

AN EXPERIMENTAL STUDY OF SOCIAL ATTRACTION IN TWO SPECIES OF STORM-PETREL BY ACOUSTIC AND OLFACTORY CUES

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Abstract. Many birds, notably colonial nesting seabirds, use public information (the visual, auditory, and olfactory presence of breeding conspecifics) when selecting nesting habitat. When colonies are extirpated, social cues that indicate nesting sites' quality are lost. In the Aleutian Islands, Alaska, storm-petrel populations were destroyed by introduced arctic foxes (*Alopex lagopus*) and have been slow to return after the foxes' eradication. We tested various social-attraction techniques as a method to encourage recolonization of Leach's (*Oceanodroma leucorhoa*) and Fork-tailed Storm-Petrels (*O. furcata*) in Ulva Cove at Amatignak, a former fox-farming island. We tested attraction to playback of each species' calls by broadcasting them in various patterns adjacent to a mist net and attraction to their odors with a T-maze design. We combined these two cues to test whether birds were more likely to enter and inhabit artificial burrows depending on playback and odor treatment. Both species of storm-petrel were attracted strongly to playback of conspecific calls and somewhat to playback of heterospecific calls; Fork-tailed Storm-Petrels were attracted to conspecific odor and entered more artificial burrows when we combined odor and playback cues. We discuss the implications of these results, including the development of protocols to encourage restoration of seabird colonies in the Aleutian Islands after eradication of introduced foxes and Norway rats (*Rattus norvegicus*).

Key words: artificial burrows, island restoration, odor, playback, social attraction, storm-petrel, T-maze

Estudio Experimental de Atracción Social en Dos Especies de *Oceanodroma* con Señales Acústicas y Olfativas

Resumen. Muchas aves, particularmente las aves marinas que anidan en colonias, usan información pública (presencia visual, auditiva y olfativa de individuos anidando de la misma especie) para seleccionar el hábitat de nidificación. Cuando se extirpan las colonias, se pierden las señales sociales que indican la calidad de los sitios de nidificación. En las islas Aleutianas, Alaska, las poblaciones de *Oceanodroma* fueron destruidas por los zorros del Ártico introducidos (*Alopex lagopus*) y se han recuperado lentamente luego de la erradicación de los zorros. Evaluamos varias técnicas de atracción social como método para promover la recolonización de *O. leucorhoa* y *O. furcata* en la Cala de Ulva en Amatignak, una isla donde antiguamente se criaban zorros. Evaluamos la atracción a llamados previamente grabados de cada especie reproduciéndolos en varios patrones adyacentes a una red de niebla y la atracción a sus olores con un diseño de laberinto "T." Combinamos estas dos señales para evaluar si las aves tenían una mayor probabilidad de entrar a y habitar madrigueras artificiales dependiendo del tratamiento de reproducción de llamados y olor. Ambas especies fueron fuertemente atraídas por la reproducción de llamados de individuos de la misma especie y en menor medida por la reproducción de llamados de individuos de la otra especie; los individuos de *O. furcata* fueron atraídos por el olor de los individuos de la misma especie y entraron a más madrigueras artificiales cuando combinamos señales de olor y reproducción de sonidos. Analizamos las implicancias de estos resultados, incluyendo el desarrollo de protocolos para promover la restauración de las colonias de aves marinas en las islas Aleutianas luego de la erradicación de zorros y ratas (*Rattus norvegicus*) introducidos.

INTRODUCTION

Historically, avian conservation strategies have focused on the creation, enhancement, and protection of key habitats. There is an underlying assumption in avian conservation that, if suitable habitat structure and protection from anthropogenic disturbance can be provided, birds will return ("if you build it, they will come"; Ahlering and Faaborg 2006). Although this strategy is important and often effective, it may be inadequate

in some cases. It fails to consider basic avian social behavior that may delay recovery of some bird species (e.g., colonial species) no matter how suitable the habitat appears (Muller et al. 1997, Clout 2001, Doligez et al. 2002).

There are many examples where habitat management through protection from anthropogenic disturbance has not resulted in the return of avian populations. In California Common Murres (*Uria aalge*) had not returned to breed 10 years after an oil spill and El Niño extirpated a large colony

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(Parker et al. 2007), in Australia bark-foraging woodland birds had not colonized revegetated grazed paddocks after 50 years (Martin et al. 2004), and in New Zealand Common Diving Petrels (*Pelecanoides urinatrix*) did not return to Mana Island over 10 years after the eradication of house mice (*Mus musculus*) (Miskelly and Taylor 2004).

We conclude that recovery of extirpated populations should not be limited to habitat management alone but that social and behavioral factors must also be considered. For many colonial birds, especially island-nesting seabirds, strong fidelity to a site and colony is a basic element of their behavior that may limit recolonization (Greenwood and Harvey 1982, Danchin and Wagner 1997). Young seabirds of philopatric species simply return to their natal site to breed (Jenouvrier et al. 2008), while dispersing seabirds use "public information" provided by breeding conspecifics to signal safe nesting habitat (Forbes and Kaiser 1994, Danchin et al. 1998, 2004, Wagner and Danchin 2010). Seabirds choose a breeding site on the basis of many criteria: absence of predators, topography, substrate, and proximity to feeding grounds (Birkhead and Furness 1985, Stephenson and Irons 2003). Gathering information about resources on multiple islands scattered over wide expanses of open ocean would be energy demanding and costly (Boulinier and Danchin 1997). Therefore, settling at a natal site or monitoring conspecifics and acquiring visual, auditory, or olfactory information (Podolsky and Kress 1989, Kress 1998, Nevitt 2008) is likely a much more parsimonious method of assessing nest-site quality (Betts et al. 2008). These behaviors result in little pioneering of unoccupied sites and habitat (Forbes and Kaiser 1994). Once formed, however, new colonies become highly attractive to prospecting birds (through the use of public information) and can grow quite rapidly (Kildaw et al. 2005).

