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AN EXPERIMENTAL STUDY OF THE USE OF SOCIAL INFORMATION BY PROSPECTING NOCTURNAL BURROW-NESTING SEABIRDS

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Abstract. Cues and social information are important in the decisions many animals make to settle. In colonial seabirds, such decisions are based upon information gathered during a prospecting phase, in which for young individuals social information from conspecifics is key. Yet the specific cues that prospectors use, and why, remain debated questions. We used an experimental approach to evaluate a conspecific-attraction hypothesis, predicting that during nocturnal prospecting Ancient Murrelets (*Synthliboramphus antiquus*) use social information in the form of audio cues. Specifically, we used playback experiments to test whether prospectors use conspecific vocalizations to locate potential breeding sites, and we hypothesized that prospectors' activity should increase during playback of conspecific calls. Using an information-theoretic approach we found that, as predicted, playback increased Ancient Murrelet activity, supporting a conspecific-attraction hypothesis. During playback, activity increased over background levels by 271% at Langara Island and by 458% in the Aleutian Islands. In addition, Ancient Murrelet activity decreased with increasing wave height, as moon phase approached full, and with increasing distance to the nearest occupied colony. We conclude that prospectors use conspecific vocalizations to locate potential colony sites and that playback may be used in management to speed the process of recolonization of areas from which the species has been extirpated historically.

Key words: *Aleutian Islands, Ancient Murrelet, Haida Gwaii, island restoration, recolonization.*

Estudio Experimental del Uso de la Información Social por parte de Aves Marinas que Anidan en Madrigueras y que Realizan Prospecciones durante la Noche

Resumen. Las pistas y la información social son importantes en las decisiones que muchos animales realizan para asentarse. En las aves coloniales marinas, estas decisiones están basadas en información recolectada durante una fase de prospección, en la cual la información social de individuos de la misma especie es clave para los jóvenes. Sin embargo, las pistas específicas que usan las aves que prospectan y las razones de ello continúan siendo temas de debate. Usamos un enfoque experimental para evaluar una hipótesis de atracción de la misma especie, prediciendo que durante las prospecciones nocturnas los individuos de *Synthliboramphus antiquus* utilizan información social en la forma de pistas sonoras. Específicamente, usamos experimentos de reproducción de sonidos previamente grabados para evaluar si las aves que prospectan usan las vocalizaciones de individuos de la misma especie para localizar sitios potenciales de anidación y planeamos la hipótesis de que la actividad de los individuos que prospectan debería aumentar durante la reproducción de las llamadas de los individuos de la misma especie. Empleando un enfoque teórico de información encontramos que, como predicho, la reproducción de grabaciones aumentó la actividad de los individuos de *S. antiquus*, apoyando la hipótesis de atracción de la misma especie. Durante la reproducción de grabaciones, la actividad aumentó por sobre los niveles de fondo en un 271% en la Isla Langara y en un 458% en las Islas Aleutianas. Adicionalmente, la actividad de los individuos de *S. antiquus* disminuyó con un aumento de la altura de las olas, a medida que la fase lunar se acercó a llena, y con un aumento de la distancia a la colonia ocupada más cercana. Concluimos que los individuos que prospectan utilizan las vocalizaciones de los individuos de la misma especie para localizar sitios coloniales potenciales y que se pueden emplear las grabaciones para acelerar el proceso de recolonización de áreas en donde la especie ha sido extirpada históricamente.

INTRODUCTION

Most animals, at some point in their life history, show site fidelity. For example, fidelity to sites of breeding and birth have been found in many species of elasmobranchs and fishes (Ridgway et al. 1991, Feldheim et al. 2002, King and Withler 2005, Carlisle and Starr 2009), birds (Williams and Rodwell 1992, Illera and Diaz 2008), and marine mammals (Chittleborough 1965, Carr and Carr 1972). Species with philopatry return to their colony of birth, some breeding meters from their natal site, such as the Thick-billed Murre (*Uria lomvia*; Steiner and Gaston 2005). Other species evaluate a number

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of colonies before choosing one (e.g., Henaux et al. 2007). Once an individual chooses a colony, it often shows high site fidelity by returning to the same location year after year, and decisions to remain or move are based largely upon reproductive success and timing of reproductive failure (Danchin et al. 1998, Schmidt 2004, Naves et al. 2006).

