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RESEARCH ARTICLE

Experimental evidence that social information affects habitat selection in Marbled Murrelets

Jonathon J. Valente,[1,2,*] S. Kim Nelson,[3] James W. Rivers,[1] Daniel D. Roby,[3] and Matthew G. Betts[4,*]

[1] Department of Forest Engineering, Resources, & Management, Oregon State University, Corvallis, Oregon, USA
[2] Smithsonian Conservation Biology Institute, Migratory Bird Center, National Zoological Park, Washington, D.C., USA
[3] Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, USA
[4] Forest Biodiversity Research Network, Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon, USA
* Corresponding authors: Jonathon J. Valente, Jonathon.J.Valente@gmail.com; Matthew G. Betts, Matt.Betts@oregonstate.edu

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ABSTRACT

Habitat selection decisions can impact individual fitness and ultimately scale up to mediate population dynamics. Understanding how birds select habitat is thus critical for discerning the biological processes structuring populations and for developing conservation strategies, particularly for species in decline. Marbled Murrelet (*Brachyramphus marmoratus*; hereafter murrelet) populations have declined in recent decades due to loss of late-successional forest nesting habitat and changing ocean conditions that impact foraging success. Most other seabirds in the family Alcidae nest colonially and evidence suggests nesting murrelets may aggregate in stands, yet no studies have examined murrelet use of social information in nest-site selection. In 2016, we experimentally simulated the presence of murrelets at 14 randomly chosen potential breeding sites by broadcasting murrelet calls throughout the breeding period. Between broadcasting bouts, we recorded calls of wild murrelets and compared call rates with those recorded at 14 control sites (no broadcast). One year after playbacks ceased (2017) we conducted breeding season surveys to document behaviors indicative of murrelet breeding activity. Broadcasting murrelet calls in 2016 increased daily odds of wild murrelets vocalizing during the treatment period by up to 15.4× (95% CI: 2.3, 125.4) relative to control sites. During the 2017 breeding season, the odds of occupancy were 10.0× (CI: 1.2, 81.4) greater at treatment sites than control sites. These results indicate that social information influences murrelet breeding site selection because the simulated conspecific presence in potential nesting habitat appeared to attract prospectors in 2016 that continued occupying treatment sites the following year. This conspecific attraction implies murrelet nesting sites are likely to remain occupied over time and that large tracts of nesting habitat may be important for supporting murrelet populations. Murrelets may also be susceptible to information-mediated Allee effects whereby a lack of conspecific information about nesting habitat could exacerbate long-term population declines.

Keywords: audio playback, *Brachyramphus marmoratus*, conspecific attraction, Marbled Murrelet, social attraction, social information, threatened seabirds

LAY SUMMARY

- We found that Marbled Murrelets are attracted to potential breeding areas based on the presence of other Marbled Murrelets.
- The odds of murrelets occupying sites where we previously broadcast murrelet calls were about 10 times greater than at sites where we did not play calls.
- Murrelet populations have been declining, and recovery may be hindered by the fact that there are few murrelets available to provide information to others about where to nest.
- Managers could consider broadcasting vocalizations to encourage murrelets to nest in unused, high-quality habitat.
- Because murrelets are attracted to other murrelets, protecting areas adjacent to known nesting sites may also be an effective conservation approach.

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Evidencia experimental que la información social afecta la selección de hábitat en *Brachyramphus marmoratus*

RESUMEN

Las decisiones de selección de hábitat pueden impactar la adecuación biológica individual y en última instancia escalar para mediar las dinámicas poblacionales. Entender cómo las aves seleccionan el hábitat es por ende crucial para discernir los procesos biológicos que estructuran las poblaciones y para desarrollar las estrategias de conservación, particularmente para las especies en disminución. Las poblaciones de *Brachyramphus marmoratus* han disminuido en las últimas décadas debido a la pérdida de hábitat de anidación en estados sucesionales tardíos de bosque y a condiciones cambiantes del océano que impactan el éxito de forrajeo. La mayoría de las otras aves marinas en la familia Alcidae anidan en colonias y la evidencia sugiere que los individuos de *B. marmoratus* que anidan pueden juntarse en los rodales, a pesar de lo cual no hay estudios que hayan examinado el uso de información social por parte de *B. marmoratus* en la selección del sitio de anidación. En 2016, simulamos experimentalmente la presencia de *B. marmoratus* en 14 sitios de cría potenciales elegidos al azar por medio de la reproducción de llamadas de *B. marmoratus* a lo largo del período reproductivo. Registramos las llamadas de individuos silvestres de *B. marmoratus* entre los espacios sin reproducción de sonidos y comparamos las tasas de llamada con aquellas registradas en 14 sitios control (sin reproducción de llamadas). Un año después del cese de las reproducciones de llamadas (2017), realizamos censos en la estación reproductiva para registrar comportamientos que indiquen actividad reproductiva de *B. marmoratus*. La reproducción de llamadas de *B. marmoratus* en 2016 aumentó las probabilidades diarias de vocalización de individuos silvestres durante el período de tratamiento en hasta 15.4× (95% IC: 2.3, 125.4) en relación a los sitios control. Durante la estación reproductiva de 2017, las probabilidades de ocupación fueron 10.0× (IC: 1.2, 81.4) más grandes en los sitios de tratamiento que en los sitios control. Estos resultados indican que la información social influencia la selección del sitio reproductivo por parte de *B. marmoratus*, debido a que la presencia simulada de individuos conespecíficos en el hábitat de anidación potencial pareció atraer individuos buscadores en 2016 que continuaron ocupando los sitios de tratamiento al año siguiente. Esta atracción de individuos conespecíficos implica que los sitios de anidación de *B. marmoratus* permanecerán probablemente ocupados a lo largo del tiempo y que grandes pedazos de hábitat de anidación pueden ser importantes para sustentar poblaciones de *B. marmoratus*. *B. marmoratus* puede también ser susceptible al efecto Allee mediado por información, por el cual una falta de información de individuos conespecíficos sobre el hábitat de anidación podría exacerbar las disminuciones poblacionales a largo plazo.