At sites where seabird colonies have been extirpated or severely reduced (as by introduced predators), public information that signals suitable nesting habitat is destroyed (Forbes and Kaiser 1994). Therefore, prospecting individuals may no longer consider such places for nesting, and recolonization after habitat enhancement will be slow or none. If the abandoned site is still suitable for nesting, established colonies can be simulated artificially to attract birds (Kress 1997, Parker et al. 2007). The use of decoys, mirrors, and playbacks to simulate public information from active colonies is referred to as social attraction, its goal being to encourage prospecting birds to land among artificial cues and remain long enough to attract additional birds (Kress 1998). As more birds congregate at the site, potential breeders should have an increased chance of pairing and breeding, eventually establishing a colony (Parker et al. 2007, Kress 1998).

Storm-petrels (Procellariiformes: Hydrobatidae) are colonial nocturnal burrow-nesting seabirds known to use public information, such as conspecific vocalizations, when selecting nesting habitat (Warham 1990). Like many other island birds, storm-petrels are extremely vulnerable to predation because of their small size, lack of anti-predator behavior, low reproductive rates, ground-nesting habits, and long nestling periods (Atkinson 1985, Warham 1990). Thus, the introduction of predatory mammals can result in the destruction

of entire colonies or species such as the Guadalupe Storm-Petrel (*Oceanodroma macrodactyla*; Jehl and Everett 1985). When colonies of storm-petrels are extirpated, populations often do not return, as a result of a combination of social constraints (Podolsky and Kress 1989) and demographic factors (Warham 1990). Thus there is now a need to understand the use of cues in the formation of storm-petrel colonies to facilitate the development of techniques to attract individuals to empty sites.

Island ecosystems across the Aleutian chain in Alaska have been devastated by the introduction of mammalian predators. Most islands were stocked with Arctic foxes (*Alopex lagopus*) for the fur trade, and Norway rats (*Rattus norvegicus*) were accidentally introduced to several (Ebbert and Byrd 2002). Consequently, colonies of Leach's (*Oceanodroma leucorhoa*) and Fork-tailed Storm-Petrels (*O. furcata*) were eliminated or severely reduced (Murie 1959, Bailey 1993, Bailey and Kaiser 1993, Williams et al. 2003). Eradication of introduced foxes from the Aleutian Islands has been a priority of the Alaska Maritime National Wildlife Refuge since the first successful eradication in 1949 (Ebbert and Byrd 2002). The rate of storm-petrel recolonization after fox removal has ranged from relatively fast (Fork-tailed Storm-Petrel, Kasatochi Island; Drummond 2007) to none (Nizki/Alaid Island; Byrd et al. 1994). We conclude that a protocol is needed to encourage storm-petrels to recolonize Aleutian Islands where they remain extirpated after eradication of the fox.

It is widely known that storm-petrels are attracted to playback of their calls, and attempts to establish new colonies by this type of social attraction have been successful (Podolsky and Kress 1989, Bolton et al. 2004). It is also known that some species of breeding storm-petrel navigate to their burrow by olfaction and are attracted to their own nesting material (Grubb 1974). However, olfaction has not been used in social-attraction experiments. The general objective of our study was to consider whether social-attraction techniques are suitable for both species of storm-petrel common to the harsh and expansive environment of the Aleutian Islands. We addressed the following questions: (1) Does call playback successfully attract storm-petrels to Ulva Cove, Amatignak Island, a location typical of the Aleutian Islands, and, if so, what type of playback treatment is most attractive and what status (breeding or nonbreeding) of bird is most attracted? (2) Are nonbreeding storm-petrels attracted or repelled by conspecific odor? (3) With simultaneous auditory and olfactory cues, is it possible to attract storm-petrels to artificial burrows at Ulva Cove? Within the context of our results at Amatignak Island, we discuss the possibility of using social attraction as a conservation technique to speed the rate of storm-petrel recolonization in the Aleutian Islands.

METHODS

STUDY AREA

We carried out our experiments at Ulva Cove on Amatignak Island in the western Aleutian Islands (Fig. 1). Amatignak is an average-sized Aleutian island (1433 ha) adjacent

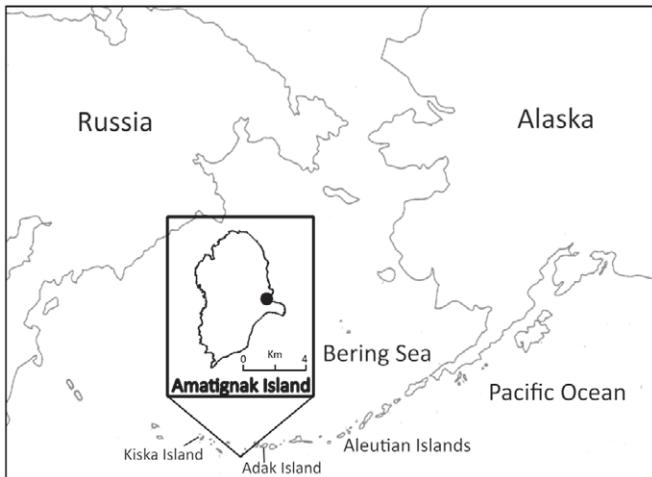


FIGURE 1. Map of experimental site, Ulva Cove (51.27 °N, 179.10 °W), in relation to the Aleutian Archipelago. Ulva Cove, represented by a dot, is on the east side of Amatignak Island.

