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RESEARCH ARTICLE

Using bioacoustics to enhance the efficiency of spotted owl surveys and facilitate forest restoration

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Abstract

The California spotted owl (*Strix occidentalis occidentalis*) is an older-forest associated species that resides at the center of forest management planning in the Sierra Nevada and Southern California, USA, which are experiencing increasingly large and severe wildfires and drought-related tree mortality. We leveraged advances in passive acoustic survey technologies to develop an acoustically assisted survey design that could increase the efficiency and effectiveness of project-level surveys for spotted owls, allowing surveys to be completed in a single year instead of in multiple years. We deployed an array of autonomous recording units (ARUs) across a landscape and identified spotted owl vocalizations in the resulting audio using BirdNET. We then evaluated spatio-temporal patterns in spotted owl vocalizations near occupied territories and the ability of a crew naïve to the location of occupied territories to locate spotted owls based on patterns of acoustic detections. After only 3 weeks of acoustic surveys, ≥1 ARU within 750 m of all 17 occupied territories obtained spotted owl detections across ≥2 nights. When active surveys using broadcast calling were conducted near ARUs with spotted owl detections by surveyors naïve to territory occupancy status and locations, surveyors located owls in 93% to 100% of occupied territories with ≤3 surveys. To further improve the efficiency of spotted owl surveys, we developed a statistical model to identify and prioritize areas across the Sierra Nevada for different survey methods (active only, acoustically assisted, no surveys) based on the expected probability of occupancy predicted from remotely sensed measurements of tree height and historical occupancy. Depending on managers' tolerance for false negatives, this model could help identify large areas that might not benefit from surveys based on low expected occupancy probabilities and areas where acoustically assisted surveys might enhance survey effectiveness and efficiency. Collectively, these findings can help managers streamline the survey process and thus increase the pace of forest restoration while minimizing potential near-term adverse effects on California spotted owls.

KEYWORDS

acoustic, BirdNET, California, management, PAM, passive acoustic monitoring, Sierra Nevada, *Strix occidentalis*

Dry forest ecosystems adapted to frequent fire in western North America have experienced vegetation densification from fire suppression, warming and drying associated with climate change, and increasing human populations in the wildland-urban interface, which have led to larger and more severe wildland fires and extensive drought-related tree mortality (Abatzoglou and Williams 2016, Westerling 2016, Schoennagel et al. 2017, Stevens et al. 2017, Steel et al. 2023). While management practices such as tree thinning and fire use can reduce the risk of large, severe fires and drought-induced mortality, these activities are often highly regulated in and around habitat for sensitive wildlife species (Collins et al. 2010, Stephens et al. 2019, Kuchinke et al. 2020). Simultaneously, many of these sensitive species are negatively affected directly (individuals) and indirectly (habitat) by large high-severity fires (Jones et al. 2016, 2020; Rockweit et al. 2017) such that forest management to reduce the risk of large high-severity fires by reducing forest fuels may promote species conservation and ecosystem resilience objectives. Identifying the critical habitat of target species for proposed forest management, however, is often time consuming and potentially hazardous to field personnel (e.g., when surveys must be performed at night), thus driving up the cost and delaying the pace and scale of these forest management efforts. The public land area treated annually in California, USA, has decreased since it peaked at 1,214 km^2 in 2008 (as of 2019; Knight et al. 2022), despite a commitment by the state of California and the United States Department of Agriculture Forest Service (USFS) to treat 4,046 km^2 annually by 2025 (State of California and USFS 2020). Therefore, improving survey effectiveness for species of concern could enhance the pace and scale of forest management activities intended to promote the resilience of dry forests in western North America, thus reducing the risk of severe wildfire to humans, homes, and infrastructure. Moreover, improved survey methods that facilitate forest management in turn benefit habitat conservation objectives for many forest-associated sensitive species, given the adverse effects of extensive areas of severe fire (Jones et al. 2022) and drought-related tree mortality (Steel et al. 2023).

The California spotted owl (*Strix occidentalis occidentalis*) is an older-forest associated species of concern and a focus of forest management planning in the Sierra Nevada and Southern California. The United States Fish and Wildlife Service (USFWS) has recently proposed to list the California spotted owl as threatened in the Sierra Nevada and endangered in Southern California under the Endangered Species Act in part because of the threat posed by severe wildfire (U.S. Fish and Wildlife Service USFWS 2023). The proposed listing of this species includes a 4(d) rule that encourages forest management when that management would help conserve the spotted owl, despite limited short-term harm to the species (USFWS 2023). Listing this species would likely increase the need for efficient and effective surveys for spotted owls in proposed forest management (project) areas throughout the species' range. The current standard active survey protocol on national forests, which support the majority of California spotted owl habitat and known territories, was designed to achieve a high probability of detecting occupied territories in an area proposed for forest management (or project area). To do so, the active survey protocol (i.e., active-only surveys) requires 6 broadcast call surveys separated by 5 calendar days to determine non-occupancy, or active follow-up surveys to locate nest and roost sites when a survey detects an owl (USFS 1991, USFWS 2012). These active-only surveys often involve extensive nighttime work and are therefore potentially hazardous to surveyors (Forsman 1983, USFS 1991). Furthermore, although this protocol can be completed in a single year, the extensive survey effort required within the limited spring breeding season typically necessitates 2 years to complete (USFS 1991), potentially delaying projects that facilitate forest management and mitigate high severity fire risk (Collins et al. 2010).

Recent advances in passive acoustic survey methods and data processing have the potential to boost survey effectiveness in detecting owls where they are present, either by augmenting or supplanting active-only surveys for spotted owls, and thus potentially reducing the survey time and effort required to determine if a proposed project area is occupied by spotted owls. Passive acoustic surveys involve the deployment of autonomous recording units (ARUs) and provide a surveillance network for acoustically active species across the landscape (Wood et al. 2021). Detection algorithms can then be applied to the resultant audio data to predict whether specific species vocalized (Kahl et al. 2021, Ruff et al. 2022). Passive acoustic surveys can detect a diverse array of vocalizing species (Sugai et al. 2019, Kahl et al. 2021, Wood et al. 2021), including spotted owls (Wood et al. 2019*c*, Duchac et al. 2020, Hezler 2022, Appel et al. 2023), with high confidence. Additionally, these passive surveys appear suitable for monitoring changes in spotted owl occupancy rates (Wood et al. 2019*b*, Weldy et al. 2023) with the added benefit of limiting potential disturbance to owls from active surveys. Although these passive acoustic surveys have been successful in related areas, they have not yet been used (or assessed) as a tool for explicitly conducting or improving the effectiveness of long-standing standard survey protocols being used by land and wildlife management agencies.

