

Factors Affecting Colony Formation in Leach's Storm-Petrel

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First-time breeding seabirds either return to the vicinity of their natal colony to nest (Fisher and Lockley 1954, Lack 1968) or travel between many active colonies as well as uncolonized sites looking for breeding sites (Harris 1984, Podolsky 1985, Kress and Nettleship 1988). The factors associated with nest-site selection include physical aspects of the environment such as vegetation structure, topography, or soil type (Klopfer and Hailman 1965) and social factors such as the sight and sound of conspecifics (Darling 1938; Lack 1954, 1966; Orians 1966).

The presence of a group of conspecifics is a strong indicator that a particular site is both safe and productive. This social facilitation hypothesis, first proposed by Darling (1938), predicts that first-time breeding colonial birds should be attracted to the stimuli associated with an active group of conspecifics (Brockway 1964, Klopfer and Hailman 1965, Lehrman 1965, Lott et al. 1967, Erickson 1970, Burger and Shisler 1980). The alternative hypothesis is that social stimuli do not attract first-time breeders.

We tested this hypothesis by observing the response of Leach's Storm-Petrels (*Oceanodroma leucorhoa*) to experimentally presented vocalizations and hand-dug nesting burrows. We reasoned that if tape-recorded vocalizations and artificial burrows led to colonization at islands without active petrel colonies it would support the social facilitation hypothesis. Likewise, the lack of visitation or breeding in the presence of social stimuli would indicate that other factors, such as purely physical aspects of the habitat, may operate in the colony formation process.

Leach's Storm-Petrels have two distinct vocalizations at the nesting colony (Townsend 1924, Gross 1935, Hall-Craggs and Sellar 1976). The chuckle call is usually given in flight and more rarely uttered from the burrow. The purr call is given exclusively from the burrow.

Adult storm-petrels are strongly attracted to recordings of their vocalizations (Grubb 1973, Furness and Baillie 1981). Grubb (1973) found a significant increase in the number of storm-petrels flying in the vicinity of amplified vocalizations. Ainley et al. (1976) have shown that amplified recordings of Leach's Storm-Petrels greatly increase the capture rate of Leach's and Fork-tailed (*O. furcata*) storm-petrels.

Our objective was to induce Leach's Storm-Petrels to breed at uncolonized islands by presenting am-

plified vocalizations in combination with hand-dug burrows. We conducted capture experiments and colonization experiments. In the capture experiments the rate of storm-petrels captured in a mist net was compared among eight different sound treatments. In the colonization experiments the number and breeding behavior of storm-petrels in artificial burrows was compared among burrows where no vocalizations were played, burrows where purr calls or chuckle calls only were played, and burrows where both purr and chuckle calls were played.

The experiments were conducted on five islands in Muscongus Bay, Maine (Knox and Lincoln counties), near the southern limit of the nesting range of Leach's Storm-Petrel in the western North Atlantic. The islands are within 8 km of each other and include Eastern Egg Rock, Ross Island, Wreck Island, Franklin Island, and Old Hump Ledge. Eastern Egg Rock, Ross Island, and Old Hump Ledge are treeless islands dominated by grasses including timothy (*Phleum pratense*) and terrell grass (*Elymus virginicus*) and shrubs including raspberry (*Rubus idaeus*) and elderberry (*Sambucus canadensis*). The dominant vegetation on Wreck Island and Franklin Island is red spruce (*Picea rubra*).

At the initiation of this project in 1980, Leach's Storm-Petrels bred on Eastern Egg Rock and had bred previously on the experimental islands except for Ross Island (Cruickshank 1950). Leach's Storm-Petrels currently breed on only 16 of the ca. 3,000 Maine islands with a total population estimated at 19,000 pairs (Korschgen 1979). Our observations have shown that nonbreeding storm-petrels visit or "prospect" at islands other than their natal island before they breed. The islands in this study were visited frequently by storm-petrels.