to Amchitka Pass. Foxes were removed from Amatignak in 1991, thus the island is now free of all terrestrial mammals. Like most Aleutian Islands, Amatignak is treeless, characterized by subarctic tundra including patches of grasses (*Leymus* sp.) and Umbelliferae (*Heracleum*, *Angelica*), with hyperoceanic blanket-bogs at low elevations. We selected Amatignak for study of storm-petrel restoration on the basis of its relatively long time of recovery since fox eradication, its resemblance in vegetation and terrain to the site of the large active storm-petrel colony at Buldir (Byrd and Trapp 1977), its similarity in size to other islands storm-petrels inhabit, and the presence of vocal storm-petrels, indicating the presence of prospecting birds (Buxton 2010).

PLAYBACK

We evaluated the Leach's and Fork-tailed Storm-Petrels' response to auditory playback at Ulva Cove by broadcasting various storm-petrel calls adjacent to a mist net.

We recorded typical storm-petrel calls at North Bight, Buldir Island, in 2006 with a Sony TCD-D10PROII digital audio tape recorder or Fostex FR-2 solid-state recorder with a Sennheiser MKH 70 or MKH 816 directional microphone (Seneviratne et al. 2009) and in 2008 with a Song Meter (Wildlife Acoustics, Inc., firmware version 1.5.0, model SM1). We randomly selected between five and 10 recorded calls (from different individuals) with no background noise and combined them into 2-min medleys with the application Garage Band (Apple, Inc.), and uploaded to an iPod shuffle (Apple, Inc.).

To test response to a variety of playback types, we used five treatments: silent control (no sound), noise control (20 sec on/5 sec off increments of John Mellencamp's "Jack and

Dianne," Riva Records, 1982), Leach's Storm-Petrel playback (a combination of chuckle and purr calls; Taoka et al. 1988), Fork-tailed Storm-Petrel playback (a combination of three-syllable flight calls and the male's single-syllable calls; Simons 1981), and colony playback (a combination of all calls of both species of storm-petrel). We used a combination of two call types for each species because Podolsky and Kress (1989) captured Leach's Storm-Petrel at a higher rate by using both *chuckle* and *purr* calls. In 2008, we ran playback experiments for a total of 15 nights from 26 June to 2 August (each treatment played for three nights); in 2009, we ran experiments for a total of 25 nights from 6 June to 26 July (each treatment played for five nights), playing different treatments on each night according to a randomized schedule. Recordings were broadcast from a TOA ER-2230 wireless megaphone facing toward the ocean, on a 30 min on/30 min off schedule from 01:30 to 04:30 (HAST) each night. This period represents the mean peak of storm-petrel calling according to counts of calls recorded by devices placed at other sites around Amatignak (Buxton 2010).

To evaluate response to playback, we recorded the number of storm-petrels captured in an 8-m by 2-m mist net placed in the middle of Ulva Cove, at the boundary between the rocky beach and grassy vegetation. The megaphone was placed midway between the net poles, ~2 m back in the grass. In 2008, to detect recaptures, we marked captured storm-petrels with a spot of quick-drying nail polish on the outer rectrix. In 2009, we banded captured storm-petrels with U.S. Geological Survey (USGS) stainless steel bands. To detect breeders, we examined all birds for a medial brood patch. Because we recognize the problems associated with linking a de-feathered brood patch to a storm-petrel's current breeding status (Boersma et al. 1980, Warham 1990), we scored birds captured on Amatignak by using the swollen and vascularized brood patches of breeding birds found in burrows on Buldir Island (an active colony) as a reference (RTB pers. obs.). We did not infer breeding from partial brood patches.

T-MAZE

To test nonbreeding storm-petrels' response to conspecific odors, we experimented with a T-maze (e.g., Grubb 1974) inside a 4-m by 5-m Weatherport shelter from 12 June to 27 July 2009. The maze was constructed of 1.5-cm birch plywood and consisted of a clear acrylic top (to permit observation of the bird inside), an electric fan, a 20-cm by-20 cm choice arena, and three removable coriboard (4 mm) boxes (Fig. 2). Each removable 12-cm by 12-cm box had a clear acrylic top, a sliding divider on the side facing the maze, and a 1-cm plastic mesh opposite for ventilation. One box, the "start box," contained the test bird and was placed in front of the fan, and the two other

boxes contained scented materials (see below) and were placed at either end of each 30-cm arm (Fig. 2). The maze's floors were lined with removable white corriboard that was washed with 70% methanol and water between trials. Air and odor were drawn through the maze, from the ends of the arms toward the choice area and start box, by a 12-volt-battery-powered CPU cooling fan (Thermaltake, Inc.) set to its minimum of 243 L min^{-1} .

