**Full title**: Evaluating the link between occupancy and nesting activity in an endangered, forest-nesting seabird

**Short title**: Murrelet occupancy and nesting activity

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**ABSTRACT**

Presence-absence surveys are frequently used to monitor populations of rare and elusive species because they require minimal effort and disturbance to target populations. Such data may also be used as a proxy for more complex biological processes (e.g., breeding activity), but explicit links to these processes must be validated if they are to be useful. Here we test whether presence-absence surveys can aid in the identification of nesting sites for the Marbled Murrelet (*Brachyramphus marmoratus*), a threatened seabird that nests in older-aged forests along the Pacific Coast. Between 2018 and 2022 we identified 17 trees containing active murrelet nests in the Oregon Coast Range (USA) and 26 trees that purportedly contained no nests. Naïve observers conducted audio-visual surveys within 200 m of each focal tree following standard protocols, and we modeled the effects of site status (active nest or control) and distance from the nest on probability of recording murrelet presence or breeding behaviors (occupancy). Results indicated the probability of recording murrelet occupancy was 0.20 (95% CI: 0.14, 0.27) regardless of site status or distance to a known nest. We found some evidence that the probability of recording presence was higher at nest sites (0.81, 95% CI: 0.71, 0.88) than control sites (0.71, 95% CI: 0.64, 0.78), although a null model had similar support. Thus, while presence-absence surveys may still be useful for identifying murrelet nesting sites and habitat, they appear to be inappropriate for identifying nest trees. Moreover, we estimated that observers would need to conduct up to 20 repeated surveys to reasonably conclude there are no active breeders within 200 m. These findings serve as an important reminder of the limitations that can come with relying on presence-absence data alone to identify nesting areas.

**INTRODUCTION**

Anthropogenic degradation of natural areas has driven unprecedented biodiversity declines in recent decades (Barnosky et al. 2011; Lewis & Maslin 2015; Newbold et al. 2015; Pimm & Raven 2000) with cascading negative effects on ecosystem function and human well-being (Cardinale et al. 2012). Effective monitoring of population changes is necessary to help understand and mitigate such declines where possible. For rare and declining species, identifying important habitats can be complicated by sampling inefficiencies associated with small populations and cryptic behavior of target species. In many cases, presence-absence surveys are used as an alternative to monitoring abundance because of cost savings, the ease of implementation at larger scales, and the feasibility of data collection methods (MacKenzie et al. 2002; Joseph et al. 2006). Additionally, presence-absence surveys can be preferable to more intensive and invasive sampling methods (e.g., capturing and marking) that have the potential to alter behavior and fitness outcomes (Zemanova 2020). Fortunately, improved modeling techniques over the last several decades have enhanced our ability to generate unbiased estimates of occupancy in the presence of imperfect detection (Mackenzie et al. 2002, Tyre et al. 2003, Noon et al. 2012, Bailey et al. 2014), increasing the appeal of presence-absence surveys for practitioners.

Despite the many advantages of presence-absence sampling, understanding what biological inferences can be drawn from such data remains an important challenge. For example, identifying critical breeding habitat is necessary to support reproduction, yet in many cases it is ambiguous whether presence of a species can be a reliable indicator of its breeding activity. Theory predicts that the probability an individual occupies a site should increase with habitat quality (Fretwell & Lucas 1969) which has been supported by empirical evidence in many species, including birds (Sergio & Newton 2003; Bled et al. 2011; Bennett et al. 2022), mammals (Thornton et al. 2012; Regolin et al. 2021), and insects (Pasinelli et al. 2013; Poniatowski et al. 2018). Thus, presence-absence data could serve as a reasonable proxy for preferred, or even quality, breeding habitat in some situations. For mobile animals, however, presence at any point in space may be insufficient for establishing reproductive activity. For example, commuting movements to nest or den sites could lead to presence in travel corridors, and prospecting behaviors could lead to temporary presence in sites that are ultimately not selected for breeding. Detections may be further decoupled from true breeding status because non-territorial individuals or “floaters” are present in many populations (Moreno 2016), and territorial breeders may shift locations during a season in search of higher quality habitat (Betts et al. 2008). Indeed, spatially explicit simulations have demonstrated that reproductive success is generally a weak predictor of species presence (Tyre et al. 2001). Thus, the relationship between occupancy and breeding activity can be complex and often is influenced by species-specific behaviors.

The Marbled Murrelet (*Brachyramphus marmoratus*; hereafter, murrelet) is a seabird that employs a “habitat split strategy” wherein it forages in nearshore marine areas throughout the year but also nests within late-successional and old-growth coastal forests during the summer breeding season (Nelson 2020). Murrelet populations are greatly reduced from historical levels and this species is considered threatened in the portion of its range south of Alaska (Nelson 2020). Population declines are likely attributable to loss and fragmentation of old-growth breeding habitat (Valente et al. 2023) and climate-induced changes in ocean conditions that reduce food availability which also impacts breeding activity (Peery et al. 2004; Becker et al. 2007; Betts et al. 2020, Garcia-Heras et al. 2024). Locating breeding sites is extremely difficult because murrelets nest on platform limbs high off the ground, and approach their nests at high speeds predominantly during the darkness of pre-dawn and dusk hours (Nelson 2020). Consequently, murrelet populations have largely been monitored for the past 20 years by surveying populations at sea (McIver et al. 2021).

