Ornithological Applications

AmericanOrnithology.org

Volume 123, 2021, pp. 1–15
DOI: 10.1093/ornithapp/duab020

RESEARCH ARTICLE

Assessing the effectiveness of a forest Habitat Conservation Plan for a threatened seabird, the Marbled Murrelet

Kristin Brunk,[1]* Sal Chinnici,[2] Anna Pidgeon,[1] and M. Zachariah Peery[1]

[1] Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, Wisconsin, USA
[2] Forest Sciences, Humboldt Redwood Company LLC, Scotia, California, USA
*Corresponding author: kbrunk@wisc.edu

Submission Date: September 28, 2020; Editorial Acceptance Date: March 31, 2021; Published May 17, 2021

ABSTRACT

Habitat Conservation Plans (HCPs) commonly facilitate habitat conservation on private land in the United States, yet the effectiveness of individual HCPs is rarely evaluated. Here, we assess the effectiveness of a high-profile HCP created by a lumber company to protect old-growth forests used for breeding by Marbled Murrelets (*Brachyramphus marmoratus*) on private land. We used 17 years of HCP-monitoring data to compare trends in murrelet occupancy and inland counts between private HCP areas and public reference areas over time. Based on occupancy models applied to audio-visual survey data, average occupancy was higher in public reference areas (0.85; 85% confidence intervals [CI]: 0.79–0.90) than in private HCP areas (0.46; 85% CI: 0.38–0.54). Numerically, trends in occupancy were slightly positive in public areas (= 1.01; 85% CI: 0.94–1.08) and slightly negative in private areas (= 0.97; 85% CI: 0.87–1.06), but CI did not preclude stable occupancy on both ownerships. Based on generalized linear mixed models applied to inland radar survey data, murrelet counts in private HCP areas (least-squares [LS] mean = 8.7; 85% CI: 6.2–12.2) were lower than those in public reference areas (LS mean = 14.8; 85% CI: 10.1–21.7), but CI overlapped. Murrelet counts declined by 12–17% annually on both ownerships over the study period based on the top model, but a closely competing interactive model suggested more rapid declines in public reference (14–20%) than in private HCP (10–15%) areas. Both models indicated that murrelet counts were negatively related to sea surface temperature, suggesting that warm ocean conditions negatively affect murrelet breeding effort. Collectively, these results suggest that while HCP habitat may be lower quality than public reference areas, the HCP has likely not exacerbated ongoing declines of murrelets in the region. This work highlights the importance of including reference areas when evaluating conservation policies.

Keywords: Brachyramphus marmoratus, Habitat Conservation Plan, Marbled Murrelet, occupancy, private land, radar, recovery

LAY SUMMARY

- Habitat Conservation Plans (HCPs) are a common conservation tool used to protect habitat on private land in the United States, but the effectiveness of individual HCPs is rarely evaluated.
- We assessed the ability of 1 high-profile HCP to protect breeding habitat for a threatened seabird, the Marbled Murrelet (*Brachyramphus marmoratus*), on land owned by a lumber company. To do this, we compared trends in murrelet occupancy and abundance between private HCP conservation areas and public reference areas.
- We found that habitat protected within public reference areas was higher quality, but lack of differences in trends between ownerships indicated that the HCP did not exacerbate ongoing declines of murrelet populations in our study area. Additionally, habitat in private HCP areas is likely to improve as forests continue to mature.
- We also found that the abundance of murrelets on both landownerships was declining rapidly over time, likely due to reduced breeding effort because of broad-scale environmental factors.
- Rigorous assessments of conservation policies are imperative for guiding future conservation initiatives and investments, especially on private land where species are most vulnerable to habitat loss.

Evaluando la efectividad de un Plan de Conservación de Hábitat de bosque para *Brachyramphus marmoratus*, un ave marina amenazada

RESUMEN

Los Planes de Conservación de Hábitat (PCH) comúnmente facilitan la conservación de hábitat en tierras privadas en Estados Unidos, pero rara vez se evalúa la efectividad individual de estos PCH. En este estudio, evaluamos la efectividad de un PCH de alto vuelo creado en tierras privadas por una compañía forestal para proteger bosque maduro usado para criar por parte de *Brachyramphus marmoratus*. Usamos datos de 17 años de monitoreo del PCH para comparar a lo largo del tiempo las tendencias de ocupación de *B. marmoratus* y los conteos tierra adentro entre áreas de PCH privadas y áreas públicas de referencia. Basados en modelos de ocupación aplicados a datos de censos auditivos y visuales, la ocupación promedio fue mayor en las áreas públicas de referencia (0.85; 85% IC: 0.79–0.90) que en las áreas de PCH privadas (0.46; 85% IC: 0.38–0.54). En términos numéricos, las tendencias en ocupación fueron ligeramente positivas en las áreas públicas (= 1.01; 85% IC: 0.94–1.08) y ligeramente negativas en las áreas privadas (= 0.97; 85% IC: 0.87–1.06), pero los intervalos de confianza no descartaron una ocupación estable en ambos tipos de propiedades. Basados en modelos mixtos lineales generalizados aplicados a los datos de los censos de radar tierras adentro, los conteos de *B. marmoratus* en las áreas de PCH privadas (media de mínimos cuadrados = 8.7; 85% IC: 6.2–12.2) fueron más bajos que aquellos de las áreas públicas de referencia (media de mínimos cuadrados = 14.8; 85% IC: 10.1–21.7), pero los intervalos de confianza se superpusieron. Los conteos de *B. marmoratus* disminuyeron un 12–17% por año en ambos tipos de propiedades a lo largo del período de estudio basados en el mejor modelo, pero un modelo interactivo también muy bueno sugirió disminuciones más rápidas en las áreas públicas de referencia (14–20%) que en los PCH privados (10–15%). Ambos modelos indicaron que los conteos de *B. marmoratus* estuvieron negativamente relacionados con la temperatura de la superficie del mar, sugiriendo que las condiciones cálidas del océano afectaron negativamente el esfuerzo reproductivo de *B. marmoratus*. En conjunto, estos resultados sugieren que mientras el hábitat de PCH puede ser de menor calidad que el de las áreas públicas de referencia, el PCH probablemente no ha exacerbado las disminuciones en curso de *B. marmoratus* en la región. Este trabajo subraya la importancia de incluir áreas de referencia cuando se evalúan las políticas de conservación.

Palabras clave: Brachyramphus marmoratus, ocupación, plan de conservación de hábitat, radar, recuperación, tierra privada

INTRODUCTION

There is growing recognition of the need to empirically evaluate the effectiveness of conservation policies (Ferraro and Pattanayak 2006, Fisher et al. 2013, Baylis et al. 2016, Ribas et al. 2020). Even common biodiversity conservation policies are rarely evaluated with the same rigor as ecological hypotheses, leading to uncertainty about the effectiveness of these measures and conservation investments (Ferraro and Pattanayak 2006). One common conservation tool in the United States is the Habitat Conservation Plan (HCP) policy under the Endangered Species Act (ESA). The ESA protects habitat for listed threatened and endangered species on both federal and nonfederal land, including land owned by private citizens, which is where species are most vulnerable to habitat loss (Eichenwald et al. 2020). However, because restrictions on land use imposed by the ESA can promote perverse incentives for private landowners, such as the preemptive removal of habitat or listed species from private land (Wilcove et al. 1996, Brook et al. 2003, Lueck and Michael 2003), the HCP policy was developed to promote partnerships between private landowners and the federal government to address the conservation of listed species. Incidental take permits issued with approved HCPs allow development and other land management activities to continue if threats to listed species are minimized and mitigated to the maximum extent practicable, for example by conserving a portion of important habitat or seasonally restricting activities that could impact the covered species. Because of the flexibility they provide to landowners, HCPs have become a common tool for managing listed species on nonfederal land in the United States, with more than 1,000 approved HCPs covering more than 18.5 million hectares (U.S. Fish and Wildlife Service (USFWS) 2016). Despite the frequent application of this policy, assessments of the effectiveness of individual plans are rare (Shilling 1997). Thus, whether HCPs constitute an effective mechanism for increasing landowner flexibility without impacting the viability of listed species remains a critical, unanswered question (Harding et al. 2001, Schwartz 2008).

Understanding the effectiveness of individual HCPs is challenging for at least 2 reasons. First, many HCPs lack adequate monitoring programs (Harding et al. 2001), and even when monitoring has been performed, few HCPs have been implemented for a sufficient duration to detect changes in populations, which can take decades (Kareiva et al. 1999). Second, the geographic ranges of listed species usually exceed the area governed by individual HCPs such that listed species are affected by broad-scale environmental factors (e.g., climate change) beyond the activities allowed under the HCP. Further, in some cases, population declines of listed species may be an a priori expectation because of persistent, large-scale environmental stressors. Therefore, rather than only monitoring populations within HCP areas, also monitoring populations within a control or reference area that experiences similar broad-scale environmental conditions would allow for more rigorous evaluations of HCP impacts on species.

The Marbled Murrelet (*Brachyramphus marmoratus*; hereafter murrelet) is a federally threatened seabird that, in the conterminous United States, nests almost exclusively in old-growth forests (Hamer and Nelson 1995) and forages in the nearshore waters of the Pacific Ocean (Raphael et al. 2015). Murrelet breeding and abundance are negatively affected by fragmentation and loss of breeding habitat resulting from management activities like harvest of economically valuable old-growth trees (Raphael et al. 2002a, Zharikov et al. 2007, Betts et al. 2020). Additionally, murrelet populations are affected by a myriad of broad-scale environmental processes. For example, higher murrelet reproductive success has been linked to cooler ocean conditions and concomitant high availability of prey, such as krill and juvenile rockfish (Meyer et al. 2002, Becker et al. 2007, Raphael et al. 2015). Loss of nesting habitat due to timber harvest in old-growth forests and declines in prey abundance at sea have both been implicated in murrelet population declines (Carter and Erickson 1992, Becker and Beissinger 2006, Betts et al. 2020). Therefore, the effects of broad-scale oceanic factors on murrelets can complicate the assessment of local breeding habitat management and conservation strategies, such as those included in an HCP, if reference areas are not also monitored.