We captured the experimental subjects in an 8-m by 2-m mist net set up 25 m east of the Weatherport, using playback of conspecific calls from a TOA ER-2230 wireless megaphone as an attractant. Captured storm-petrels lacking brood patches were given a 5- to 7-min acclimation period in the start box prior to experimental trials. At 1 min before trials began, we

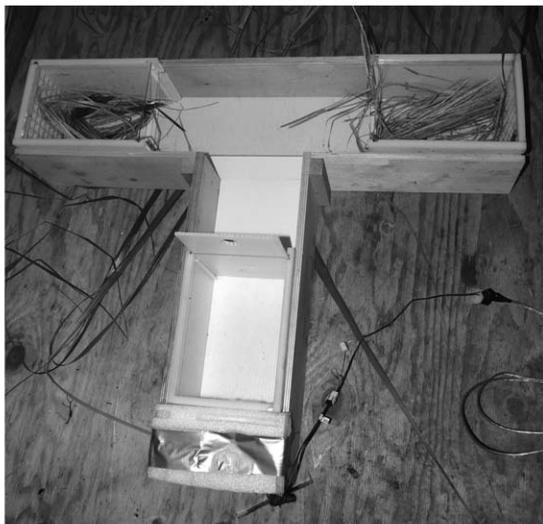
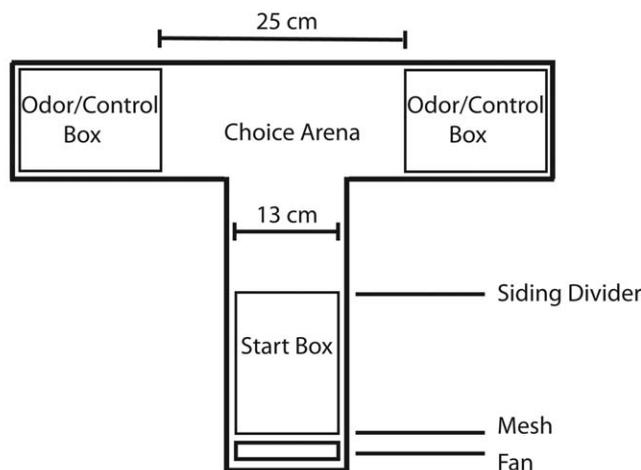


FIGURE 2. Above: T-maze design used to test attraction of non-breeding storm-petrels to conspecific odor. It includes three removable plastic 12-cm by 20-cm boxes, each with mesh at one end to allow for air circulation and a sliding divider at the other to release the bird into the choice arena. Below: T-maze set up in the field, on the weatherport shelter floor.

inserted odor boxes into the end of each arm and activated the fan to draw odor evenly through the maze. The odor boxes, choice arena, and area beyond the start box were covered with black garbage bags so that the observer was blind to the location of the scent boxes and the bird could not see the observer. After the acclimation period, we inserted the start box containing each subject into the maze and opened the divider. The blind observer (RTB) recorded the following: species (Leach's or Fork-tailed), stress level of the subject (see below), whether or not the bird had to be nudged (poked lightly with a pencil), the time (min) it took the bird to make a decision, and the bird's final decision (defined as >30 sec spent in the scent box or arm of the maze). We defined a bird as "stressed" if it exhibited any combination of the following behaviors: scratching at the edges of the box, fluttering wings, vocalizing, or pacing. Each bird was given 2 min to move, after which, if it was still in the start box, it was nudged. If no reaction was observed the bird was recorded as "no choice." Between each trial each individual had a 5-min rest period while we cleaned the maze's walls and replaced the control materials. Each bird was the subject in three different odor-choice trials: (1) "stomach oil"—paper towel saturated with regurgitation versus plain paper towel, (2) "feather odor"—collected by rubbing 3–5 birds with a paper towel versus plain paper towel, and (3) "nesting material"—made by putting 7–10 captured birds in a scent box on top of dry *Leymus* grass for 15 min each versus fresh dry *Leymus* grass. These materials were collected before each night of trials with the maze during the mist-net/playback experiments and kept in a sealed fresh Zip-lock bag. The order in which the trials were presented was randomized, as was whether the scented materials were positioned on the left or right, to control for the possibility of multiple testing of the same subject influencing selection by learning and cross-over effects (Minguez 1997, Diaz-Uriarte 2001). To control for the possibility of birds orienting to external or internal cues, we randomized the orientation of the maze facing north, south, east, or west for each successive trial. After completing three odor trials, each subject was marked with a USGS stainless steel band and released.

ARTIFICIAL BURROWS

To assess the possibility of auditory playback and olfactory cues attracting storm-petrels to artificial burrows in the valley around Ulva Cove, we set up a series of artificial nest-site study plots within habitat suitable for storm-petrel nesting. Two plots were located 50 m apart, on the north face (plot 2: 51.2605° N , 179.0799° W , plot 3: 51.2607° N , 179.0788° W) on a substrate dominated by tussocks of *Leymus* sp. (rye grass) and *Heracleum lanatum* (cow parsnip). One plot was located 800 m away on the south face of the valley (plot 1: 51.2576° N , 179.0771° W) on a substrate dominated by poorly drained *Lycopodium selago* (fir club moss) and *Leymus* sp. All plots were at least 75 m from the site of the playback experiment. All

plots were 5 m by 5 m at an elevation of 15 m above sea level. In 2008, we placed 15 plastic tubes 40 cm long and 10 cm in diameter in grass tussocks or buried them into the ground at each plot; in 2009, we added 5 more tubes to each site. At the end of each plastic tube, we dug a small chamber (approximately 15 cm by 15 cm) into the soil. The design of the artificial burrows was based León and Mínguez (2003), and their dimensions were based on the mean burrow length of 43 cm and chamber depth of 13 cm of Leach's Storm-Petrels nesting on islands in Newfoundland and Maine (Huntington et al. 1996).

