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Effects of investigator disturbance on hatching success and nest-site fidelity in a long-lived seabird, Leach's storm-petrel

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Abstract

Long-lived animals are expected to reduce reproductive effort when breeding conditions are unfavorable, therefore seabirds may be especially sensitive to investigator disturbance. In a non-threatened procellariiform, Leach's storm-petrel *Oceanodroma leucorhoa,* we examined whether the frequency and the time of day of investigator disturbance influenced hatching success, and if disturbance affected hatching success and nest-site fidelity in the subsequent breeding season. Birds used in this study had received little or no investigator disturbance during the prior decade. Hatching success was significantly influenced by the frequency, but not the time of day, of disturbance. *Weekly* and *daily* handling of parents reduced hatching success by 50 and 56% compared to the *control* group. Most failures (91%) were caused by egg desertion, and all the deserted eggs belonged to pairs in the *weekly* and *daily* groups. During the subsequent breeding season, the hatching success of disturbed pairs that continued to breed together returned to normal levels. However, 37% more disturbed pairs than *control* pairs deserted the nesting burrows they had used in the previous year. Since most changes in nest site also result in mate change, investigator disturbance may have had long-term negative effects on reproductive success as well. Our results demonstrate that both *weekly* and *daily* investigator disturbance during incubation greatly reduced the hatching success and subsequent nest-site fidelity of naïve Leach's storm-petrels.

Keywords: Investigator disturbance; Leach's storm-petrel; Long-lived birds; Egg desertion; Hatching success

1. Introduction

Avian taxa are differentially sensitive to investigator disturbance, and these differences likely relate to their life history strategies (Götmark, 1992). Because reproduction is costly, parents are expected to adjust their level of current investment such that the probability of success justifies the cost to survival and future reproduction (Williams, 1966; Stearns, 1992). Long-lived iteroparous animals have many opportunities to breed in a lifetime and therefore should take less risk during the current breeding attempt than shorter-lived animals that have a lower potential for future reproduction (Stearns, 1976). Consequently, individuals of long-lived species are more likely to reduce parental effort when breeding conditions are unfavorable and thus may be particularly vulnerable to disturbances caused by researchers. Investigators studying long-lived birds should understand how their research procedures affect their study animals and take precautions to mitigate adverse effects, especially when threatened species are involved.

Procellariiforms (e.g., albatrosses, shearwaters, and petrels) are particularly long-lived seabirds, many of whose populations are in decline (Warham, 1990). Many populations are declining because their island breeding habitat is being lost or degraded as a result of human development and the introduction of mammalian predators (Warham, 1990). Procellariiforms are further threatened by high levels of mortality incurred in long-line fisheries (Cooper, 2000; Tuck et al., 2001). Investigator disturbance that reduces reproductive success could exacerbate these population declines and interfere with the accurate assessment of demographic parameters and appropriate allocation of management resources (Croxall and Rothery, 1991; Rodway et al.,

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1996). Thus, knowledge of the short-term and long-term effects of investigator disturbance on reproductive success is crucial to designing appropriate research programs that advance conservation efforts. Yet, little is known about the effects of investigator disturbance on procellariiforms. Several studies have reported that research activities, such as monitoring and banding birds during incubation, have reduced the hatching success of northern fulmars (*Fulmarus glacialis*, Ollason and Dunnet, 1980) and Leach's storm-petrels (*Oceanodroma leucorhoa*, Wilbur, 1969; MacKinnon, 1988; Huntington et al., 1996). However, no attempt has been made to quantify the frequency of investigator disturbance that affects hatching success, nor to identify the long-term effects of disturbance on reproduction.