Here, we utilized a 17-year dataset of Marbled Murrelet inland surveys to evaluate the effectiveness of private conservation areas created as part of a high-profile HCP to protect murrelet breeding habitat on private land in northwestern California. To assess this HCP, we utilized murrelet occupancy and inland count data collected from HCP conservation areas, as well as nearby protected public areas that were not part of the HCP. These data were collected as part of an effectiveness monitoring program implemented with the HCP. Because murrelets in public and private areas were affected by similar broad-scale oceanic factors, we used these protected public areas as a baseline to evaluate the utility of the HCP conservation areas for protecting murrelet breeding habitat. Importantly, protected public areas were larger and had higher occupancy and inland counts than HCP conservation areas at the inception of the HCP (see Bigger et al. 2006a) and, thus, here we compare *trends* in murrelet occupancy and inland counts between HCP sites and protected public sites as our metric to assess the effectiveness of the HCP. We predicted that if the HCP conservation areas were effective, then trends in murrelet occupancy and counts would not be different between private HCP areas and public reference areas, or trends in private HCP areas would be more positive. This monitoring program provides a key opportunity to compare murrelet inland habitat use between areas characterized primarily by differences in forest management and protection afforded by an HCP. By evaluating a prominent HCP for Marbled Murrelets, we aim to provide insights into the effectiveness of HCPs as a conservation policy, and an example framework for more rigorous evaluations of HCPs in the future.

METHODS

Study Area

The Pacific Lumber Company, located in northwestern California, completed and implemented a 200,000-acre, multi-species HCP that includes Marbled Murrelets in 1999. Prior to the HCP, the extensive harvest of old-growth forests took place beginning in the late 1800s. This HCP, and the subsequent transfer of 3,024 ha of old-growth forests known as the Headwaters Forest Grove to the federal government, helped resolve a highly public, decade-long forest management controversy. After the transfer, 2 of the few large remaining tracts of unharvested old-growth forests in northern California were officially protected within the newly created Headwaters Forest Reserve (managed by the Bureau of Land Management) and the already preserved Humboldt Redwoods State Park (managed by the California Dept. of Parks and Recreation). Additionally, on private land subject to the HCP, 6 of the remaining stands of old-growth forests (~2,671 ha total) were designated as Marbled Murrelet Conservation Areas (MMCAs), in which timber harvesting was prohibited except to accelerate murrelet habitat development (Figure 1). Forests outside of the MMCAs, including small amounts of potentially occupied murrelet nesting habitat, remained subject to timber management activities. In 2008, ownership of the land subject to the HCP was transferred to the Humboldt Redwood Company, which manages the property, no longer harvests any old-growth trees or stands, and continues to fulfill the requirements of the HCP. Forests on both public and private land experienced a similar history of mixed use and are composed mainly of coastal redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*) in the overstory and tanoak (*Notholithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), salal (*Gaultheria shallon*), and western sword fern (*Polystichum munitum*) in the understory. Habitat within both ownerships is characterized by a mosaic of forest types, including varying degrees of unharvested old-growth and partially harvested (residual) old-growth as well as second-growth forest.

We used 2 protected public areas, Headwaters Forest Reserve (3,024 ha) and Humboldt Redwoods State Park (21,448 ha; hereafter collectively referred to as "public"; Figure 1), as reference sites to compare trends in murrelet occupancy and inland counts between non-HCP and HCP areas. Within HCP areas, we conducted murrelet surveys at 4 MMCA sites: Bell Lawrence MMCA (193 ha), Shaw Gift MMCA (531 ha), Allen Creek MMCA (928 ha), and Cooper Mill Creek MMCA (308 ha; hereafter collectively referred to as "private"; Figure 1). We note that the MMCAs were the only areas monitored for murrelet occupancy and abundance on private land; no murrelet monitoring surveys took place on HCP land outside of the MMCAs. Thus, we compare murrelet trends on public reference sites to those on MMCAs, rather than broadly to all of the land subject to the HCP. This is a valuable comparison, though, because the creation of MMCAs was the focal strategy for murrelet protection within the HCP. While no timber harvest took place within the MMCAs during the life of the HCP, it is possible that historic (prior to 1999) selective harvesting of large, old trees on private

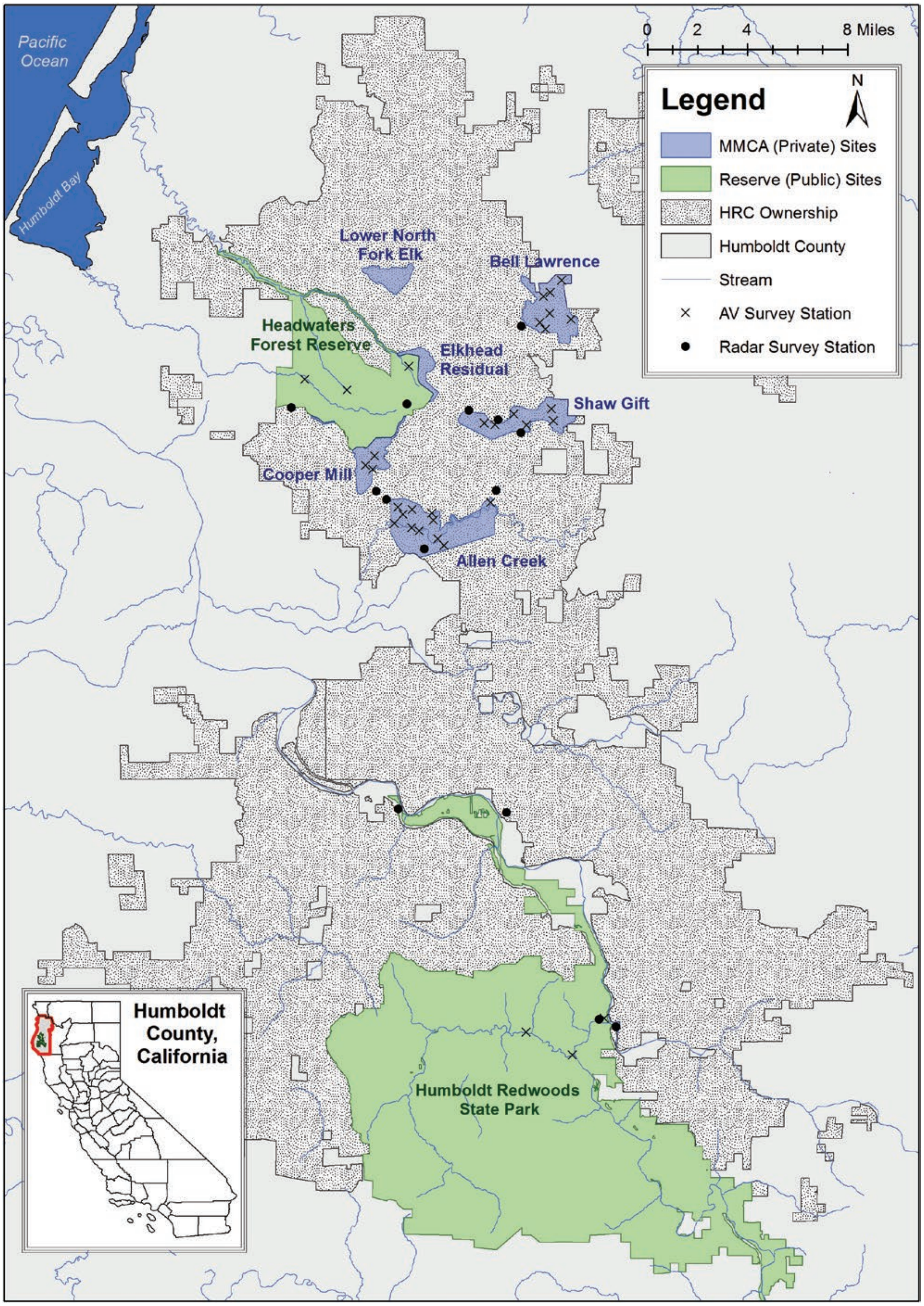

FIGURE 1. Map of the study area. Surveyed private (HCP) sites included Allen Creek, Bell Lawrence, Cooper Mill, and Shaw Gift MMCAs. Surveyed protected public (non-HCP) sites included the Headwaters Forest Reserve and Humboldt Redwoods State Park.

land or timber harvest at the edges of the MMCAs could result in delayed murrelet abandonment of private HCP areas given this species' long-life span and presumed nest site fidelity (Meyer et al. 2002). Additionally, the MMCAs constitute smaller and less-contiguous old-growth habitat that may be less suitable for murrelet breeding. Therefore, we expected to see more negative trends in occupancy dynamics and inland counts in the MMCAs than in public reference areas if the MMCAs, and thus the HCP, were not effective for promoting continued murrelet breeding on private land.

Survey Methods

We used 2 independent survey methods to monitor murrelet use of inland breeding habitats annually. Inland audio-visual surveys yield information about the presence and potential breeding status of murrelets, and radar surveys provide information about the abundance of murrelets flying inland and can be used as an index of the size of the potential breeding population (Peery et al. 2004a). We used audio-visual surveys from 2000 to 2016 to determine trends in murrelet occupancy dynamics and radar surveys from 2002 to 2018 to assess trends in inland murrelet counts. Audio-visual and radar surveys on both ownerships each year were conducted by the same set of surveyors, all of whom were trained and evaluated annually in Marbled Murrelet survey techniques, as suggested by Pacific Seabird Group protocols.