In principle, ARUs could be deployed in the spring and the audio analyzed rapidly to identify spotted owl vocalizations, thus allowing a crew to actively survey near ARUs that detected spotted owls later in the summer. Such an acoustically assisted survey could guide a crew to focus their active survey effort (i.e., acoustically assisted active surveys) in areas where owls were already detected, thus streamlining the process and providing a means of meeting a high cumulative detection probability within a single year. Many unknowns remain, however, including the timing and placement of ARUs and the appropriate thresholds to determine whether a passive acoustic survey should be followed up by active surveys. Additionally, the effectiveness of acoustically assisted active surveys starting at a given ARU location must also be assessed, as these surveys will be different from active-only surveys where an approximate direction and distance of the owl response is recorded during an initial survey (Forsman 1983, Franklin et al. 1996). Effective ARU placement and thresholds are also likely needed to ensure a high detection probability within a single-season survey effort because of the tight timeline of deploying ARUs on the landscape, collecting and processing the data, and conducting sufficient acoustically assisted active surveys when needed. For spotted owls, this period would be further restricted to earlier in the summer when owls are still responsive to survey methods (Forsman et al. 1984, Reid et al. 2021).

Our goal was to develop an acoustically assisted survey design for California spotted owls that can fully cover a project area and meets or exceeds the detection and non-detection efficacy of the traditional active-only survey protocol within a single year using primarily daytime field activities. Our objectives were to assess how well passive acoustic surveys detect occupied territories, assess how well acoustically assisted active surveys locate occupied territories, and develop a prioritization approach for acoustically assisted surveys.

STUDY AREA

We conducted work in the Eldorado spotted owl demography study area, located on the Eldorado National Forest in the central Sierra Nevada, California (Figure 1). Spotted owl territory occupancy and reproduction have been monitored annually within a 345-km^2 density area (where all known owls were monitored; Figure 1B) from 1986 to 2021 and at additional satellite territories (111 km^2; where only certain known territories were monitored) from 1997 to 2021 (Blakesley et al. 2010, Berigan et al. 2012). Personnel employed directly or indirectly by the USFS determined occupancy and reproductive status at most territories annually and banded most territorial individuals with unique leg bands. The number of territories monitored annually across the combined density and satellite territories varied between 62 and 83 territories monitored each year (since 1997), and the number of occupied territories ranged between 29 and 53 each year. The 2014 King Fire burned through about half of the density area and a few of the satellite territories, with much of this area burning at high severity (characterized by >75% mortality of overstory trees; https://www.mtbs.gov/faqs; accessed 27 Nov 2023).

For the purposes of this study, we divided the Eldorado study area into 2 overlapping sub-study areas, referred to as the ARU study area and the survey prioritization study area (Figure 1). The ARU study area was established to address ARU performance in areas with known occupancy where ARUs were deployed during summer 2021.

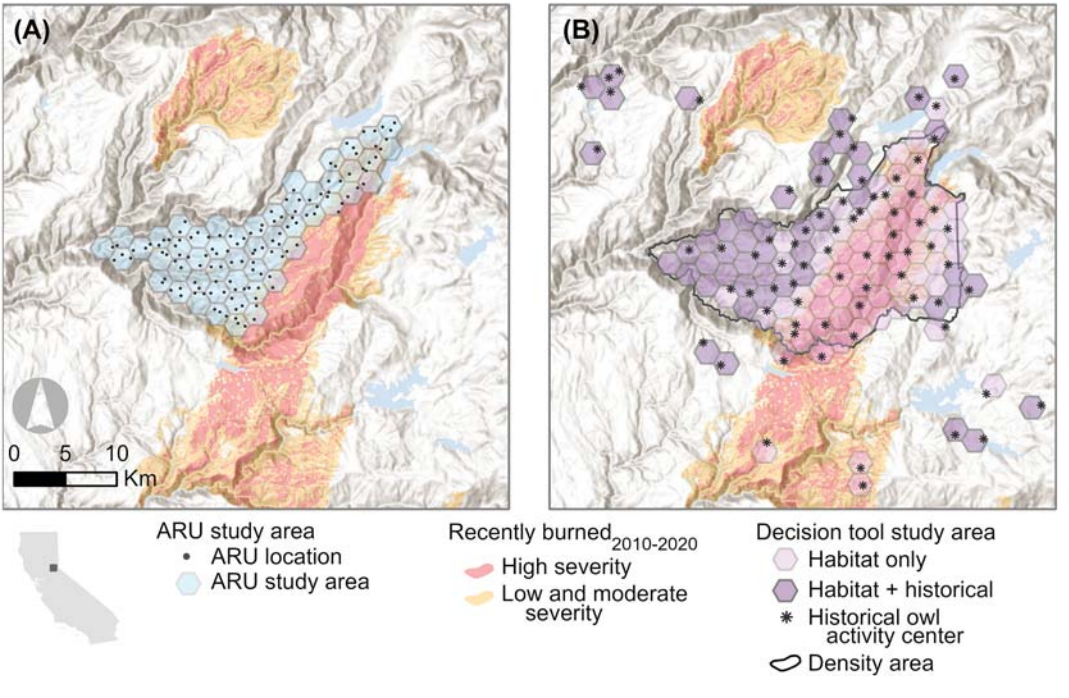

FIGURE 1 The study areas in the Sierra Nevada, California, USA, 1997–2021, gridded into 400-ha hexagonal cells. We used the A) autonomous recording unit (ARU) study area to answer research questions pertaining to naïve location of California spotted owls and determining recording duration and thresholds. We present the locations of the 126 ARUs that collected data during summer 2021 and the severity of all fires that burned from 2010 to 2020. The B) survey prioritization study area pertains to optimization of ARU placement in the context of a 1-year protocol framework. Historical activity centers in the density study area (which was monitored in its entirety from 1997 to 2021) and outlying areas (monitored from 1997 to 2021) are indicated. Cells used to build a model set pertaining to habitat only and a second model set that also incorporated historical owl data are shown. The base map hillshade and hydrology use data from Esri, the Consultative Group on International Agricultural Research, and the United States Geological Survey.

The ARU study area included the density area that was either unburned or burned at low or moderate severity (characterized by ≤75% mortality of overstory trees; https://www.mtbs.gov/faqs; accessed 27 Nov 2023) since 2010 (204 km^2). We used the survey prioritization study area to address the prioritization of survey effort, and it included the entire density area (burned and unburned) and the satellite territories monitored from 2003 to 2021. The study areas were topographically complex and ranged in elevation from 334 m to 2,379 m, with a Mediterranean climate characterized by warm, dry summers and cool, wet winters. The forest was managed primarily by the USFS and composed primarily of ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), incense cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), California black oak (*Quercus kelloggii*), and white fir (*Abies concolor*), in addition to canyon live oak (*Q. chrysolepis*), interior live oak, (*Q. wislizenii* var. *wislizenii*), and tanoak (*Notholithocarpus densiflorus*; Mayer and Laudenslayer 1988). There were many ecologically and socially important fauna species in the study area (Usinger 1963).