We examined the influence of investigator disturbance during incubation on the hatching success and subsequent nest-site fidelity of a procellariiform seabird, the Leach's storm-petrel. Leach's storm-petrels were selected as a model species because, unlike many procellariiforms, they are abundant worldwide (Huntington et al., 1996) and can act as a surrogate for threatened members of their order. Specifically, we tested whether the frequency and the time of day of investigator disturbance during incubation influenced hatching success, and if this disturbance affected hatching success and nest-site fidelity in the subsequent breeding season. The frequency of disturbance could reduce hatching success in at least two ways. The disturbance either could cause parents to permanently desert their eggs, resulting in certain failure, or it could cause parents to temporarily neglect their eggs, which can reduce hatching success in procellariiforms (e.g., Matthews, 1954; Boersma and Wheelwright, 1979). The time of day of disturbance also could affect hatching success by increasing the amount of temporary egg neglect. An incubating bird may perceive the investigator as a threat (e.g., a predator) and be motivated to escape. Since Leach's storm-petrels avoid gull predation by flying between their nesting colony and pelagic foraging areas only at night (Huntington et al., 1996), a bird that is disturbed in the morning is likely to remain inside its burrow until nightfall. By then, the bird may no longer be motivated to escape, and therefore would continue to incubate until it is relieved by its partner. In contrast, a bird disturbed near nightfall may respond by departing earlier than it would have otherwise, thereby prematurely terminating its incubation shift. This premature departure would leave the egg temporarily neglected, for a period of time lasting from hours to days, until the bird's partner returns from sea to begin its incubation shift. Therefore, we predicted that pairs disturbed in the evening would have lower hatching success than pairs disturbed in the morning.

2. Methods

2.1. Study area and species

This study was conducted in 1999 and 2000 on Kent Island, New Brunswick, Canada (44° 35′ N, 66° 45′ W). The breeding ecology of Leach's storm-petrels has been detailed elsewhere (Huntington et al., 1996). Briefly, Leach's storm-petrels can live for more than 30 years, form long-term pair bonds, and are highly philopatric to their nesting burrows. Each year, a single egg is laid in the burrow, and both parents incubate the egg for an average of 43 days in shifts lasting about 3 days each. After hatching, the nestling is brooded for an average of 6 days, after which the chick remains alone in the burrow for 55–65 days and is fed during brief nocturnal visits by the parents.

2.2. Field methods

Pairs used in this study had received little or no investigator disturbance during the prior decade (Charles Huntington, personal communication). We located active burrows in mid-June 1999 after eggs had been laid. We adopted standard research procedures used to monitor Leach's storm-petrels nesting in other portions of the island's colony (Ronald Butler, personal communication; Charles Huntington, personal communication). These procedures included making access holes into burrows in which the nest chambers were difficult to reach through the burrow entrances. We sealed each access hole with a wooden board covered with a thick layer of soil and duff, and secured the board with a log or rock. The number of access holes did not differ significantly among the treatment groups ($G_w = 0.58$, $df = 2$, $P = 0.75$); 65% of *control* burrows ($n = 20$), 75% of *weekly* burrows ($n = 20$), and 94% of *daily* burrows ($n = 18$) had access holes.

Each breeding pair was assigned to 1 of 6 treatment groups based on the time of day (*morning* or *evening*) when we first disturbed it and the frequency of investigator disturbance it was to receive (*control*, *weekly*, or *daily*). Pairs were systematically distributed among the frequency treatment groups as we encountered them throughout the study area. This methodology ensured that pairs within the treatment groups were not spatially clustered with regard to microhabitat type or temporally clustered with regard to nest initiation date. Daylight hours extended from >0500 to <2200, therefore we visited burrows in the *morning* treatment group between 0800 and 1200 and burrows in the *evening* treatment group shortly before dark between 1900 and 2100. Pairs in the *control* group received the minimum disturbance possible, whereas field procedures for the *weekly* and *daily* treatment groups simulated investigator disturbance that might be experienced by incubating birds during routine monitoring in a scientific study (e.g., Morse and Buccheister, 1979; Chaurand and Weimerskirch, 1994; Yorio and Boersma, 1994; Weimerskirch, 1995; Waugh et al., 1997). Visitation schedules for the *control*, *weekly,* and *daily* treatment groups were as follows:

2.2.1. Control treatment group

We visited each pair in the *control* group only once during incubation, and did not remove the incubating partner from the burrow to band it. Thus, only one member of a *control* pair received human contact, and was not handled. After determining that a burrow was active by briefly feeling for the presence of an adult and egg, we waited at least 43 days (i.e., the average length of the incubation period) to revisit the burrow to determine hatching success.