Despite these challenges, being able to delineate murrelet nesting habitat is critical given this species’ endangered status and because its breeding range overlaps with some of the most productive timber forests in the world (Adams & Latta 2007; Lorenz et al. 2021). In 1990, the Pacific Seabird Group (PSG) developed (Paton et al. 1990) and then revised (Evans Mack et al. 2003, Pacific Seabird Group 2024) a presence-absence survey protocol (hereafter, the PSG survey protocol) designed to help identify forested areas that had a high likelihood of being used by breeding murrelets. These surveys involve trained observers watching and listening for murrelets in the early morning hours during the breeding season while recording observed detections, along with associated behaviors. Sites are classified as “occupied” when observers record murrelets calling from a stationary location, flying below the canopy, or circling above the canopy, behaviors that typically occur around breeding sites (Nelson & Peck 1995, Nelson & Hamer 1995, O’Donnell et al 1995, Naslund 1993). Occupied sites are thus assumed to have importance for breeding (Evans Mack et al. 2003). At present, however, it remains unclear how well such behaviors reflect proximity to an active nest. Understanding these relationships will help improve our ability to locate and learn about nesting sites for this threatened species and identify the spatial scales at which these behaviors are relevant for defining breeding sites. Such information is crucial given that PSG surveys are now the accepted method for identifying murrelet breeding sites on public and private timberlands (Pacific Seabird Group 2024).

In this study, we evaluated the link between occupancy and nesting activity in murrelets. We used an experimental approach where naïve observers conducted PSG protocol surveys at variable distances from known, active nest trees, and at variable distances from random potential nest trees within murrelet habitat. We tested the hypothesis that murrelet detections were influenced by proximity to nest, and we predicted that the probability of recording presence, occupancy, or both would be (1) greater at active murrelet nest trees than at random potential nest trees and (2) would decrease as surveyors moved away from nest trees, but not random potential nest trees. We also examined the frequency with which different behaviors were observed within nesting and control sites to develop an improved understanding of how audio-visual surveys may be used to pinpoint nest trees. Results from this study will help us develop a better understanding of the relationship between breeding activity and occupancy patterns for a highly mobile species and our findings will inform future PSG protocol surveys, thereby enhancing conservation of the species.

**MATERIALS AND METHODS**

*Study area and experimental design*

We conducted this experiment as part of a larger study on breeding and movement ecology of the Marbled Murrelet along the central coast of Oregon, USA, centered on the city of Newport (N 44°38’12.42”, W 123°3’12.43”). In this region, murrelet breeding habitat is found in the late successional and old-growth forest of the Oregon Coast Range, across a diversity of ownerships. We collected data over the course of four murrelet breeding seasons, May - August of 2018, 2019, 2021, and 2022. In the early breeding season of each year (between April 21 and June 7), we captured murrelets at sea between Lincoln City, OR and Yachats, OR, fitted them with VHF radio-tags, and then tracked individuals to their inland nesting sites. This approach is preferable to searching for nests at inland sites because it provides an unbiased sample of nest locations because observers only search inland sites that are used by tagged individuals. We approximated locations of nests using telemetry receivers in fixed-wing aircraft, and pinpointed exact nest locations with ground-based visual surveys (Fig 1a). Once we located a nest, we installed nest cameras with infrared capabilities in adjacent trees and recorded footage 24 h per day to monitor the presence of murrelets at the nest. Additional details regarding capture and tracking can be found in Garcia-Heras et al. (2024), and all institutional, state, and federal permits were approved prior to field work.

**Fig 1**. (A) Study area on the central coast of Oregon with locations of nest trees and focal control trees; (B) Example of a study site depicting the location of a focal tree with one survey station within each distance bin (white circles; 0-67 m, 67-133 m, and 133-200m) around the focal tree.

Our study consisted of nest and control sites; every site focused on a central tree surrounded by locations where we conducted PSG protocol surveys (Fig 1b). Every nest we found was used as a focal tree in a nest tree site unless the nest failed before we could complete at least one survey. We identified control sites from a randomized list of forest stands that had been deemed “occupied” by PSG protocol surveys in previous years. We only used “occupied” stands because our objective was to examine whether murrelet detections reflect proximity to a nest, conditional on murrelets being present within the stand. Stands where murrelets were not previously detected tend to remain unused (S1 Appendix) and thus provide no useful information for answering that question. Although our control stands had been previously deemed occupied, their status in the year we surveyed them for this study was initially unknown. Using aerial imagery, we randomly selected focal trees at these control sites that were >25 m from an edge and contained large horizontal branches that could serve as potential murrelet nesting platforms. In the first year of the study, we chose control sites *a priori*, anticipating more nest sites than we ultimately found. Thus, there were more control sites than treatment sites that first year. In subsequent years we added control sites iteratively as we located nests, so that there was an equal number of control and nest sites in subsequent years.

