by the presence of moist, unsettled soil at the burrow entrance and frequently by dirt on nearby vegetation not yet blown or washed away. Fresh nests are those that have green vegetation in the nest material.

Gross (1947) reports that in 1947 the first "mating pair" was found on 21 May and an incubating bird on 29 May; by 6 July 33 of the 49 nests known to be in use also had eggs and by 11 July the first nestling was found. We did not try to determine the dates of laying for fear that the adults would desert the burrow if disturbed in the pre-egg or early incubation period. As the incubation period is 41–42 days (Huntington,

TABLE 3
DURATION OF INCUBATION SPELLS IN THREE LEACH'S PETREL BURROWS

Observation period	Parent	Duration of spells (days)				Mean length of spell
17 June–10 July	A	1	1	2	5	2.25
	B	1	3	3	5	3.00
18 June–12 July	C	2	2	4	5	3.25
	D	2	4	3	2	2.75
11–23 July	E	1	3	2		2.00
	F	3	3	3		3.00

1962) the dates of laying can be extrapolated from the known age of chicks (Table 2). Hence egg laying extends from about the middle of May to the middle of August with a peak during the first 2 weeks of June. Petrels are found in the colony as late as the first week of December (Gross, 1935) and known late fledging dates are 15, 18, 19 November 1945 and 18, 21, 17 November 1946 (Gross, 1947). As the period between laying and fledging is 104–112 days (Huntington, 1962), those nestlings fledging after 20 November are assumed to be from eggs laid during the first 10 days of August.

Past investigations of the incubation schedules of petrels (Lockley, 1930; Ainslie and Atkinson, 1937; Roberts, 1940; Allen, 1962; Huntington, 1963; and others) all used stick lattices that were checked at regular intervals. If the lattices were disturbed, the adult was removed from the burrow and banded or its band identified. This method often makes an incubating parent leave prematurely, thus producing underestimates of incubation spells. Huntington has devised an automatic method of determining incubation spells by means of two-way gates over the entrances of burrows; these activate the mercury switches of solenoid-driven markers that record on pressure-sensitive kymograph paper. An activity record does not necessarily indicate an incubation relief, as petrels may come to the burrow entrance without leaving (personal observation). Table 3 shows the intervals between the presumed entries and departures from three burrows in a 37-day period in 1966. These data suggest an average incubation spell of about 3 days. Gross (1935) reports one spell of 144 hours. I recorded maximum incubation spells of at least 5 days.

In transatlantic homing experiments adult petrels averaged more than 200 miles per day over a 13-day period with a net gain in weight of several grams (Billings, 1968). If the feeding period between incubation duties is about 3 days, the birds could travel at least 600 miles in that time, which would allow the Kent Island petrels to forage anywhere in the Bay of Fundy or the Gulf of Maine.

The mates of nonreturned experimental homing birds gave us an opportunity to observe the faithfulness of a parent to its egg in the absence of its mate. One parent continued incubating, with normal feeding periods at sea, for 18 days; others tended their eggs for 11 and 17 days after their mate was removed from the burrow. One adult removed from its burrow on 11 July 1966 died en route to a release point. When the burrow was next checked on 14 August it contained a 20-day-old chick that on 21 August weighed 28.75 g, about 10 g below the average weight of a 3-week-old chick (Gross, 1935). The retarded growth of this chick suggests that the single surviving parent tended it over the 40-day period.

Ineffective Breeders

Most petrel colonies generally contain a large body of "ineffective breeders" or "unemployed birds" (Davis, 1957; Allen, 1962; Richdale, 1963; Serventy, 1967; and others). Davis (1957) believes this body of ineffective breeders has three components: prebreeders, adult nonbreeders, and failed breeders that have lost or deserted their egg or chick.

Leach's Petrel probably breeds for the first time when 3 years old, probably 1-year-olds and most certainly 2-year-olds make nocturnal visits to the breeding colonies (Huntington, pers. comm.). At least one group of prebreeders can be recognized by their downy brood patches. *Oceanodroma castro* molts the down of the brood patch from 20 to 40 days before laying (Allen, 1962). If Leach's Petrel approximates this schedule, breeders should have bare brood patches by late May. Known breeders at Kent Island have new down on the brood patch by mid-August. Petrels with downy brood patches were rarely caught in mist nets under the canopy, but they composed from 7 to 56 per cent of the catch in two 30-foot-high mist nets at the periphery of the study area. These birds may be young of the previous year that visit the island throughout the summer but do not enter the woods until their second summer. A 2-year-old bird and a 3-year-old, banded as nestlings at Kent Island by C. E. Huntington and caught in the 30-foot nets, had bare brood patches. Variation, perhaps sexual, in the age of first breeding was suggested by one 4-year-old with a downy brood patch (banded as a nestling at Gull Island, Witless Bay, Newfoundland) and another 4-year-old with a bare brood patch.