2.2.2. Weekly treatment group

We designed the *weekly* treatment group so that pairs would be disturbed on a weekly basis, with each partner receiving approximately 4 disturbances (provided that the pair did not desert its egg). During our initial visit to a burrow in the *weekly* treatment group we first removed the egg (to avoid damaging it while removing the parent; Charles Huntington, personal communication) and then the incubating bird. We banded the bird, weighed it using a cloth bag and Pesola® spring scale, and measured its right wing and tarsus. Next, we returned the egg and parent to the burrow and set a twig lattice at the entrance. We re-entered the burrow only when the twig lattice was displaced, indicating that an incubation shift change-over may have occurred (Ainslie and Atkinson, 1937; Billings, 1968; Wilbur, 1969; Chaurand and Weimerskirch, 1994). When a change-over had occurred, we banded, weighed, and measured the other partner. We then waited 1 week before revisiting the burrow. After this 7-day disturbance-free period, we began a new cycle of disturbance by entering the burrow and weighing whichever member of the pair was present; we did not repeat body measurements. We then reset the twig lattice and checked it daily until the sticks were displaced, at which time we entered the burrow again to weigh the other partner. Generally the displaced twig lattice reliably indicated that an incubation shift change-over had occurred, and each member of a pair received only one disturbance per cycle. Occasionally the lattice was displaced but a change-over had not occurred, in which case we weighed the incubating bird again and reset the lattice, then repeated this process until we caught the other partner. When we found an unattended (i.e., cold) egg, we checked the nest again the following day to determine whether a parent had returned to incubate (in which case the bird was weighed) or if the egg remained unattended (in which case we checked the nest again the following day).

We continued visiting each burrow until the egg's fate could be determined (i.e., hatched or failed to hatch). Eggs that failed to hatch were considered deserted if they had been unattended for 15 consecutive days. Although the tolerance of Leach's storm-petrel eggs to extended chilling is unknown (Huntington et al., 1996), fork-tailed storm-petrel *Oceanodroma furcata* eggs become inviable after 7 days of continuous neglect (Boersma and Wheelwright, 1979). The average duration of the incubation period in Leach's storm-petrels is shorter than in fork-tailed storm-petrels (43 and 50 days, respectively; Huntington et al., 1996; Boersma and Wheelwright, 1979). Thus, 7 days of continuous neglect represents a greater proportion of the incubation period in Leach's storm-petrels than in fork-tailed storm-petrels. Since these two closely related species probably are under similar developmental constraints, it is unlikely that Leach's storm-petrel eggs could have survived being chilled for 7 consecutive days. Our definition of egg desertion (i.e., 15 consecutive days of egg neglect) therefore was conservative.

2.2.3. Daily treatment group

Procedures were the same as in the *weekly* treatment group except that we disturbed *daily* treatment group pairs once per day throughout incubation. After initially banding, weighing, and measuring each parent, we weighed the incubating partner daily, regardless of the status of the twig lattice or whether that same bird had been disturbed the day before.

2.2.4. Long-term effects of investigator disturbances

During the following breeding season, we recorded whether each *control*, *weekly*, and *daily* burrow used in 1999 was occupied or empty in 2000. In occupied *weekly* and *daily* burrows we used the twig lattice system to capture and record the identity of each breeding partner with minimal disturbance. We did not weigh or measure the birds, and did not disturb pairs again during incubation. We returned to each *control*, *weekly*, and *daily* nest after the egg's projected hatching date (estimated by candling; Weller, 1956, modified for Leach's storm-petrels by A. L. Blackmer, unpublished) to determine hatching success. We also searched for and were able to locate several banded birds from the *weekly* and *daily* groups that were breeding in different burrows in 2000 than in 1999; we measured the distance (m) these birds moved between burrows.