The capture experiment was conducted at Eastern Egg Rock in July 1982. During July, breeders were distinguished from prebreeders and nonbreeders by the complete absence of down on the brood patch (Ainley et al. 1976). It was not possible to distinguish between pre- and nonbreeders. We set two 12-m-long mist nets with 2.5-cm mesh: one over 24 artificial burrows and the other ca. 25 m away from artificial burrows. There were no active, natural petrel burrows near the study site. We attracted storm-petrels by playing a TDK 3-min endless loop cassette tape of the two vocalizations from a portable cassette deck. The recordings were made in 1978 at Eastern Egg Rock. The amplitude of the playback was constant among the treatments at 70 and 90 dB measured 1 m from the tape deck with a hand-held Realistic decimeter (model 42-3019). For 10 nights, storm-petrels were

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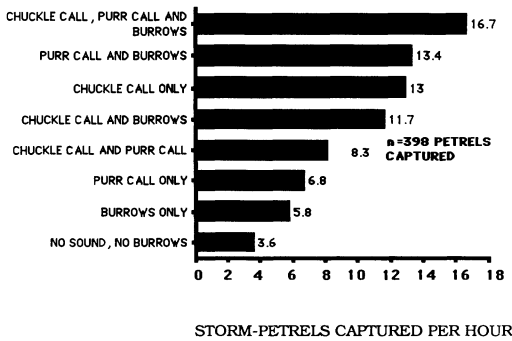


Fig. 1. Storm-petrels captured per hour of mist-netting for each sound treatment ($\chi^2 = 127.44$, $df = 7$, $P < 0.01$, $n = 40$ h).

captured from 2200 through 0200, yielding a 40-h sample. Each 30 min during that time, 1 of the 8 treatments (see below) was selected at random.

The treatments included: (1) no sound and no burrows (control), (2) burrows only, (3) purr calls only, (4) chuckle calls only, (5) purr calls and burrows, (6) chuckle calls and burrows, (7) chuckle calls plus purr calls, and (8) chuckle calls plus purr calls plus burrows. The number of petrels captured per 30 min was recorded. Unbanded petrels were banded on the right leg with a USFWS stainless steel band. We recorded whether individuals were breeders or prebreeders from the condition of the brood patch (bare or downy).

The capture data were analyzed by Chi-square tests on the actual capture rate vs. the expected capture rate. The number of petrels captured per hour of control was used as the expected capture rate. Probability levels < 0.05 were considered significant.

The colonization experiments were conducted on Old Hump Ledge in 1980, Ross Island in 1981, Wreck Island in 1982, and Franklin Island in 1983. On each island we built two or more sets of artificial burrows with 18–36 burrows/set. We made a total of 264 artificial burrows on the four islands. Burrow sets were built in habitat where the dominant vegetation, slope and exposure appeared uniform based upon visual inspection.

Artificial burrows were hand-dug and spaced 60–100-cm apart. Each burrow had a single entrance 10 cm in diameter, which led into a 40–50-cm tunnel. In each burrow, the entrance tunnels led into a nest chamber set to the left of the entrance tunnel, thus forming an "L-shaped" burrow. The nest chambers were ca. 25 cm in length, height, and width. A hole was cut into the top of the nest chamber and covered with a flat rock which, when lifted, allowed inspection of the burrow.

Burrow sets were assigned randomly to 1 of 4 treatments: no sound (control), chuckle call only, purr call only, and both purr and chuckle calls. The burrows

that received sound stimuli had a single 13-cm outdoor speaker placed centrally among the burrows. Vocalizations were played continuously from 2200 to 0400 from mid-May to mid-August for a single field season. The extended use of the tape was made possible by using 3-min endless loop tape cassettes broadcast on a cassette player powered by a 12-volt car battery. An automatic timer (see Kress 1983 for technical specifications) activated the sound system. The amplitude produced by this sound system generated ca. 80 dB at 1 m from the speaker.

The artificial burrows and sound equipment were examined no less than every two weeks during the year of sound stimulation and approximately once a month in years after sound stimulation. Burrows were classified as being either colonized or inactive. Burrows were colonized if they contained a petrel egg or chick, had excavations, contained petrel feathers, or contained one or more adults. Inactive burrows showed none of these. Each unbanded storm-petrel found in a burrow was banded on the right leg with a USFWS stainless steel band. The condition of the brood patch (bare or downy) was recorded.

We pooled the colonization data for the four islands and analyzed by Chi-square test on the number of burrows colonized per treatment vs. the expected number colonized. Expected values were the proportion of burrows in each treatment multiplied by the total number of colonized burrows. Probability levels of < 0.05 were considered significant.

The distance from each burrow to the speaker was recorded for all burrow sets in a sound treatment. We compared the observed distribution of colonized and inactive burrows to the expected distribution. The expected distribution was the proportion of the total burrows present at a particular distance from the speaker multiplied by the total number of colonized burrows. Attraction occurred when the colonized burrows were closer to the speaker than was expected from a random pattern of colonization and visitation. Conversely, we assume that storm-petrels avoided the sound when colonized burrows were distributed farther away from the speaker than expected (Marler 1968, 1972).