Treatments included (1) "control," with no sound or manipulation of burrows, (2) "playback," in which we broadcast recordings of both species of storm-petrel from the plot, and (3) "playback and nesting material," in which we broadcast recordings and placed nesting material inside each artificial burrow. We ran one of three treatments per night at each consecutive site according to a randomized schedule. Experiments were run for 21 nights (7 nights per treatment) from 3 July to 6 August in 2008 and for 34 nights (17 nights of control, 10 nights of playback, and 7 nights of playback and nesting material) from 6 June to 28 July in 2009. At 00:30 we placed a toothpick upright 5 cm back from the entrance to each burrow (Moller et al. 2003). On "playback" nights, from 00:30 to 05:00, we broadcast recordings of a colony (a medley of both species' calls) on a TOA ER-2230 wireless megaphone from an iPod shuffle. On "playback and nesting material" nights, in addition to broadcasting calls, in 2008 we placed nesting material collected from storm-petrel burrows on Buldir Island in each burrow and in 2009 we placed nesting material from the T-maze experiment in each burrow. After "playback and nesting material" nights, we removed nesting materials and scraped the soil chamber at the end of each burrow in an attempt to disperse odors.

Between 05:30 and 11:00 after each night, we checked burrows for whether the toothpick had been knocked down and for other signs of activity such as presence of feathers or evidence of digging. Diurnal songbirds were also active at this time of morning, and, although it is unlikely, they may have occasionally investigated burrows.

STATISTICAL ANALYSES

For data analysis we used the statistical program R version 2.11.1 (R Development Core Team 2010) and assumed statistical significance $\alpha = 0.05$. All data are presented as mean \pm SE.

We used a generalized linear mixed model (GLMM) with a Poisson error structure, log link, and fit with a Laplace approximation to examine the relationship between number of captures of each species of storm-petrel and playback treatments. We included day of the year as a continuous random variable to remove the effects of nightly environmental conditions. Because there was no difference between the two control types ($Z_1 = 0.032$, $P = 0.97$), we combined silent and noise

controls into a single treatment category, "control." To determine how many more birds were captured during playback treatments than during the control, we set the control as the intercept and inverse-log-transformed parameter estimates from the GLMM. To analyze effects of factors such as stress, nudging, and different trial types on the birds' ultimate choice between odor and control in the T-maze, we ran a GLMM with a binomial error structure, logit link, and fit with a Laplace approximation. We included an individual's identity as a random variable because each bird was tested three times (Diaz-Uriarte 2001). To assess preference for odor or control while controlling for repeated testing (cross-over effects) for each species we ran a null binomial GLMM with only the random variable (individual) (Diaz-Uriarte 2002). We used odds ratios to determine if more birds were orienting toward the odor. To analyze knocking down of the toothpick at the entrance to each artificial burrow as a function of year, night, and treatment, we ran a GLMM with a Poisson error structure and log link fit with a Laplace approximation, with site as a random variable.

RESULTS

PLAYBACK

Both Leach's and Fork-tailed Storm-Petrels were strongly attracted to "conspecific" and "colony" playback. Within 10–15 min of the start of the playback, birds were actively circling and calling. We caught significantly more birds of each species on nights when we broadcast that species' call (Leach's Storm-Petrel, $Z_4 = 8.41$, $P < 0.001$, SD of random effect = 1.66; Fork-tailed Storm-Petrel, $Z_4 = 5.64$, $P = 0.001$, SD of random effect = 1.39; Fig. 3). On nights of conspecific playback that were especially dark (no moon and heavy fog), reaction to playback was so dramatic that not only were many birds caught in the net, but dozens of birds were circling and calling, bouncing out of the net, and hitting net poles, the banding shed, and personnel. We caught 41 times more Leach's Storm-Petrels on nights we broadcast Leach's Storm-Petrel calls and 29 times more on nights we broadcast colony calls than on nights of the silent control and noise control (Table 1; Fig. 3). We caught twice as many Leach's Storm-Petrels on nights we broadcast Fork-tailed Storm-Petrel calls than on control nights; however, this difference was barely nonsignificant (Table 1; Fig. 3). We caught about 20 times more Fork-tailed Storm-Petrels on nights we broadcast that species' calls and 5 times more on nights we broadcast colony calls than on control nights. Although we caught 1.3 times more Fork-tailed Storm-Petrels on nights we broadcast Leach's Storm-Petrel calls, this difference was not significant (Table 1).

Among 346 captures of Leach's Storm-Petrel and 28 of the Fork-tailed Storm-Petrel in 2008 there was only 1 recapture (rectrix marked with nail polish), of a Leach's Storm-Petrel on 25 July during Leach's Storm-Petrel playback. The

