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The Effect of Burrow Loss on Mate Choice in the Leach's Storm-Petrel

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Long-lived seabirds often nest for many years with the same mate at the same site (Fisher and Lockley 1954, Lack 1968). Repeated pairings might result either from strong mate fidelity or from a tendency to return to the same burrow or nest site, here called site tenacity (Hildén 1965, Morse 1980). Retention of a site sometimes exceeds retention of a mate (e.g. Allan 1962, Morse and Buchheister 1979), which tentatively suggests that site tenacity is primarily responsible for repeated pairings in these instances. If repeated pairing is a consequence of site tenacity, birds deprived of their nest sites should remate randomly; if repeated pairing results from mate fidelity, birds deprived of their nest sites should retain their previous mates.

We know of no controlled experiments that assess the roles of mate fidelity and site tenacity in retaining mates from one breeding season to the next. Here, we demonstrate experimentally that retention of the same mate during successive breeding seasons by the Leach's Storm-Petrel (*Oceanodroma leucorhoa*) is largely or totally dependent on site tenacity.

This experiment was carried out on Little Duck Island, Hancock County, Maine, an island of 34 ha, located 15 km from the mainland. Pairs in 62 numbered burrows were captured and banded during June 1980. Before the arrival of birds at the colony in April 1981, 25 of these burrows were randomly selected, and their entrances were covered with a 25- × 15-cm wooden shingle. Then, a 30- × 30-cm piece of coarse

metal screening (1- × 1-cm mesh) was placed over each shingle and secured with 15-cm wire spikes in each corner to prevent access to these burrows. The remaining burrows were not covered. In June 1981 the 37 burrows not covered in April were censused as in 1980, and inhabitants of neighboring burrows were captured in order to locate as many of the birds displaced from the experimental burrows as possible. In all, over 500 unnumbered burrows, those closest to the 62 numbered burrows, were searched for displaced birds.

Mate retention was strongly site-dependent. A significantly higher proportion of undisturbed individuals retained their mates from 1980 than did displaced individuals (Table 1) ($P < 0.001$ in a one-tailed Fisher Exact Probability Test).

Two groups of birds could not be used in this analysis (and thus are not included in the two right columns of Table 1), but nevertheless are consistent with this conclusion: (1) both members of six undisturbed pairs changed their burrows, and all but one of these pairs nested with a different mate; and (2) members of five displaced pairs managed to burrow under the screening into their original burrows, in spite of the efforts taken to exclude them, and all of them nested with their mates from 1980. In addition to these two groups, neither member of 10 displaced pairs or 7 undisturbed pairs was recovered, a significantly higher proportion of displaced than undisturbed pairs ($\chi^2 = 4.48$, $df = 1$, $P < 0.05$).

TABLE 1. Mates of Leach's Storm-Petrels in 1980 and 1981.

| Sample | Number of pairs censused in 1980 | Number of pairs suitable for analysis in 1981 | Number with same mate in both 1980 and 1981 |
|-------------|----------------------------------|---|---|
| Displaced | 25 | 10 ^a | 2 (20%) |
| Undisturbed | 37 | 24 ^b | 23 (96%) |

^a Birds found that were displaced from their 1980 burrows. Both members of one displaced pair were found; in the other nine cases only one member of the pair was found.

^b Undisturbed birds found. Both members of 23 undisturbed pairs were found; in the other case only one member of the pair was found.

If site tenacity is the prevailing factor associated with retaining a mate, any displaced individuals that do retain their mates at new sites should be located closer to their original burrow than those with new mates, given equal availability of new burrows for the two groups. (A certain number of pairings would be predicted by chance alone if both birds initially returned to their original site.) Because of the small number of pairs switching to new sites, we have few data with which to test this hypothesis. The 3 established pairs recovered at new sites (2 displaced, 1 undisturbed), however, do support this hypothesis. They were separated from their 1980 sites by significantly fewer burrows (1, 3, 13 other burrows were nearer; $\bar{x} = 5.7 \pm 6.4$ SD) than were 13 birds captured with new mates ($\bar{x} = 120.5 \pm 169.0$ SD other burrows were nearer) ($P = 0.034$ in a one-tailed Mann-Whitney *U*-Test). Four of the 13 individuals with new mates did nest in the immediate vicinity of their 1980 burrows, however (2, 6, 6, 8 other burrows were nearer). These results do not eliminate the possibility of mate fidelity; they indicate only that, if existent, mate fidelity is largely ineffectual when mates do not have their former burrow as a common reference point.

The results thus support the hypothesis that mate retention in these Leach's Storm-Petrels is a consequence of site tenacity. They further suggest that mate fidelity plays little or no part in the repeated pairings of these birds. Although one might argue that the tendency of the displaced birds to take new mates is simply a response to an unnatural disturbance, the covered entrance to the burrow, this conclusion seems unwarranted. In this study a similar proportion of undisturbed birds that moved to new sites in 1981 had a new mate. Further, this same result has been reported in undisturbed individuals elsewhere, both Leach's Storm-Petrels (Morse and Buchheister 1979) and other species of storm-petrels (Davis 1957, Allan 1962, Harris 1969).