Audio-Visual Surveys

Marbled Murrelets were monitored from 2000 to 2016 using audio-visual surveys at 33 survey stations (n = 27 private, n = 6 public; Figure 1). Survey stations were placed in good murrelet habitat and positioned to maximize surveyors' ability to see murrelets because occupancy was determined based on visual observations. Survey station placement and audio-visual surveys were conducted according to the standard protocol for monitoring this species at inland locations (Ralph et al. 1994, Pacific Seabird Group 1998). While the Marbled Murrelet monitoring protocol was revised in 2003, per the requirement of the HCP, Humboldt Redwood Company continued to monitor murrelets according to the protocol that was in place when monitoring began to ensure consistency in monitoring throughout the study period. Surveys took place during the breeding season, between April 15 and August 5 each year. Station visits were spread throughout the nesting season such that visits to an individual survey station were at least 6 and no more than 30 days apart, and at least one survey took place in the last 2 weeks of July or the first week of August. Surveys began 45 min before and continued until 75 min after sunrise. During each survey, surveyors considered stations to be unoccupied when no murrelets were detected and occupied when they observed certain behaviors such as circling above the canopy, flying below the canopy, or landing on a branch. While these behaviors are not necessarily indicative of a current nesting attempt, they are considered indicators of habitat that are important for breeding (Bahn 1998, Pacific Seabird Group 1998). Because it is unclear whether murrelets observed flying over a station but not circling (i.e., flyovers) are utilizing habitat near the station, we considered stations where only flyovers were recorded as unoccupied. Surveyors visited each survey station 5 times per season or until an occupied behavior was observed, after which no further surveys were conducted.

Audio-Visual Survey Analysis

Occupancy and detection covariates. We used 2 categorical station-level covariates to describe habitat in our study area. Ownership was a categorical covariate indicating whether a survey station was located on private (HCP) or public (non-HCP) land, which we used to test the effect of the HCP conservation areas on occupancy dynamics. Ownership encompasses many HCP-driven factors that could be related to murrelet occupancy, including habitat differences between public and private land such as amount of old-growth, age of trees, availability of nesting platforms, amount of edge habitat, and patch area. Habitat was a categorical covariate that indicated whether a survey station was located within 200 m of unharvested old-growth forests regardless of ownership. Because over half of the private HCP survey stations were located within 200 m of unharvested old-growth (Supplementary Material Table S2), we used habitat to test whether proximity to old-growth alone, and not ownership per se, was important for determining murrelet occupancy dynamics. We also tested both ownership and habitat as potential influences on surveyor's ability to detect murrelets because public stations generally had larger tracts of old-growth forests and murrelet detectability has been shown to be positively correlated with the amount of old-growth near a survey station due to changes in murrelet flight behavior near old-growth, like flying more slowly and vocalizing more as they prospect for or maintain a bond with a nest site (Bigger et al. 2006b).

We used survey-level covariates to describe factors that may have affected surveyors' ability to detect murrelets during surveys. We considered inclusion of proportion cloud cover (cloudcov) and precipitation (precip) in detection models because both have been shown to influence murrelet detection during surveys (Naslund and O'Donnell 1995, Bahn 1998). Cloud cover and precipitation data were collected at the beginning of all audio-visual surveys, as most murrelets move inland before sunrise, corresponding with the beginning of the survey period (Rodway et al. 1993, Naslund and O'Donnell 1995, Burger 2001). Cloud cover was estimated as the proportion of the sky obscured by clouds, and precipitation was categorized as none, fog, drizzle, or light rain. We also included quadratic day of year (DoY) as a temporal covariate affecting detection probability because we expected that murrelet

TABLE 1. Covariates used to model detection probability (p), initial occupancy (ψ_1), colonization (γ), and local extinction (ε). Each "x" indicates that the effect of the covariate was tested for the parameter.

Covariate	Variable type	Definition	Parameters		
			p	Ψ_1	γ, ε
cloudcov	Continuous	Percentage cloud cover	x		
precip	Categorical	Precipitation condition	x		
DoY	Continuous	Day of year (quadratic)	x		
visibility	Categorical	Visibility at each survey station, ranked by murrelet surveyors	x		
PropOG	Continuous	Proportion of habitat within a 1000-m radius of the survey station that is old-growth forest	x		
ownership	Categorical	Whether a site is on private (HCP) or public (reference) land	x	x	x
habitat	Categorical	Whether a site is located within 200 m of unharvested old-growth or has only residual old-growth within 200 m	x		x

detections would likely peak late in the breeding season as murrelets flew to and from the nest to provision nestlings and then decline (Naslund 1993, Rodway et al. 1993). DoY variables were centered and standardized before inclusion. To account for heterogeneity in visibility from each survey station, we asked murrelet surveyors to rank each survey station as low, medium, or high visibility, and we included this as a station-level covariate in detection models (visibility). Stations with low visibility were often located in the center of a stand and had little view of the sky, while stations with high visibility were located on a ridge, road, or other opening and had a good view of a large swath of sky (S. Chinnici, personal observation). Finally, we also included a continuous station-level covariate for the proportion of forest that was old-growth within 1,000-m radius of each survey station (PropOG) because murrelet detectability has been shown to be positively correlated with the amount of old-growth forests near survey stations due to changes in murrelet flight behavior, like flying more slowly and vocalizing more near large tracts of old-growth (Bigger et al. 2006b). We used ArcMap 10.3 and Humboldt Redwood Company forest cover maps created in 2002 to delineate old-growth, which we defined as forest that was classified as either unharvested old-growth or residual old-growth with at least 50% canopy cover, and to calculate the proportion of old-growth for each survey station. All covariates and definitions can be found in Table 1.

Model selection. We used dynamic occupancy modeling in program PRESENCE 2.13.6 to characterize murrelet occupancy dynamics. Dynamic occupancy modeling estimates survey station occupancy over multiple primary survey periods while correcting observations for imperfect detection by using detection/non-detection data from repeated sampling within secondary survey periods (Mackenzie et al. 2003). Our occupancy models estimated 3 parameters: ψ_1 was the probability of a station being occupied in the first year of surveys (initial occupancy), γ_t was the probability of an unoccupied site being colonized in year t (colonization), and ε_t was the probability of an occupied site becoming unoccupied in year t (temporary or local extinction; Mackenzie et al. 2003). We note again that for murrelets, colonization and local extinction represent changes in occupied behaviors, not necessarily whether stations were used for breeding. Our primary sampling periods, t, were breeding seasons (i.e., April 15 to August 5), and our secondary sampling periods were approximately 3-week windows within each breeding season (April 15 to May 6; May 7–29; May 30 to June 20; June 21 to July 13; and July 14 to August 5). If a site was visited multiple times within a secondary sampling period, we randomly selected one survey to include in the analysis. We also parameterized detection probability as in MacKenzie et al. 2003, where p represented the probability of detecting murrelet occupancy, given that a site was occupied.

We first chose the best modeling structure for detection probability (p). To do so, we assessed the effect of combinations of several covariates (ownership, habitat, DoY, precip, cloudcov, visibility, PropOG) on within-year detection, and then assessed temporal variation in detection probability among years by comparing a null model with no time trend, a model with an annual effect (year), a model with a linear time trend (T), and a model with a logarithmic time trend ($\ln T$). We examined several different possible time trends because re-growth of trees near survey stations could impact visibility and result in decreasing detection probabilities over time, but if a trend was present, it could be linear or non-linear. When evaluating competing detection models, we allowed colonization (γ_t) and local extinction (ε_t) to vary by year, and we allowed initial occupancy (ψ_1) to vary by ownership. We ranked models using Akaike's information criterion (AIC) and AIC model weights (w_i) (Burnam and Anderson 2002).

To directly compare occupancy trends between private HCP areas and public reference areas, we used the best detection model and fit one model for each ownership using year-specific colonization and local extinction. We used these models to obtain derived estimates of annual occupancy (ψ_t) and annual rate of change in occupancy (λ_t) for each ownership (Mackenzie et al. 2003, MacKenzie et al. 2018). We then calculated the geometric mean of the rate of change in occupancy () for each ownership, where = 1 indicates stable occupancy over the 16-year survey period and < 1 indicates a decline in occupancy over time (Jones et al. 2018). We calculated variance for using the delta method (Powell 2007).

Lastly, to characterize differences in occupancy dynamics between public reference stations and private HCP stations, we examined the effects of temporal and habitat covariates on colonization () and local extinction (ε_t), while using the best detection model. Because public stations were known to have higher occupancy when the HCP was implemented (Bigger et al. 2006a), we allowed initial occupancy (ψ_1) to vary by ownership for all models. We tested (1) a null model with no covariate effects on colonization or local extinction; (2) models with ownership or habitat effects on colonization, local extinction, or both; (3) models with ownership or habitat and an annual (year) effect on colonization, local extinction, or both; and (4) additive and interactive effects between time trends (T, ln$T$) and ownership or habitat effects on colonization, local extinction, or both (37 models in total; Supplementary Material Table S1). If an interactive model between a time trend and ownership was well supported, it would indicate that differences exist in occupancy trends between ownerships. We used models with habitat to understand if proximity to old-growth, rather than ownership per se, was the important factor determining trends in colonization and local extinction. We again ranked models using AIC and w_i (Burnam and Anderson 2002), and we calculated variances of dynamic occupancy probabilities and covariate effects using the delta method (Powell 2007). After selecting the best model, we assessed goodness of fit using parametric bootstrapping (100 simulations) within program PRESENCE, followed by an analysis of deviance to assess the amount of variation in occupancy explained by the covariates in the best-supported model. Analysis of deviance compares the difference in deviance between a constant (null) model and the model of interest to the difference in deviance explained by the constant (null) model and a global (most complex) model and hence provides an estimate of r^2 (Skalski et al. 1993, Tempel et al. 2016). The constant model for our analysis of deviance included the best detection structure and only intercepts for initial occupancy (ψ_1), colonization (γ_t), and local extinction (ε_t). The global model included the habitat covariates from the top-ranked model and was fully time varying for colonization and local extinction, while using the same structure for detection as the top-ranked model (Tempel et al. 2016, Jones et al. 2018).