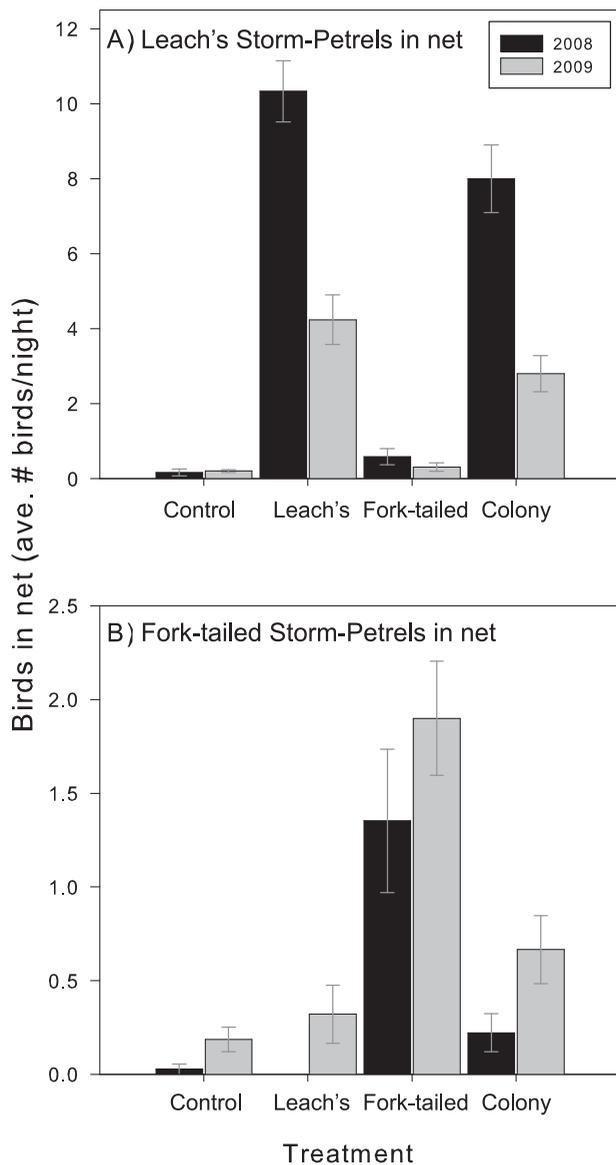


FIGURE 3. Average number of captures in net per night of (A) Leach's and (B) Fork-tailed Storm-Petrels during various playback treatments, including control (no sound and 20-sec increments of music), Leach's Storm-Petrel (*chuckle* and *purr* calls), Fork-tailed Storm-Petrel (flight and male calls), and colony (a combination of Leach's and Fork-tailed).

polish was still slightly wet, suggesting this was a recapture from the same night. Among 228 captures of Leach's Storm-Petrel and 97 of the Fork-tailed in 2009 there were 2 recaptures on 2 separate nights, both of Leach's Storm-Petrels recaptured within 35 min of initial capture. We recaptured no Fork-tailed Storm-Petrels.

We found no evidence of brood-patch swelling or vascularization in any individuals caught in the net.

T-MAZE

Of all factors tested (stress, nudging, and trial type), only stress had an effect on the choice between odor and control in the T-maze ($Z_1 = 2.65$, $P = 0.008$, SD of random effect = 0.38). Therefore, when analyzing odor preference, we ran GLMM with and without stressed individuals. When stressed individuals were included in GLMM analysis, we found no significant orientation of either species toward odor (all $P > 0.5$; Fig. 4). When we excluded stressed individuals from the analysis, Fork-tailed Storm-Petrels oriented more frequently towards the odor cue ($Z_1 = 2.11$, $P = 0.03$, SD of random effect = 1.21) while Leach's Storm-Petrels oriented more frequently away from the odor cue, although not significantly ($Z_1 = -1.81$, $P = 0.07$, SD of random effect = 1.21; Fig. 4). With stressed individuals removed, Fork-tailed Storm-Petrels chose the odor cue 69% of the time, while Leach's Storm-Petrels chose it 41% of the time (Table 2).

Leach's Storm-Petrels took an average of 17.7 ± 3.4 min to complete the three odor trials, whereas Fork-tailed Storm-Petrels took 22.1 ± 3.1 min, excluding rest periods. In total, only three trials with Leach's Storm-Petrel trials and zero with the Fork-tailed Storm-Petrels were recorded as "no choice." Sixteen Leach's Storm-Petrels and 18 Fork-tailed Storm-Petrels had to be nudged to start the maze. When the dividing gate was opened, these subjects sat in the start box quietly without moving. No other factors tested, such as nudging, trial type ("stomach odor" versus "feather odor" versus "nesting material"), or any interaction term had any effect on choice (all $P > 0.87$).

ARTIFICIAL BURROWS

The number of burrow entries varied significantly by treatment type ($Z_2 = 1.96$, $P = 0.05$, SD of random effect = 0.496). Both year and day of year also had a significant effect on burrow entries (year $Z_1 = 3.59$, $P < 0.001$; day of year $Z_1 = 2.52$, $P = 0.012$). In 2009, when calls were broadcast and scented materials were placed inside burrows, the average number of burrow entries increased. The number of times toothpicks were knocked down increased from 0.18 ± 0.10 on control nights (3 knockdowns on 3 separate nights) to 0.50 ± 0.22 on playback nights (5 knockdowns on 4 nights) to 1.00 ± 0.38 on playback and nesting-material nights (7 knockdowns on 4 nights). In 2008, knockdowns increased only slightly from 1.29 ± 0.43 on control nights to 1.40 ± 0.53 on playback and nesting-material nights.

In 2009, we observed evidence of freshly dug burrows (dirt displaced up to 15 cm), one at plot 2 and one at plot 3. In 2009, on a "playback and material" night, at 00:30 when we placed nesting material inside a burrow on plot 1, an unidentified bird flew out. Except for this one occasion, we found no evidence of storm-petrels inhabiting or taking up daytime residence in artificial burrows.

TABLE 1. GLMM (Poisson error structure, log link, fit by Laplace approximation) outputs for mean captures of Leach’s and Fork-tailed Storm-Petrels netted during four different call-playback treatments.