*Sampling*

We established survey stations around each focal tree in our study at which we conducted PSG protocol surveys (Evans Mack et al. 2003). We placed one station at randomly selected locations in each of three distance bins around the focal tree: 0-67 m, 67-133 m, and 133-200 m (Fig 1b); hereafter, we refer to individual survey locations as “stations” and a group of survey stations surrounding a focal tree as a “site”. We chose 200 m as a maximum distance because it coincides with previous observations of murrelets flying below the canopy for nearly 200 m when approaching or departing nest sites (Singer et al. 1995). Surveyors used random number tables to identify the initial distance and direction from the focal tree for each station, then followed the methods set in the PSG Survey Protocol to ensure stations contained at least a partial view of the sky and were located away from sources of noise (e.g., a loud stream) to maximize murrelet detectability; surveyors could move stations up to 50 m from the initial coordinates if necessary. At some sites we were unable to identify 3 locations that were suitable for a sampling station. Therefore, nest sites had a mean (SD) of 2.94 (0.24) sampling stations and control sites had a mean of 2.88 (0.43) sampling stations.

We hired independent observers to conduct surveys at our stations. Surveyors were instructed to survey each station 4-5 times during the breeding season (Table 1), and all surveyors were naïve as to which sites had nests. All surveys were conducted between 10 May and 25 August, and we only conducted surveys at nest sites while the nest remained active. Surveys followed the methods established in the Pacific Seabird Group’s inland survey protocol (Evans Mack et al. 2003). In brief, surveys began 45 min prior to sunrise and concluded 75 min after sunrise, during which time observers recorded audio and visual murrelet detections. During surveys, observers recorded “occupancy” if they observed: a murrelet nest, egg or chick; or an adult landing in a tree, calling from a stationary position, flying below the canopy, or circling above the canopy. Observers recorded a murrelet as “present” if they observed other detection types that are less likely to be associated with breeding activity, including straight-line above-canopy flights, or an aural detection where the individual’s behavior was not observed. In the analyses described below, we analyzed occupancy and presence detections separately, but we considered murrelets present at any site where occupancy was recorded.

**Table 1.** The number of sites sampled using Marbled Murrelet audiovisual surveys between 2018 and 2020. Each site had multiple stations within 200m of focal trees, and each station was surveyed multiple times. Observers recorded murrelet occupancy (indicative of breeding activity) and/or presence during each survey. No sites were monitored in 2020 due to the COVID-19 pandemic.

|  | Year | Sites | Stations | Surveys | Occupied surveys | Presence surveys |
| --- | --- | --- | --- | --- | --- | --- |
|  |  |  |  |  |  |  |
| Nest sites | |  |  |  |  |  |
|  | 2018 | 4 | 12 | 42 | 15 (35.7%) | 34 (81.0%) |
|  | 2019 | 2 | 6 | 13 | 4 (30.8%) | 13 (100%) |
|  | 2020 | -- | -- | -- | -- | -- |
|  | 2021 | 5 | 15 | 44 | 7 (15.9%) | 27 (61.4%) |
|  | 2022 | 6 | 17 | 46 | 12 (26.1%) | 38 (82.6%) |
|  | Total | 17 | 50 | 145 | 38 (26.2%) | 112 (77.2%) |
|  |  |  |  |  |  |  |
| Control sites | | |  |  |  |  |
|  | 2018 | 12 | 35 | 131 | 25 (19.1%) | 95 (72.5%) |
|  | 2019 | 2 | 6 | 19 | 3 (15.8%) | 13 (68.4%) |
|  | 2020 | -- | -- | -- | -- | -- |
|  | 2021 | 6 | 16 | 61 | 14 (23.0%) | 37 (60.7%) |
|  | 2022 | 6 | 18 | 48 | 13 (27.1%) | 34 (70.8%) |
|  | Total | 26 | 75 | 259 | 45 (17.4%) | 179 (69.1%) |
|  |  |  |  |  |  |  |

*Data analysis*

We used mixed effects logistic regression to examine the effects of site status (active nest vs. control) and distance from the focal tree on both the probability of recording occupancy and the probability of recording presence during a survey. For each response variable we built four models to represent the predictions that detection probabilities are (1) not affected by site status or station distance, (2) greater at nest sites but do not vary with station distance, (3) greater at nest sites and decline linearly with station distance, and (4) greater at nest sites and vary non-linearly with station distance (Table 2). We included random site and station effects in all models of occupancy; for presence models we included random station effects but excluded site effects to mitigate problems with model convergence. We fit all models in R version 4.3.1 using the lme4 package (Bates et al. 2015). For both the occupancy and presence analyses we compared among the 4 models using Akaike’s Information Criterion corrected for small sample size (AICc; Burnham & Anderson 2002). We calculated ΔAICc for each model by subtracting the AICc value for the most parsimonious model from the target model’s AICc value, and we considered any model with a ΔAICc less than 2 to have strong support. We also calculated the AICc weight for each model i as:

AICc weight is interpreted as the probability that model i is the best of the set of candidate models. Finally, we tested the fit of each model by comparing the chi-square statistic calculated from the empirical data to a distribution of chi-square statistics calculated from 500 datasets parametrically bootstrapped from the fitted model (Davidson & Hinkley 1997). We considered the model a reasonable fit if it fell within a 95% confidence interval of the bootstrapped values.