We are confident that our study meets the assumptions of these types of models. In particular, we assumed (1) the true occupancy state of each survey station did not change within a breeding season because occupied behaviors are strong indicators of breeding behavior, (2) the detection histories observed at stations were independent of one another because occupied behaviors are a local phenomenon, and (3) there were no false detections of murrelets during surveys because personnel were well trained in conducting murrelet surveys. We report all results with 85% confidence intervals (CI) to ensure compatibility with AIC model selection (Arnold 2010), and we report model effect sizes using odds ratios (Jones and Peery 2019).

Radar Surveys

We used radar surveys from 2002 to 2018 to assess inland murrelet counts at 14 survey stations (n = 8 private, n = 6 public; Figure 1). Radar survey stations were located within forest stands or along riparian corridors that led to potential breeding areas, as murrelets are known to fly through corridors to reach inland breeding sites (Nelson and Hamer 1995). Radar stations were positioned such that the radar unit had unobstructed scanning areas of the forest stands or flyways being surveyed. Radar surveys were conducted from 75 min prior to 75 min after sunrise. Each station was surveyed 4 times per year between April 15 and August 5 from 2002 to 2018, except in 2009 which had a reduced sampling effort and was excluded from this study. Repeat visits to a radar station were at least 9 days apart. Radar surveyors utilized a Furuno® FR-1510 Mark-3 high-performance X-band radar that transmits 9,410 ± 30 MHz with a peak power output of 12 kW. This radar used a 2-m antenna mounted onto a pickup truck ~3.5 m above ground level. The antenna was set to rotate 24 times per minute and to scan a circular area with a 1.5-km radius. Pulse length was set at 0.07 µs. During each survey, the total number of murrelet detections was counted. Radar targets traveling at least 64 km hr^{-1} and leaving an echo trail of ≥3 blips after 4 antenna sweeps were classified as murrelets (Cooper et al. 2001). Because single and small groups of murrelets flying within a few meters of each other appear as a single echo on a radar screen (Burger 1997), each echo trail was counted as a single detection. An overlap in radar ranges for some survey stations could have led to some murrelets being double-counted when those stations were surveyed the same morning, so to prevent double-counting, we randomly removed one survey on mornings when overlapping stations were surveyed simultaneously.

Radar survey analysis. We analyzed murrelet counts obtained from radar surveys with a generalized linear mixed model (GLMM) in the *lme4* package (Bates et al. 2015) in the R statistical environment (R Core Team 2020). Because our count data were overdispersed, we used a negative binomial distribution with a logarithmic link to correct for overdispersion. We were interested in determining (1) if there was a negative trend over time in murrelet counts, and if so, (2) if that negative trend was different between public and private land. Thus, with the goal of keeping models as simple as possible due to the limited number of survey stations, we compared 2 models: (1) a full model including ownership, linear year (T), and an interaction effect between them and (2) a reduced model without the interaction effect. We compared these 2 models using AIC (Burnam and Anderson 2002). We included sea surface temperature (SST) in our model because at-sea conditions influence the proportion of murrelets that fly inland to breed in a given year (Peery et al. 2004a). While there are many oceanic factors we could have used, including lag effects from oceanic conditions the previous year (e.g., Betts et al. 2020), we chose SST because of prior murrelet work conducted in California. Generally, cooler average SSTs lead to better foraging conditions (Becker and Beissinger 2003), and prey availability has been linked to breeding success in Marbled Murrelets (Becker et al. 2007). SST data (°C) were averaged from NOAA buoys 46022 (Eel River—17NM West-Southwest of Eureka, California, USA) and 46027 (St. George's—8NM West Northwest of Crescent City, California, USA) for the months of January through April (pre- and early-breeding season) for each year (2002–2018). We also included quadratic DoY in the model because murrelet activity likely peaks and then tapers off each year (Mack et al. 2003). SST and DoY variables were centered and standardized before inclusion in the model. We also included surveyor as a fixed effect to account for any variation in counts that may have existed among surveyors. Finally, we also included a random slope and intercept for each survey station over time.

After we completed modeling, we examined diagnostic plots including a QQ plot, a residual plot, and individual plots regressing model residuals against each explanatory variable to ensure that our model adequately met GLMM assumptions for our purposes. We also ensured that the overdispersion parameter, calculated as the Pearson chi-square divided by the degrees of freedom, was reasonably close to 1. We then used our GLMM to estimate the number of murrelets counted per survey in each year and we characterized slopes of inland murrelet counts on each ownership using the *emmeans* package (Lenth 2020). Finally, we also conducted a power analysis using the *simr* package (Green and Macleod 2016) to estimate our power to detect a difference in trends between public and private land, given our survey design and observed data.

RESULTS

Occupancy Modeling of Audio-Visual Data

We conducted 1,968 audio-visual surveys from 2000 to 2016, with an average of 125 surveys per year (range: 97–142). We detected murrelet occupancy at an average of 34% of private HCP stations and 82% of public reference stations annually (Figure 2A). On average, public stations had a higher proportion of old-growth forests within a 1,000-m radius of survey stations (public: 0.71 [SE = 0.11], private: 0.20 [SE = 0.02]). A full description of annual observed occupancy and habitat covariates for each survey station is available in Supplementary Material Table S2.

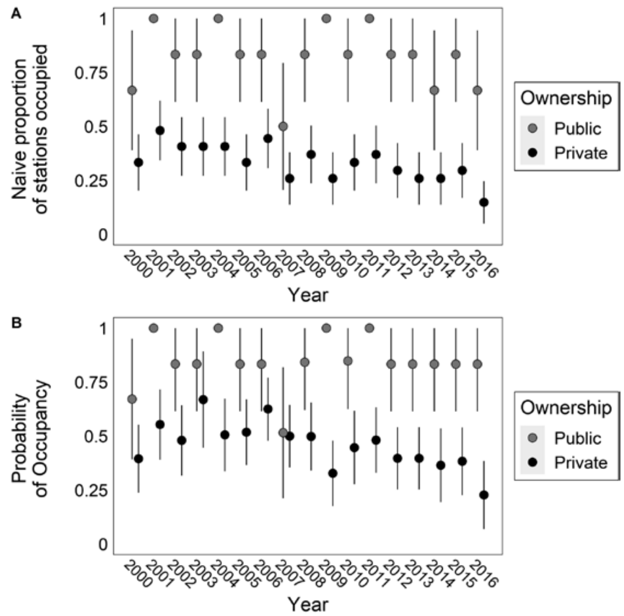

FIGURE 2. (A) Proportion of sites where murrelet occupancy was observed, without correcting for detection. (B) Derived annual estimates of occupancy for stations on public and private land over time from fully time-varying models (see Methods section). Error bars represent 85% CI.

Detection probabilities throughout the study ranged from 0.10 to 0.79, which are similar to those published by others for audio-visual surveys (e.g., Cooper and Blaha 2002, Bigger et al. 2006b). The top model for detection parameters included within-year effects of ownership and quadratic DoY (Supplementary Material Table S3) and a linear year effect (T; Supplementary Material Table S4). Detection probability was higher on public than on private land ($\beta_{ownership}$ = 1.17, 85% CI: 0.88–1.45). The inclusion of a linear year effect indicated that detection probabilities declined over time (β_T = –0.09, 85% CI: –0.11 to –0.06), which could have been due to re-growth of trees and vegetation at survey stations that reduced visibility or due to changes in murrelet behavior (e.g., less circling or less calling, making birds harder to detect).

Our fully time-varying models with year-specific colonization and local extinction revealed that over the 16-year study period, average occupancy at public reference sites was 0.85 (85% CI: 0.79–0.90), while average occupancy at private HCP sites was 0.46 (85% CI: 0.38–0.54). Occupancy

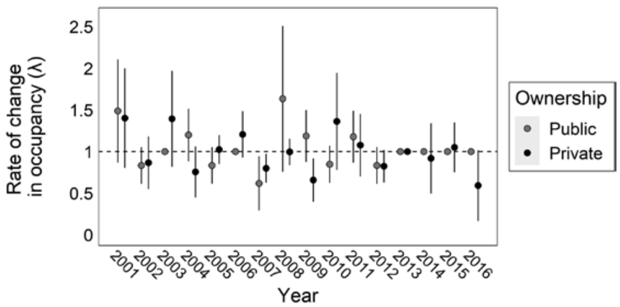

FIGURE 3. Derived annual rate of change in occupancy (λ_t) for both ownerships from the fully time-varying models. Error bars represent 85% CI calculated using the delta method. The horizontal dotted line denotes λ = 1, which represents stable occupancy between years.

in public reference areas was consistently higher than occupancy in private HCP areas (Figure 2B). Numerically, trends in occupancy were slightly positive at public reference sites (= 1.01, 85% CI: 0.94–1.08) and slightly negative at private HCP sites (= 0.97, 85% CI: 0.87–1.06; Figure 3) but estimates for both ownerships had wide CI, and thus, there was no strong evidence for a trend in occupancy on either ownership.