Palabras clave: atracción de individuos conespecíficos, atracción social, aves marinas amenazadas, *Brachyramphus marmoratus*, información social, reproducción de sonidos grabados

INTRODUCTION

Understanding how individuals select habitat is a fundamental goal in avian ecology (Cody 1985, Jones 2001, Morris 2003). Historically, research in this area has focused on linking bird distributions to environmental characteristics such as vegetation structure, climatic variables, and landscape context (Ahlering et al. 2010). Experiments on colonial waterbirds in the early 1980s revealed that inadvertent social information, which is gained by observing cues from conspecifics and heterospecifics interacting with their environments (Danchin et al. 2004), can also influence habitat selection (Kress 1983, Kotliar and Burger 1984, Burger 1988). Conspecific attraction methods, wherein researchers purposefully display cues from conspecifics to attract settlers, have since become a critical component of restoration projects for colonial seabirds worldwide (Jones and Kress 2012). More recent work suggests that conspecific social cues also influence habitat selection for many non-colonial species (Ahlering et al. 2010). In some instances, the inclination to select breeding sites near conspecifics appears to be so strong that broadcasting vocalizations can result in colonization of ostensibly low-quality habitat (Nocera et al. 2006, Betts et al. 2008, Farrell et al. 2012); conversely, high-quality habitat may remain vacant in the absence of conspecific cues (Ward and Schlossberg 2004). It is thus apparent that social information is used by many species when selecting habitat, and it can have an especially strong influence on settlement decisions that influence fitness.

Habitat selection theory predicts negative tradeoffs between individual fitness and conspecific density stemming from resource competition (Fretwell and Lucas 1969). However, there are two primary reasons individuals might be attracted to conspecific social cues. First, social cues can help an individual identify likely habitat. They indicate the presence of individuals with similar resource requirements and can even yield information about habitat quality when the cues imply fitness of the cue producer (Danchin et al. 2004). Although such information can be imperfect, it is easy to collect and more efficient than identifying and comparing potential habitat through personal exploration (Danchin et al. 2004, Wagner and Danchin 2010). Secondly, there can be benefits to settling in proximity to conspecifics themselves. Increases in per-capita fitness with increasing conspecific density, known as Allee effects, are common in nature and can arise through a variety of mechanisms including increased predator vigilance, access to mates, and genetic diversity (Courchamp et al. 1999, Stephens et al. 1999, Kramer et al. 2009). Such

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positive associations typically occur at low population densities and thus can be especially critical in growth and maintenance of dwindling populations (Doligez et al. 2003, Schmidt et al. 2015a, 2015b).

The Marbled Murrelet (*Brachyramphus marmoratus*; hereafter murrelet) is a small, endangered seabird (IUCN 2020) in the family Alcidae that occurs at population densities that are thought to be well below historical levels throughout its range (Nelson 2020). Murrelets inhabit coastal environments stretching from central California, USA north through the Aleutian Islands (Nelson 2020). Year-round, they typically forage on the ocean within 5 km of shore, opportunistically feeding on small fish, euphausiids, and other invertebrates (Burkett 1995, Nelson 2020). Like other alcids, murrelets exclusively inhabit marine environments in the non-breeding season (Winkler et al. 2020). However, murrelets have an uncommon breeding strategy; whereas most alcids nest colonially in close proximity to the ocean, murrelets typically nest on the limbs of large trees at inland sites that can exceed 80 km from the coastline (Evans Mack et al. 2003, Lorenz et al. 2016, Raphael et al. 2018). Murrelets lay a single egg on moss or litterfall and thus require trees with large branches; nesting habitat is therefore typified by old-growth conifer stands, or late-successional stands with old-growth components such as remnant old trees, large nesting platforms, and multilayered canopies (Hamer and Nelson 1995, Nelson 2020). Unfortunately, the murrelet's split habitat strategy renders them vulnerable to declines in habitat quality in both marine and terrestrial environments (Peery et al. 2004, Betts et al. 2020); reductions in the availability of marine prey (Becker et al. 2007, Norris et al. 2007, Gutowsky et al. 2009), loss of nesting habitat in older forests (Raphael et al. 2016, 2018, Nelson 2020), and high rates of nest predation (McShane et al. 2004; Peery et al. 2004, 2006; Peery and Henry 2010) have led to long-term population declines. Murrelets additionally have a relatively slow life history strategy characterized by delayed reproduction (2–4 yr old), single-egg clutches, and skipped breeding seasons (Stearns 1992, Nelson 2020). Murrelet population sizes have thus changed little in the last 20 yr despite heightened protection throughout the United States and Canada (Miller et al. 2012, Raphael et al. 2018).

Although murrelets are often considered solitary nesters, there are reasons to suspect conspecific social cues could influence breeding site selection. First, nearly all members of the auk family nest colonially (De Santo and Nelson 1995, Winkler et al. 2020), and this propensity to aggregate is so strong that some of these species will not attempt to breed in locations that lack conspecifics (e.g., Kress and Nettleship 1988, Parker et al. 2007). Murrelets are social like other alcids, interacting and calling with one another in groups at inland nesting areas and at sea (Rodway et al. 1993, Naslund and O'Donnell 1995, Nelson and Hamer 1995, Nelson 2020). Furthermore, there is evidence that murrelets co-occur in nesting stands and some indication that nests can be spatially aggregated; for example, Manley (1999) reported 52% of nests in British Columbia were located within 100 m of a second nest, and Nelson and Wilson (2002) identified 2 active nests within 30 m of one another. Nevertheless, we still lack basic information about how murrelets select areas to nest, including the role that social attraction may play in this process, despite its importance for understanding breeding requirements and for implementing effective management actions to assist in population recovery.