The rate of hourly capture differed significantly among the treatments from the expected capture rate of 3.6 storm-petrels/h ($\chi^2 = 127.44$, $df = 7$, $P < 0.01$; Fig. 1). The highest capture rate (16.7 birds/h) was where we presented purr and chuckle vocalizations in combination with artificial burrows. This rate was significantly higher than the capture rate of 3.6 birds/h for the control ($\chi^2 = 61.70$, $df = 1$, $P < 0.001$). The capture rate (13.4 birds/h) for purr call and burrows was significantly higher than the capture rate (6.8) for purr call ($\chi^2 = 9.10$, $df = 1$, $P < 0.001$). The capture rate for the chuckle call was significantly higher than for the purr call ($\chi^2 = 8.20$, $df = 1$, $P < 0.001$). Of the 398 storm-petrels captured, 93% had either completely downy or partially downy brood-patches indicat-

ing that they were either prebreeders or nonbreeders (Ainley et al. 1976).

No burrows in the chuckle treatment or no sound treatment were colonized on any island. However, 17.5% of the purr only treatment and 23.8% of the purr and chuckle treatment were colonized (Table 1). On Old Hump Ledge in 1979, 28% of the burrows in the purr and chuckle treatment were colonized. On Ross Island in 1980, 30% of the burrows in the purr and chuckle treatment were colonized, whereas 17.5% of the Ross Island burrows in the purr treatment were colonized. On Wreck Island in 1981, 20% of the burrows in the purr and chuckle treatment were colonized. On Franklin Island in 1982, 19% of the burrows in the purr and chuckle treatment were colonized.

The observed pattern of burrows colonized departed significantly from the expected ($\chi^2 = 14.51$, $df = 3$, $P < 0.001$, $n = 46$; Table 1). Only burrows in the purr and chuckle treatment or the purr call treatment were colonized on the four islands. Colonized burrows were closer to the speakers than expected assuming a random effect of distance ($\chi^2 = 37.52$, $P < 0.01$, $n = 46$; Fig. 2).

The number of burrows colonized dropped from 46 to 17 in the first year. Two years after sound stimulation, 14 of these 17 burrows remained colonized (Table 2). On Old Hump Ledge 8 yr after sound stimulation (1988), 7 of 24 burrows contained either an egg or chick and 4 additional natural burrows near the artificial burrows contained either an egg or chick.

Coloniality evolves when the advantages of group breeding outweigh the disadvantages (Alexander 1974). Where there is an advantage to be gained by group breeding, such as reduced risk of predation (Hamilton 1971) or enhanced food finding (Ward and Zahavi 1973), individuals that select a breeding site close to conspecifics will have higher reproductive success than individuals that nest elsewhere. Although there are no published data for storm-petrels, in some seabirds those individuals that breed away from conspecifics (Bergman 1980) or at the edge of the colony (Coulson 1968, Kosinski and Podolsky 1979, Podolsky 1980) have lower reproductive success than those that nest in the colony center.

Storm-petrels were more likely to colonize burrows

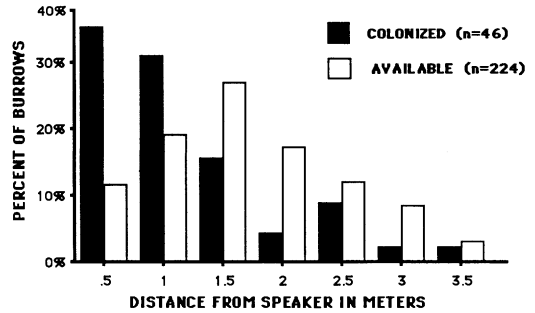


Fig. 2. The percentage of burrows available and colonized at 0.5-m intervals away from the speakers ($\chi^2 = 37.52$, $P < 0.01$, $n = 46$).

where both purr and chuckle vocalizations or the purr only vocalization were presented and did not colonize burrows stimulated with only chuckle calls or without calls. Chuckle and purr calls are the stimuli typically heard at an active colony when petrels are prospecting for nest sites. Purr calls are given only underground and may indicate the presence of an established breeder. We believe that prospectors are most attracted to artificial burrows stimulated with the complete set of sounds typical of an active petrel colony.

