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Homing Experiment with Leach's Storm-Petrels

ELIZABETH CARY PIERSON,[1] CHARLES E. HUNTINGTON,[2] AND NATHANIEL T. WHEELWRIGHT
Department of Biology, Bowdoin College, Brunswick, Maine 04011 USA

Leach's Storm-Petrels (*Oceanodroma leucorhoa*) show high rates of return to their nest sites after being experimentally released at various distances from the breeding colony (Griffin 1940, Billings 1968). Homing at speeds of up to 350 km/day and navigating distances of up to 4,800 km across unfamiliar territory, many birds actually gain mass along the way (Billings 1968). In some cases storm-petrels, which are almost never sighted over land, apparently cross land to avoid much longer all-water routes (Billings 1968). Inspired by Griffin's research at the Bowdoin Scientific Station, Kent Island, New Brunswick (44°35'N, 66°45'W), Billings tested the hypothesis of overland navigation by transporting 15 storm-petrels to the coastal town of Stephenville, Newfoundland (48°33'N, 58°36'W), which is separated from Kent Island by two major land barriers, Prince Edward Island and Nova Scotia. Billings reported return speeds nearly double those of Griffin in several different homing experiments. Given the discrepancy between their results and the fact that experiments in ecology are too rarely repeated and independently corroborated by different investigators, we report the results of a replication of Billings' Stephenville homing experiment.

Thirty-two incubating Leach's Storm-Petrels from Kent Island were selected on the basis of nest accessibility and previous breeding experience. The birds included males and females that averaged 10.9 yr old (SD 5.2 yr) and ranged in age from a minimum of 4 yr to at least 22 yr. We estimated age by adding the number of years since the birds were first banded as breeders to the 4 yr needed to achieve reproductive maturity (Huntington and Burtt 1970). Males and females did not differ in age ($n = 20$ and 12, respectively; Kruskal-Wallis Test: $P = 0.56$). None had been used in Billings' experiments. For several days before the experiment, all nests were checked daily to determine when each bird had arrived to begin its incubation shift. Storm-petrels have incubation shifts that last up to 5 days (Gross 1935, C. Huntington unpubl. data) and attend their nests erratically (Boersma and Wheelwright 1979), so it was difficult to find large numbers of birds at identical stages in their incubation shifts. Consequently, we used birds that had spent varying periods of time on the nest at the start of the experiment.

The experimental procedure was similar to that of Billings (1968). Birds were removed from their nest burrows beginning at 2330, 3 July 1974. Each bird was weighed with Pesola spring scales, placed in a cloth bag, and put into a cardboard box. At 0500 the following day, the birds were transported by boat to Grand Manan Island, a distance of 9 km. Two hours later the birds were flown to Stephenville, with a brief stop in St. John, New Brunswick, to change planes. The birds were not fed in captivity. On the afternoon

[1] Present address: RR 2, Box 248, South Harpswell, Maine 04079 USA.

[2] Author to whom reprint requests should be addressed.

of 4 July 1974, within 15 h of being removed from their burrows, the birds were released singly at the water's edge at 5-min intervals. At the time of release, skies were partly cloudy with a light southwest wind. Vanishing directions were determined by compass. Twenty-nine of the 32 birds disappeared in a southerly or southwesterly direction.

The return of the storm-petrels was detected by setting up lattices of small twigs in front of the entrances to the birds' burrows. If a lattice had been disturbed, indicating that a bird had entered, the burrow was inspected to determine if the experimental bird had returned. Leach's Storm-Petrels return to the breeding colony only at night (Gross 1935). During the first 2 weeks of the experiment, burrows were checked hourly throughout the night. Thereafter burrows were checked daily for an additional 3 weeks.

The first bird to be recovered appeared on 7 July 1974, slightly more than 3 days after its release. The following day, eight more individuals returned (Fig. 1). Twenty-three days after release, 28 of the birds (88%) had returned. The mean time between their release and recovery was 7.1 days (SD 4.2 days). Two of the four birds that failed to return in 1974 were caught in 1975, and a third reappeared in 1976; all returned to their 1974 burrows. Nest desertion, because of the disturbance of the experiment rather than faulty navigation, was presumably the reason they were not recaptured in 1974. Only one bird was never seen again. Eventually, 97% of the birds returned; 84% returned within 17 days. Billings recorded a similar short-term recovery rate: 12 of 15 of her experimental birds (80%) returned within 17 days of their release.

There are an infinite number of possible return routes from Stephenville to Kent Island, but three are most probable. The first and shortest would be a direct 785-km flight over eastern Prince Edward Island and the isthmus that connects Nova Scotia to New Brunswick. Because the route would require considerable overland travel (ca. 130 km) and storm-petrels are very seldom noted over land (Boyd 1954), it was the least likely of the three. The second, around the Nova Scotia peninsula, would be the shortest route involving no overland travel (ca. 1,070 km). A third route would have taken the homing storm-petrels southwest from Stephenville, skirting Prince Edward Island, entering Northumberland Strait, and crossing Nova Scotia at its narrowest point at the New Brunswick border into Chignetco Bay and the Bay of Fundy. The birds would have covered a total distance of about 820 km, only 31 km of which are over land. Previous experiments, in which birds released on either side of the narrowest point of the Nova Scotia isthmus returned at "roughly the same time" (Billings 1968; see also Griffin 1940), suggested that the storm-petrels took the third route.