In this study, we experimentally simulated conspecific presence at potential breeding sites by using acoustic playback to test the hypothesis that murrelets use social information to select breeding habitat. First, we selected a sample of forest stands that were of similar age and structure and contained suitable murrelet nesting habitat. In the first year of our study, we broadcast murrelet vocalizations on a randomized subset of sites, with the others serving as control sites where no vocalizations were played. Simultaneous recordings allowed us to identify calls of wild murrelets during these treatments. In the year following experimental broadcasts, we returned to all sites and assessed them for murrelet occupancy following established protocols (Evans Mack et al. 2003) and without the use of playback. If, as we hypothesize, murrelets use social information to select breeding habitat, we would predict (1) a greater probability of recording a murrelet vocalization in the first year during the playback period and (2) a greater probability of a site being occupied in the second year in treatment sites relative to control sites. Our findings will lead to a better understanding of how murrelets select breeding habitat and ultimately enhance conservation and management of this threatened species.

METHODS

Study Area

Our study took place in the western slope of the Coast Range in central and southern Oregon. The region experiences cool, wet winters, and mild dry summers with annual precipitation ranging from 100 to 400 cm (Daly 2019). Dominant tree species include Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), western redcedar (*Thuja plicata*), red alder (*Alnus rubra*), and bigleaf maple (*Acer macrophyllum*; Ripple et al. 2000). The region is widely considered one of the most productive temperate forest systems in the world and is a hub for timber production in the United States (Adams and Latta 2007). The Coast Range now contains ~5% old growth and

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11% late-successional forest, both well below the historical range of variability (Wimberly et al. 2000).

To select sites for our experiment, we compiled a list of Coast Range forest stands on state and federal land that had been previously surveyed using the Pacific Seabird Group's inland survey protocol (Evans Mack et al. 2003), the standard approach for surveying murrelets. These surveys note murrelet presence if any individual is detected, and stands can additionally be deemed occupied if the subcanopy flight or above canopy circling is observed, as these behaviors are indicative of breeding activity (Nelson and Hamer 1995, Evans Mack et al. 2003). We started by selecting the 219 stands that were not found to be occupied (although murrelet presence had been detected at some sites). We further narrowed this group of potential sites to those most likely to be used by murrelets in the future. These included stands that (1) contained suitable murrelet nesting habitat, characterized by mature forests with available nesting platforms; (2) were within 32 km (20 miles) of the coast because this is where the majority of murrelet nests have been found to date (Nelson 2020); and (3) were within 1 km of a site known to be occupied by murrelets, as this improved the likelihood that some individuals would be aware of the available habitat. This left 93 potential stands from which we chose 28 for our study with the constraints that all had to be ≥1 km apart and travel time among them was not logistically prohibitive (Figure 1A). All selected stands were comprised of mature forest (>80 yr old) dominated by Douglas-fir, Sitka spruce, and western hemlock. Although occupancy had not been documented in any selected stand, previous survey effort varied, with stands receiving 4–18 prior surveys (mean = 8.09, SD = 3.48) across 1–2 breeding seasons (mean = 1.77, SD = 0.43).

Prior to initiation of field work, we randomly assigned half (n = 14) of the stands to receive the vocalization playback treatment and the other half as controls lacking playback (n = 14). We identified an ideal location (hereafter a site) for deployment of custom-built playback and recording devices (hereafter PRDs; Revolution Robotics, Corvallis, Oregon USA) in each stand; these sites were near canopy gaps, surrounded by sparse understory shrub cover, and away from running water to maximize the efficacy of broadcast and recording. Field trials indicated our playback treatments could be detected up to 400 m from the broadcast location, so we considered this our effective treatment area. Using Gradient Nearest Neighbor maps of vegetation structure (https://lemma.forestry.oregonstate.edu/data/structure-maps) we determined that the proportion of each treatment area consisting of forest ≥80 yr old ranged from 0.23 to 0.88, but did not significantly differ between control (mean = 0.51, SD = 0.15) and treatment (mean = 0.56, SD = 0.18) sites (Welch two-sample t-test, $t = -0.81$, df = 24.75, $P = 0.42$).

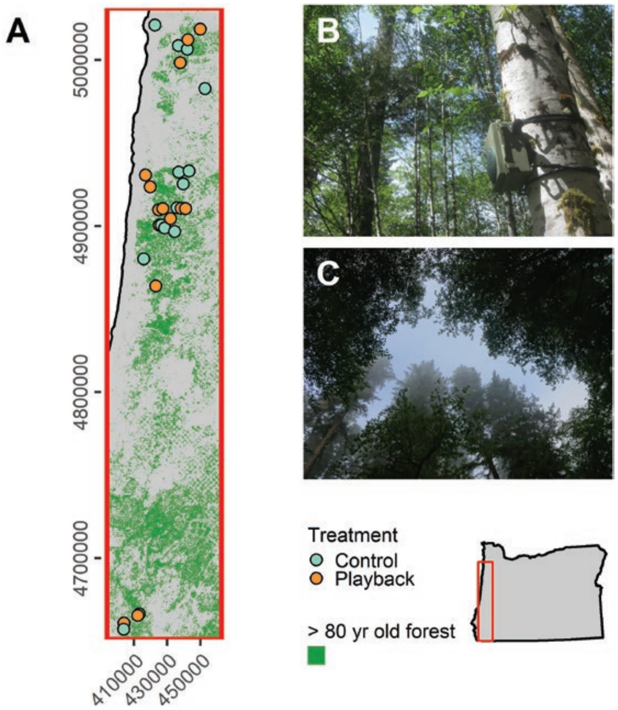

FIGURE 1. (**A**) Location of 28 sampling sites in late successional forest stands of the Oregon Coast Range that we used to evaluate the effects of simulated conspecific presence on Marbled Murrelet settlement decisions. UTM coordinates (NAD83 zone 10) are displayed on the axes. (**B**) During the 2016 breeding season we attached a playback and recording device (PRD) to a tree at each site to monitor and record murrelet vocalizations for 135 min starting 60 min prior to dawn. At treatment sites we also intermittently broadcast murrelet sounds from the same devices. (**C**) To test for occupancy in the following year (2017) in response to playbacks, we conducted dawn occupancy surveys in canopy gaps near the vicinity of where the PRDs had been placed the previous year.