Our modeling of colonization and local extinction dynamics indicated that ownership and either a linear or log-linear time trend were important factors in determining colonization dynamics and that ownership and a linear or log-linear time trend were important in determining local extinction dynamics (Figure 4; Supplementary Material Table S5). The top model was additive and included ownership and a log-linear time trend for both colonization and local extinction:

$$\mathrm{logit}\left(\gamma_t\right) \ = \ 0.78 - 1.41 \ \left(\ln T\right) \ + \ 1.52 \ \left(\mathrm{Ownership}_{\mathrm{public}}\right)$$

$$\mathrm{logit} \ \left(\varepsilon_t\right) \ = \ 0.41 - 0.78 \ \left(\ln T\right) - 1.08 \ \left(\mathrm{Ownership}_{\mathrm{public}}\right)$$

This model indicated that the odds of colonization increased by a factor of 4.57 (85% CI for odds ratio: 1.46–14.30) regardless of the year for public reference areas compared to private HCP areas (Figure 4A), and the odds of colonization declined on both ownerships by a factor of 0.25 per log-year (85% CI for odds ratio: 0.14–0.44; Figure 4A). This model also indicated that the odds of local extinction decreased by a factor of 0.34 (85% CI for odds ratio: 0.12–0.94) for public reference areas compared to private HCP areas (Figure 4B), and the odds of local extinction declined on both ownerships by a factor of 0.46 per log-year (85% CI for odds ratio: 0.25–0.85; Figure 4B). This model received 0.38 of model weight, covariates in this model explained 59% of the variation in colonization and local extinction rates according to the analysis of deviance,

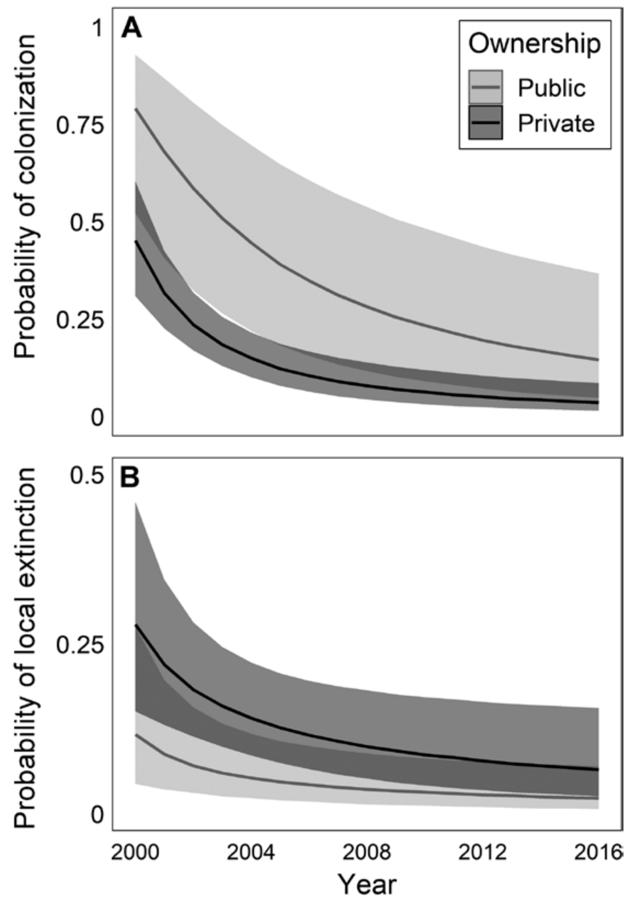

FIGURE 4. Occupancy dynamics from the top occupancy model, which included ownership and an additive log-linear time trend on both (A) colonization and (B) local extinction. Shaded areas represent 85% CI.

and our goodness-of-fit test did not indicate any issues with model fit (P = 0.37). A model that included ownership and an additive linear time trend (T) was within 1 AIC of the top model and received 0.23 of model weight, but this model produced very similar estimates of colonization and local extinction as the top model (Supplementary Material Table S6).

GLMM of Radar Data

We completed 814 radar surveys from 2002 to 2018 (n = 346 public, n = 468 private). We counted an average of 29.3 (SE: 1.57, range: 0–135) and 14.2 (SE: 0.68, range: 0–109) murrelets per 2.5-hr survey at all stations in public reference and private HCP areas, respectively, over the entire study period. Generally, average annual murrelet counts were higher in public reference areas than in private HCP areas (Figure 5A). The full (ownership by year interaction) and reduced (additive ownership and year effects) models had similar AIC scores: the reduced model was ranked higher, but the full model had some support

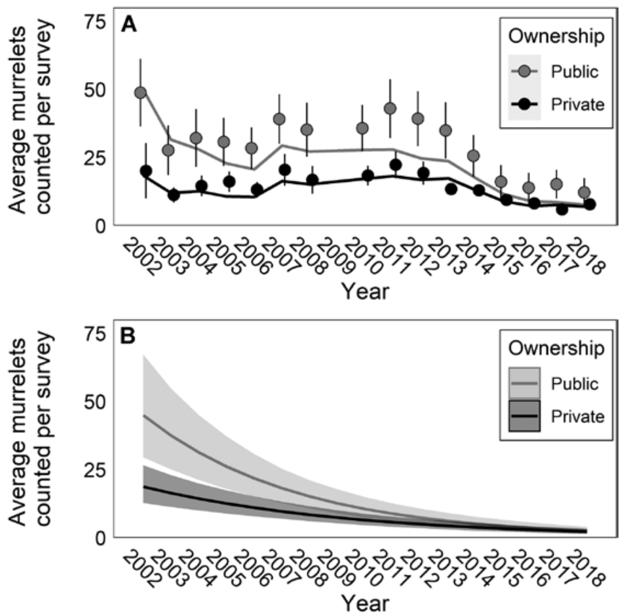

FIGURE 5. Radar survey and analysis results. (A) Dots and 85% error bars represent the observed number of murrelets counted per radar survey, averaged across stations on public and private land each year. Lines represent GLMM-derived estimates of average murrelets counted per radar survey given the observed values of all model parameters for stations on public and private land each year, with bootstrapped 85% CI. (B) GLMM-derived effect plot for the interaction between ownership and linear year showing the mean number of murrelets counted per radar survey on each ownership while all other model parameters were held at their median values, with bootstrapped 85% CI. GLMM-derived estimates in (A) and (B) are from the full model including the interaction effect between ownership and year.

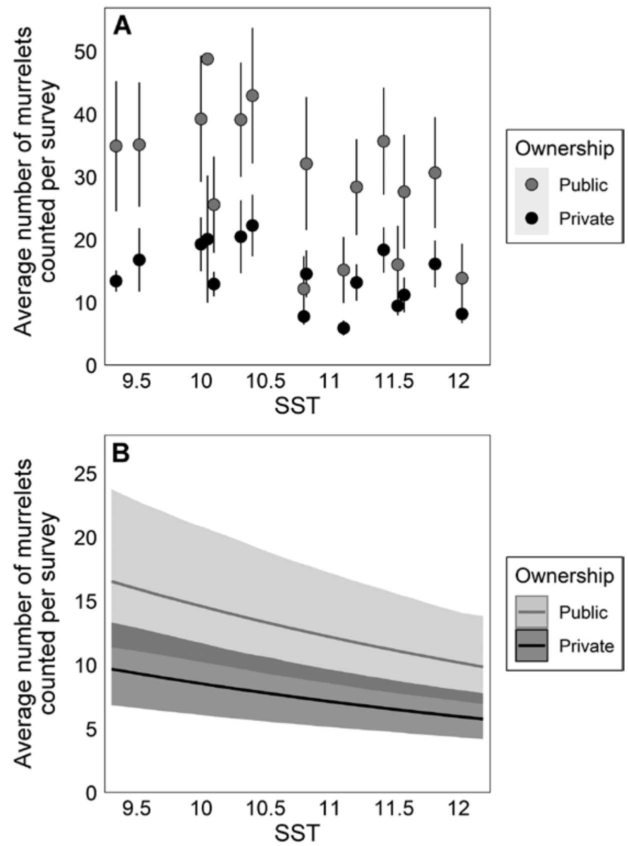

FIGURE 6. Relationship between SST and murrelet inland counts. (A) Observed SSTs and associated murrelet counts, with 85% CI. (B) GLMM-derived effect plot for SST showing the mean number of murrelets counted per radar survey at each SST, while all other model parameters were held at their median values, with bootstrapped 85% CI. Estimates were derived from the full model including the interaction effect between ownership and year.

(ΔAIC: 0.4; likelihood ratio test: $\chi^2 = 2.39$; $P = 0.12$), and we therefore report parameter estimates and effect sizes from both models. There was no evidence of overdispersion for the full model.

The reduced model without the interaction effect estimated the least-squares mean of murrelet counts in private HCP areas as 8.7 (85% CI: 6.2–12.2), while that for public reference areas was 14.8 (85% CI: 10.1–21.7). Similarly, the coefficient for ownership indicated that murrelet counts in private HCP areas were 0.41 times those in public reference areas (85% CI: 0.08–0.65; $P = 0.11$). The linear year term (T) indicated that annual rate of change in counts was 0.86 (85% CI: 0.83–0.88), which means counts were declining on both ownerships by ~14% annually (85% CI: 12–17%; $P < 0.01$). The reduced model also indicated that each 0.8° increase in SST was associated with a 13% decline in murrelet inland counts (85% CI: 10–16%; $P < 0.01$); thus, years with warmer ocean temperatures were associated with lower murrelet counts.