2.3. Statistical analyses

We examined whether investigator disturbance influenced the likelihood that an egg would hatch using a multiple logistic regression model in which the nominal dependent variable was hatched or failed to hatch and the explanatory variables were the frequency of disturbance (categorical treatment: *control*, *weekly*, or *daily*) and the time of day of disturbance (categorical treatment: *morning* or *evening*). Because the time of day of disturbance did not influence hatching success, nor was there an interaction between the time of day of disturbance and the frequency of disturbance (see Section 3), we pooled the *morning* and *evening* treatment groups in all subsequent analyses. We then used two-tailed *G*-tests with William's correction factor to conduct pairwise comparisons of the number of eggs that hatched versus the number of eggs that failed to hatch in 1999 among the *control*, *weekly*, and *daily* treatment groups. For these 3 pairwise comparisons we used the Bonferroni method to determine the experimentwise error rate ($\alpha' = 0.05/3$; Sokal and Rohlf, 1995); thus, we considered a result significant if $P \leqslant 0.017$. For all other tests $\alpha = 0.05$. We also used a *G*-test to examine whether the frequency of investigator disturbance affected the subsequent nest-site fidelity of disturbed and *control* pairs. For this analysis we compared the number of pairs in 2000 that re-used their 1999 burrows to the number of pairs that did not re-use their 1999 burrows between the disturbed and *control* groups. Means are reported ± 1 S.D.

To determine whether investigator disturbance in 1999 affected hatching success in 2000, we used a *G*-test to compare among treatment groups the number of eggs that hatched versus the number of eggs that did not hatch in 2000. For this analysis, we used 7 *weekly* and 12 *daily* treatment group pairs whose membership was the same in both years of the study. We excluded individuals that changed mates between 1999 and 2000 from this analysis because individual or pair attributes (e.g., breeding experience, individual or burrow quality) can influence hatching success (Black, 1996). We also used the 18 *control* burrows that were occupied in 2000 for this analysis. Although we did not band *control* birds in 1999 (and therefore could not confirm that pair membership in these burrows was the same in both years), pair membership probably did not change since Leach's storm-petrels typically show extremely high nest-site fidelity (e.g., 95% on Matinicus Rock, Maine; Morse and Buccheister, 1979).

3. Results

We monitored 58 Leach's storm-petrel pairs during the 1999 breeding season. Pairs in the *control* group ($n = 20$) were disturbed during a single visit and were not handled, whereas pairs in the *weekly* group ($n = 20$) were disturbed on 33% of the days their burrows were under observation, and pairs in the *daily* group ($n = 18$) were disturbed on 100% of the days their burrows were under observation. As expected, the number of disturbances received by *control*, *weekly*, and *daily* pairs differed significantly (Kruskal-Wallis: $H = 44.26$, $P < 0.001$). Of the 76 individuals in the *weekly* and *daily* groups, 80% had never been handled by humans; the remaining 20% of birds had been previously banded, but had not been handled within 6–13 years of our study.

3.1. Short-term effects of investigator disturbance

Hatching success was significantly influenced by the frequency, but not the time of day, of investigator disturbance (*multiple logistic regression:* frequency of disturbance: Wald $\chi^2 = 9.42$, $P < 0.01$; time of day of disturbance: Wald $\chi^2 = 0.53$, $P = 0.46$; $n = 58$), after dropping the non-significant interaction term from the model (frequency of disturbance×time of day of disturbance: Wald $\chi^2 = 0.41$, $P = 0.82$; $n = 58$). Pairwise comparisons revealed that the *weekly* and *daily* treatment groups each had significantly lower hatching success than the *control* group (*control* vs. *weekly*: $G_w = 12.80$, $P < 0.001$; $n_{control} = 20$ pairs, $n_{weekly} = 20$ pairs; *control* vs. *daily*: $G_w = 14.70$, $P < 0.001$; $n_{control} = 20$ pairs, $n_{daily} = 18$ pairs), whereas there was no difference between the *weekly* and *daily* groups' hatching success ($G_w = 0.14$, $P = 0.70$). Overall, investigator disturbance reduced hatching success by 50% in the *weekly* group and by 56% in the *daily* group compared to the *control* group (Fig. 1).

Egg desertion was the primary cause of nest failure; of 23 eggs (out of 58) that did not hatch, 91% failed because the parents had deserted them. All of the deserted eggs belonged to pairs in the *weekly* and *daily* groups, and desertion occurred with similar frequencies in these treatment groups (100% of 11 *weekly* and 91% of 11 *daily* eggs that failed to hatch had been deserted).