Playback Treatments and Acoustic Monitoring

During the spring and summer of 2016, we deployed a single PRD at each site and attached it to the trunk of a small tree ~2 m above the ground (Figure 1B). Our PRDs could both broadcast sounds, allowing us to simulate murrelet presence (treatment sites only), and record sound, allowing us to detect murrelets using or prospecting both treatment and control sites. Treatments would ideally be applied while murrelets are prospecting for nesting habitat, although it is unknown when this occurs; both pre-breeding (Podolsky 1990, Parker et al. 2007) and post-breeding (Fijn et al. 2014, Ponchon et al. 2017) prospecting have been documented in other seabirds. We thus chose to operate PRDs from May 13 to August 10, 2016, because in our study region this period (1) encompasses the heart of the breeding season (April through mid-September), (2) brackets the peak of inland murrelet activity (July), and (3) would likely ensure both pre-breeders and post-breeders are exposed to treatments given the asynchronous nature

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of murrelet nesting (Nelson and Hamer 1995, Evans Mack et al. 2003, Nelson 2020). During the field season, we were forced to move PRDs at 4 sites (2 treatments and 2 controls) 278–499 m from their original deployment location when it was discovered that persistent machinery or songbird noise reduced our ability to detect murrelet vocalizations on the recordings.

PRDs broadcasted (treatment only) and recorded (treatment and control) each morning from 60 min before sunrise until 75 min after sunrise (hereafter active period), a period coinciding with daily peaks in inland murrelet activity (Naslund and O'Donnell 1995, Evans Mack et al. 2003). At treatment sites only, we programmed PRDs to broadcast nine short clips (21–45 s) of a murrelet vocalization once every 10 min during the active period. Each treatment site received a total of ~4 min of playback per morning at a broadcast volume of ~93 dB. Vocalizations used in the treatments were local recordings of murrelets flying over and/or circling forest and were thought to represent sounds produced by a mix of prospecting and breeding individuals. Following precedent (e.g., Ward and Schlossberg 2004, Betts et al. 2008, Farrell et al. 2012), we chose not to broadcast any sounds at control sites because heterospecific or anthropogenic noises could inadvertently attract or repel murrelets (Gess 2007, Seppänen et al. 2007).

We programmed PRDs at all sites to record continually during the active period. PRDs stopped recording at treatment sites while broadcasting vocalizations, resulting in recordings of 135 min per morning at control sites and ~131 min at treatment sites. PRDs occasionally malfunctioned and, consequently, not all PRDs were fully operational each day of the treatment and sampling period. From recording logs, we could determine how many minutes of recording each unit made each day, and we defined an active PRD day as one on which it recorded for at least 100 min (out of a possible 135 min); we discarded data from all other days. PRDs were operational at control sites for an average of 52.4 days (SD = 16.1), and treatment sites for an average of 46.1 days (SD = 15.9).

A single technician, blind to treatment assignment, visually reviewed spectrograms for all 3,048 recording hours and compared them to spectrograms of known murrelet vocalizations using Song Scope 4.0 (Wildlife Acoustics, Maynard, Massachusetts, USA). This visual inspection was necessary because signal recognizers in Song Scope and other recommended software packages (Knight et al. 2017) regularly misidentified several turdidae (thrush) species as murrelets. When a candidate murrelet vocalization was observed, the technician verified the detection by listening to the audio. The technician documented the total recording time and the number of murrelet detections recorded on each morning.

Dawn Surveys to Evaluate Murrelet Occupancy

In the spring and summer of the year following playback treatments (2017), we conducted dawn surveys at 12 treatment and 11 control sites; 3 control and 2 treatment sites were dropped due to logistical constraints. We chose a single survey station close to the original PRD location (mean distance = 38.6 m, SD = 21.2) that maximized the probability of detection by having an unobstructed view of the sky (Figure 1C) and being free of excessive noise as required by murrelet occupancy survey guidelines (Evans Mack et al. 2003). On the four sites where PRDs had been moved, the survey station was placed with respect to the second PRD location.

We conducted murrelet occupancy surveys at these stations during June 21–July 31, 2017, a period that encompasses the peak of breeding activity and detectability (Evans Mack et al. 2003). Protocol surveys take place from 45 min before sunrise to 75 min after sunrise, during which time a single observer records any visual or aural murrelet detections as well as whether the individual is observed below the canopy. Sites were classified as having murrelet presence when observers recorded any murrelet via visual or aural detection during a survey. In addition, sites were classified as occupied when murrelets were visually observed below the canopy or circling above it, both strong indicators that a survey site has importance for breeding (Evans Mack et al. 2003). We continued surveying sites on average every 4.31 days (SD = 2.65) until we either recorded occupancy behaviors or had completed nine surveys following the murrelet occupancy protocol (Evans Mack et al. 2003).