Storm-petrels tended to colonize the burrows closest to the speakers. Of the burrows within 0.5 m of the speakers, 70% were colonized compared to only 16% colonized at 3 m or more beyond the speakers. The tendency to colonize close to conspecifics reduces individual risk of predation by close association with more potential prey (Coulson 1968, Hamilton 1971).

The implication of the attraction experiments to endangered bird management is far-reaching. There are currently 60 species of endangered colonial birds worldwide, 30 of which are seabirds (King 1981). Many are endangered because of habitat destruction, especially the destruction of their colonies by introduced predatory mammals (King 1981). Attraction of prospecting birds to remaining safe sites or to sites that have been restored shows great potential for managing threatened seabirds. This is especially true

TABLE 1. The number of burrows available and colonized (in parentheses) per sound treatment on the four experimental islands ($\chi^2 = 14.51$, $df = 3$, $P < 0.001$, $n = 46$).

	Burrows only	Chuckle only	Purr only	Purr and chuckle
Old Hump Ledge 1979	—	—	—	32 (9)
Ross Island 1980	20 (0)	20 (0)	40 (7)	40 (12)
Wreck Island 1981	20 (0)	—	—	20 (4)
Franklin Island 1982	—	—	—	72 (14)
Total burrows available	40	20	40	164
Total burrows colonized	0	0	7	39
Expected burrows colonized	7	3.5	6.9	28.6

TABLE 2. The reproductive performance of storm-petrels in colonized burrows on the 4 experimental islands during the season of sound stimulation, and 1 and 2 years after sound stimulation.

	Year of sound stimulation	1 yr after sound stimulation	2 yr after sound stimulation
Total no. of artificial burrows	264	264	264
Artificial burrows colonized	46	17	14
No. of burrows with prospectors	36	11	8
No. of burrows with breeders	10	6	6
No. of eggs produced	10	6	6
No. of eggs hatched	2	4	4
No. of chicks fledged	0	0	2

where prebreeders are known to prospect at safe sites or at sites where introduced predators are being controlled or have been eliminated.

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Plumage Color Correlates with Body Size in the Ruff (*Philomachus pugnax*)

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The behavioral and plumage polymorphism in the Ruff (*Philomachus pugnax*) is well-known but not yet fully understood. Males develop an elaborate and conspicuous breeding plumage with enlarged neck-feathers (the ruff) and ear-tufts, both of which vary from black and brown to white (Selous 1906–1907, Søgaard Andersen 1948). This plumage polymorphism is correlated with a behavioral polymorphism. Dark males form territories on a lek (i.e. independents; van Rhijn 1973), either as "residents" or "marginals," while white males behave as satellites and do not defend territories of their own (e.g. Hogan Warburg 1966, van Rhijn 1973).

Male Ruffs are larger than females, a situation which is rare in the Scolopacidae (Jehl and Murray 1986: fig. 2). Furthermore, resident males have, on average, longer wings than marginal males which in turn have longer wings than satellites (van Rhijn 1983). Territorial males also weigh more than satellites (Dobrin-ski in Cramp 1983) and dark males have longer wings than white males (Gibson in van Rhijn 1983 and Cramp 1983). Body size (measured as wing length) also appears to determine status on the lek among territorial males (van Rhijn 1983). Because wing length may increase with age in waders (e.g. Pienkowski and Minton 1973), differences in wing length among color

types could be due to age differences, with darker, territorial males on average being older than satellites. However, plumage color did not change between years among males that returned to the same lek (Søgaard Andersen 1948), though male age was unknown in that study (all observations were based on adult birds only). Thus, plumage color, body size, and age may all be correlated and contribute to the mating tactics used by individual males.

Van Rhijn (1973, 1983) suggested that both the color and behavior of Ruff males were controlled genetically by separate but linked sets of genes, now at equilibrium. Reproductive success was thought to be the same for territorial males as for satellites. This may constitute an example of a mixed evolutionary stable strategy (mixed ESS; Maynard Smith and Parker 1976) where dark and light males are maintained in the population by equal genetic payoffs, though different costs and benefits are associated with the two strategies (Maynard Smith 1983).

We measured four body-size characters in ruff specimens in full breeding plumage from the collections of the British Museum in Tring, England, and the Natural History Museum in Stockholm, Sweden. One of these characters, tarsus length, is an age-independent character (Garnett 1981, Alatalo and Lundberg 1986) and should be a useful control for age differences between differently colored males. We measured bill (culmen) and tarsus (tibio-tarsus) length to

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