Birds with bare brood patches, perhaps 2-year-olds, enter the woods, dig burrows, and initiate pair bond formation the summer before they first breed. This prebreeding activity extends throughout the summer. In August many burrows have fresh nests or show signs of fresh digging; 26.5 per cent of the 461 burrows examined in August had evidence of prebreeder activity. The presence of two adults staying over a day in the burrow together (Table 2) is frequently observed in the prebreeding behavior of petrels (Roberts, 1940; Davis, 1957; Allen, 1962). Pre-

breeders do not necessarily return to the same part of the colony the next year. We captured in the study area 34 petrels Huntington had banded, presumably as prebreeders, on other parts of the island in previous years; 8 were captured in burrows while engaged in prebreeder activity, 4 others were known to be breeding, the remaining 22 were not known to be associated with a burrow. Established breeders do not tend to move from one section of the colony to another even if changing burrows (Huntington, 1962). No bird known to be breeding on another part of the island was ever caught in either of the two 30-foot nets or in the woods of the study area. An exception, perhaps proving the rule, was a petrel captured on the ground in the study area 11 or 12 days after a predator had destroyed its nest on a neighboring island.

The relative abundance of adult nonbreeders is difficult to assess. Ten adults that were nesting in 1965 were caught in 1966, but were not known to be associated with a burrow in the study area. Of the nine burrows these birds occupied in 1965, five were not in use in 1966, three were occupied by a new pair, and one was not examined. Therefore of the 78 adults known to have bred in 1965 that were captured in 1966, less than 13 per cent were possible nonbreeders in 1966. The group of 72 adults known to be breeding in 1965 but not captured in 1966 may also have contained nonbreeders as well as undiscovered breeders and mortality losses.

The third class of ineffective breeders are those that have lost or deserted their egg or chick. Normally this group is very small; in the 222 active burrows examined in August (Table 2) we found only three unincubated eggs, 1.4 per cent, and no dead chicks. The eggs may have been unincubated because one parent left to feed before its mate arrived to incubate.

In 1966 our investigations caused the abandonment of about 77 eggs; 141 of the 154 parents affected had been banded previous to their disturbance. The subsequent recaptures of these birds are presented in Table 4; most of these were taken by searching burrows at night or by mist nets in the study area. Of the failed breeders 39 per cent were known to have returned at least to the colony. Certainly not all returning birds were recaptured, and some of the failed breeders may have gone to other parts of the island. Fresh digging found as soon as two nights after a disturbance suggests that the male may begin excavating a new nesting cavity on the night that he first returns to a disturbed burrow.

RENESTING ATTEMPTS

Most of the failed breeders that were recaptured apparently were renesting (Table 4). Some of the renesting attempts involved complex changes of mates and burrows. The complexity of these shifts suggests a normal shortage of potential mate replacements, and that only the simul-

TABLE 4
RECAPTURES OF FAILED BREEDERS

Number of nests abandoned	77
Parents banded before disturbance	141
Parents used in homing experiments	32
Parents not captured after disturbance	66
Parents recaptured after abandoning nests	43
Recaptured in study area but not associated with a burrow	10
Recaptured in original burrow	15
With new mates	3
With old mates (1 pair)	2
Original mates unknown	10
Recaptured in burrow other than original one	9
With new mates	7
With old mates (1 pair)	2
Original mates unknown	0

taneous desertion of so many nests and the consequent entry into the population of a large number of failed breeders in similar stages of their reproductive cycle permitted its occurrence.

Possible renestings and egg replacements have been reported in *Puffinus puffinus* (Harris, 1966), *Macronectes giganteus* (Warham, 1962), *Hydrobates pelagicus* (Gordon, 1931; Davis, 1957), and in *Oceanodroma castro* (Allen, 1962). Gross (1935) reported that "an egg removed from one burrow was replaced two weeks later by another" and that "several times the birds broke their egg. . . . They deserted the burrow for nearly a week and then returned to it. The length of the tunnel was increased and an egg soon appeared in the remodeled home." As he does not mention the identity of any of the petrels involved, the second egg was not necessarily a replacement clutch. C. E. Huntington (pers. comm.) observed an apparent replacement under circumstances similar to the fourth renesting reported below.

On 30 June and 2 July two adults were found incubating in burrow 483; neither could be sexed by the condition of the vent. On 8 July an infrared observation window was installed over the nest chamber and the incubating bird was returned to the nest. This bird presumably left the burrow that night and was not subsequently recaptured. When the burrow was examined on 13 July the nest still contained the unincubated egg. On 15 July the nest cavity had been enlarged and the egg was outside the nest chamber. On 19 and 21 July fresh digging was again evident. The night of 22 July the known mate of the bird that had been initially disturbed was found digging in the extended nesting cavity. The bird was replaced but left the burrow later that night. On 14 August fresh nest

material consisting of green fern fronds was found in the new cavity. Thus 7 days after the presumed abandonment of the egg the first indications of renesting were found. Digging of a new nesting cavity continued intermittently for 9 days; about a month after the abandonment a new nest was constructed. There was no evidence of the return of the mate or the initiation of a new pair bond by 14 August when the study was terminated.