Data Analysis

We used recording data collected in 2016 to test the hypothesis that murrelet activity was elevated at playback sites in relation to control sites during the treatment period. We condensed all detections recorded at each site for each day into detection (1) or non-detection (0) observations and used mixed logistic regression (*lme4* 1.1.23 package; Bates et al. 2015) in R 3.6.3 (R Core Team 2013) to model the daily probability of detecting a murrelet. We used a detection/non-detection response variable instead of a count of the number of calls recorded each day because (1) recordings did not allow for distinguishing how many individuals were present, so counts provided little additional information, and (2) count data were zero-inflated and contained several enormous observations (likely due to birds circling) and thus could not be well represented by any standard discrete probability distribution. We fit 3 models and compared them using Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002). Preliminary data exploration indicated there was a distinct peak in detection frequency in early-mid July, so all models

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included a quadratic effect of standardized day of the year (DOY). Our full time-by-treatment model

$$\begin{aligned}\operatorname{logit}(\theta_{i,j}) = & \beta 0 + \mathrm{Site}_i + \beta 1 \cdot \mathrm{Playback}_i + \beta 2 \cdot \mathrm{DOY}_{i,j} \\ & + \beta 3 \cdot \mathrm{DOY}_{i,j}^2 + \beta 4 \cdot \mathrm{Playback}_i \cdot \mathrm{DOY}_{i,j} \\ & + \beta 5 \cdot \mathrm{Playback}_i \cdot \mathrm{DOY}_{i,j}^2 \end{aligned} \tag{1}$$

was designed to test the hypothesis that the effects of playback on murrelet detections are mediated by DOY. Here $\theta_{i,j}$ is the probability of detecting a murrelet on observation j of site i, Site is a normally distributed random site effect, and Playback is an indicator (0/1) of whether the site was treated. We then fit a reduced treatment-only model that excluded the interaction between Playback and DOY; this tested the hypothesis that playback treatments affect murrelet detections consistently through time. Finally, we fit a null model that excluded Playback and all of its interactions to test the hypothesis that treatment does not influence murrelet detections. We considered the top model and any model within 2 AIC_c units to have substantial support and determined the relative likelihood of each model using Akaike weights (w_i; Burnham and Anderson 2002). We tested the fit of the top model using the *PBmodcomp* function in the *pbkrtest* 0.4.8.6 R package (Halekoh and Højsgaard 2014). We calculated a chi-square test statistic for the original dataset (χ^*) and compared this value to similar χ statistics calculated from 500 datasets parametrically bootstrapped from the fitted model; we concluded the model was a reasonable fit if χ^* did not fall in the upper or lower 0.025 quantiles of the simulated χ distribution (Davidson and Hinkley 1997).

We then used the 2017 dawn survey data to test for playback effects on-site use in the breeding season following treatment. We created two survey-specific binary (0/1) response variables representing presence and occupancy, as specified by the murrelet survey protocol (Evans Mack et al. 2003). The presence variable took a value of 1 if any murrelet was detected during the survey and 0 otherwise. The occupancy variable took a value of 1 if the surveyor observed behaviors indicative of breeding activity. Thus, the variables presence and occupancy represent comparatively weaker and stronger evidence, respectively, of murrelet breeding on study sites based on the known relationship between sub-canopy behaviors, circling, and nesting (Nelson and Hamer 1995, Evans Mack et al. 2003). We used single-season occupancy models (MacKenzie et al. 2002, Tyre et al. 2003) with the *unmarked* 0.13.2 R package (Fiske and Chandler 2011) to model these response variables. The occupancy models assumed closure among the ≤9 surveys per site conducted during our 5-week 2017 survey period, which allowed us to explicitly model the detection process, an important consideration given murrelets are cryptic and difficult to detect even when they are known to be present at active nest sites (Nelson and Hamer 1995, Nelson 2020). In our full models, the probability of presence/occupancy (ψ) at site i was a function of playback treatment

$$\operatorname{logit}(\psi_i) = \beta 0 + \beta 1 * \mathrm{Playback}_i$$

and we included a quadratic effect of DOY on the conditional probability of detecting presence/occupancy (p) given it occurs at the site

$$\operatorname{logit}(p_{i,j}) = \alpha 0 + \alpha 1 \cdot \mathrm{DOY}_{i,j} + \alpha 2 \cdot \mathrm{DOY}_{i,j}^2$$

To evaluate the effect of treatment on presence/occupancy, we compared this model with a reduced model in which playback was excluded. We compared among models using AIC_c and evaluated the fit of the top model using parametric bootstrapping as described above.

RESULTS

Behavioral Response During 2016 Treatment

During the treatment period in 2016, we recorded murrelets on 39.4% of mornings at treatment sites and only 27.0% of the sampling mornings at control sites. We found evidence that the daily probability of recording a murrelet during this treatment period was influenced by time-mediated playback effects; indeed, no other candidate model came within 30 AIC_c units of the time-by-treatment model and it thus had nearly 100% of the support within the model set (Table 1). During late May and early June, daily recording probability was similar between treatment groups; in late June and July, that probability increased at all sites, although the increase was much stronger at treatment sites (Figure 2A). By mid-July, there was a large difference between treatment and control sites in the expected probability of recording a murrelet (Figure 2B) and, by the end of our survey period, the daily odds of detecting a murrelet were 15.39× (95% CI: 2.28, 125.35) greater at playback than at control sites. We found no evidence that the full model was a poor fit for our data ($P = 0.18$), and report full parameter estimates in Table 2.

Site Use One Year Post Treatment (2017)

When evaluating presence between treatment and control sites during the 2017 breeding season (the year following playbacks), we detected murrelets at a greater proportion of treatment sites (treatment = 83%; control = 55%) and on a greater proportion of surveys conducted within treatment sites (treatment = 36.2%; control = 20.5%). The full model estimated that odds of presence were 4.24× (CI: 0.60, 29.91) greater at treatment sites than control sites (Figure 3A). However, the reduced model, which excluded treatment effects on presence, had almost twice as much support (Table 1), indicating it is more likely that playback

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TABLE 1. A comparison of all fitted models used to test playback and quadratic day of the year (DOY) effects on Marbled Murrelet behavior. We used mixed generalized linear regression to model the daily probability of recording a murrelet (θ) during the 2016 treatment period. We then used occupancy models to examine the effects of playback on murrelet presence and occupancy (ψ) while accounting for detection probability (*p*) during the 2017 breeding season, one year after treatments had ceased. We report the number of model parameters (*K*), the difference in the small-sample corrected AIC score between the model and the top-ranked model (ΔAIC_c) and the Akaike weight of evidence for the model (w_i)