Assuming that all of the recaptured birds traveled 820 km on their return, their mean homing speed was 115 km/day; the median homing speed was 137 km/day. The fastest return time indicated an average speed of 274 km/day. Billings reported similar return times from the same site, with mean, median, and fastest speeds of 147, 140, and 255 km/day, respectively. The slowest birds in our experiment traveled at an average speed of 36 km/day.

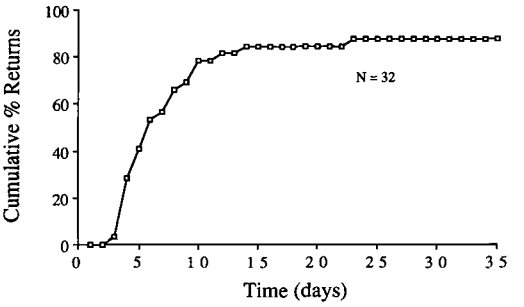

Fig. 1. Cumulative percentage of Leach's Storm-Petrels recaptured at Kent Island, New Brunswick, as a function of number of days after release in Stephenville, Newfoundland. Of the 32 birds, 31 birds eventually returned to their original burrows.

The high variance in return times in this experiment (Fig. 1) as well as in Griffin's experiments could be because birds took different routes. (Billings did not indicate the variance.) The difference between the overland route and the all-water route from Stephenville, for example, is only 250 km, a distance that storm-petrels apparently can cover in less than a day. Because birds in this experiment arrived at Kent Island over a two-week period, their differences in homing speeds must have been due to more than the fact that they followed distinct routes. Such large differences in return speeds could be explained by individual variation in navigational abilities, or the use of distinct types of homing (such as piloting or random search; Able 1980) or differential commitment to reproductive activities. These in turn could be due to individual differences in sex, nutritional status, age, or experience (Able 1980).

We found that males and females did not differ significantly in their return times, although there was a suggestion that females returned faster (mean return time for males and females: 8.3 ± 5.0 days and 5.5 ± 2.2 days, respectively; Kruskal-Wallis Test: $P = 0.07$, $n = 32$). There was no relationship between return time and whether a bird had been removed from its nest on the first or second day of its incubation shift (t-test: $P > 0.05$; $n = 28$). Return time was not correlated with the bird's mass at the time of removal from its nest (in contrast to Billings 1968) or mass at return (linear regression: $r = 0.21$ and 0.35, respectively, $P > 0.05$), nor was return time correlated with a bird's estimated age (Spearman Rank Test: $r_s = -0.03$, $P = 0.89$).

This experiment supports Billings' (1968) conclusion that Leach's Storm-Petrels have well-developed

homing abilities; most birds returned relatively rapidly after being displaced more than 800 km from their nests. Furthermore, storm-petrels can navigate over unfamiliar territory at speeds twice those reported by Griffin (1940). The distance to Stephenville precludes direct sensory contact with familiar landmarks near Kent Island and, presumably, is outside the day-to-day experience of the experimental birds. This experiment indicates true navigation abilities (Able 1980). Explanations of individual variation in homing speeds await experimental studies in which we know both the characteristics (age, sex, stage of reproduction, physical condition, etc.) of individual birds, and their homing routes (e.g. Able et al. 1984).

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Sex Differences in Risk-taking Behavior in Foraging Flocks of House Sparrows

RANDALL BREITWISCH[1] AND JOANN HUDAK[2]
Department of Biology, Indiana University of Pennsylvania, Indiana, Pennsylvania 15705 USA

Birds that forage in flocks often lend themselves to analysis of costs and benefits associated with grouping behavior and how cost-benefit trade-offs may shift with changes in group size (Pulliam and Millikan 1982, Pulliam and Caraco 1984). Granivorous species have frequently been selected for these studies because of the limited variety of food items taken, and House Sparrows (*Passer domesticus*) have been a particularly popular species for study (Barnard 1980a, b, c; Barnard and Sibly 1981; Elgar and Catterall 1981, 1982; Caraco and Bayham 1982; Elcavage and Caraco 1983; Studd et al. 1983; Elgar et al. 1984, 1986; Elgar 1986; Lima 1987).

However, there has been surprisingly little study of possible sex differences in behavior for any flocking species. The single exception appears to be Caraco and Bayham's (1982) treatment of House Sparrow foraging flocks. Although the only difference they showed was that males occurred in flocks in greater proportion than in the local population, Caraco and Bayham indicated that there were other apparent behavioral differences not rigorously investigated in their study. Primary among these was the suggestion that females were more hesitant to forage where there were frequent disturbances.

Following the lead of Caraco and Bayham (1982), we studied two aspects of risk-taking behavior in for-

[1] Present address: Department of Biology, University of Dayton, 300 College Park, Dayton, Ohio 45469 USA.

[2] Present address: R.D. 2, Box 222, Delta, Pennsylvania 17314 USA.