**Table 2**. Ranking of the models fit to test whether nest presence and distance from the nest influence probability of recording Marbled Murrelets during audio-visual surveys. We used mixed effects logistic regression to model the probability that naive observers recorded murrelet occupancy or presence. For each model we report the small-sample corrected AIC score (AICc), difference between the model’s AICc and that of the top model (ΔAICc), Akaike weight of evidence (wi), number of model parameters (K), and the log likelihood.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Model | | AICc | ΔAICc | wi | K | log likelihood |
|  |  |  |  |  |  |  |
| Occupancy | |  |  |  |  |  |
|  | ~1 | 431.74 | 0.00 | 0.48 | 3 | -212.84 |
|  | ~nest | 433.05 | 1.31 | 0.25 | 4 | -212.47 |
|  | ~nest + distance + distance2 + nest\*distance + nest\*distance2 | 433.69 | 1.95 | 0.18 | 8 | -208.66 |
|  | ~nest + distance + nest\*distance | 435.09 | 3.36 | 0.09 | 6 | -211.44 |
|  |  |  |  |  |  |  |
| Presence | |  |  |  |  |  |
|  | ~nest | 473.74 | 0.00 | 0.46 | 3 | -233.84 |
|  | ~1 | 474.35 | 0.61 | 0.34 | 2 | -235.16 |
|  | ~nest + distance + nest\*distance | 475.61 | 1.87 | 0.18 | 5 | -232.73 |
|  | ~nest + distance + distance2 + nest\*distance + nest\*distance2 | 479.68 | 5.94 | 0.02 | 7 | -232.70 |
|  |  |  |  |  |  |  |

**RESULTS**

Over the 4-year sampling period, we conducted audio-visual surveys at 17 active nest sites and 26 control sites (Table 1). An additional 3 nests were located, but surveyors were unable to visit all of them during the period when nests were active. Naïve observers conducted an average of 2.9 (1.22) surveys per station at nest sites, recording occupancy and presence during 26.2% and 77.2% of those surveys, respectively. At control sites, observers conducted 3.45 (1.07) surveys per station and recorded occupancy and presence during 17.4% and 69.1% of surveys, respectively (Table 1).

The occupied behaviors used to indicate breeding activity were infrequently detected by surveyors, even when they unequivocally occurred. Using video recordings, we were able to confirm that murrelets arrived at and/or departed from the nest sites while at least 109 (27%) PSG protocol surveys were being conducted at associated stations. Observers recorded some form of murrelet activity during 85 (78%) of those confirmed arrival/departure surveys but recorded occupied behaviors during only 29 (27%; Fig 2).

**Fig 2**. By reviewing video recordings of active nests, we confirmed that a murrelet arrived at and/ or departed from an active nest during at least 109 ground-based audio-visual surveys. Here, locations of those surveys are stratified by horizontal distance from the nest tree. Overall, observers recorded murrelet presence during 78% of those surveys, but occupancy during only 27%.

Across all surveys, nearly all (98%) occupied behaviors that were recorded consisted of either sub-canopy flights or above canopy circling. Observers recorded one occasion of an adult landing in a tree and one occasion of an adult calling from a stationary location; both observations occurred at nest sites. We found that the ratio of sub-canopy flight to above-canopy circling detections differed between nest and control sites. Sub-canopy flights comprised 63.2% of observed occupied behaviors at nest sites while circling comprised 31.6% of observed behaviors. At control sites, however, sub-canopy flights comprised a significantly greater percentage of occupied behaviors (90.9%; Z = 2.22, p = 0.03) while circling only accounted for 9.1% of detections.

We found no strong evidence that proximity to a known nest tree influenced the probability of recording occupancy during an audiovisual survey. Based on AICc model comparison, the null model, which excluded both site status (nest/control) and distance, had the greatest support among competing models. Results from this model indicated that the probability of detecting occupancy on any given survey was 0.195 (95% CI: 0.139, 0.266) regardless of the presence of, or proximity to, a known nest (Fig 3). Two additional models - one containing status only and the second containing status plus its interaction with quadratic distance - also had support, as indicated by ΔAICc values less than 2 (Table 2). However, the summed weight of these two models (0.43) was still less than the weight of the null model (0.48), indicating the latter is a more likely representation of the data than the former two combined. Findings from our bootstrapping procedure indicated that the null model was a good fit for the data (p = 0.642).