Response variable	Model	*K*	ΔAIC_c	w_i	Σw_i
2016 daily probability of recording a murrelet during treatment					
	θ ~ Playback + DOY + Playback*DOY	7	0.00	>0.99	>0.99
	θ ~ DOY	4	33.66	<0.01	>0.99
	θ ~ Playback + DOY	5	33.86	<0.01	1.00
2017 probability of presence 1-yr post treatment					
	p ~ DOY, ψ ~ 1	4	0.00	0.62	0.62
	p ~ DOY, ψ ~ Playback	5	1.00	0.38	1.00
2017 probability of occupancy 1-yr post treatment					
	p ~ DOY, ψ ~ Playback	5	0.00	0.77	0.77
	p ~ DOY, ψ ~ 1	4	2.46	0.23	1.00

TABLE 2. Parameter estimates from the top models selected in 3 analyses examining the effects of playback treatments on Marbled Murrelet behavior. We used a generalized linear mixed model to evaluate the effects of treatment on daily probability of recording a murrelet during the treatment period in the first year of the study (2016). The 2017 estimates come from occupancy models that examined treatment effects on probability of murrelet presence and occupancy in the breeding season one year after the treatment application. Full model sets with which these were compared are presented in Table 1.

Response variable	Parameter	Estimate	95% LCL	95% UCL
2016 daily probability of recording a murrelet during treatment				
	Intercept	−1.56	−2.79	−0.33
	Playback	0.93	−0.78	2.64
	DOY	−0.24	−0.48	0.00
	DOY^2	−0.47	−0.71	−0.23
	Playback*DOY	1.00	0.67	1.33
	Playback*DOY^2	0.07	−0.26	0.40
	Site variance	4.76	—	—
2017 probability of presence 1-yr post treatment				
	Probability of presence			
	Intercept	0.84	−0.06	1.74
	Detection probability			
	Intercept	−0.66	−1.33	0.01
	DOY	−0.18	−0.67	0.31
	DOY^2	0.51	0.00	1.02
2017 probability of occupancy 1-yr post treatment				
	Probability of occupancy			
	Intercept	−1.44	−3.03	0.15
	Treatment	2.30	0.20	4.40
	Detection probability			
	Intercept	−1.29	−2.82	0.24
	DOY	−0.02	−1.25	1.21
	DOY^2	0.33	−0.63	1.29

treatments did not augment the probability of presence. The estimated probability of detecting presence was greatest on the first day of sampling (0.81; CI: 0.52, 0.94) and lowest in mid-July (0.34; CI: 0.21, 0.49).

In contrast to the presence variable, we did find evidence that the probability of occupancy was greater at treatment sites than at control sites in 2017. We recorded occupancy (i.e. behaviors indicative of breeding activity) at 8 of 12 playback sites (66.7%) but only 2 of 11 control sites (18.2%). The full model estimated that odds of occupancy were 9.97× (CI: 1.22, 81.38) greater at playback than control sites (Figure 3A), and there was over 3 times more support for this model than the reduced model. Probability of detecting occupancy ranged from a maximum of 0.47 (CI: 0.13, 0.84) early in the sampling period to 0.22 (CI: 0.06, 0.56) in mid-July (Figure 3B). We found no evidence for

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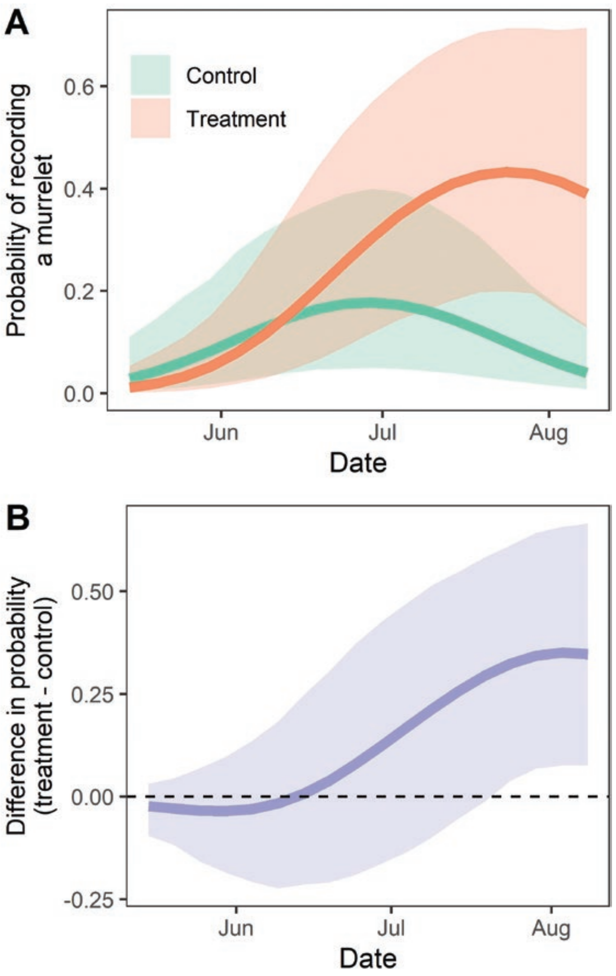

FIGURE 2. (**A**) Expected probability of recording a Marbled Murrelet in 2016, the year treatments were applied, for locations where vocalizations were broadcast (orange line) vs. control sites that lacked playback (green line). Error around the predicted values represent bootstrapped 95% confidence intervals from the fitted model. (**B**) The probability of a murrelet being recorded was similar between treatment and control sites early in the 2016 breeding season but was much greater at treatment sites later in the breeding season (July–August).