The full model indicated that the estimated annual rate of change in counts in public reference areas was 0.83 (85% CI: 0.80–0.86), corresponding with an ~17% annual decline in counts (85% CI: 14–20%; $P < 0.01$; Figure 5). Additionally, the interaction effect for this model revealed an ~5% annual difference in trends in murrelet counts between public and private land (85% CI: 1–10%; $P = 0.11$; Figure 5B), suggesting that average murrelet counts may be declining faster in public reference areas than in private HCP conservation areas. Thus, the estimated annual rate of change in private HCP areas was 0.88 (85% CI: 0.85–0.90), corresponding to an ~13% annual decline in murrelet counts (85% CI: 10–16%). Similar to the reduced model, the full model also estimated a negative relationship between SST and murrelet counts such that each 0.8° increase in SST was associated with a 13% decrease in inland radar counts (85% CI: 11–17%, $P < 0.01$; Figure 6). All coefficient estimates and standard errors are presented in Supplementary Material Table S7.

Our power analysis indicated that the power to detect a 10% annual difference in trends between ownerships over time was high (estimated power = 96.9%; 95%

CI: 95.6–97.9%) given our study design. However, power to detect the observed 5% annual difference in trends between ownerships was limited (estimated power = 61.5%; 95% CI: 58.4–64.5%). Thus, we suggest that, while counts of inland flying murrelets declined substantially over the study period, the extent to which they declined more on public areas is uncertain.

DISCUSSION

Our results present a nuanced understanding of how conservation areas set aside as part of a high-profile HCP have affected murrelet occupancy and abundance in the context of broad-scale environmental factors. Generally, public areas seem to represent better murrelet habitat–occupancy was consistently higher, colonization was more likely, local extinction was less likely, and murrelet counts were higher in public reference areas. However, these differences existed at the outset of the HCP, and we therefore focused on trends in occupancy and inland counts to evaluate the effectiveness of the HCP in conserving murrelets. Models with additive effects for ownership had consistently more support than those that included interactions, except that murrelet counts were potentially declining more slowly in private HCP conservation areas than in public reference areas. Taken together, this evidence suggests that the HCP has likely not exacerbated negative trends in occupancy and inland counts for the Marbled Murrelet. While HCP conservation areas may not be appreciably contributing to murrelet population recovery due to relatively low occupancy and abundance, the minimum requirement for HCPs is that they do not appreciably reduce the likelihood of survival and recovery of the species. Another important consideration is that habitat within the HCP conservation areas will likely improve over time as forests mature into more suitable habitat, and retaining as much breeding habitat as possible will likely benefit the recovery of the Marbled Murrelet, which has lost ~85% of its breeding habitat in California (USFWS 1997). Most of the extant high-quality nesting habitat in California is now protected within parks, reserves, or other conservation areas (Falxa and Raphael 2016), and thus, factors affecting murrelets at sea, nest predation, and historic and ongoing habitat loss are likely responsible for continued murrelet declines in California (Betts et al. 2020).

Despite the declines we observed in murrelet inland counts in our study area, regional population estimates from at-sea surveys (the standard protocol for censusing murrelet population size) off the coast of southern Oregon and northern California increased from 2000 to 2017 (Pearson et al. 2018). This apparent discrepancy is likely due to the fact that inland radar counts do not reflect regional population size, but more likely represent breeding effort and the size of the potential breeding population, including nonbreeders and failed breeders (Peery et al. 2004a, Barbaree et al. 2014, Lorenz et al. 2017). Thus, the decline we observed in inland radar counts is likely indicative of a long-term decline in local murrelet breeding effort. The decline we observed in colonization over time on both landownerships further supports this explanation. Indeed, dispersal of murrelets from Oregon or Washington into coastal areas near our study site could have resulted in high regional population estimates at-sea near our study area even while, locally, murrelet breeding effort declined. Murrelets are known to temporarily disperse long distances, which can contribute to changes in at-sea populations (Hébert and Golightly 2008, Peery et al. 2008, Hall et al. 2009, Vásquez-Carrillo et al. 2013), and there is evidence that large movements at sea may indicate low breeding propensity for murrelets (Lorenz et al. 2017). It seems likely that murrelets have fidelity for nesting areas (Hébert et al. 2003, Piatt et al. 2007, Lorenz et al. 2019), and murrelet populations have experienced an ~30% decline in Washington, Oregon, and California (Miller et al. 2012). Thus, temporary immigration seems more likely than a permanent increase in regional population size offshore from our study area and is consistent with our inland survey results.

Differences in occupancy and abundance between public and private land are likely attributable, at least in part, to differences in amount and configuration of habitat. The HCP conservation areas consisted of smaller and less-contiguous old-growth patches than public reserves, meaning there was a higher edge to core ratio. Smaller patch size, and therefore less core habitat, has been shown to negatively impact other interior forest species (Valente and Betts 2019), and although some ambiguity exists about the effect of habitat fragmentation on murrelet occupancy and breeding success (Meyer and Miller 2002, Meyer et al. 2002, Raphael et al. 2002b, Zharikov et al. 2006, 2007, Burger and Page 2007, Malt and Lank 2009), it seems unlikely that murrelets have high breeding success in highly fragmented landscapes. Murrelets may be susceptible to edge effects including reduced epiphyte availability (van Rooyen et al. 2011), increased exposure to heat and evaporative water loss (Meyer and Miller 2002), and higher abundance of nest predators (Zharikov et al. 2007). In particular, the potential for nest predation by corvids increases in fragmented habitat (Malt and Lank 2007), and murrelets are sensitive to corvid predation (Luginbuhl et al. 2001, Raphael et al. 2002b, Peery et al. 2004b, Malt and Lank 2009, Peery and Henry 2010). On both ownerships, we found that colonization decreased over the study period, likely because of declining breeding effort but, surprisingly, local extinction also decreased over time. This could be a result of low-quality sites being abandoned by murrelets first, resulting in higher fidelity at sites that remained occupied, which presumably contain high-quality breeding habitat. We note that we cannot infer differences in actual breeding success related to landownership because neither monitoring technique indicates whether a detected murrelet actually nested or more importantly, successfully reproduced. More detailed nest-level work would need to be done to explore breeding success within HCP conservation areas and whether conservation areas could constitute population sinks for murrelets.

There are a few important limitations of our study. The first is that this is a retrospective analysis of survey data collected from an HCP effectiveness monitoring program where treatments (i.e., public and private) were not randomly assigned and survey stations were not randomly placed across the landscape. The small number of stations surveyed for both analyses resulted in the wide CI we calculated for several model parameters. Therefore, our results should be interpreted with some caution and the understanding that larger sample sizes or a more rigorous experimental design would allow stronger conclusions to be drawn about the effect of the HCP conservation areas on murrelet populations. However, our dataset is also unique in its longevity and in the parallel monitoring of public reference areas for direct comparison. The second caveat is that associating murrelets detected by radar with specific habitat is potentially flawed, as radar detections do not guarantee that murrelets are utilizing habitat near a survey station. However, radar surveys are a highly recommended method for monitoring inland habitat use by murrelets because they result in higher detection probabilities and more accurate counts than audio-visual surveys (Burger 2001, Bigger et al. 2006a, 2006b). Additionally, there is little other suitable murrelet nesting habitat located near our study area (Raphael et al. 2011; S. Chinnici, personal observation), so murrelets are unlikely to be transiting through our study area to get to other areas. While radar counts on public land may be inflated if murrelets are detected flying through Headwaters Forest Reserve on their way to use habitat within the MMCAs, we find this scenario unlikely because radar counts at Headwaters Forest Reserve were lower than those in Allen Creek and Bell Lawrence MMCAs, for example.

Finally, we reiterate that murrelet surveys on private land were only conducted within the habitat set aside for murrelets (i.e., the MMCAs), so the effect of the HCP on the occupancy status of any murrelets utilizing private land outside those specific areas remains unknown. While some seasonal restrictions exist to minimize the effects of timber harvest on murrelets that breed outside the MMCAs, these conservation areas were the main protective measure outlined in the HCP for murrelets and the majority of suitable murrelet habitat is protected within them. Therefore, this study still provides vital information about how the HCP has affected Marbled Murrelet populations. Moreover, this multi-species HCP also covers 16 additional species, including fish, amphibians, a reptile, birds, and mammals. The focal species are anadromous salmonids, including Coho (*Oncorhynchus kisutch*) and Chinook (*Oncorhynchus tshawytscha*) Salmon, the Northern Spotted Owl (*Strix occidentalis caurina*), and the Marbled Murrelet. The individual conservation plans of the HCP each include a habitat-based approach with an effectiveness monitoring component. Aquatic effectiveness monitoring for the salmonids and other species has indicated that riparian conditions may be improving following significant impacts during first-cycle logging. Monitoring indicates that the invasive Barred Owl (*Strix varia*) is negatively impacting Northern Spotted Owl occupancy and reproduction as is the case throughout the range of the Northern Spotted Owl (Gutiérrez et al. 2007).

Similar long-term trends in murrelet occupancy and inland counts in public reference and private HCP areas over time and the negative relationship between SST and inland counts underscore the importance of monitoring reference areas when evaluating an HCP. In fact, there is a general need for conservation to better implement rigorous experimental designs and counterfactual analyses to assess the success of conservation policies (Ferraro and Pattanayak 2006, Baylis et al. 2016). However, in light of the lack of funding for conservation initiatives, including even quasi-experimental reference sites in HCP monitoring is an important step in the right direction. We hope that this study will prompt more thorough evaluations of other large-scale HCPs and careful consideration when designing monitoring programs of future HCPs to improve the rigor of such evaluations. Given the importance of habitat protection and the high risk of habitat loss on private land (Eichenwald et al. 2020), thorough evaluations of HCPs and other private land conservation initiatives are essential to ensure conservation on private land is successful.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

ACKNOWLEDGMENTS

Data from murrelet surveys were provided by the Humboldt Redwood Company, and we would like to thank S. McAllister, B. O'Brien, and A. Brown for many years of field surveys. We are grateful to D. Tempel, J. Hines, G. Jones, and B. Hobart for insights into occupancy modeling, and we thank Jim Baldwin for his assistance with the GLMM analysis. We also thank A. Ives, V. Radeloff, and K. Strier for their helpful comments on an earlier draft. Finally, we thank 4 anonymous reviewers

whose comments and suggestions greatly improved the analyses and writing.