Species and treatment	Coefficient	Transformed coefficient	SE	Z	P ^a
Leach’s Storm-Petrel					
Control (intercept) ^b	-2.046		0.3401	-6.016	<0.001*
Colony ^c	3.362	28.832	0.3874	8.677	<0.001*
Fork-tailed Storm-Petrel ^d	0.830	2.293	0.445	1.865	0.0622
Leach’s Storm-Petrel ^e	3.716	41.116	0.4421	8.407	<0.001*
Fork-tailed Storm-Petrel					
Control (intercept) ^b	-2.688		0.4273	-6.291	<0.001*
Colony ^c	1.649	5.203	0.5092	3.239	0.0012*
Fork-tailed Storm-Petrel ^d	2.992	19.927	0.5302	5.644	<0.001*
Leach’s Storm-Petrel ^e	0.249	1.282	0.7399	0.336	0.7368

^aAsterisks highlight values of $P < 0.05$.
^bSilence and 20-sec increments of music.
^cPlayback of calls of both Leach’s and Fork-tailed Storm-Petrels mixed.
^dPlayback of flight and male calls.
^ePlayback of *chuckle* and *purr* calls.

DISCUSSION

Pre-breeding storm-petrels were strongly attracted to playback of conspecific calls at Ulva Cove, and Fork-tailed Storm-Petrels (showing no external signs of stress) were attracted to conspecific odor in an experimental maze. Attracting individuals to artificial burrows by means of these auditory and olfactory cues was not straightforward, with more dramatic results observed only during the second year of experimental attraction, but no evidence of birds using

burrows permanently. Social-attraction experiments were successful in attracting pre-breeding and prospecting storm-petrels, but recruitment of these individuals as breeders was not achieved in our short-term experiment and merits more discussion.

At Ulva Cove, we found a strong attraction of Leach’s and Fork-tailed Storm-Petrels to conspecific playback, as found in other species of petrels such as the European Storm-Petrel (*Hydrobates pelagicus*; Furness and Baillie 1981), Wilson’s Storm-Petrel (*Oceanites oceanicus*; Bretagnolle 1989), and Galapagos Petrel (*Pterodroma phaeopygia*; Podolsky and Kress 1992). Dramatic attraction to social cues suggests that birds are drawn to areas where there are high densities of conspecifics and is likely associated with colonial nesting strategies and the use of public information (Podolsky and Kress 1989, Danchin et al. 1998). Both species were attracted to playback of a colony, and furthermore, although the trend was barely nonsignificant, there were more Leach’s Storm-Petrels captured on nights of playback of heterospecific calls. Heterospecific attraction is a widely accepted concept in passerine biology (Mönkkönen and Forsman 2002), where the presence of other species with similar habitat requirements can reflect the quality of a nesting site (Mönkkönen et al. 1999). Over most of the Fork-tailed Storm-Petrel’s range, its colonies are often mixed with Leach’s Storm-Petrels (Boersma et al. 1980, Vermeer et al. 1988, McChesney and Carter 2008). Although there are subtle differences, Fork-tailed and Leach’s Storm-Petrels have similar nesting habitat (burrow in well-drained soil or hummock; Stenhouse and Montevecchi 2000) and diet (Vermeer et al. 1988). Furthermore, both species make a variety of loud nocturnal vocalizations used in communication (Huntington et al. 1996,

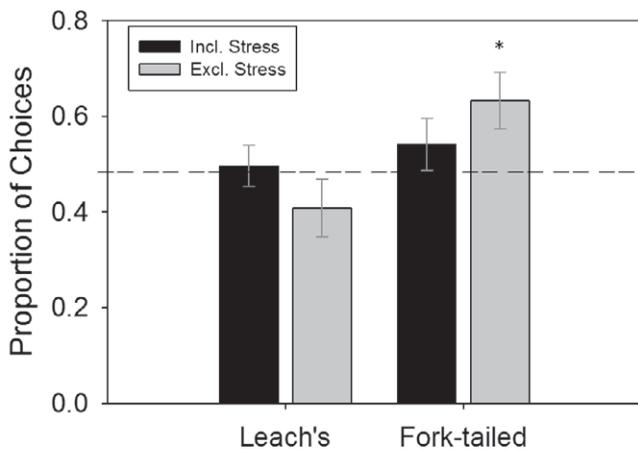


FIGURE 4. Proportion of Leach’s and Fork-tailed Storm-Petrels that chose scented materials in the t-maze experiment. Gray bars, proportion of choices with stressed individuals included; black bars, proportion with stressed individuals removed. The asterisk (*) indicates a proportion that differs significantly ($P < 0.05$) from 0.5.

TABLE 2. GLMM (Binomial error structure, logit link, fit by Laplace approximation) outputs for choice of Leach's and Fork-tailed Storm-Petrels for conspecific odor or control odor in a T-maze, stressed individuals excluded.

Species	Coefficient	Odds ratio	Probability of choosing conspecific odor	SE	Z	P
Leach's Storm-Petrel	-0.372	0.69	0.408	0.206	-1.808	0.071
Fork-tailed Storm-Petrel	0.773	2.167	0.684	0.367	2.109	0.035

Boersma and Silva 2001), which are available as public information. Given that high-quality habitat for the two species, in terms of prey and burrow location, is similar, public information should be useful to both. Prospecting birds should be able to listen for either conspecific or heterospecific storm-petrels in order to gather information about breeding habitat. To our knowledge, our study provides the first evidence for colonial seabirds use of a heterospecific cue.

We found no evidence of captured storm-petrels with swollen or vascularized brood patches, suggesting that none of the birds were incubating eggs and all were non-breeders. The high number of nonbreeding birds captured suggests the presence of many prospecting storm-petrels in Ulva Cove. Furthermore, the complete lack of breeding birds attracted to broadcast calls is consistent with other research on storm-petrels (Fowler et al. 1982, Okill and Bolton 2005). Storm-petrels have a high rate of nest-site fidelity (Warham 1990), so it would serve little function for breeding birds to be attracted to calls of conspecifics. Conversely, auditory displays by conspecifics are available (and useful) for pre-breeding birds prospecting for both future mates and nest sites.