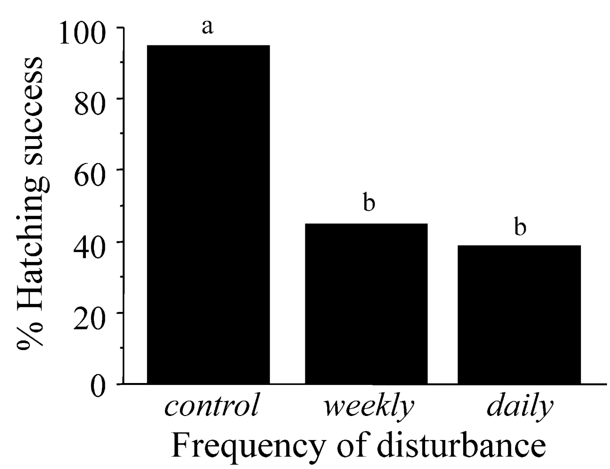

Fig. 1. Hatching success of eggs in relation to the frequency of investigator disturbance to pairs in 1999 at Kent Island, New Brunswick, Canada. The hatching success of the *weekly* and *daily* treatment groups each was significantly lower than that of the *control* group (both $P < 0.001$; $n_{control} = 20$ pairs, $n_{weekly} = 20$ pairs, $n_{daily} = 18$ pairs), whereas there was no difference between the *weekly* and *daily* groups' hatching success ($P = 0.70$). Different letters indicate statistically distinguishable treatment groups.

The minimum number of disturbances accrued before egg desertion occurred was 2 visits per pair in the *weekly* group and 3 visits per pair in the *daily* group. Nearly half of the deserted eggs (48% of 21 eggs) were buried in the dirt floor of the nest chamber. Most of the other deserted eggs remained on the surface of the nest chamber's floor, and one egg was ejected from the burrow. We detected no evidence of a newly excavated nest chamber, fresh nesting materials, or a fresh egg in any burrow within 15 days after egg desertion.

Daily treatment pairs that did not desert their eggs continued to incubate them normally, with incubation shifts averaging 3.2 ± 1.2 days in length ($n = 59$ shifts, $n = 8$ pairs). Throughout incubation, 7 of these pairs rarely neglected their eggs (range: 0–2 days total), and all of the eggs hatched. One pair neglected their egg more frequently (6 days total), and their chick died while hatching.

3.2. Long-term effects of investigator disturbance

Investigator disturbance not only reduced hatching success in 1999, it also reduced nest-site fidelity in the following breeding season. Fewer disturbed (i.e., *weekly* and *daily*) pairs re-used their 1999 nesting burrows in 2000 than did *control* pairs ($G_w = 8.85$, df = 1, $P < 0.01$, $n_{control} = 20$ pairs; $n_{disturbed} = 38$ pairs); 60% of *weekly* ($n = 20$) and 33% of *daily* ($n = 18$) pairs had one or both partners desert the burrows they had used in 1999, whereas 10% of *control* burrows ($n = 20$) were unoccupied in 2000. Of the 21 pairs that had deserted their eggs in 1999, 71% subsequently deserted their burrows (i.e., did not re-use those burrows in 2000). In contrast, only 15% of 34 pairs that hatched their eggs in 1999 subsequently deserted their burrows. In 2000, we located 5 birds from the disturbed treatment groups breeding in the same general area as in 1999 but in different burrows and with new partners. These birds had moved an average of 26 m (range: 6.2–90.0 m) from their 1999 burrows.

The negative effect of investigator disturbance on hatching success, evident in 1999, did not persist during the subsequent breeding season. In 2000, the hatching success of pairs whose membership was the same in both years did not differ among treatment groups ($G_w = 1.36$, df = 2, $P = 0.50$, $n_{control} = 18$ pairs; $n_{weekly} = 7$ pairs; $n_{daily} = 12$ pairs). Hatching success increased from 71 to 100% in the *weekly* pairs and from 58 to 92% in the *daily* pairs. In contrast, the hatching success of the *control* pairs was high in both years of the study (94% in 1999 and 89% in 2000).