Generally, colonial individuals prefer settling amid conspecifics (e.g., Podolsky and Kress 1989), a preference likely due to the risks associated with pioneering new habitat (Forbes and Kaiser 1994) and the advantages of acquiring high-quality habitat and choice among a selection of mates (Schjørring et al. 1999). Conspecific attraction increases an individual's ability to access social information used in settlement decisions by acting as an indication of an area's general suitability (Shields et al. 1988), a way to assess site quality (Stamps 1988, Doligez et al. 2003), and as the first step in identifying seemingly suitable breeding sites (Danchin et al. 1991). The use of conspecific cues as a proxy of habitat quality reinforces coloniality, with areas of suitable habitat remaining unoccupied (Danchin and Wagner 1997, Greene and Stamps 2001). Studies aimed at testing a conspecific-attraction hypothesis have successfully used decoys and call playbacks to attract birds to areas of interest to a researcher (Kotliar and Burger 1984, Podolsky and Kress 1989, Crozier and Gawlik 2003, Harrison et al. 2009) and to induce group displays and nesting behavior (O'Connell-Rodwell et al. 2004). Social information in the form of conspecific cues has also been found to be more important than structural cues about vegetation to some species of passerines (Betts et al. 2008, Harrison et al. 2009) and has been used effectively to enhance recolonization of many species (e.g., Parker et al. 2007).

In seabirds, conspecific-attraction techniques have been studied widely and are an effective means of luring individuals to potential colony sites and facilitating breeding (Kress 1978, 1983, 1997, Sato et al. 1998, Parker et al. 2007). Many studies have found that nocturnal seabirds (i.e., those that are active at colonies after dark), particularly of the order Procellariformes, use vocalizations for individual recognition, location recognition, and nest defense (Grubb 1973, 1979, Aubin et al. 2000, Jouventin and Aubin 2000, Bonadonna et al. 2004, Cure et al. 2009). But little research has been completed on conspecific attraction in nocturnal seabirds, the roles of audio, visual, and olfactory cues, and how these species make settlement decisions. Prior to deciding to settle, prospectors (e.g., inexperienced subadults searching for a location within which to settle and breed) visit many colony sites near the end of the breeding season when information about reproductive success (i.e., fledglings and/or hatched eggshells) at the site is greatest (Boulinier et al. 1996). Therefore, prospectors' use of conspecific cues is presumably high.

In the vocal repertoire of the Ancient Murrelet (*Synthliboramphus antiquus*), a nocturnal seabird of the family Alcidae, Jones et al. (1989) found nine distinct vocal displays that are highly locatable and individually distinctive. If these displays are an adaptation to a nocturnal lifestyle, audio cues may be important for finding a mate, locating a colony, and communicating with conspecifics. Throughout the species' North American range, populations of the Ancient Murrelet have been declining, predominantly because of introduced arctic foxes (*Vulpes lagopus*), raccoons (*Procyon lotor*), and rats (*Rattus* sp.), but the successful eradication of these predators from islands where the murrelet bred has not consistently resulted in its recolonization, although increases in burrow occupancy have been observed (Regehr et al. 2007). The eradication of introduced predators from breeding colonies of the Ancient Murrelet in both Haida Gwaii (British Columbia, Canada) and the Aleutian Islands (Alaska) provides a unique opportunity to study habitat selection and recolonization of this species.

Ancient Murrelets do not show philopatry (i.e., fidelity to their natal site) and are believed to disperse from their natal colony (Gaston and Adkins 1998, Pearce et al. 2002), visiting and assessing a number of breeding colonies prior to settling in one location. This phase is known as prospecting, and most Ancient Murrelets visit colonies for only 1 or 2 years before they begin to breed (Gaston 1992, Gaston and Shoji 2010). While the majority of nonbreeders visiting a colony are probably in their second year, there is variation in when individuals begin to breed, most breeding by the time they reach their fourth summer (Gaston 1992, Gaston and Shoji 2010). Once an individual begins breeding it often does so every year, with high site fidelity (Gaston 1990, 1992). Prospecting activity peaks during the peak of chick departures, when chicks and adults are calling back and forth during the first half of the evening. Once all family groups have left the colony late in the breeding season, all activity at the site (including that of prospectors) ceases (Gaston 1992). The Ancient Murrelet is not sexually dimorphic, and both males and females are thought to prospect for breeding sites (Gaston 1992). The objectives of this study were to understand the role of acoustic cues in habitat selection by prospecting Ancient Murrelets as a test of the efficacy of artificial cues as a means of inducing recolonization. We tested the conspecific-attraction hypothesis by examining the response of prospecting Ancient Murrelets to acoustic cues, and we predicted that these prospectors should use audio cues to locate potential breeding areas, their activity increasing during playback. Furthermore, from a management perspective, we tested whether distance from an occupied colony influenced prospectors' activity at our playback sites and whether prospectors return to sites previously visited, leading to a lingering post-experiment effect of playback.