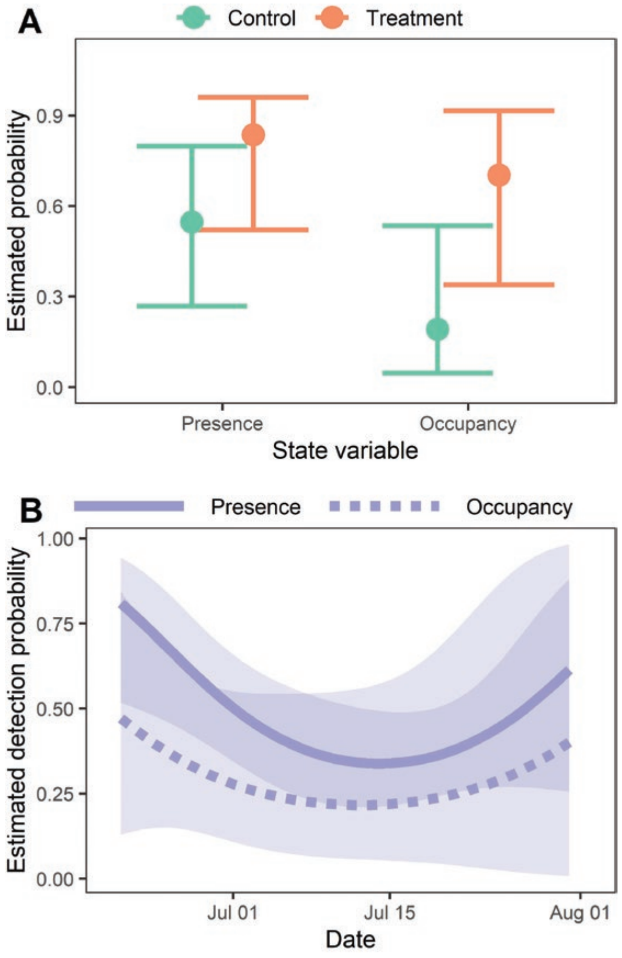

FIGURE 3. (**A**) Treatment sites where murrelet vocalizations were broadcast in the previous year had greater estimated probabilities of murrelet presence and occupancy than control sites; there was little statistical support for treatment effects on presence, but substantial support for treatment effects on occupancy. (**B**) Estimates were generated from occupancy models that simultaneously quantified the effects of day of the year on the probability of detecting presence or occupancy. Error bars and shaded regions denote 95% CIs.

lack of fit for the models fit to either the presence ($P = 0.87$) or occupancy ($P = 0.86$) datasets; see Table 2 for parameter estimates from these models.

DISCUSSION

Our study provides robust experimental evidence that Marbled Murrelets use information about conspecific presence when selecting nesting habitat. Not only did playbacks boost local murrelet activity in the year of the experiment, but evidence of breeding activity increased substantially the following year. It is possible that in the year of our treatments, playbacks simply induced individuals that were already in the vicinity of our survey areas to vocalize, and thus did not increase the number of birds visiting treatment sites. However, this cannot explain the greater occupancy rate that we documented at treatment sites in 2017 one year after playbacks had ceased. Thus, we posit that the augmented vocalization rates recorded in 2016 were most plausibly generated by prospectors attracted to the playbacks. Although we were unable to verify nesting attempts in 2017, the sub-canopy and circling flight behaviors we used to distinguish occupancy are widely assumed to indicate nesting is occurring at or near the site (Nelson and Hamer 1995, Meyer et al. 2002, Evans Mack

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et al. 2003, Raphael et al. 2016). The most parsimonious explanation, then, is that our treatments induced settlement. Even if some of the occupancies documented in 2017 were additional prospectors that ultimately never nested, our findings indicate the odds that a murrelet would nest or consider nesting were ~10× greater at treatment sites than control sites one year after broadcasting social cues.

Unfortunately, little is known about prospecting behavior in murrelets. The year-round presence of individuals at potential inland nesting sites has led to speculation that prospecting occurs at all times of the year except during the post-breeding molt (Naslund 1993). Our results suggest that prospecting for many individuals occurs close to the breeding season; however, we cannot be more precise given that our treatments were designed to target individuals both during the pre-breeding and post-breeding periods. Ancillary dawn survey data conducted in 2016 documented murrelet occupancy on some of the sites where murrelets were recorded on PRDs (Appendix). These surveys were not designed to rigorously compare occupancy between treatment and control sites. Nonetheless, they indicate a possibility that birds exposed to pre-breeding cues could have made breeding attempts more frequently at treatment sites in 2016 and the differences noted in 2017 may represent philopatric individuals. On the other hand, many avian species, including some seabirds (e.g., Fijn et al. 2014, Ponchon et al. 2017), are known to prospect in the post-breeding period of the year prior to selecting nesting habitat, presumably because that is when information about conspecific fitness is readily available (Danchin et al. 1998, 2004, Doligez et al. 2002, Betts et al. 2008). If this is true for murrelets, any breeding attempts are unlikely to have occurred until 2017.

Similarly, little is known about the timing of prospecting within a murrelet's life span, and we can only speculate about the age and experience level of the birds attracted to our treatment sites. It is assumed that murrelets prospect potential breeding sites as sub-adults in the years prior to their first breeding attempt (Nelson 2020). Furthermore, alcids tend to exhibit high fidelity to previously used nesting sites (Nettleship and Birkhead 1985, Breton et al. 2006) and anecdotal evidence suggests this is likely true for murrelets as well (Nelson and Peck 1995, Nelson 2020). It, therefore, seems plausible that a large proportion of the birds we attracted were first-time breeders. However, we cannot rule out the possibility that more mature birds were also influenced by our playbacks. Future research investigating when murrelets prospect, both within a year and within their life cycle, will be important for interpreting our findings.

Although no breeding activity was detected at any of our study sites prior to 2016, the level of survey effort and thus our level of confidence that sites were previously unoccupied varied among sites. It is therefore possible that prior murrelet breeding activity had occurred yet went undetected at several of our study sites. If this did occur, it does not invalidate our results given that we randomly assigned treatments to sites; indeed, this source of unmodeled heterogeneity would likely have made it more difficult to detect a treatment effect. Similarly, we initially experienced technical problems with the PRDs, so treatment applications were more conservative than initially intended. That we still detected treatment effects, despite these issues, makes our results all the more robust.