METHODS

Active-only survey methods

Active-only survey methods were consistent with traditional survey methods (USFS 1991). We used active-only surveys (performed by the traditional crew) to establish the true location of occupied spotted owl activity centers (nest or roost sites). We also used active-only survey techniques to obtain historical occupancy and reproductive status of birds to build models of the probability of occupancy. The traditional crew visited known historical activity centers while broadcasting vocal lures along walking transects in these areas (Forsman 1983, Franklin et al. 1996). Across the rest of the ARU study area, the traditional crew used 10-minute broadcast calling surveys at stations distributed along roads and trails at night (Franklin et al. 1996) to comprehensively survey the area for spotted owls. If an owl was detected either by sight or auditory response during nocturnal hours, the traditional crew followed up the detection during diurnal or twilight hours as soon as possible in an attempt to determine whether the area was occupied by a nesting or roosting owl (Tempel and Gutiérrez 2013). At least 3-4 independent surveys (≥1 week apart) were conducted at each calling station if no detections occurred, with an emphasis on completing ≥2 surveys before 1 July when possible. We determined reproductive status by feeding owls live mice and observing the behavior of the owls after they took the mice (Forsman 1983). Breeding owls typically took offered mice and carried them to the nest or fledged young. In contrast, non-reproductive owls either ate or cached mice. We inferred non-reproduction if an individual took ≥2 offered mice, and cached the last mouse taken (Franklin et al. 1996). Crews re-visited breeding pairs to determine the number of fledged birds, band young, or to determine failed nesting status using the mouse-offering technique described above.

Passive acoustic surveys

In May 2021, a crew naïve to owl activity in the study area (i.e., naïve crew) placed 126 ARUs (SwiftOne Recorder; K. L. Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Ithaca, NY, USA) across the ARU study area based on a grid of 400-ha hexagonal cells. The settings for the ARUs included a sample rate of 32 kHz, 16-bit resolution, gain of +33 dB, microphone sensitivity of −25 dB relative to 1 V/Pa, microphone signal-to-noise ratio of 62 dB(A) (decibels weighted based on human hearing), and analog-to-digital converter clipping level ± 0.9 V. These 400-ha cells represented the approximate size of a spotted owl territory (Jones et al. 2018) and are consistent with previous acoustic surveys of spotted owls in the Sierra Nevada, where ARU spacing according to the relative limitations of the ARU and study system were established (Wood et al. 2019*b*, Reid et al. 2021). Although the spotted owl breeding season (and concentration of vocalizations) in the Sierra Nevada occurs in April and May, snowpack often prevents access to higher elevation areas until May. We eliminated communication between the traditional and naïve crews and ensured that any indicators of current or historical owl occupancy were not revealed to the naïve crew. Wherever possible, we placed 3 ARUs within each hexagonal cell, with ≥500 m between each unit to minimize acoustic overlap among ARUs. Cells with challenging topography and access and cells that were only partially within the demographic area had fewer ARUs. For the 51 hexagonal cells in the ARU study area, 28 contained 3 ARUs, 19 contained 2 ARUs, and the remaining 4 cells that were mostly outside the ARU study area contained a single ARU. The ARUs recorded continuously between 1800 and 0800 for a median of 31 recording nights, ranging between 3 (early ARU failure) and 36 nights. We exchanged memory cards in each of the 126 ARUs in the middle of their deployment (after 14–21 days), which allowed us to process the data sooner and facilitated same-season acoustically assisted active surveys.

We processed the acoustic data during the field season using the template detector feature in an unreleased beta version of Raven Pro 2.0 (Raven Pro beta; K. L. Yang Center for Conservation Bioacoustics) and applied a spotted owl template that had previously been developed for this project (Wood et al. 2019*b*). While this method allowed the data to be processed using on-site desktop computing, the standard review threshold for that detector had a high rate of false positives (i.e., low precision), and thus required validation by additional crew members (which took ~2 weeks) to confirm spotted owl vocalizations by listening to the recordings that met or exceeded the detector's review threshold. The naïve crew then carried out acoustically assisted active surveys at all ARUs with a confirmed detection. Because of this time delay on acoustic processing, the naïve crew only had time to follow up acoustic data that was collected during the first half (14–21 days) of the full ARU deployment period.

Audio processing has progressed, so to improve our analysis to assess how well passive acoustic surveys detect occupied territories (objective 1), we re-processed the acoustic data using the command line interface of the machine learning algorithm BirdNET (Kahl et al. 2021). We used a specifically customized version of BirdNET that is optimized for our recording hardware and settings and trained to identify vocalizations of 236 California bird species including the spotted owl (i.e., BirdNET-Sierra; which included explicit classes for multiple vocalizations of the California spotted owl). As is standard for BirdNET, BirdNET-Sierra analyzed audio in 3-second increments, generating a unitless quantitative prediction score (confidence score), with higher scores corresponding to a higher probability of a correct prediction, albeit in a species-specific manner. Therefore, the prediction score superficially resembles a probability even though it is not, and accuracy at any given score is not necessarily the same across species. To account for all vocalization types in this analysis, we used the highest-scoring spotted owl vocalization from each 3-second clip (either specific or general). Previous analyses suggested that any spotted owl vocalization type (either specific or general) with a BirdNET-Sierra confidence score ≥0.989 provided a true positive detection rate of 0.813 (e.g., 81 of 100 BirdNET-Sierra detections that met or exceeded that threshold were true positives; Kelly et al. 2023). BirdNET confidence scores are influenced by the acoustic characteristics of the recording system, background noise conditions, and sample rate, so a given threshold will produce different accuracies if applied to different recording settings (Wood et al. 2019*a*, Kahl et al. 2021).

Objective 1: passive acoustic survey detection of occupied territories

We assessed the extent to which passive acoustic surveys detected spotted owls at occupied territories based on the proportion of the corresponding activity centers (determined in the same summer season by the traditional crew) that had acoustic detections within 750 m. Our rationale was that acoustic detections close to spotted owl activity centers are more likely to result in successful active follow-up surveys because owls are central place foragers and are therefore likely to be physically near their activity center (especially at dusk and dawn), and a crew is more likely to get an owl to respond and be able to follow an owl back to its activity center across a shorter distance. Our specific choice of 750 m was initially based on our several decades of combined spotted owl survey experience and was subsequently confirmed as a reasonable detection threshold. We calculated the proportion of activity centers with a nearby (<750 m) acoustic detection based on 1) the number of nights (1, 2, 3) with acoustic detections (detection nights) that would determine whether an ARU would receive a follow-up survey (i.e., flagged ARUs), and 2) the number of weeks (2, 3, 4, 5) of ARU deployment duration. With respect to the detection night criterion, our rationale was to identify a set of thresholds for the number of nights with spotted owl detections that maximized the probability of detecting occupied territories (true positives), and minimized the number of false positives to avoid triggering unnecessary active follow-up surveys (Reid et al. 2021). With respect to the ARU deployment duration, our rationale was that acoustic detections from a shorter deployment duration would provide more time for acoustically assisted active surveys and thus increase the likelihood of detecting and locating territorial owls early in the breeding season (May was as early as was feasible in our study area) before they become less vocal, shift activity centers, and range over wider areas later in summer (Forsman et al. 1984; Reid et al. 2021, 2022). For ARU deployment durations shorter than the full recording period of 5 weeks, we removed acoustic data from the dates that were latest in the season (e.g., for a unit that was deployed from 15 May to 22 Jun, a 3-week simulated deployment used data from 15 May to 5 Jun).