**Fig 3**. A comparison of the predicted probabilities (± 1 standard deviation) of detecting Marbled Murrelet occupancy and presence during audiovisual surveys. Top models indicated that the probability of recording occupancy did not vary between known nesting sites and control sites, although the probability of recording presence was slightly greater at nest sites. Distance from a known nest did not influence recordings of either response variable.

We found weak evidence that the probability of recording presence was greater near known nesting trees. The model with the lowest AICc value estimated that the probability of recording presence during a survey was 0.805 (95% CI: 0.709, 0.875) at sites with a known nest and 0.714 (95% CI: 0.635, 0.782) at control sites (Fig 3). However, the null model (which excluded both site status and distance effects) also had strong support with a ΔAICc value of 0.61. Indeed, the AICc weight of the null model was 0.34 which indicates it is only slightly less probable than the top model with a weight of 0.46 (Table 2). Comparatively, there was much less support for the two models that included distance covariates, as their summed AICc weights were only 0.2. Bootstrapping suggested that the top model was a good fit for the raw data (p = 0.624).

**DISCUSSION**

Monitoring reproductive behavior for cryptic species can be logistically challenging and financially infeasible. While presence-absence data tend to be much easier to collect, it is critical to link such detections to the focal species’ biology (e.g., reproductive activity) to make informed decisions regarding what information such detections contain. In this study, we found no strong evidence that observers were more likely to detect murrelets, nor specific behaviors thought to indicate breeding activity (i.e., sub-canopy flights or overhead circling), near active murrelet nests than at random potential nest trees within murrelet habitat. Thus, murrelet observations alone in potential nesting habitat are likely insufficient for identifying fine-scale nesting locations. Whether they are sufficient for identifying nesting stands at a broader spatial scale, however, remains unknown. Regardless, our findings demonstrate that murrelets are using forested habitat that extends well beyond the immediate vicinity of active nest trees. To what extent such use is due to nesting vs. non-nesting individuals is also unknown.

One potential explanation for our findings is that available murrelet breeding habitat is saturated such that even randomly placed points in old-forest habitat are relatively close to active nests. This is made more plausible by the fact that murrelet breeding habitat has been dwindling in recent decades (Valente et al. 2023). In our study, we were unable to know the location of all active nests that may have been present in surveyed sites, and thus we lack information about whether other nests existed in proximity to our nest sites or to randomly selected trees that were used as the basis for surveys. There are a few reasons to suspect this may have driven our findings. First, as noted, we only used control sites that had been deemed “occupied” in previous years because we wanted to ensure these were in plausible murrelet habitat. Of course, this means that occupied behaviors (indicative of breeding) had been previously recorded in these areas (Pacific Seabird Group 2024). Given murrelets have high fidelity to nest sites and are suspected to be philopatric across years (Nelson 2020), it is possible that we chose control sites that contained nests. Secondly, there is evidence that murrelets use social attraction to identify nesting sites (Valente et al. 2021), which could lead to nesting aggregations in stands containing nests. Therefore, it is possible that survey stations located away from known nesting trees were relatively close to a concurrently active nest whose presence was unknown. That said, we still contend that using control stands that had been previously deemed occupied was the most appropriate choice for our study. Sampling locations in unoccupied stands would likely yield no detections (S1 Appendix), predisposing our results to indicate that murrelet detections are more common near active nests. By relying on occupied stands as control sites, we were able to evaluate whether murrelet detections were more frequent around active nests, conditional on the sample being conducted within likely murrelet habitat.

Alternatively, murrelet activity may not be a strong indicator of proximity to an active nest at the scale of our surveys, regardless of the behavior exhibited. To be clear, this does not necessarily imply that murrelet detections are ineffective for identifying important breeding habitat. Indeed, sub-canopy flight was the most dominant occupied behavior recorded and given murrelets forage at sea and at substantial distances to inland nesting sites (Lorenz et al. 2017), it seems unlikely that individuals would fly below the canopy unless they are either prospecting for or approaching nest sites. At a minimum, sub-canopy flights indicate that murrelets recognize the stand as potential habitat. Sub-canopy flights could also indicate there is a nest somewhere in the stand; approaching and departing nests have been recorded at distances up to 182 m from the nest (Nelson & Peck 1995; Singer et al. 1995). If long under-canopy flights are common, they could be recorded frequently in breeding stands even when they are not particularly close to nests.

Nearly all of the other detections of occupancy in our study involved observations of above-canopy circling. Like other auks, murrelets are social (Rodway et al. 1993; Naslund & O’Donnell 1995; Nelson & Hamer 1995; Nelson 2020; Valente et al. 2021) and above-canopy circling is thought to be a form of social interaction in which groups of birds aggregate before returning to the ocean (Nelson 2020). Although this behavior has been observed predominantly above known nest stands, non-breeders and possibly individuals nesting in other stands are thought to join such aggregations (Nelson 2020). Consequently, the relative frequency of these circling behaviors over active nest sites compared to random locations remains ambiguous.