METHODS

STUDY SITES

Our study took place at three islands, Langara, Little Sitkin, and Amatignak. Langara Island, Haida Gwaii, British

Columbia (54° 14′ N, 133° 01′ W), covers 3105 ha and reaches 160 m above sea level at its highest point. Langara Island is predominantly forested, the dominant trees being Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) with western red cedar (*Thuja plicata*) in the interior. Ground cover is predominantly moss and mossy stumps and logs (Rodway et al. 1994). Langara Island was declared free of introduced Norway rats (*R. norvegicus*) in 1997 after a 4-year eradication campaign (Taylor et al. 2000). Ancient Murrelets attend their colonies in Haida Gwaii from March until the end of June with chick departures and prospecting peaking in late May (Gaston 1992), so we ran our playback and burrow trials during May and June 2007 and 2008. We also investigated Ancient Murrelet behavior at two sites in the Aleutian Islands, Alaska, more than 2500 km to the west of our British Columbia study sites. Little Sitkin Island (51° 57′ N, 178° 30′ E) covers 6354 ha, reaches 1188 m above sea level at its highest point, and is located in the Rat Islands group, part of the Alaska Maritime National Wildlife Refuge. Also located within this refuge, Amatignak Island (51° 15′ N, 179° 04′ W) of the Delarof Islands group covers 3433 ha and reaches 515 m above sea level at its highest point. The arctic fox was introduced to both islands in 1923 and successfully eradicated from Little Sitkin Island in 2000 and from Amatignak Island in 1991. Both Little Sitkin and Amatignak islands are treeless with mostly low-lying grasses and sedges, leafy plants, and mosses below 450 m elevation; above this there is little to no vegetation. In the Aleutian Islands Ancient Murrelets breed much later, attending colonies from May until the end of July. Chick departures and prospecting peak in early July (Byrd and Day 1986, Gaston 1992), so on both Aleutian islands we ran our playback trials during late June and July 2008.

For our statistical purposes, we define location as geographic region (i.e., Haida Gwaii or the Aleutian Islands) and site as the specific locality where a playback trial took place (i.e., Explorer Bay, Dibrell Bay, South Holland Point, Dadens, Williwaw Cove, or Ulva Cove). To account for variation between the two locations we grouped our playback sites as independent sites within the two locations (Langara Island and the Aleutian Islands).

CALL-PLAYBACK TRIALS

Playback stimuli. Using two Sennheiser ME62 omnidirectional microphones connected to a Marantz PMD660 portable solid-state recorder (sample frequency 44.1 kHz and 16-bit resolution) we assembled one 10-min track of unaltered Ancient Murrelet vocalizations including chirrup calls, songs, and chick calls recorded from several individuals at McPherson Point, Langara Island, during May and June 2006. All recordings are deposited in the Macaulay Library, Cornell Lab or Ornithology, Ithaca, New York (accession number 1994). We broadcast the recordings on an iPod Shuffle (Apple Computer, Inc.) set on repeat mode over a TOA ER-2230 wireless megaphone (both iPod and megaphone set to 75% of maximum gain, giving a range of approximately 400–600 m in which the playback was audible). In all cases, the megaphone was situated at the vegetation edge behind the shoreline, was kept ~1 m above the ground, and was pointed out to sea.

Langara Island. During May and June 2007 and 2008 we broadcast the recording at two unoccupied sites in each year for a total of four sites with playback trials at varying distances from the colony currently active at McPherson Point on Langara Island (Fig. 1a). We chose four playback sites that were historically occupied by Ancient Murrelets but were unoccupied during the most recent surveys at Langara Island in 2004 (Gaston 1992, Regehr et al. 2007). We confirmed that the sites of our playbacks were unoccupied by noting the lack of departing family groups during our experiment.