For all objective 1 analyses, we only considered audio data collected during dusk (2000–2159) or dawn (0400–0559) because spotted owls are more likely to be near their activity centers (Gutiérrez et al. 1995, Berigan et al. 2019, Wood et al. 2019*c*). Further, we summarized each survey night by combining audio data from the preceding dusk and ensuing dawn. We did not consider audio data collected by an ARU within 1.5 km of the traditional crew's active-only survey locations (or other survey efforts in the area) for the entirety of the survey night to ensure that vocalizations were from owls unprovoked by imitated calls and to eliminate false positive detections from the surveyors' calls.

Objective 2: acoustically assisted active survey detection of occupied territories

The naïve crew conducted acoustically assisted active surveys during dawn and dusk in the areas surrounding the locations of ARUs with detections to assess occupancy status and locate nests and roosts. The naïve crew performed acoustically assisted active surveys at all confirmed ARU-based owl detections using the same protocol as for active-only surveys, except they initiated surveys at ARU locations, prioritizing those with the most detection nights or the most recent detections (Forsman 1983, Franklin et al. 1996). If there was no response to broadcast calling at the initial ARU location, the naïve crew continued surveying, mainly along roads near the ARU, with the intention of covering the best available spotted owl nesting and roosting habitat in the area, as assessed visually by the crew. In the cases where there were clusters of ARUs with detections, the crew would move toward the next nearest ARU with detections and continue active surveying. Because of time limitations in the field, the naïve crew was only able to conduct follow-up surveys for approximately 1 month (from 7 Jun to 8 Jul) and was therefore limited in the number of acoustically assisted active surveys they could conduct for each ARU with confirmed owl detections. We considered an activity center to have been located by the naïve crew with very high confidence if they found a spotted owl roosting at dusk or dawn within 400 m of the activity center located by the traditional crew or within 400–700 m of the original activity centers if an individual was identified as a resident of the territory based on its colored leg band. We then determined the number and proportion of known owl activity centers that were successfully identified by the naïve crew and calculated the rate of field-based acoustically assisted active survey success.

We also plotted the distance between each owl activity center and nearby ARUs, indicating which had follow-up visits based on detections from Raven Pro beta's template detector and which met the most efficient BirdNET-Sierra detection nights and survey duration identified in objective 1. We noted which of these activity centers were located by the naïve crew to assess the relationship between ARU distance from the activity center and the effectiveness of acoustically assisted active surveys.

Objective 3: prioritization approach for acoustically assisted surveys

Our goal was to identify cells with high probabilities of occupancy where active-only surveys might be most efficient (across a small area to facilitate the completion of the 6 necessary surveys), intermediate probabilities of occupancy where acoustically assisted active surveys might be most efficient, and low probabilities of occupancy that might not benefit from either type of survey. We used the survey prioritization study area for this analysis, which encompassed the density and satellite areas (with the same 400-ha hexagonal grid used for ARU deployment; Figure 1). To accommodate project areas with and without previous owl surveys, we estimated the probability of occupancy in 2 model sets based on habitat data alone and a combination of habitat data and historical occupancy and reproductive data. We used logistic regression for models in each set because we assumed perfect detection and treated the annual survey results as true presence or absence data. We made this assumption because bimonthly survey period detection probabilities for spotted owls were estimated to be 0.68 (Tempel et al. 2016) and the survey season spans 4 months, yielding an overall detection probability of 0.99.

We calculated our response variable (recent occupancy) as the proportion of years a cell was occupied from 2015 to 2021 (continuously ranging between 0 and 1). We calculated occupancy for a given grid cell based on any activity center (geometric center of the annual activity center location [nest site or best roost site]) that fell within that grid cell. When multiple activity centers occurred within a single grid cell, we combined occupancy. For example, a cell that contained 2 activity centers (A, B), where A was occupied in 2015 and 2021 and B was occupied in 2018–2021, would have a combined occupancy of 0.71 (the cell was occupied 5 of 7 possible years). Because the entire density area was surveyed each year, we assumed that any hexagonal cell that did not contain an activity center, but was primarily (≥50% of its area) within the density area boundary, had an occupancy of zero. Thus, our survey prioritization study area included all hexagonal cells primarily within the density area and in satellite territories that had ≥3 years of occupancy data (n = 114).

For the habitat-only model set, we used the proportion of years the cell was occupied from 2015 to 2021 as the response variable and vegetation metrics derived from California Forest Observatory (CFO) data as explanatory variables (Table 1; Figure 1). These data layers were derived from cross-walking aerial light detection and ranging (LiDAR) point clouds with remotely sensed data to predict forest structure at a 10-m spatial resolution (California Forest Observatory CFO 2020). Specifically, we calculated mean canopy cover and canopy height within each 400-ha hexagonal grid cell. We also calculated the proportional area of tall, dense forest (height >20 m and >40% canopy cover), short forest or open areas (canopy height <10 m), and medium-short forest or open areas (canopy height

TABLE 1 Covariates used to characterize habitat composition (2018) and California spotted owl historical occupancy and reproduction (2003–2014) within each hexagonal cell of the study area on the Eldorado National Forest, California, USA. Data sources include California Forest Observatory data calculated from 2018 imagery (CFO).

Metric	Data source	Definition
Mean canopy height	CFO	Average canopy height (m) within each hexagonal cell
Mean canopy cover	CFO	Average canopy cover (%) within each hexagonal cell
Tall dense forest	CFO	Proportional area with height >20 m and cover >40%
Short-open <10 m	CFO	Proportional area with height <10 m
Short-open <20 m	CFO	Proportional area with height <20 m
Occupancy[a]	Demography	Proportion of previous years that the site was occupied (2003–2014)
Reproductive history[a]	Demography	Proportion of previous years that nesting was attempted (2003–2014)

[a]We used only sites with ≥3 years of occupancy and reproduction data in the analysis.

<20 m; Table 1). We chose these covariates as potential predictors of occupancy based on our knowledge of spotted owls, and thus they are not intended to sum to 100% or to be mutually exclusive. California Forest Observatory data are updated annually, which can facilitate future predictions of occupancy as forests change because of disturbance and management activities. Owing to the 2014 King Fire, 51% of these cells (59 of 114) were partially or completely burned, producing a range of conditions from open forests to a mosaic of forest structures.