Although we found no strong evidence that detection of occupied behaviors is greater near active nests, there was some evidence that the probability of recording any detection was greater at nest sites than control sites. However, this evidence was weak given there was nearly equal support for the null model. Moreover, the additional presence detections included in this analysis were largely of birds flying overhead, and therefore likely not using the survey site for nesting. Thus, it seems that presence detections are also insufficient for identifying likely nest sites. Our findings do, however, provide useful data on the frequency at which false negatives are recorded at known nesting sites that could be useful for protocol design. Our trained observers failed to record murrelet occupancy on 79% of surveys where they were standing within 67 m of an active nest and at least one adult murrelet was confirmed to have arrived at or departed from that nest (Fig 2). These findings coincide with results from our fitted model (which used data from all surveys, regardless of whether a murrelet arrived/departed) which estimated during a PSG protocol survey, observers will fail to detect murrelet occupancy 80% of the time (95% CI : 73%, 86%) when standing adjacent to a tree with an active nest. This means observers would need to conduct up to 20 repeated surveys at a station near an active nest to ensure that the probability of failing to record murrelet occupancy drops below 0.05 (i.e., 0.8620 = 0.049) . Fortunately, findings from a parallel study we undertook found that trained observers never falsely recorded murrelet occupancy during 151 surveys in potential murrelet habitat (S1 Appendix), suggesting that false positives during surveys are rare.

Ultimately, to achieve a more statistically definitive answer to whether occupancy can inform managers of the nesting status in a patch of habitat, a study would need to identify the locations of all nests in an area, so researchers know exactly how far all sampling points are from those nests. Thus, until substantial resources are available to more closely examine the relationship between active nest trees and observable murrelet activity within a stand, it is prudent to continue using occupied behaviors as an indication of likely nesting. Given that murrelet habitat has declined by nearly 20% (Valente et al. 2023) since 1988, and that murrelet populations have failed to recover in recent decades (McIver et al. 2021), it seems advisable to consider occupied stands are used for breeding until data to the contrary are obtained.

Our results indicate occupancy was not a reliable indicator of murrelet nesting at a fine-scale, reiterating that researchers should take care when using presence-absence data as a proxy for more complex biological phenomena without a clear link. Although previous research has demonstrated a relationship between occupancy and higher-order variables like abundance (Gaston et al. 2000; Steenweg et al. 2018) or fitness (Sergio & Newton 2003; Bled et al. 2011; Bennett et al. 2022), such relationships may not hold for all species. Further, presence can be a misleading indicator of important breeding habitat when factors influencing habitat selection are decoupled from those that improve fitness (Van Horne 1983). Thus, understanding when, where, and how presence-absence data can be informative is critical given the limited time and resources available to conserve Earth’s remaining biodiversity.

**SUPPORTING INFORMATION**

**S1 Appendix**. Assessing the rate of false positive murrelet detections during audio-visual surveys of potential breeding sites

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**REFERENCES**

Adams DM, Latta GS. Timber trends on private land in western Oregon and Washington: A new look. Western Journal of Applied Forestry. 2007; 22: 8-14. <https://doi.org/10.1093/WJAF/22.1.8>

Bailey LL, MacKenzie DI, Nichols JD. Advances and applications of occupancy models. Methods in Ecology and Evolution. 2014; 5: 1269-79.

Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB, Marshall C, McGuire JL, Lindsey EL, Maguire KC, Mersey B, Ferrer EA. Has the Earth’s sixth mass extinction already arrived? Nature. 2011; 471: 51-7.

Bates D, Maechler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. Journal of Statistical Software. 2015; 67: 1-48. https://www.jstatsoft.org/article/view/v067i01

Becker BH, Peery MZ, Beissinger SR. Ocean climate and prey availability affect the trophic level and reproductive success of the marbled murrelet, an endangered seabird. Marine Ecology Progress Series. 2007; 329: 267-279. https://www.int-res.com/abstracts/meps/v329/p267-279

Bennett S, Harris MP, Wanless S, Green JA, Newell MA, Searle KR, Daunt F. Earlier and more frequent occupation of breeding sites during the non-breeding season increases breeding success in a colonial seabird. Ecology and Evolution. 2022; 12: e9213.

Betts MG, Rodenhouse NL, Sillett TS, Doran PJ, Holmes RT. Dynamic occupancy models reveal within-breeding season movement up a habitat quality gradient by a migratory songbird. Ecography. 2008; 31: 592-600. <https://doi.org/10.1002/ece3.9213>

Betts MG, Northrup JM, Guerrero JAB, Adrean LJ, Nelson SK, Fisher JL, Gerber BD, Garcia-Heras M-S, Yang Z, Roby, DD, Rivers JW. Squeezed by a habitat split: Warm ocean conditions and old-forest loss interact to reduce long-term occupancy of a threatened seabird. Conservation Letters. 2020; 13: e12745. https://doi.org/10.1111/conl.12745

Bled F, Royle JA, Cam E. Assessing hypotheses about nesting site occupancy dynamics. Ecology. 2011; 92: 938-51. <https://doi.org/10.1890/10-0392.1>

Burnham KP, Anderson DR. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. New York: Springer-Verlag; 2002.