Observers listened from a location 5–10 m behind the speaker, where noise from the playback would not hinder counts, each night for a total of 159 hour-long intervals between 22:30 and 02:30 Pacific Standard Time over 34 days. They counted arrivals and departures (using wing beats and landward or seaward direction of flight) and vocalizations to obtain an indication of the amount of activity at the site, not the number of individuals. We did not restrict our counts to a single category of cue as it is unlikely that an individual will be counted as an arrival, departure, or calling but more likely that it will be counted if all these activities are pooled. The experiment at these four sites consisted of one replicate of three nights of silent monitoring, followed by three nights of playback monitoring, and finally three nights of silent monitoring (2007: Dibrell Bay—silent 17–19 and 23–25 May, playback 20–22 May; Explorer Bay—silent 1–2 and 6–8 June, playback 3–5 June; 2008: Dadens—silent 6–8 and 12–14 May, playback 9–11 May; South Holland Point—silent 19–21 and 25–27 May, playback 22–24 May), allowing us to test for effects of playback on Ancient Murrelet activity. Each of the four study sites was located on the eastern side of the island and was abandoned by Ancient Murrelets over 26 years ago, longer than the average lifespan of an Ancient Murrelet (Gaston 1992, Regehr et al. 2007). Consequently, our experiments were not confounded by differences in prominent wind and storm directions, which are south (average during our observations), nor were there individuals within the population with prior experience breeding at these sites. In addition, in Haida Gwaii, Ancient Murrelets do not appear to select for large-scale habitat features (Major 2011). These factors, taken together, indicate that the only difference relevant to the Ancient Murrelet between the four playback sites at Langara Island is their distances to a colony currently active. Our playback design, therefore, allows us to test for differences in Ancient Murrelet activity during silent and playback trials and among distances to the colony currently occupied. At Langara Island, colony attendance by prospecting Ancient Murrelets decreases with increasing wave height, presumably because increased wave height masks calls originating from the colony (Major 2011). We downloaded information on wave height

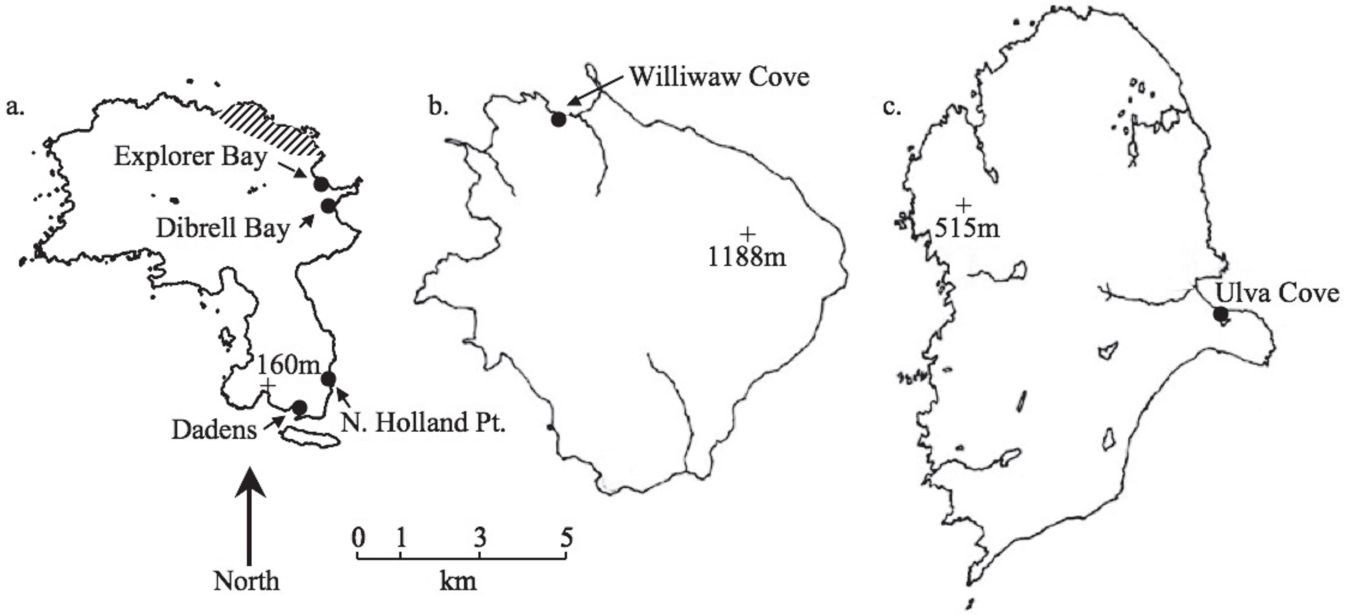

FIGURE 1. Locations of sites of playback at (a) Langara Island (location of current Ancient Murrelet colony boundaries shaded at McPherson Point), (b) Little Sitkin Island, and (c) Amatignak Island.