Similar experiments with other species would be

desirable in order to test the generality of the result reported in this paper (T. C. Grubb, Jr. pers. comm.). This comment is especially pertinent for diurnal surface-nesting seabirds, whose possibilities of finding their mates away from the nest site may depend on cues different from those used by a nocturnal burrowing species, which may use either olfactory or auditory information in locating nest sites (Grubb 1973, 1974).

The failure to recapture either member of 17 pairs could have occurred for several reasons, none likely to modify the conclusions. (1) The birds might have suffered mortality between breeding seasons. (2) These birds sometimes skip breeding years (Morse and Buchheister 1979). (3) Further searching might have produced additional birds. Because this colony contains as many as 4,000 pairs (Erwin and Korschgen 1979) scattered over 17 ha, it was impossible to recover all of the birds present, given the slow procedure of capturing them in their burrows. (4) Some birds might have failed to return to the vicinity in 1981 as a result of being handled in 1980. (5) Some of the displaced birds may have deserted as a result of encountering the covered burrows.

These results have implications for reproductive success and for conservation. Pairs of many species of seabirds nesting together for the first time experience lower levels of success than in subsequent years, independent of their age (Lack 1966, 1968; Hunt 1980). Severe disturbances to nest sites (storms, fires, grazing, colonization by large surface-nesting seabirds, artillery practice) may cause shifts to new sites. Such shifts could result in the breakup of pairs and in consequent lowered reproductive success, even if the disturbances do not occur during the breeding season or destroy all of the suitable habitat.

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Observations on the Cooling Tolerance of Embryos of the Diving Petrel *Pelecanoides georgicus*

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The tolerance of procellariiform embryos to extended periods of cooling has been documented for storm-petrels (Hydrobatidae) (Pefaur 1974, Boersma and Wheelwright 1979, Vleck and Kenagy 1980, Simons 1981), members of the family Procellariidae (Matthews 1954, Tickell 1962, Richdale 1963, Bartle 1968), and anecdotally for the Waved Albatross (*Diomedea irrorata*, Diomedidae; Harris 1973, no details given). Cooling tolerance in these taxa is assumed to be an adaptation to long-distance foraging on unpredictable food supplies, which may cause adults to leave eggs unattended for periods of one to several days. Cooling tolerance may not be ubiquitous among the Procellariidae, however, as advanced embryos of the Southern Giant Fulmar (*Macronectes giganteus*) cannot tolerate cooling to 3°C for 48 h (Williams and Ricklefs MS), and tolerance has not been confirmed in the albatrosses (Diomedidae, cf. Richdale 1952) or in the diving petrels (Pelecanoididae).

Apropos of the diving petrels, Thoresen (1969) discovered a deserted, pipping egg of *Pelecanoides u. urinatrix*, which subsequently hatched after being unattended for 10 days at an ambient temperature of about 17°C. Unusual variability in incubation periods has been cited as indirect evidence of egg neglect in some species (Boersma 1982). Payne and Prince (1979) found little variation in the incubation period of 10 *P. georgicus* eggs (44-49 days), except for one period of 65 days, which suggested the possibility of about 20 days of neglect. Because this egg was neither marked nor checked early in the incubation period, however, the possibility of egg loss and subsequent relaying cannot be ruled out. In this paper, we report observations that demonstrate a well-developed tol-

erance for chilling by embryos of the South Georgian Diving Petrel (*Pelecanoides georgicus*).

During the course of a study of the reproductive biology of *P. georgicus* on Bird Island, South Georgia (54°00'S, 38°02'W) during January and February 1982, our activities at nests caused some adults to abandon eggs late in the incubation period. Nests were usually checked daily, 8 or more hours after dawn. Adult diving petrels are strictly nocturnal at the breeding colony (pers. obs.), so an egg found cold in an unattended burrow was assumed to have been unincubated for at least 8 h. If the egg was found cold on subsequent consecutive days, it was assumed that the egg had not been incubated in the interim period. With these assumptions, we estimated the total chilling period for each egg before placement in the incubator (Table 1).

Eggs from 25 nests, abandoned for between 8 and 56 h in most cases, were removed and placed in an incubator. We measured temperatures of 7.8, 8.1, and 8.9°C in three unoccupied burrows. The temperature in the incubator was 36 ± 0.5°C, but, owing to the daily shutdown of the field station generator for maintenance, all eggs cooled to room temperature (ca. 20°C) for about 8 h each night. Eggs were left in the incubator and turned daily.

Despite initial chilling in the nest and subsequent daily temperature fluctuation in the incubator, 14 eggs hatched after periods of 4-19 (average = 10.2) days in the incubator, with the exception of 1 egg, which hatched after 32 days (Table 1). We estimated the ages of embryos to be 24 days in one case and between 34 and 44 days for the remaining eggs at the time they were abandoned (see Table 1). The average