For the habitat and historical survey model set, we again used the 2015–2021 occupancy as the response variable. In addition to the vegetation metrics used in the habitat-only model, we used historical occupancy and reproduction data collected from 2003 to 2014, excluding any grid cells that were surveyed <3 years during this 12-year period. Similar to the response variable, when multiple activity centers occurred within a single grid cell during this historical period, we combined occupancy and produced a single proportion value ranging between 0 and 1 for each grid cell. To calculate reproduction in cases where multiple activity centers occurred within a single grid cell, we calculated the proportion of survey years (2003–2014) that nesting was attempted (in cells with ≥3 years of occupancy and reproduction surveys) if the site was occupied. We assigned a reproduction proportion of zero to cells that were never occupied. Because the King Fire changed the habitat in burned territories (making historical data irrelevant), we excluded the 59 hexagonal cells that intersected the fire perimeter and the 7 additional cells with insufficient data (<3 years of historical occupancy and reproductive data), resulting in a sample size of 48 cells.

For each model set, we first tested for pairwise correlations between explanatory variables and avoided including any correlated variables in the same model (with Pearson correlation coefficient >0.6; Stats package version 3.6.2 in R). Because we assumed perfect detection, we applied a quasi-binomial general linear model in R (R Core Team 2021) to every possible combination of explanatory variables. The quasi-binomial model allowed our occupancy response variable to range between 0 and 1. We evaluated support for models within each set based on Akaike's Information Criterion corrected for small sample size (AIC_c) and reported the McFadden's pseudo R2 (developed for logistic regression models; Smith and McKenna 2013) and the 10-fold cross validation error (Boot package version 1.3-27 in R).

Finally, we used the habitat-only model set to predict occupancy estimates across the entire mixed conifer zone of the Sierra. We defined this habitat zone as areas with ≥10% coniferous canopy cover, using the gradient nearest neighbor dataset (LEMMA Lab, Oregon State University, Corvallis, OR, USA) using the VEGCLASS variable (Ohmann and Gregory 2002). We were then able to predict the number of ARUs that might have been used in the ARU study area with this prioritization approach and speculate how this might have changed the overall effort and effectiveness of surveys in the ARU study area.

RESULTS

Objective 1: passive acoustic survey detection of occupied territories

The traditional crew located 17 occupied spotted owl territories and their associated activity centers across the ARU study area, with 5 occupied by nesting pairs, 8 by non-nesting pairs, 3 by pairs of unknown nesting status, and 1 by a single male. Using BirdNET-Sierra to analyze the audio data after the field season had been completed, the proportion of spotted owl activity centers with an acoustic detection nearby (<750 m) increased as a function of ARU survey duration and decreased with the number of detection nights required (Figure 2A). With a 2-week survey duration, the most lenient threshold of a single detection night resulted in 16 of the 17 (94%) occupied owl activity centers being observed by an adjacent ARU (Figure 2A; Table S1, available in Supporting Information). With a 3-week survey duration, all activity centers had a nearby ARU with ≥2 detection nights, but only 82% of occupied activity centers had a nearby ARU with ≥3 detection nights (Figure 2A). A single occupied territory (by non-breeding individuals) had 2 detection nights across the entire 5 weeks that nearby ARUs were deployed (Figure 2A). Thus, the

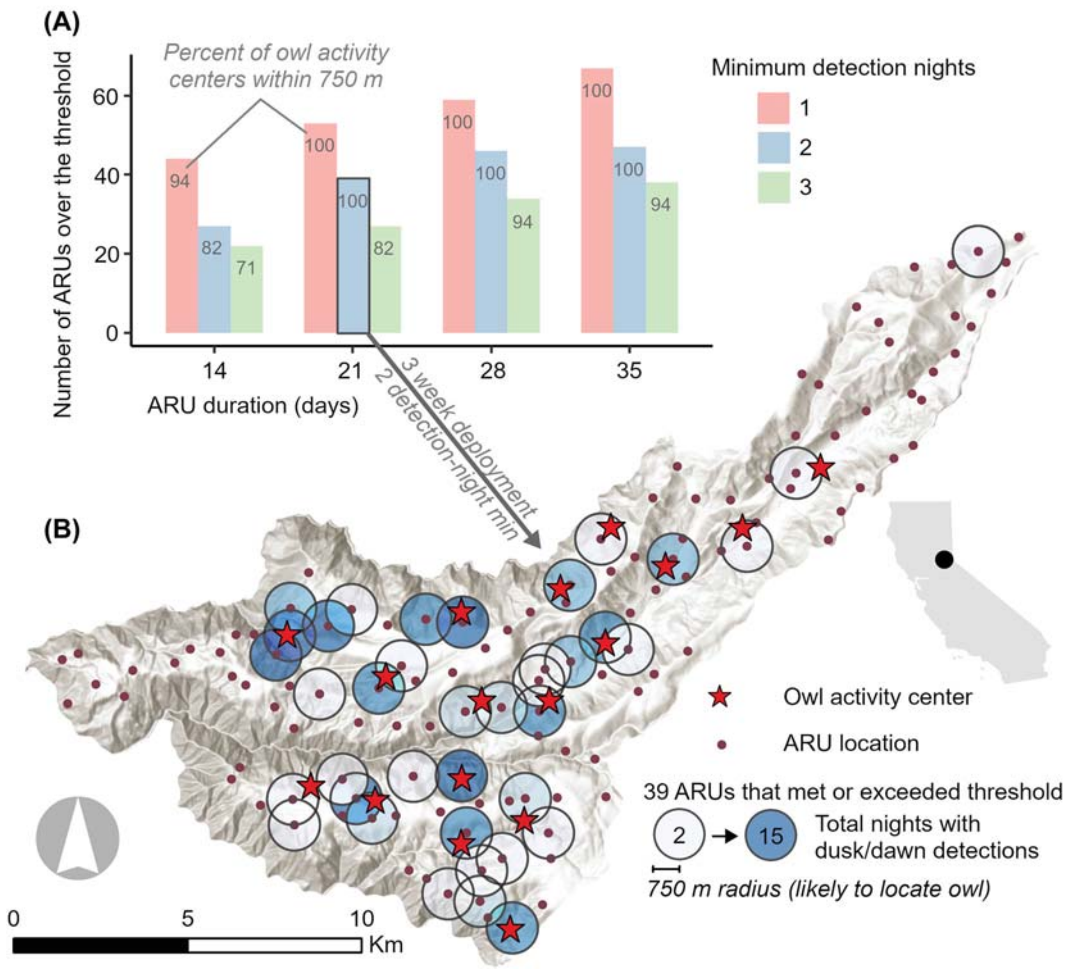

FIGURE 2 A) Number and percent of 126 autonomous recording units (ARUs) that met different spotted owl detection night thresholds and the percent of spotted owl activity centers with an acoustic detection within 750 m in 2021 on the Eldorado National Forest, California, USA. The most efficient criterion is noted by the black rectangle: a 3-week deployment with ≥2 detection nights. B) Locations of spotted owl activity centers, ARUs, and detection nights are indicated for the most efficient criterion. Circles around ARUs that met the threshold have a 750-m radius. The base map hillshade uses data from Esri, the Consultative Group on International Agricultural Research, and the United States Geological Survey.

criteria that most efficiently identified ARUs near all occupied activity centers were a 3-week deployment with ≥2 detection nights, which resulted in 39 (31%) ARUs that met or exceeded the detection night threshold and that would require acoustically assisted active surveys if the analysis had been performed during the summer survey season (Figure 2A, B). Nesting status did not appear to influence the number of detection nights with this 3-week deployment duration (Figure S1, available in Supporting Information).