4. Discussion

Weekly and *daily* investigator disturbance reduced Leach's storm-petrel hatching success by 50 and 56% compared to the *control* group (Fig. 1). Egg desertion accounted for 91% of all reproductive failures, and all the deserted eggs belonged to pairs in the disturbed treatment groups. Egg desertion occurred with similar frequency in the *weekly* and *daily* groups. This reduction in parental effort by Leach's storm-petrels in response to investigator disturbance is consistent with the predictions of life history theory. Adults of long-lived species have a high probability of survival, and reproduction in any given year represents only a small fraction of an individual's lifetime reproduction. Since reproduction is costly, it reduces the prospects of future survival and reproduction (review by Coleman and Gross, 1991). Therefore, parents should invest less in years with unfavorable breeding conditions in order to increase the probability of survival to future breeding opportunities (Stearns, 1992). For example, breeding Leach's storm-petrels (Mauck and Grubb, 1995) and Antarctic petrels *Thalassoica antarctica* (Sæther et al., 1993) responded to a flight handicap (i.e., reduced wing span and increased mass due to leg weights, respectively) by feeding their chicks less frequently. In our study, Leach's storm-petrels reduced parental effort by deserting their eggs when we adversely altered breeding conditions through *weekly* or *daily* investigator disturbances. Wilbur (1969) also found a high level of egg desertion (50%) by Leach's storm-petrels when they were banded and handled, although the amount of investigator disturbance that induced desertion was not reported.

It is possible that Leach's storm-petrels that deserted their eggs may have re-nested, and therefore did not reduce their overall parental effort during the 1999 breeding season. Gross (1935) and Wilbur (1969) found that after egg loss or desertion some Leach's storm-petrels returned to their burrows and began re-nesting (e.g., digging in the nest chamber, preparing fresh nesting materials), sometimes as soon as two nights later. Of these returning birds, most (77%) relayed 10–20 days after losing their original clutch (Huntington et al., 1996). We monitored burrows for at least 15 consecutive days after egg desertion, and during this period we detected no evidence of re-nesting in any burrow, including the construction of a new nest chamber, fresh nesting materials, or a replacement egg. Our observations suggest that birds that deserted their current clutches in response to investigator disturbance also reduced their overall parental effort during the 1999 breeding season.

Investigator disturbance during breeding has been shown to negatively affect other long-lived seabirds, as well. For example, investigator disturbance reduced the hatching success and fledging success of least auklets *Aethia pusilla* (Piatt et al., 1990), and reduced the burrow occupancy rate and hatching success of tufted puffins *Fratercula cirrhata* (Pierce and Simons, 1986).

Investigator disturbance also has been shown to adversely affect indices of reproductive success in Atlantic puffins *F. arctica* (Rodway et al., 1996), black guillemots *Cepphus grylle* (Cairns, 1980), adélie penguins *Pygoscelis adeliae* (Giese, 1996), and pelicans *Pelecanus* spp. (Schreiber and Risebrough, 1972; Boellstorff et al., 1988). Thus, our results are consistent with the predicted and observed responses of a variety of long-lived seabirds to unfavorable breeding conditions caused by investigator disturbance (reviews by Nisbet, 2000; Carney and Sydeman, 1999). On the other hand, nest visitation schedules similar to ours did not affect the hatching success of ring-billed gulls *Larus delawarensis* (Brown and Morris, 1994) and black terns *Chlidonias niger* (Shealer and Haverland, 2000). In general, gulls seem to be relatively unaffected by investigator disturbance (Nisbet, 2000).

Previous studies have not examined whether the time of day of investigator disturbance influences avian reproductive success. We predicted that pairs that were disturbed in the evening would temporarily neglect their eggs more often than pairs disturbed in the morning because they could respond to the disturbance by departing their burrows under the cover of night when predation risk is relatively low (Huntington et al., 1996). Consequently, pairs disturbed in the evening would temporarily neglect their eggs more often and have lower hatching success (sensu Matthews, 1954; Boersma and Wheelwright, 1979; Vleck and Kenagy, 1980) than pairs that were disturbed in the morning. However, we found that the time of day of investigator disturbance did not affect hatching success. This result indicates that fieldwork on Leach's storm-petrels does not need to be restricted to a particular time of day, probably because parents can be replaced into their burrows after being handled. The time of day of disturbance may have a greater effect on surface-nesting birds because they often flush as the investigator approaches, inevitably resulting in temporary egg neglect. The flushing of surface-nesting birds also may cause high rates of egg loss to predators (Nisbet, 2000) or exposure to environmental extremes.