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S. Biodiversity loss and its impact on humanity. Nature. 2012; 486: 59-67.

Davidson AC, Hinkley DV. Bootstrap Methods and Their Application. New York: Cambridge University Press; 1997.

Evans Mack D, Ritchie WP, Nelson SK, Kuo-Harrison E, Harrison P, Hamer TE. Methods for surveying Marbled Murrelets in forests: a revised protocol for land management and research. 2003; Pacific Seabird Group Technical Publication Number 2.

Fretwell SD, Lucas HL. On territorial behavior and other factors influencing distribution in birds: theoretical development. I. Theoretical development. Acta Biotheoretica. 1969; 19: 16-36.

Garcia-Heras M-S, Wolf C, Bailey Guerrero JA, Adrean LJ, Nelson SK, Roby DD, Betts MG, Rivers JW. Marine habitat use and movement in response to ocean warming by a threatened forest-nesting seabird. Global Ecology and Conservation. 2024; 50: e02857.

Gaston KJ, Blackburn TM, Greenwood JJD, Gregory RD, Quinn RM, Lawton JH. Abundance-occupancy relationships. Journal of Applied Ecology. 2000; 37: 39-59. <https://doi.org/10.1046/j.1365-2664.2000.00485.x>

Joseph LN, Field SA, Wilcox C, Possingham HP. Presence-absence versus abundance data for monitoring threatened species. Conservation Biology. 2006; 20: 1679-1687. <https://doi.org/10.1111/j.1523-1739.2006.00529.x>

Lewis SL, Maslin MA. Defining the Anthropocene. Nature. 2015; 519: 171-80.

Lorenz TJ, Raphael MG, Bloxton TD, Cunningham PG. Low breeding propensity and wide-ranging movements by marbled murrelets in Washington. The Journal of Wildlife Management. 2017; 81: 306-21.

Lorenz TJ, Raphael MG, Young RD, Lynch D, Nelson SK, McIver WR. Status and trend of nesting habitat for the marbled murrelet under the Northwest Forest Plan, 1993 to 2017. General Technical Report PNW-GTR-998. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station; 2021.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA. Estimating site occupancy rates when detection probabilities are less than one. Ecology. 2002; 83: 2248-55.

McIver WR, Pearson SF, Strong C, Lance MM, Baldwin J, Lynch D, Raphael MG, Young RD, Johnson N. Status and trend of marbled murrelet populations in the Northwest Forest Plan area, 2000 to 2018. General Technical Report PNW-GTR-996. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station; 2021.

Moreno J. The unknown life of floaters: the hidden face of sexual selection. Ardeola. 2016; 63: 49-77. <https://doi.org/10.13157/arla.63.1.2016.rp3>

Naslund NL. Why do Marbled Murrelets attend old-growth forest nesting areas year-round? Auk. 1993; 110: 594-602.

Naslund NL, O’Donnell BP. Daily patterns of Marbled Murrelet activity at inland sites. In: Ralph CJ, Hunt GL, Raphael MG, Piatt JF, editors. Ecology and Conservation of the Marbled Murrelet. Albany, CA. USDA Forest Service General Technical Report PSW-152. 1995. p. 129-34.

Nelson SK. Marbled Murrelet (*Brachyramphus marmoratus*), version 1.0. In: Poole AF, Gill FB, editors. Birds of the World. Ithaca, NY. Cornell Lab of Ornithology. 2020.

Nelson SK, Peck RW. Behavior of Marbled Murrelets at nine nest sites in Oregon. In: Nelson SK, Sealy SG, editors. Biology of the Marbled Murrelet: Inland and at sea. Northwestern Naturalist. 1995; 76: 43-53.

Nelson SK, Hamer TE. Nesting biology and behavior of the Marbled Murrelet. In: Ralph CJ, Hunt GL, Raphael MG, Piatt JF, editors. Ecology and Conservation of the Marbled Murrelet. Albany, CA. USDA Forest Service General Technical Report PSW-152. p. 57-67.

Newbold T, Hudson LN, Hill SLL, Contu S, Lysenko I, Senior RA, Bӧrger L, Bennett DJ, Choimes A, Collen B, Day J, De Palma A, Díaz S, Echeverria-Londoño S, Edgar MJ, Feldman A, Garon M, Harrison MLK, Alhusseini T, Ingram DJ, Itescu Y, Kattge J, Kemp V, Kirkpatrick L, Kleyer M, Correia DLP, Martin CD, Meiri S, Novosolov M, Pan Y, Phillips HRP, Purves DW, Robinson A, Simpson J, Tuck SL, Weiher E, White JH, Ewers RM, Mace GM, Scharlemann JPW, Purvis A. Global effects of land use on local terrestrial biodiversity. Nature. 2015; 520: 45-50.