Using the 3-week, 2-detection-night criteria, the nearest ARU to 16 of the 17 activity centers was flagged and the remaining activity center (Q; Figure 3) had a flagged ARU within 558 m of the activity center. Nearly all ARUs with Raven Pro beta detections that the naïve crew used to plan their follow-up surveys were also flagged based on a criterion of ≥2 detection nights (from BirdNET-Sierra) and a 21-day ARU deployment duration, so any additional

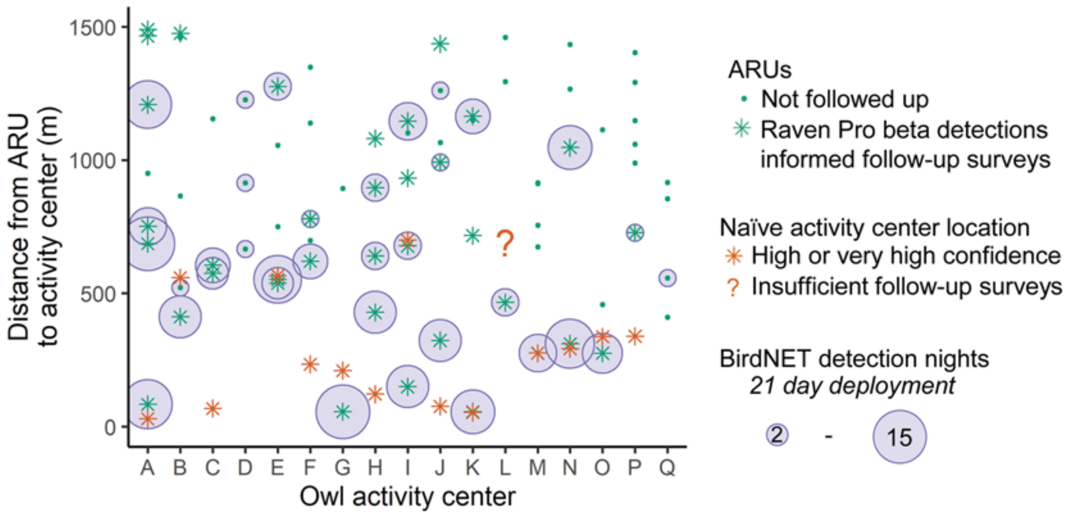

FIGURE 3 Scatterplot of autonomous recording units (ARUs) near each of the 17 occupied owl activity centers and results from acoustically assisted active surveys for California spotted owls. These detections were based on a shorter recording period and processed using Raven Pro beta in 2021 on the Eldorado National Forest, California, USA. Autonomous recording units that met the BirdNET-Sierra threshold using a 3-week recording duration and ≥2 detection nights are indicated by the circles, sized by the number of detection nights identified by BirdNET-Sierra.

information provided by clustered or nearby ARUs would be similar between the Raven Pro beta and BirdNET-Sierra methods.

Objective 2: acoustically assisted active survey detection of occupied territories

Only 15 of the 17 activity centers had an ARU unit or cluster within 750 m that detected an owl during the initial 2–3 weeks of audio data that we processed using the Raven Pro beta template detector. Thus, the naïve crew performed acoustically assisted active surveys at ARU deployment sites within 750 m (range = 55–727 m) of these 15 activity centers, in addition to a single ARU farther from these activity centers where owl vocalizations were detected (Figure 3). The naïve crew conducted 1–3 acoustically assisted active surveys ($\bar{x}$ = 1.7) at ARUs and ARU clusters near each activity center (though they did not know that these ARUs were near activity centers). By the second acoustically assisted active survey, there was ≥1 spotted owl response near each of the 15 activity centers with nearby ARUs with detections. A single dusk survey was sufficient to locate a putative roost location with very high confidence at 5 activity centers, and an additional 8 putative roost locations were established with very high confidence after 2–3 surveys. Of the 2 activity centers that were located with less than very high confidence, 1 was for a non-nesting pair (as determined by the traditional crew; activity center E in Figure 3) that likely moved roost locations. A pair was identified by the naïve crew at twilight 566 m from (and in the same protected activity center as) the activity center located by the traditional crew. There was only time to perform a single survey in this area, however, and the bands of the birds were not visible to confirm their identities. We strongly suspect that this was the same pair that was located by the traditional crew, so we classified the naïve crew's determination of an activity center as high confidence. An owl responded to an acoustically assisted active survey 691 m from the activity center located by the traditional crew (L in Figure 3), but there was insufficient time for the naïve crew to follow up on this detection. Depending on the criteria used to ascribe success, the naïve survey crew located either 14 or 15 of the activity centers for which they conducted a follow-up survey (i.e., 93–100%). Overall, the naïve crew located

14 of the 17 (82.3%) activity centers that occurred within the ARU study area with high or very high confidence (Figure 3; Figure S2, available in Supporting Information).

Objective 3: prioritization approach for acoustically assisted surveys

Because all habitat metrics were correlated ($r > 0.6$), we only fit quasi-binomial models with a single covariate (Table 2). The best model for the habitat-only estimate (which included burned areas and did not include prior occupancy) indicated that spotted owls were more likely to occupy grid cells with greater mean canopy height, where P(occ) was the predicted probability of occupancy (ranging between 0 and 1), and height was the canopy height in m:

$$\mathrm{P(occ)} = \frac{1}{1 + e^{-(-4.98696 + 0.30075 \times \mathrm{height})}} \tag{1}$$

The McFadden's R^2 value of the model in Equation 1 was 0.285 and the 10-fold cross validation error was 0.12. Given the distribution of canopy height across the survey prioritization study area, Equation 1 calculated that 30% of the landscape had a predicted occupancy <0.1 (Figure 4; Table S2, available in Supporting Information).