Our finding that murrelets select habitat based on social cues might be expected given prior evidence they can be socially gregarious (Rodway et al. 1993, Naslund and O'Donnell 1995, Nelson and Hamer 1995, Nelson 2020) and that coloniality is common among breeding alcids (De Santo and Nelson 1995, Winkler et al. 2020), many of which rely on conspecific social information to identify potential nesting locations (e.g., Kress and Nettleship 1988, Parker et al. 2007). Indeed, it is estimated that >96% of all seabird species nest colonially (Coulson 2002). Several hypotheses have been posited to explain this prevalence ranging from nesting site shortages, to predator defense, to increased efficiency of finding food (Coulson 2002). Regardless of the evolutionary mechanism, the use of social information is likely a plesiomorphic trait within the auks that has been retained in murrelets despite their specialized breeding strategy.

That murrelets incorporate social information in their selection of breeding habitat has important implications for the conservation and management of this endangered species for several reasons. First, our study suggests that murrelets are likely to choose nesting habitat in the vicinity of conspecifics. This information may be used to assist researchers when searching for murrelet nests, in turn improving our knowledge of the breeding biology of this species. To date, fewer than 600 nest sites for this species have been confirmed throughout its range (Nelson 2020, unpublished data), so information that aids in the discovery of new nests is especially valuable. From a management perspective, our results suggest that protected areas comprised of large, contiguous stands or that are spatially aggregated may be more effective in providing murrelet nest habitat than those that are small, isolated, or diffuse. Because cues indicative of murrelet presence, such as vocalizations, appear to increase the attractiveness of habitat to potential breeders, protected habitat adjacent to known nesting sites may be more likely to be used by additional individuals. Managers may also consider broadcasting vocalizations to encourage murrelets to settle in suitable, unused habitat, although care must be taken to ensure that such efforts do not lead to the creation of ecological traps (Ahlering et al. 2010).

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Our results also imply that areas selected by breeding murrelets are likely to remain occupied over time. It is assumed that murrelets have strong site fidelity, largely because breeding behavior has been noted in the same stands, and even the same trees, in subsequent years (Singer et al. 1995, Hébert and Golightly 2006, Nelson 2020, unpublished data). Although this seems likely given that many other auks are strongly philopatric (Nettleship and Birkhead 1985), our findings suggest another potential mechanism for these observations; stands may be used continually because there is apositive feedback wherein cues from breeding individuals invoke subsequent settlement and breeding of additional individuals (i.e. the establishment of habitat selection "tradition"; Thorpe 1945, Galef 1976). These two possibilities are not mutually exclusive, so it may be prudent to assume that occupied sites will be continually occupied in years with good ocean conditions if they remain undisturbed (Evans Mack et al. 2003, Betts et al. 2020).

Finally, our work highlights a behavioral mechanism that could help explain continued declines in murrelet abundance (Miller et al. 2012, McIver et al. 2019) despite the slowing of old-growth logging on federal lands under the Northwest Forest Plan (Phalan et al. 2019). While social attraction can be critical for the growth and maintenance of small populations (Doligez et al. 2003, Schmidt et al. 2015a, 2015b), a strong reliance on conspecific social information during habitat selection can exacerbate population declines in species experiencing environmental stressors (Schmidt et al. 2015a). Such information-mediated Allee effects occur when per-capita fitness is reduced specifically due to the reduction in available information about the distribution of conspecifics. Although our study was not designed to test for such effects, this warrants further investigation. For a sensitive species such as the murrelet that is already facing stressors from changing ocean conditions and loss of nesting habitat (Betts et al. 2020), a reduction in information about the distribution of quality nesting habitat from conspecifics could plausibly accelerate declines.

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Author contributions: MGB, SKN, JWR, and DDR formulated the questions and designed the study. SKN and JWR supervised collection of the data. JJV and MGB analyzed the data. JJV created the first manuscript draft and all authors contributed to editing.

Data availability: Analyses reported in this article can be reproduced using the data provided by Valente et al. (2021).

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APPENDIX

Methods and Results from 2016 Dawn Surveys

During the treatment period of 2016, we selected 11 sites at which to conduct dawn surveys (similar to those conducted during the 2017 breeding season). Murrelets had already been recorded with PRDs at each of these sites, and these surveys were designed to develop a cursory understanding of the behaviors exhibited by birds visiting during the treatment period. Between May 26 and July 29, 2016, we conducted 2–10 (mean = 3.73, SD = 2.53) dawn surveys at each of the 11 sites (Appendix Table 3). We recorded occupancy at 6 sites (55%), presence at 4 sites (36%), and no murrelet detections at 1 site (9%), though this latter site was only sampled twice.

APPENDIX TABLE 3. We conducted dawn murrelet protocol surveys at 11 sites in 2016 where murrelets had been recorded with playback and recording devices (PRDs). Here we report the proportion of days on which PRDs recorded murrelets, number of 2016 dawn surveys conducted, and the highest murrelet classification level (No detections < Presence < Occupied) recorded in 2016 and subsequent 2017 dawn surveys.

Site	Treatment	Proportion of days recorded 2016	Dawn surveys 2016	Status 2016	Status 2017
1	Playback	0.37	2	Presence	Presence
5	Control	0.59	4	Occupied	Occupied
6	Playback	0.68	5	Occupied	Occupied
10	Playback	0.63	2	Occupied	Occupied
14	Control	0.74	2	Presence	Presence
15	Playback	0.90	10	Occupied	Occupied
16	Control	0.60	6	Occupied	Occupied
17	Control	0.08	4	Presence	No detections
20	Playback	0.20	2	No detections	Occupied
21	Control	0.47	2	Occupied	Presence
25	Playback	0.38	2	Presence	Occupied

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