Noon BR, Bailey LL, Sisk TD, McKelvey KS. Efficient species-level monitoring at the landscape scale. Conservation Biology. 2012; 26: 432-41.

O’Donnell BP, Naslund NL, Ralph CJ. Patterns of seasonal variation of activity of Marbled Murrelets in forested stands. In: Ralph CJ, Hunt GL, Raphael MG, Piatt JF, editors. Ecology and Conservation of the Marbled Murrelet. Albany, CA. USDA Forest Service General Technical Report PSW-152. P. 117-28.

Pacific Seabird Group. A revised protocol for surveying Marbled Murrelets in forests. Pacific Seabird Group Technical Publication Number 6. 2024.

Pasinelli G, Meichtry-Stier K, Birrer S, Baur B, Duss M. Habitat quality and geometry affect patch occupancy of two orthopteran species. PLOS ONE. 2013; 8: e65850.

Paton PWC, Ralph CJ, Carter HR, Nelson SK. Surveying Marbled Murrelets at inland forested sites: a guide. General Technical Report PSW-GTR-120. U.S. Department of Agriculture Forest Service; 1990.

Peery MZ, Beissinger SR, Newman SH, Burkett EB, Williams TD. Applying the declining population paradigm: diagnosing causes of poor reproduction in the Marbled Murrelet. Conservation Biology. 2004; 18: 1088-1098.

Pimm SL, Raven P. Extinction by numbers. Nature. 2000; 403: 843-5.

Poniatowski D, Stuhldreher G, Lӧffler F, Fartmann T. Patch occupancy of grassland species: habitat quality matters more than habitat connectivity. Biological Conservation. 2018; 225: 237-244. https://doi.org/10.1016/j.biocon.2018.07.018

Regolin AL, Oliveira-Santos LG, Ribeiro MC, Bailey LL. Habitat quality, not habitat amount, drives mammalian habitat use in the Brazilian Pantanal. Landscape Ecology. 2021; 36: 2519-33.

Rodway MS, Regeher HM, Savard JPL. Activity patterns of Marbled Murrelets in old-growth forests in the Queen Charlotte Islands, British Columbia. Condor. 1993; 95: 831-48.

Sergio F, Newton I. Occupancy as a measure of territory quality. Journal of Animal Ecology. 2003; 72: 857-865. <https://doi.org/10.1046/j.1365-2656.2003.00758.x>

Singer SW, Suddjian DL, Singer SA. Fledging behavior, flight patterns and habitat characteristics of Marbled Murrelets tree nests in California. In: Nelson SK, Sealy SG, editors. Biology of the Marbled Murrelet: Inland and at sea. Northwestern Naturalist. 1995; 76: 54-62.

Steenweg R, Hebblewhite M, Whittington J, Lukacs P, McKelvey K. Sampling scales define occupancy and underlying occupancy-abundance relationships in animals. Ecology. 2018; 99: 172-83.

Thornton DH, Wirsing AJ, Roth JD, Murray DL. Habitat quality and population density drive occupancy dynamics of snowshoe hare in variegated landscapes. Ecography. 2012; 36: 610-21.

Tyre AJ, Possingham HP, Lindenmayer DB. Inferring process from pattern: can territory occupancy provide information about life history parameters? Ecological Applications 2001; 11: 1722-37.

Tyre AJ, Tenhumberg B, Field SA, Niejalke D, Parris K, Possingham HP. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. Ecological Applications. 2003; 13: 1790-1801.

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., Parris, K., & Possingham, H. P. (2003). Improving precision and reducing bias in biological surveys: estimating false-negative error rates. Ecological Applications, 13(6), 1790–1801.

Valente JJ, Nelson SK, Rivers JW, Roby DD, Betts MG. Experimental evidence that social information affects habitat selection in Marbled Murrelets. Ornithology. 2021; 138: ukaa086.

Valente, J. J., Nelson, S. K., Rivers, J. W., Roby, D. D., & Betts, M. G. (2021). Experimental evidence that social information affects habitat selection in Marbled Murrelets. Ornithology, 138, ukaa086. https://doi.org/10.1093/ornithology/ukaa086

Valente JJ, Rivers JW, Yang Z, Nelson SK, Northrup JM, Roby DD, Meyer CB, Betts MG. Fragmentation effects on an endangered species across a gradient from the interior to edge of its range. Conservation Biology. 2023; 37: e14091. [**https://doi.org/10.1111/COBI.14091**](https://doi.org/10.1111/COBI.14091)

Van Horne B. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management. 1983; 47; 893-901. https://doi.org/10.2307/3808148

Zemanova MA. Towards more compassionate wildlife research through the 3Rs principles: moving from invasive to non-invasive methods. Wildlife Biology. 2020; 2020: wlb.00607.