Funding statement: This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. DGE-1747503.

Ethics statement: All survey techniques were noninvasive, so no animals were handled as part of this study.

Conflict of interest statement: The authors have no known conflicts of interest to declare.

Author contributions: M.Z.P., S.C., A.P., and K.B. conceived the idea; S.C. coordinated all surveys; K.B. analyzed the data and wrote the paper; M.Z.P., A.P., and S.C. provided substantial feedback on the paper.

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

LITERATURE CITED

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. The Journal of Wildlife Management 74:1175–1178.

Bahn, V. (1998). Habitat requirements and habitat suitability index for the Marbled Murrelet (*Brachyramphus marmoratus*) as a management target species in the Ursus Valley, British Columbia. M.S. thesis, Wright State University, Dayton, OH, USA. https://corescholar.libraries.wright.edu/biology/27

Barbaree, B. A., S. K. Nelson, B. D. Dugger, D. D. Roby, H. R. Carter, D. L. Whitworth, and S. H. Newman (2014). Nesting ecology of Marbled Murrelets at a remote mainland fjord in southeast Alaska. The Condor: Ornithological Applications 116:173–184.

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Baylis, K., J. Honey-Rosés, J. Börner, E. Corbera, D. Ezzine-de-Blas, P. J. Ferraro, R. Lapeyre, U. M. Persson, A. Pfaff, and S. Wunder (2016). Mainstreaming impact evaluation in nature conservation. Conservation Letters 9:58–64.

Becker, B. H., and S. R. Beissinger (2003). Scale-dependent habitat selection by a nearshore seabird, the Marbled Murrelet, in a highly dynamic upwelling system. Marine Ecology Progress Series 256:243–255.

Becker, B. H., and S. R. Beissinger (2006). Centennial decline in the trophic level of an endangered seabird after fisheries decline. Conservation Biology 20:470–479.

Becker, B. H., M. Z. Peery, and S. R. Beissinger (2007). Ocean climate and prey availability affect the trophic level and reproductive success of the Marbled Murrelet, an endangered seabird. Marine Ecology Progress Series 329:267–279.

Betts, M. G., J. M. Northrup, J. A. B. Guerrero, L. J. Adrean, S. K. Nelson, J. L. Fisher, B. D. Gerber, M. Garcia-Heras, Z. Yang, D. D. Roby, and J. W. Rivers (2020). Squeezed by a habitat split: Warm ocean conditions and old-forest loss interact to reduce long-term occupancy of a threatened seabird. Conservation Letters 13:e12745.

Bigger, D., M. Z. Peery, J. Baldwin, S. Chinnici, and S. P. Courtney (2006a). Power to detect trends in Marbled Murrelet breeding populations using audiovisual and radar surveys. The Journal of Wildlife Management 70:493–504.

Bigger, D., M. Z. Peery, S. P. Courtney, S. Chinnici, and S. P. Courtney (2006b). Efficacy of audiovisual and radar surveys for studying Marbled Murrelets in inland habitats. The Journal of Wildlife Management 70:505–516.

Brook, A., M. Zint, and R. De Young (2003). Landowners' responses to an Endangered Species Act listing and implications for encouraging conservation. Conservation Biology 17:1638–1649.

Brunk, K., S. Chinnici, A. Pidgeon, M. Z. Peery (2021). Data from: Assessing the effectiveness of a forest Habitat Conservation Plan for a threatened seabird, the Marbled Murrelet. Ornithological Applications 123:1–15. doi:10.5061/dryad.wwpzgmsjq

Burger, A. E. (1997). Behavior and numbers of Marbled Murrelets measured with radar. Journal of Field Ornithology 68:208–223.

Burger, A. E. (2001). Using radar to estimate populations and assess habitat associations of Marbled Murrelets. The Journal of Wildlife Management 65:696–715.

Burger, A. E., and R. E. Page (2007). The need for biological realism in habitat modeling: A reinterpretation of Zharikov *et al*. (2006). Landscape Ecology 22:1273–1281.

Burnam, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edition. Springer-Verlag, New York, NY, USA.

Carter, H. R., and R. A. Erickson (1992). Status and conservation of the Marbled Murrelet in California, 1892–1987. Proceedings of the Western Foundation of Vertebrate Zoology 5:92–108.

Cooper, B. A., and R. J. Blaha (2002). Comparisons of radar and audio-visual counts of Marbled Murrelets during inland forest surveys. Wildlife Society Bulletin 30:1182–1194.

Cooper, B. A., M. G. Raphael, and D. Evans Mack (2001). Radar-based monitoring of Marbled Murrelets. The Condor 103:219–229.

Eichenwald, A. J., M. J. Evans, and J. W. Malcom (2020). US imperiled species are most vulnerable to habitat loss on private lands. Frontiers in Ecology and the Environment 18:439–446.

Falxa, G. A., and M. G. Raphael (2016). Northwest Forest Plan - The first 20 years (1994–2013): Status and trend of Marbled Murrelet populations and nesting habitat. General Technical Report PNW-GTR-933, Forest Service, Pacific Northwest Research Station, U.S. Department of Agriculture, Portland, OR, USA.

Ferraro, P. J., and S. K. Pattanayak (2006). Money for nothing? A call for empirical evaluation of biodiversity conservation investments. PLoS Biology 4:482–488.

Fisher, B., A. Balmford, P. J. Ferraro, L. Glew, M. Mascia, R. Naidoo, and T. H. Ricketts (2013). Moving Rio forward and avoiding 10 more years with little evidence for effective conservation policy. Conservation Biology 28:880–882.

Green, P., and C. J. Macleod (2016). SIMR: An R package for power analysis of generalized linear mixed models by simulation. Methods in Ecology and Evolution 7:493–498.

Gutiérrez, R. J., M. Cody, S. Courtney, and A. B. Franklin (2007). The invasion of Barred Owls and its potential effect on the spotted owl: A conservation conundrum. Biological Invasions 9:181–196.

Hall, L. A., P. J. Palsbøll, S. R. Beissinger, J. T. Harvey, M. Bérubé, M. G. Raphael, S. K. Nelson, R. T. Golightly, L. McFarlane-Tranquilla, S. H. Newman, et al. (2009). Characterizing dispersal patterns in a threatened seabird with limited genetic structure. Molecular Ecology 18:5074–5085.

Hamer, T. E., and S. K. Nelson (1995). Characteristics of Marbled Murrelet nest trees and nesting stands. In Ecology and Conservation of the Marbled Murrelet (C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, Editors). General Technical Report PSW-GTR-152, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA, USA. pp. 69–82.

Harding, E. K., E. E. Crone, B. D. Elderd, J. M. Hoekstra, A. J. McKerrow, J. D. Perrine, J. Regetz, L. J. Rissler, A. G. Stanley, and E. L. Walters (2001). The scientific foundations of habitat conservation plans: A quantitative assessment. Conservation Biology 15:488–500.

Hébert, P. N., H. R. Carter, R. T. Golightly, and D. L. Orthmeyer (2003). Radio-telemetry evidence of re-nesting in the same season by the Marbled Murrelet. Waterbirds 26:261–265.

Hébert, P. N., and R. T. Golightly (2008). At-sea distribution and movements of nesting and non-nesting Marbled Murrelets *Brachyramphus marmoratus* in northern California. Marine Ornithology 36:99–105.

Jones, G. M., R. J. Gutiérrez, J. J. Keane, and M. Z. Peery (2018). Declining old-forest species as a legacy of large trees lost. Diversity and Distributions 24:341–351.

Jones, G. M., and M. Z. Peery (2019). Phantom interactions: Use odds ratios or risk misinterpreting occupancy models. The Condor: Ornithological Applications 121:1–7.

Kareiva, P., S. Andelman, D. Doak, B. Elderd, M. Groom, J. Hoekstra, L. Hood, F. James, J. Lamoreux, G. Lebuhn, et al. (1999). Using Science in Habitat Conservation Plans. American Institute of Biological Sciences, Washington, D.C., USA. https://www.researchgate.net/publication/248281542_Using_science_in_habitat_conservation_plans

Lenth, R. V. (2020). emmeans: Estimated marginal means, aka least-squares means. https://cran.r-project.org/package=emmeans

Lorenz, T. J., M. G. Raphael, and T. D. Bloxton (2019). Nesting behavior of Marbled Murrelets *Brachyramphus marmoratus* in Washington and British Columbia. Marine Ornithology 47:157–166.

Lorenz, T. J., M. G. Raphael, T. D. Bloxton, and P. G. Cunningham (2017). Low breeding propensity and wide-ranging movements by Marbled Murrelets in Washington. The Journal of Wildlife Management 81:306–321.

Lueck, D., and J. A. Michael (2003). Preemptive habitat destruction under the Endangered Species Act. Journal of Law and Economics 46:1–59. doi:10.2139/ssrn.223871

Luginbuhl, J. M., J. M. Marzluff, J. E. Bradley, M. G. Raphael, and D. E. Varland (2001). Corvid survey techniques and the relationship between corvid relative abundance and nest predation. The Journal of Field Ornithology 72:556–572.