in meters for Langara Island from the Fisheries and Oceans Canada website (http://www.dfo-mpo.gc.ca/science/data-donnees/index-eng.html?sub=climWeath#result) and for Central Dixon Entrance weather buoy 46145, located at 54° 22′ 2″ N, 132° 2″ 0″ W) off the coast of Langara Island. In the Aleutian Islands, colony attendance by prospecting Ancient Murrelets decreased as the full moon approached, presumably because the increased light from a full moon increased the risk of predation at the colony (Major 2011). To keep our data for Langara Island and the Aleutian Islands consistent, we downloaded information on moon phase for Langara Island from the Astronomical Applications Department of the U.S. Navy (http://aa.usno.navy.mil/idex.pho).

Aleutian Islands. We broadcast the same recordings used at Langara Island during June and July 2008 at one abandoned colony site on each island, Williwaw Cove on Little Sitkin Island (HLM) and Ulva Cove on Amatignak Island (ILJ) (Fig. 1b, c). It is unknown when the last Ancient Murrelets bred on each of these islands, but the presence of foxes dates to 1923 (S. Ebbert, pers, comm,), and Ancient Murrelets were certainly extirpated from these islands long before the 1990s. Thus, as at Langara Island, the population had no individuals with a memory of breeding at either of these Aleutian Island colonies. We confirmed their absence by again noting the absence of departing family groups during our playback trials. Furthermore, our playback sites were located in protected coves on the northern (Little Sitkin Island) and eastern (Amatignak Island) sides of the islands; during the summer the direction of prominent winds and storms in the Aleutians is from the south (average over the course of our observations) and does not confound our results. Observers recorded counts of arrivals and departures (by using wing beats and landward or seaward direction of flight), and vocalizations during 186 hour-long intervals over 62 days (32 at Little Sitkin Island, 30 at Amatignak Island). The playback experiment at these two sites consisted of three cycles of five nights of silent monitoring alternating with five nights of playback from 00:00 to 03:00 Hawaii–Aleutian Standard Time: Amatignak—silent 22–26 June, 2–6 July, and 12–16 July, playback 27 June–1 July, 7–11 July, and 17–21 July; Little Sitkin—silent 22–26 June, 5–9 July, and 16–20 July, playback 30 June–4 July, 11–15 July, and 21–25 July). As at Langara Island, we included both wave height in meters and moon phase in this analysis, even though Major (2011) did not find wave height to be an important factor determining arrival of prospectors in the Aleutians Islands. We downloaded wave-height information from the Western Aleutians weather buoy (46071), located at 51° 09′ N, 179° 00′ E, from the National Data Buoy Center, National Oceanographic and Atmospheric Administration (http://www.ndbc.noaa.gov/) and moon-phase information from the Astronomical Applications Department of the U.S. Navy (http://aa.usno.navy.mil/idex.pho). Despite this buoy being ~100 km from Amatignak Island and ~40 km from Little Sitkin Island, we assume the weather data from the buoy reflect conditions at the playback sites. Observers' impressions of wind speed and wave height at the two playback sites and the buoy data are consistent.

We do not believe our use of Ancient Murrelet vocalizations recorded at Langara Island for playback experiments in the Aleutian Islands confounds our study as dialect formation depends on vocal learning, which is not known in the order

Charadriiformes, which includes the auks (Kroodsma 1982). Differences in innate vocalizations could nonetheless arise from genetic differentiation of isolated populations, but we noticed no such differences in our general examination of calls recorded in the two regions. If such a difference did exist, we might expect to see response to playback of "foreign" calls reduced from that to locally recorded vocalizations—something we considered when interpreting the results of our experiments.

STATISTICAL ANALYSES

To assess whether Ancient Murrelet activity (i.e., summed nightly arrivals, departures, and vocalizations) (1) increased during playback (only the first three trials—silent, playback, silent—for each site were used in this analysis) and (2) increased during silent trials following playback (included only silent trials from all sites), we considered eight and four a priori candidate models composed of biologically plausible combinations of six (location, trial, distance, wave height, moon phase, and day nested within site) and three (trial, location, and day nested within site) explanatory variables of interest, including a null model. We used a mixed-effects nested generalized linear model with maximum pseudo-likelihood estimation method (allowing for inter-model comparisons), a Poisson distribution, and a log-link function for all analyses in SAS 9.1 (proc GLIMMIX; SAS Institute, Cary, NC). All models included the term day nested within site as a random factor and location as a fixed effect. We then used an information-theoretic approach to rank our candidate models by using (1) Akaike's information criterion (Akaike 1974) for small sample sizes, correcting for overdispersion by including an estimate of model deviance ($\hat{c}$ = model deviance/df) for the global model, QAIC$_c$, and QAIC$_c$ weights (w_i) to evaluate a model's likelihood (Akaike 1974, Burnham and Anderson 2002). All values reported under Results are means ± 95% CI. When the best-supported model received a weight less than 0.9 we used model averaging to generate parameter estimates and unconditional standard errors, which we used with parameter likelihoods to draw inference from our data set (Johnson and Omland 2004).