For the habitat and model set using historical data, historical reproduction and historical occupancy were highly correlated (correlation coefficient > 0.6), but neither was highly correlated with any habitat covariates. Accordingly, we fit a series of models where each model contained either occupancy or reproduction and a single vegetation metric. The best model in the second set (which excluded burned areas and included prior occupancy) indicated that spotted owls were more likely to occupy grid cells with a lower proportion of short-open forest (where open indicates the proportional area with canopy height <10 m) and higher historical occupancy rates (Table 3):

$$\mathrm{P(occ)} = \frac{1}{1 + e^{-(-1.8242 + 7.3280 \times \mathrm{historical\ occupancy} - 6.6035 \times \mathrm{open})}} \tag{2}$$

The McFadden's R^2 value of the model in Equation 2 was 0.858 and the 10-fold cross validation error was 0.03. Using Equation 2, slightly more than half (52%) of the survey prioritization study area had a predicted occupancy <0.1. The actual occupancy (proportion of grid cells with an activity center between 2015 and 2021) in this

TABLE 2 Ranked Akaike's Information Criterion corrected for small sample size (AIC_c) quasi-binomial models from the first model set predicting the proportion of years (2015–2021) with California spotted owl occupancy using only habitat data (from 2018 California Forest Observatory data) in the study area on the Eldorado National Forest, California, USA. We present the difference between the model's AIC_c and the best model's AIC_c (ΔAIC_c), number of parameters (K), and the proportion of predictive power of the given model compared to the full model set (AIC_c weight).

	ΔAIC_c	AIC_c	AIC_c weight	K
Mean canopy height	0.00	106.96	0.40	2
Short-open <20 m[a]	0.59	107.55	0.30	2
Tall dense forest[b]	1.38	108.35	0.20	2
Short-open <10 m[c]	2.64	109.60	0.11	2
Mean canopy cover	14.57	121.54	0.00	2
Null model	34.10	141.06	0.00	1

[a]Proportional area with canopy height <20 m.
[b]Proportional area with canopy cover >40% and canopy height >20 m.
[c]Proportional area with canopy height <10 m.

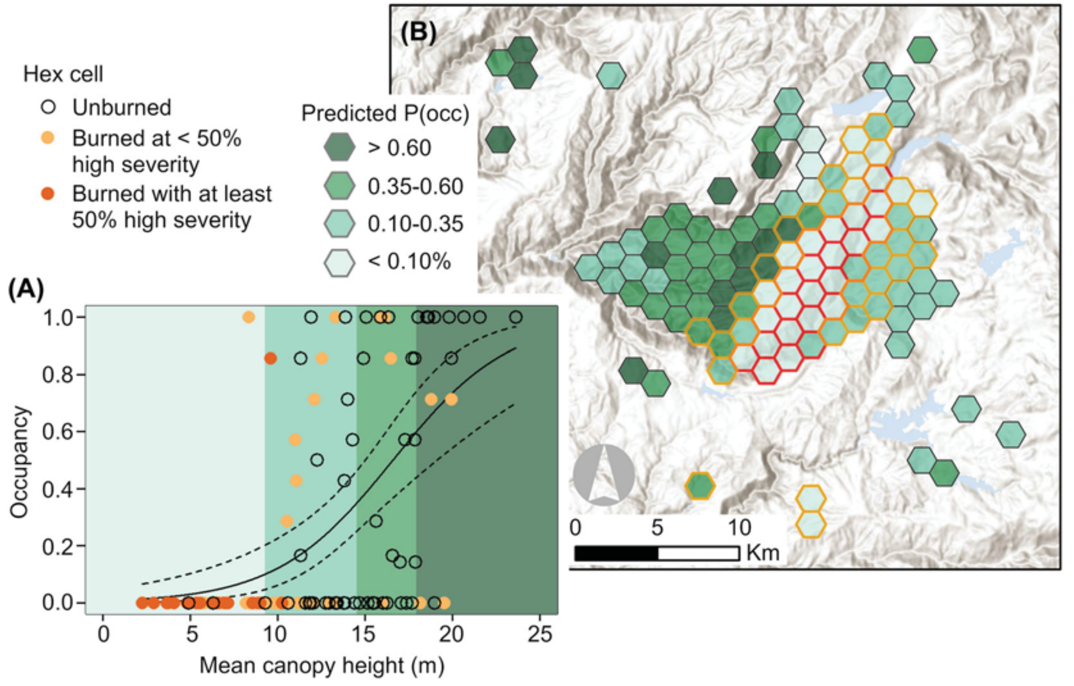

FIGURE 4 Visualization of predictions of California spotted owl occupancy, P(occ), from the best habitat-only model on the Eldorado National Forest, California, USA, based on 2018 mean canopy height. Scatterplot (A) of a hexagon's predicted and actual occupancy versus mean canopy height. Each point represents a hex cell and its actual occupancy (2015–2021), colored by the percentage of that cell that was burned at high severity in the King Fire. The solid line shows the predicted occupancy, with dashed lines showing the 95% confidence interval. The shaded vertical stripes correspond to predicted occupancy groups, and match those shown in the map (B), which displays the spatial arrangement of different probabilities across the landscape. The base map hillshade and hydrology use data from Esri, the Consultative Group on International Agricultural Research, and the United States Geological Survey.

low-probability area was <0.01. Grid cells with a predicted occupancy >0.6 covered 40% of the area and included cells that were all occupied ≥1 time between 2015 and 2021, with an average actual occupancy of 0.78 (Figure 5; Table S3, available in Supporting Information).

DISCUSSION

We demonstrated that acoustically assisted spotted owl surveys can achieve a high probability of accurately assessing territory occupancy status and locating activity centers in occupied territories within a single breeding season. Specifically, 3-week passive acoustic surveys with audio data processing conducted with BirdNET-Sierra allowed us to flag ARUs for active follow-up surveys within 750 m of all 17 known activity centers. This detection probability of 1.0 was achieved with only 31% (39 of 126) of ARUs requiring follow-up surveys when we used ≥2 nights of detections as a threshold to flag ARUs. Thus, this combination of survey duration and detection night threshold appears to identify a reasonable number of areas for acoustically assisted active surveys and allow for sufficient time for those surveys to take place later in the same breeding season.

A survey crew naïve to the status and location of occupied spotted owl territories could locate owl activity centers with confidence at 82% (14 of 17) of activity centers when audio data were processed during the season with Raven Pro

TABLE 3 Ranked Akaike's Information Criterion corrected for small sample size (AIC_c) quasi-binomial models from the second model set predicting the proportion of years (2015–2021) with California spotted owl occupancy using habitat (from 2018 California Forest Observatory data) and historical occupancy or historical reproduction (2003–2014) data in the study area on the Eldorado National Forest, California, USA. We present the difference between the model's AIC_c and the best model's AIC_c (ΔAIC_c), number of parameters (K), and the proportion of predictive power of the given model compared to the full model set (AIC_c weight).