Mack, D. E., W. P. Ritchie, S. K. Nelson, E. Kuo-Harrison, and T. E. Hamer (2003). Methods for surveying Marbled Murrelets in forests: A revised protocol for land management and research. Pacific Seabird Group, Corvallis, OR, USA. http://www.pacificseabirdgroup.org

Mackenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, A. B. Franklin, M. G. Knu, and A. B. Franklin (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

MacKenzie, D. I., J. D. Nichols, A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines (2018). Occupancy Estimation and Modeling, 2nd edition. Elsevier Academic Press, New York, NY, USA.

Malt, J., and D. Lank (2007). Temporal dynamics of edge effects on nest predation risk for the Marbled Murrelet. Biological Conservation 140:160–173.

Malt, J. M., and D. B. Lank (2009). Marbled Murrelet nest predation risk in managed forest landscapes: Dynamic fragmentation effects at multiple scales. Ecological Applications 19:1274–1287.

Meyer, C. B., and S. L. L. Miller (2002). Use of fragmented landscapes by Marbled Murrelets for nesting in southern Oregon. Conservation Biology 16:755–766.

Meyer, C. B., S. L. Miller, and C. J. Ralph (2002). Multi-scale landscape and seascape patterns associated with Marbled Murrelet nesting areas on the U.S. west coast. Landscape Ecology 17:95–115.

Miller, S. L., M. G. Raphael, G. A. Falxa, C. Strong, J. Baldwin, T. Bloxton, B. M. Galleher, M. Lance, D. Lynch, S. F. Pearson, C. John Ralph, and R. D. Young (2012). Recent population decline of the Marbled Murrelet in the Pacific Northwest. The Condor 114:771–781.

Naslund, L. (1993). Why do Marbled Murrelets attend old-growth forest nesting areas year-round? The Auk 110:594–602.

Naslund, N. L., and B. P. O'Donnell (1995). Daily patterns of Marbled Murrelet activity at inland sites. In Ecology and Conservation of the Marbled Murrelet (C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, Editors). General Technical Report PSW-GTR-152, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA, USA. pp. 129–134.

Nelson, S. K., and T. E. Hamer (1995). Nest success and the effects of predation on Marbled Murrelets. In Ecology and Conservation of the Marbled Murrelet (C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, Editors). General Technical Report PSW-GTR-152, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA, USA. pp. 89–98.

Pacific Seabird Group (1998). Marbled Murrelet Monitoring Protocol. Pacific Seabird Group, Corvallis, OR, USA.

Pearson, S. F., B. McIver, D. Lynch, J. Baldwin, N. Johnson, M. M. Lance, M. G. Raphael, C. Strong, R. Young, K. Nelson, et al. (2018). Marbled Murrelet effectiveness monitoring, Northwest Forest Plan 2017 summary report. Northwest Forest Plan Interagency Regional Monitoring Program. https://www.fs.fed.us/r6/reo/monitoring/marbled-murrelet.php

Peery, M. Z., and R. W. Henry (2010). Recovering Marbled Murrelets via corvid management: A population viability analysis approach. Biological Conservation 143:2414–2424.

Peery, M. Z., L. A. Henkel, S. H. Newman, B. H. Becker, J. T. Harvey, C. W. Thompson, and S. R. Beissinger (2008). Effects of rapid flight-feather molt on postbreeding dispersal in a pursuit-diving seabird. The Auk 125:113–123.

Peery, M. Z., S. R. Beissinger, S. H. Newman, B. H. Becker, E. Burkett, and T. D. Williams (2004a). Individual and temporal variation in inland flight behavior of Marbled Murrelets: Implications for population monitoring. The Condor 106:344–353.

Peery, M. Z., S. R. Beissinger, S. H. Newman, E. B. Burkett, and T. D. Williams (2004b). Applying the population decline paradigm: Diagnosing causes of poor reproduction in the Marbled Murrelet. Conservation Biology 18:1088–1098.

Piatt, J. F., K. J. Kuletz, A. E. Burger, S. A. Hatch, V. L. Friesen, T. P. Birt, M. L. Arimitsu, G. S. Drew, A. M. A. Harding, and K. S. Bixler (2007). Status review of the Marbled Murrelet (*Brachyramphus marmoratus*) in Alaska and British Columbia. Open-File Report 2006-1387, U.S. Geological Survey. http://pubs.water.usgs.gov/ofr20061387

Powell, L. A. (2007). Approximating variance of demographic parameters using the delta method: A reference for avian biologists. The Condor 109:949–954.
R Core Team (2020). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
Ralph, C. J., S. K. Nelson, M. M. Shaughnessy, S. L. Miller, and T. Hamer (1994). Methods for surveying Marbled Murrelets in forests: A protocol for land management and research. Technical Paper 1, Pacific Seabird Group, Marbled Murrelet Technical Committee, Arcata, CA, USA.
Raphael, M. G., G. A. Falxa, K. M. Dugger, B. M. Galleher, D. Lynch, S. L. Miller, K. S. Nelson, and R. D. Young (2011). Northwest Forest Plan - The first 15 years (1994–2008): Status and trend of nesting habitat for the Marbled Murrelet. General Technical Report PNW-GTR-848, U.S. Forest Service, Pacific Northwest Research Station, U.S. Department of Agriculture, Portland, OR, USA. http://www.fs.fed.us/pnw/pubs/pnw_gtr848.pdf
Raphael, M. G., D. E. Mack, and B. A. Cooper (2002a). Landscape-scale relationships between abundance of Marbled Murrelets and distribution of nesting habitat. The Condor 104:331–342.
Raphael, M. G., D. E. Mack, J. M. Marzluff, and J. M. Luginbuhl (2002b). Effects of forest fragmentation on populations of the Marbled Murrelet. In Effects of Habitat Fragmentation on Birds in Western Landscapes: Contrasts with Paradigms from the Eastern United States (T. L. George and D. S. Dobkin, Editors). Studies in Avian Biology 25:221–235.
Raphael, M. G., A. J. Shirk, G. A. Falxa, and S. F. Pearson (2015). Habitat associations of marbled murrelets during the nesting season in nearshore waters along the Washington to California coast. Journal of Marine Systems 146:17–25.
Ribas, L. G. d. S., R. L. Pressey, R. Loyola, and L. M. Bini (2020). A global comparative analysis of impact evaluation methods in estimating the effectiveness of protected areas. Biological Conservation 246:1–11.
Rodway, M. S., H. M. Regehr, and J.-P. L. Savard (1993). Activity patterns of Marbled Murrelets in old-growth forest in the Queen Charlotte Islands, British Columbia. The Condor 95:831–848.
van Rooyen, J. C., J. M. Malt, and D. B. Lank (2011). Relating microclimate to epiphyte availability: Edge effects on nesting habitat availability for the Marbled Murrelet. Northwest Science 85:549–561.
Schwartz, M. W. (2008). The performance of the Endangered Species Act. Annual Review of Ecology, Evolution, and Systematics 39:279–299.
Shilling, F. (1997). Do habitat conservation plans protect endangered species? Science 276:1662–1663.
Skalski, J. R., A. Hoffman, and S. G. Smith (1993). Testing the significance of individual- and cohort-level covariates in animal survival studies. In Marked Individuals in the Study of Bird Populations (J.-D. Lebreton and P. M. North, Editors). Birkhauser Verlag, Basel, Switzerland. pp. 9–28.
Tempel, D. J., J. J. Keane, R. J. Gutiérrez, J. D. Wolfe, G. M. Jones, C. M. Ramirez, W. J. Berigan, C. V. Gallagher, T. E. Munton, P. A. Shaklee, et al. (2016). Meta-analysis of California Spotted Owl (*Strix occidentalis occidentalis*) territory occupancy in the Sierra Nevada: Habitat associations and their implications for forest management. The Condor: Ornithological Applications 118:747–765.
U.S. Fish and Wildlife Service (USFWS) (1997). Recovery Plan for the Marbled Murrelet in Washington, Oregon, and California. U.S. Fish and Wildlife Service, Portland, OR, USA. http://www.fws.gov/carlsbad/SpeciesStatusList/RP/19970924_RP_MAMU.pdf
U.S. Fish and Wildlife Service (USFWS) (2016). Habitat Conservation Planning and Incidental Take Permit Processing Handbook. U.S. Department of the Interior Fish and Wildlife Service, U.S. Department of Commerce National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Washington, DC, USA. https://www.fws.gov/midwest/endangered/permits/hcp/hcphandbook.html
Valente, J. J., and M. G. Betts (2019). Response to fragmentation by avian communities is mediated by species traits. Diversity and Distributions 25:48–60.
Vásquez-Carrillo, C., R. W. Henry, L. Henkel, and M. Z. Peery (2013). Integrating population and genetic monitoring to understand changes in the abundance of a threatened seabird. Biological Conservation. 167:173–178. doi:10.1016/j.biocon.2013.08.008
Wilcove, D. S., M. J. Bean, R. Bonnie, and M. McMillan (1996). Rebuilding the ark: Toward a more effective Endangered Species Act for private land. https://omnilearn.net/esacourse/pdfs/Rebuilding_the_Ark.pdf
Zharikov, Y., D. B. Lank, and F. Cooke (2007). Influence of landscape pattern on breeding distribution and success in a threatened Alcid, the Marbled Murrelet: Model transferability and management implications. Journal of Applied Ecology 44:748–759.
Zharikov, Y., D. B. Lank, F. Huettmann, R. W. Bradley, N. Parker, P. P. W. Yen, L. A. Mcfarlane-Tranquilla, and F. Cooke (2006). Habitat selection and breeding success in a forest-nesting Alcid, the Marbled Murrelet, in two landscapes with different degrees of forest fragmentation. Landscape Ecology 21:107–120.