The Procellariiformes have excellent olfactory capabilities, which they use to find productive areas for foraging in the open ocean (Warham 1990, Nevitt and Haberman 2003) and as a guidance system in locating colonies and burrows (Grubb 1974). Storm-petrels in particular have a strong and persistent musky odor on their feathers and around their burrows, a smell that may be available as public information. Our results show that, when stressed individuals were excluded, nonbreeding Fork-tailed Storm-Petrels were attracted to conspecific odor. All odors would be associated with active colonies; where smelly nesting material would signal active burrows, stomach oil would signal adults feeding chicks and detectable musky feather odor would signal a large number of conspecifics. Although the result was not significant, many nonbreeding Leach's Storm-Petrels were attracted to the control. At a more confined level, individuals may have been attracted to the control rather than to the conspecific odor cue because of the odor's possible function as a signal of burrow occupancy. The reason for such a distinct difference between species is unknown, but may be that Leach's Storm-Petrel is more territorial (*screech* call used in territorial interactions,

Taoka et al. 1988) and less likely to enter strange unoccupied burrows (Huntington et al. 1996) than is the Fork-tailed Storm-Petrel. This suggests that timid Leach's Storm-Petrels could use odor as an occupancy signal, while less timid Fork-tailed Storm-Petrels use odor as public information when prospecting for safe nesting habitat.

By combining auditory and olfactory cues, we examined the possibility of attracting both species of storm-petrel to enter and inhabit artificial burrows. In the first year of burrow experiments we found little increase in burrow entries between control and experimental treatments. On nights with playback or playback and scent treatments we observed many birds calling and circling and found evidence of birds landing on the plot (feathers and feces on the plot); they did not, however, often enter burrows. In the second season, we found a larger increase in burrow entries from control to playback to playback and nesting material. This suggests that the effect of stimuli in artificial-colonization experiments may be cumulative, and in order to encourage burrow use, more years may be required. Most storm-petrels are recruited into the breeding population at an age of 3 to 5 years (Huntington et al. 1996, Warham 1990), while returning to prospect potential colonies after a year or two at sea (Okill and Bolton 2005). This means that birds prospecting on Amaticnak could require 2 to 4 years before they decide to settle and breed. The relationship between prospecting behavior and recruitment is not well understood (Bradley et al. 1999). However, it is clear from the lack of breeding birds and low recapture rate in our playback experiment there is a large population of pre-breeding birds. Huntington et al. (1996) found that during the prospecting period storm-petrels become progressively more faithful to a colony. Therefore, if this social-attraction experiment were to continue for another 2 to 4 years, during which prospecting individuals mature to breeding age, more storm-petrels may inhabit artificial burrows.

In contrast to our results, in a similar playback experiment in Maine examining Leach's Storm-Petrel colonization of artificial burrows, Podolsky and Kress (1989) had dramatic and almost instantaneous results. Within the first year of social-attraction experiments being tried, adult storm-petrels occupied and laid eggs in artificial burrows near playback. Their study focused on only one species of

storm-petrel, all experiments were performed on small islands a short distance from active colonies, and the islands were rocky with limited amounts of suitable habitat. Amatignak is a relatively large island (1433 ha), it is over 360 km east of the active colony on Buldir Island, and there is suitable storm-petrel habitat over the majority of the island. Thus the situation is a much more diffuse than in Maine, in both distance from natal site and large numbers of options for nesting habitat. Furthermore, at many sites on Amatignak there were small subcolonies of storm-petrels (Buxton 2010), and the odds that prospecting individuals will choose a small artificial colony rather than a small natural colony are very low (S. Kress, pers. comm.).

An issue not addressed directly in our study is the possibility of attracting prospectors to unsuitable habitat (Ahlering et al. 2010). Furthermore, we acknowledge the spatial bias inherent with using only one site, Ulva Cove. On the basis of the large number of prospecting storm-petrels, we assumed that Ulva Cove represented safe, suitable habitat for recolonization of nocturnal seabirds. We also assumed, from its vegetation and topographical structure, that Ulva Cove was typical of the western Aleutian Islands, lending itself to discussion of social attraction at a larger scale in the Aleutians. However, additional factors that require future research include soil and vegetation characteristics of microhabitat suitable for various burrow-nesting species and the interaction between microhabitat type and use of social cues. For example, Amatignak has unusually boggy water-saturated peat soils lacking on some other islands such as Buldir (ILJ and RTB, pers. obs.), which may limit recolonization. Another issue is the recolonization of gulls (*Larus* spp.), which are predators of nocturnal birds like storm-petrels (Stenhouse and Montevecchi 1999), following the eradication of mammalian predators. We suggest that these factors should be considered in the placement of social-attraction stimulæ in the Aleutians.

Although it may be possible to attract pre-breeding storm-petrels to abandoned colonies in the Aleutians, whether social attraction is a suitable method of speeding recolonization is yet to be determined. Considering storm-petrels' late age at first breeding and the wide dispersion of suitable habitat across the Aleutian Islands, storm-petrel attraction as a conservation tool in the Aleutians may be more effective on a longer time scale. If our experiment were to have continued to a point where all pre-breeding birds reached an age appropriate for recruitment, storm-petrels may have occupied and bred in some artificial burrows. There is a need for research concerning restoration techniques for storm-petrels, especially in the Aleutian Islands, where these birds were decimated by introduced foxes. Our study represents a first step working toward producing a protocol by which burrow-nesting seabirds can be restored to their former numbers across the Aleutian chain.

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