RESULTS

RESPONSE TO CALL PLAYBACK

Overall Ancient Murrelet activity increased during call playback. During 2006 and 2007 at Langara Island, Ancient Murrelet activity ranged from 0 to 24 wing beats and calls per night (2.09 ± 2.54) during silent observations and from 0 to 16 wing beats and calls per night (5.67 ± 3.28) during playback (a 271% increase associated with playback; Fig. 2). Similarly, during 2008 at Williwaw Cove, Little Sitkin Island, and Ulva Cove, Amatignak Island, Ancient Murrelet activity ranged from 3 to 254 calls and wing beats per night (72.26 ± 31.67) during silent observations but from 26 to 559 calls and wing beats per night (331.00 ± 100.00) during playback (a 458% increase associated with playback; Fig. 3).

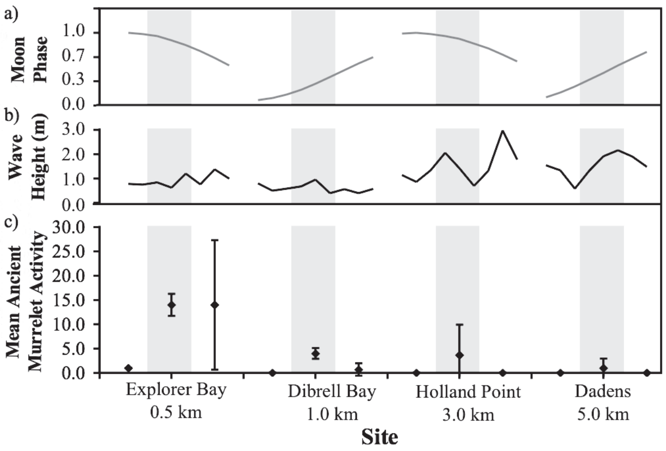

FIGURE 2. Summary of (a) moon phase (the proportion of the moon visible), (b) wave height in meters, and (c) activity (i.e., summed arrivals, departures, and vocalizations counted in one night, shown as means of three nights of observations ± 95% CI) at four formerly occupied breeding sites (including the distance in meters from the active colony at McPherson Point) at Langara Island, British Columbia, during silent observations (white areas) and playback (shaded gray areas) in 2007 and 2008.

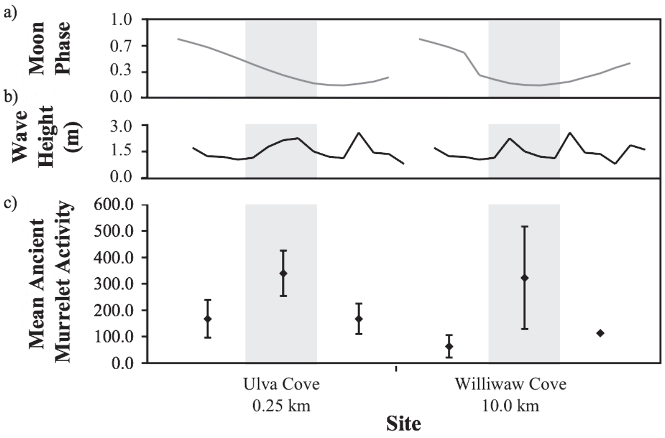

FIGURE 3. Summary of (a) moon phase (the proportion of the moon visible), (b) wave height in meters, and (c) activity (i.e., summed arrivals, departures, and vocalizations counted in one night, shown as means of five nights of observations ± 95% CI) at two abandoned colony sites in the Aleutian Islands (Ulva Cove, Amatignak Island, and Williwaw Cove, Little Sitkin Island) including distance (in meters) from the nearest active colony site during silent observations (white areas) and playback (shaded gray areas) in 2008.