Remarkably little is known about the effects of investigator disturbance on avian reproductive success and nest-site fidelity in subsequent years. Among disturbed (i.e., *weekly* and *daily*) Leach's storm-petrel pairs whose membership was the same in both years of the study, hatching success the following breeding season (2000) returned to normal levels that were similar to the hatching success of *control* pairs. In contrast, the fledging success of Atlantic puffins remained low for 1 year, but not 2 years, after investigator disturbance (Rodway et al., 1996).

Although investigator disturbance did not have long-term effects on hatching success, it did reduce nest-site fidelity. We found that disturbance in 1999 caused 37% more disturbed pairs than *control* pairs to desert their burrows the following breeding season (2000). Since we did not band individuals belonging to the *control* group in 1999 (to minimize disturbance), we assumed that occupied *control* burrows in 2000 contained the same breeding partners as in 1999. If some of these occupied burrows in 2000 housed different breeding partners than in 1999, then we would have underestimated the proportion of *control* birds that deserted their 1999 burrows, causing the fidelity rates of the *control* group and the disturbed group to be more similar. However, Leach's storm-petrels typically exhibit very high nest-site fidelity (e.g., 95%, Morse and Buccheister, 1979). Therefore, our estimate that 90% of *control* pairs reused their 1999 burrows in 2000 probably is accurate, hence disturbed pairs exhibited significantly lower nest-site fidelity than did *control* pairs.

Since most (74%) burrow changes by Leach's storm-petrels also result in mate change (Mauck, 1997), investigator disturbance that caused a bird to desert its burrow (and therefore its mate) may have been costly to lifetime reproductive success. Numerous studies on long-lived birds have demonstrated that indices of reproductive success improve as the duration of the pair bond increases (Black, 1996). Additionally, mate change could delay reproduction, and procellariiform chicks that hatch late in the season often have lower survival rates than early-hatched young (e.g., Richdale, 1963; Perrins, 1966; Harris, 1979; Hatch and Nettleship, 1998). Thus, although investigator disturbance did not affect the hatching success of birds that remained together in the same burrow during the subsequent breeding season, it may have reduced the reproductive success of individuals that changed burrows and mates.

Leach's storm-petrels that deserted their 1999 burrows may have attempted to move away from the disturbance, as has been suggested for kittiwake gulls *Rissa tridactyla* (Sandvik and Barrett, 2001), ring-billed gulls (Conover and Miller, 1978), and adélie penguins (Reid, 1968; Wilson et al., 1989). Failure to hatch an egg *per se* in 1999 also may have contributed to the decision to desert the burrow (see Huntington et al., 1996). Only 15% of pairs that hatched their eggs in 1999 subsequently deserted their 1999 burrows, whereas 71% of pairs that deserted their eggs in 1999 also deserted their burrows. Irrespective of whether birds changed burrows due to investigator disturbance or reproductive failure per se, we presume that they deserted their 1999 burrows in order to improve the likelihood of reproductive success in the future.

Our results demonstrate that *weekly* and *daily* investigator disturbance during incubation had strong negative effects on the hatching success and nest-site fidelity of Leach's storm-petrels. However, we studied Leach's storm-petrels that had experienced little or no investigator disturbance during the prior decade, so the reductions in hatching success and nest-site fidelity we observed probably were at the high end of the range. Long-lived birds such as procellariiforms have the potential to habituate to investigator disturbance within and across seasons (e.g., Burger and Gochfeld, 1999), therefore the negative effects of disturbance might diminish as individuals gain additional exposure to research activities, for example during a long-term study. Although investigator disturbance has not been shown to reduce breeding performance in all seabirds studied (review by Nisbet, 2000), several studies have obtained results that are similar to ours (reviews by Carney and Sydeman, 1999; Nisbet, 2000), suggesting that investigator disturbance may adversely affect a number of long-lived species. We encourage researchers studying long-lived seabirds to consider both the short-term and long-term effects of investigator disturbance on reproduction, especially for naïve birds.

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