On 20 June two incubating birds were removed from their burrows for experimental purposes. On 23 June their mates returned to their respective burrows to incubate. Both abandoned their eggs the following night and did not subsequently return to their burrows. On 31 July these two birds were found purring together in a third burrow 7 feet from the male's original burrow and 35 feet from the female's burrow. Both petrels were sexed by dissection on the following day. The diameter of the largest ovum of the female was 1.2 mm. The left testis of the male was 3.8 × 2.2 mm.

On 20 June a female was removed from her nest and displaced for a homing experiment. Her mate returned from feeding and incubated the egg until disturbed, after which he abandoned the nest and was not subsequently recaptured. After an absence of 9 days the experimental homer returned to her original burrow and soon abandoned the egg; 12 nights later she was found in a second burrow 20 feet from her original burrow with a new partner with an unknown history; 21 nights after this incident she was retaken back in her original burrow with her third partner of the summer, a male of unknown history. She was sexed by dissection on the following day, 2 August. The largest ovum was ruptured in removing the ovary; the second largest ovum was 1.7 mm in diameter.

On the morning of 24 June an incubating female was removed from her burrow, taken to nearby Machias Seal Island, and released there that evening. The condition of the vent rendered the sex of the bird indeterminate at this time. Hourly checks of the stick lattice over the burrow entrance were made each night, and on 29 June a male was incubating the egg. He left the following night, and sometime between then and 5 July the egg was accidently broken. On 21 July the male was caught about 5 meters from the burrow in a mist net; 2 hours later the female was caught in the same section of the net. The next morning, 22 July, the burrow was examined and neither an egg nor an adult was found. The burrow was not checked again until 14 August when the male was found incubating an egg on a fresh nest in a small chamber adjacent to the original nest cavity. He was sexed by dissection 2 days later on 17 August when the original female was found incubating the egg. As the egg was not translucent and the vent of the female was not excessively wide or discolored

the egg may have been laid anytime between 22 July and about 9 August, or at last 28 days after the first egg was laid. The fact that both adults were found incubating both eggs is convincing evidence that the female did in fact replace her lost clutch.

Discussion

In discussing the evolution of low reproductive rates in pelagic seabirds, Lack (1954, 1966) argues that the clutch in petrels is limited to one egg because one set of parents can raise only one nestling. Giving the parents an extra nestling experimentally reduces the chances of survival of either chick (Huntington, 1963). I have cited evidence above that a single parent alone probably cannot raise a chick. Normally the survival of eggs to hatching and of nestlings to fledging is extremely high in Leach's Petrel, judging by the rarity of dead eggs or chicks found in burrows.

In the rare event that an egg is lost, Leach's Petrel is apparently able to replace it. Records of late fledging dates (Gross, 1947) suggest that if replacement occurs early in the summer the brood may fledge successfully. The survival of these late fledglings and the risk of a second laying must be such that selection has favored this strategy rather than the alternative of missing a year of reproduction. Similarly if a breeding bird loses a mate it will attempt to remate and renest later in the season.

The lack of a definite synchronization of egg laying and the many instances of renesting attempts suggest that at least the Kent Island population is not bound to a highly seasonal food supply. More probably the petrels have relatively constant sources of food that may be shifting in position, widely dispersed, or located at a considerable distance from the colony. Immature birds as inexperienced feeders may not be able to provide for the demands of reproduction. The mode of foraging, the distribution of food organisms in time and space, and the relative feeding success of breeders and prebreeders must be determined before the actual mechanism of the regulation of petrel populations can be described.

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Summary

An estimated 15,000 pairs of Leach's Petrel breed on Kent Island. Of those adults known to have nested in 1965, 54 per cent returned to the colony in 1966; 67 per cent of the returned petrels were nesting with

their previous mates, 68 per cent of the returned petrels were nesting in their previous burrow. The examination of 461 previously undisturbed burrows suggests a breeding success thru the first few weeks after hatching of more than 98 per cent. One-year-old birds may visit the colony, but are not thought to enter the woods; 2-year-olds visit the colonies and initiate burrow and pair bonds; the usual age of first breeding is thought to be 3 years. Failed breeders and widowed birds frequently remate and attempt to renest later in the season. An attempted rearing of a chick by a single parent is noted. Evidence for the replacement of a lost clutch is given and the probable success of replacement broods is suggested.

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