The best-supported model from our candidate set explaining Ancient Murrelet activity during one night included the terms trial and distance (Table 1). This model received 1.5 times more support than the second-best model, which included the terms trial, distance, and wave height (Table 1). Ancient Murrelet activity was highest during trials with playback, at sites closest to a currently occupied site, when wave

TABLE 1. Set of candidate models describing summed Ancient Murrelet activity during observations of one night at four formerly occupied breeding sites at Langara Island (Dibrell Bay, Explorer Bay, Dadens, and South Holland Point) and two formerly occupied sites in the Aleutian Islands (Ulva Cove, Amatignak Island, and Williwaw Cove, Little Sitkin Island), Alaska in relation to trial (silent versus playback), distance to the nearest occupied site (distance), wave height, and moon phase in 2007 and 2008 (n = 64; $\hat{c}$ = 0.94). All models also include location (Langara Island or the Aleutian Islands) as a fixed effect and day nested within site as a random factor.

Candidate model	K	$\Delta QAIC_c$	w_i
Trial + distance + location	7	0.00[a]	0.46
Trial + distance + wave height + location	8	0.86	0.30
Trial + distance + moon phase + location	8	2.47	0.13
Trial + distance + wave height + moon phase + location	9	3.46	0.08
Trial + location	6	7.52	0.01
Trial + wave height + location	7	7.72	0.01
Trial + moon phase + location	7	10.16	0.00
Trial + wave height + moon phase + location	8	10.49	0.00

[a] Minimum value of $QAIC_c$ = 237.19.

TABLE 2. Summed quasi-Akaike weights (w_i), weighted parameter estimates, and unconditional standard errors (SE_u) of weighted parameter estimates calculated from all candidate models of total Ancient Murrelet activity during observations of one night at four formerly occupied breeding sites at Langara Island (Dibrell Bay, Explorer Bay, Dadens, and South Holland Point), British Columbia, during 2007 and 2009, and two formerly occupied sites in the Aleutian Islands (Ulva Cove, Amatignak Island, and Williwaw Cove, Little Sitkin Island), Alaska during 2008.

Parameter[a]	Summed weight	Weighted parameter estimate	SE_u
Intercept	1.00	1.63	0.49
Location: Langara	1.00	5.04	0.36
Trial: silent	1.00	–1.35	0.32
Distance to occupied site	0.97	–0.11	0.03
Wave height	0.39	–0.21	0.27
Moon phase	0.22	–0.01	0.21

[a] We set categorical variables trial: playback and location: Langara to zero in all models.

heights were low, and when moon phase was closest to the new moon (Table 2). However, the range encompassed by the standard errors of the parameter estimates overlapped zero for all terms except trial, indicating that those effects were weak.

We did not find a lingering post-experiment effect of playback, as the best-supported model was the null model, which received all of the weight among our candidate models (Table 3).

TABLE 3. Set of candidate models describing a post-experiment effect of playback on Ancient Murrelet activity during observations of one night at four sites at Langara Island, Haida Gwaii (Explorer Bay, Dibrell Bay, Holland Point, and Dadens) and two sites in the Aleutian Islands, Alaska (Ulva Cove, Amatignak Island, and Williwaw Cove, Little Sitkin Island) in relation to trial (pre-experiment silent trial 1 and post-experiment silent trials 2 and 3) and site (Ulva Cove, Amatignak Island, and Williwaw Cove, Little Sitkin Island) and location (Langara Island or the Aleutian Islands). In all models day nested within site was included as a random factor (n = 52, $\hat{c}$ = 0.90).

Candidate model	K	$\Delta AICc$	w_i
Null	4	0.00[a]	1.00
Trial	6	24.24	0.00
Location	5	169.52	0.00
Trial + location	7	188.76	0.00

[a] Minimum AIC_c value = –372.63.

DISCUSSION

Our experimental data support an important prediction of the conspecific-attraction hypothesis: Ancient Murrelets prospecting at night used conspecific vocalizations to locate and orient to potential colony sites. In seabirds generally, including the Ancient Murrelet (Gaston 1992), prospecting occurs near the end of the breeding season (i.e., during fledging) when the most reliable information about reproductive success at the site is available (Danchin et al. 1991, Boulinier et al. 1996). Most studies suggest that late-season prospecting is an adaptation that allows prospectors to evaluate conspecific reproductive success at the site (Boulinier et al. 1996, Danchin et al. 1998). We suggest Ancient Murrelets choose this time because departures of chicks (an indicator of reproductive success) coincide with increased calling at colony sites, providing a very reliable cue with information about the site's quality.

Seabird colonies can be loud places (Feare et al. 2003). In general, nocturnal seabirds have highly transmissible calls, but constraining environmental conditions at a colony (wind, vegetation, etc.) may limit communication to short distances (Wiley and Richards 1982, Jouventin and Aubin 2000). Therefore, a seabird can use conspecific vocalizations to locate a potential colony site, but communication can sometimes be achieved only close to or within the site. Using vocalizations as a locator cue ensures prospectors focus their efforts evaluating occupied sites (i.e., those perceived as of high quality), a reliable method for individuals interested in visiting many potential nesting sites in a relatively short period. The first time a seabird arrives at a colony site as a prospector, it has previously spent very little time on land. Therefore, information concerning places to attempt breeding and what constitutes "good" breeding habitat are presumably learned from conspecifics. Once at an already busy site, prospectors can assess habitat, conspecific reproductive success, and interact with potential mates, later deciding to settle on the basis of these observations (Danchin et al. 1998, Seppänen et al. 2007). The timing of prospecting and the use of vocalizations to locate colony sites support our conspecific-attraction hypothesis, as our results demonstrate that Ancient Murrelets use audio information from conspecifics when choosing which sites to visit.

Ancient Murrelets gather offshore 1 to 2 hr before sunset, flying from "gathering grounds" to the colony (Gaston 1992). Prospectors may use these grounds as yet another indication of the location of suitable nesting sites, similar to how Guanay Cormorants (*Phalacrocorax bougainvillii*) use rafts situated near their breeding colony as a compass signaling the direction of a patch for foraging (Weimerskirch et al. 2010). We found that prospecting Ancient Murrelets' response to playback declined with increasing distance to the nearest occupied site, suggesting that this distance may be a factor associated with the locations of offshore gathering grounds. The gathering ground at Langara Island lies just offshore of McPherson Point (Gaston 1992), but locations in the Aleutian Islands are poorly known. Other islands near Amatignak and Little Sitkin islands have colonies, suggesting proximity to gathering grounds. A better description of response to playback and distance might use the location of gathering grounds rather than that of occupied colonies.

It is widely accepted that petrels use odor as a cue for foraging (Nevitt and Haberman 2003), and Bonadonna et al. (2007) suggested that they have individually distinctive odors that could be used in mate and nest-site recognition. If other nocturnal seabirds use odor to locate their nest site, prospectors may use this cue to evaluate colony sites. Olfaction has not been studied in the Ancient Murrelet, but adults do not remove hatched eggshell fragments from their burrows (Gaston 1992), and this visual cue, in addition to associated olfactory cues in burrows (i.e., feather and eggshell odor), could allow prospectors to evaluate individual burrows, providing more information regarding site and burrow quality. Gaston (1992) suggested that prospecting Ancient Murrelets tend to enter burrows that successfully hatched chicks more often than those that did not. This behavior could be the result of visual and olfactory cues present in burrows that successfully hatched chicks and may be a fine-scale method of assessing site quality. We did not test for effects of visual and olfactory cues on prospectors' behavior and later settlement decisions but believe future studies should assess the role of visual and olfactory cues in habitat selection.

Our playback experiments provide ample evidence that prospecting Ancient Murrelets use audio cues to locate potential nesting sites, which implies that social information is important in the birds' decisions to settle. Given this, abandoned sites lacking audio cues are unlikely to be recolonized, especially if they are far from an occupied site and/or gathering ground. Moreover, the lack of a lingering effect of playback after our experiment suggests the draw to visit a colony is highly linked with vocalizations. Further study of site-specific settlement decisions is required for assessment of how prospectors evaluate sites and burrows, whether they use heterospecific vocalizations when searching for potential colony sites, and whether they use a hierarchy of cues when assessing potential nesting sites.

Most of the Aleutian Islands (Alaska Maritime National Wildlife Refuge) and much of Haida Gwaii (Gwaii Hanaas National Park and ecological reserves) are protected areas currently being managed for nature conservation and the restoration of seabirds affected by past anthropogenic perturbations, particularly introduced predators (foxes and rats in the Aleutians, raccoons and rats in Haida Gwaii). Expensive and largely successful efforts have been made in both areas to restore islands by eradicating alien predators, and signs of wildlife recovery are evident (Ebbert 2000, Ebbert and Byrd 2002, Regehr et al. 2007). Nevertheless, managers have been looking for tools to restore the native ecosystem, particularly seabirds that have recovered in some areas after eradication but not in others. Our study suggests that playback of Ancient Murrelet calls at areas of suitable breeding habitat is a possible management tool for restoring this species.

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