	ΔAIC_c	AIC_c	AIC_c weight	K
Historical occupancy × short-open <10 m[a]	0.00	20.91	0.25	3
Historical occupancy × mean canopy height	0.25	21.16	0.22	3
Historical occupancy × short-open <20 m[b]	0.97	21.88	0.16	3
Historical occupancy × tall dense forest[c]	1.00	21.91	0.15	3
Historical occupancy	1.41	22.32	0.13	2
Historical occupancy × mean canopy cover	2.13	23.04	0.09	3
Historical reproduction × short-open <10 m	14.96	35.86	0.00	3
Historical reproduction × mean canopy height	14.97	35.88	0.00	3
Historical reproduction × short-open <20 m	15.74	36.65	0.00	3
Historical reproduction × tall dense forest	15.79	36.70	0.00	3
Historical reproduction	17.43	38.34	0.00	2
Historical reproduction × mean canopy cover	18.34	39.25	0.00	3
Mean canopy height	32.09	53.00	0.00	2
Short-open <20 m	32.13	53.04	0.00	2
Tall dense forest	32.40	53.31	0.00	2
Short-open <10 m	33.20	54.11	0.00	2
Mean canopy cover	45.68	66.59	0.00	2
Null model	47.15	68.06	0.00	1

[a]Proportional area with canopy height <10 m.

[b]Proportional area with canopy height <20 m.

[c]Proportional area with canopy cover >40% and canopy height >20 m.

beta's template detector. The ARUs were only flagged by this less-streamlined approach near 15 occupied territories, resulting in acoustically assisted active surveys successfully locating activity centers of 93.3–100% of occupied territories when an ARU within 750 m was flagged and followed up. We acknowledge that the method of flagging ARUs for follow-up was not identical between this test and the BirdNET-Sierra-based approach we propose to use going forward. In the field, we used a template detector in Raven Pro beta that required vetting by a technician, and in our analyses we used BirdNET-Sierra, which has a lower false positive rate and therefore does not require in-season vetting. Of the 7 ARUs that were flagged based on detections derived from Raven Pro beta and not flagged by BirdNET-Sierra, only 1 ARU was within 750 m of an occupied activity center (activity center K, where a closer ARU had detections from both approaches). Because 6 of these 7 ARUs were far from owl activity centers, we assumed that they would not have changed the naïve crew's acoustically assisted active survey strategy. This high level of overlap likely indicates that the effectiveness of acoustically assisted active surveys using BirdNET-Sierra analyses at this detection threshold level and recording duration would be just as effective as the acoustically assisted active surveys that we tested here. Thus, by multiplying the probability of flagging an ARU near all occupied activity centers (1.0) by the probability of finding an owl at high

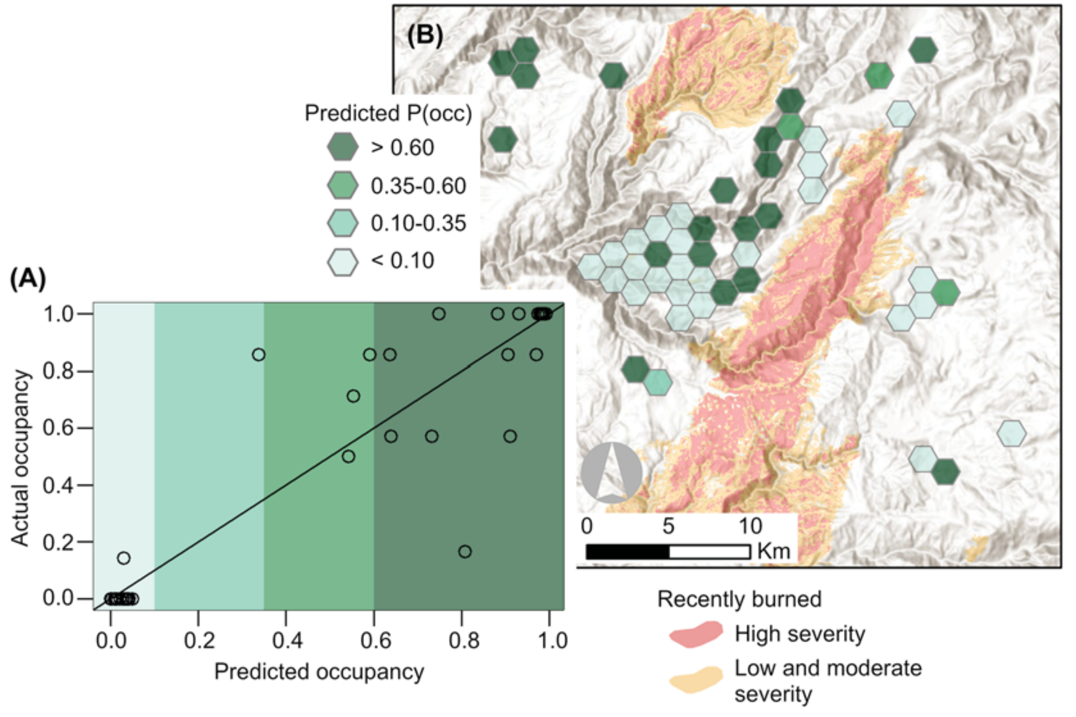

FIGURE 5 Visualization of predictions of California spotted owl occupancy, P(occ), from the best habitat and historical data model on the Eldorado National Forest, California, USA, based on proportion of short-open forest (in 2018) and historical occupancy (2003–2014). Scatterplot (A) of actual (2015–2021) versus predicted occupancy, where each point represents a hexagonal cell. The shaded vertical stripes correspond to predicted occupancy groups, and match those shown in the map (B), which displays the spatial arrangement of different probabilities across the landscape and fire severity (2010–2021). The base map hillshade and hydrology use data from Esri, the Consultative Group on International Agricultural Research, and the United States Geological Survey.

confidence (0.93–1.0), the probability of successfully finding activity centers across a project area using acoustically assisted active surveys based on BirdNET-Sierra in a single breeding season would be 0.93–1.0.

Because of limited resources, the naïve crew of 2 was responsible for deploying and retrieving 126 ARUs and conducting follow-up surveys (they completed 27) during a shortened field season (due to restrictions imposed by the COVID-19 pandemic). Additional staff assisted with applying the custom Raven Pro beta template detector to the acoustic data and manually reviewing detector results (i.e., putative acoustic detections), which would not be necessary for the BirdNET-Sierra method via the command line interface. With a larger crew, more efficient acoustic analysis methods, or implementing the prioritization approach, there would have been sufficient time to implement the few additional necessary acoustically assisted active surveys that would likely have resulted in 100% of owl activity centers being located with high confidence. In comparison, the traditional protocol typically takes 2 years of active-only surveys (primarily carried out at night or twilight) to achieve a high probability of locating territories (USFS 1991).

Prioritization approach for acoustically assisted surveys

We also developed statistical models for the efficient deployment of ARUs on the landscape, which could further improve survey efficiency by allowing surveyors to concentrate effort in areas likely occupied by spotted owls and avoid deploying ARUs in areas unlikely to be occupied. These prioritization models predict the probability of owl occupancy (defined as the presence of a current activity center) in individual 400-ha hexagonal grid cells across a landscape slated for forest management activities. The habitat-only model predicted low occupancy primarily in cells where recent high severity fire had burned ≥25% of the cell's area. While this model might help predict the probability of occupancy in unburned landscapes, areas with high proportions of green forests (and no historical occupancy data) may have high occupancy probabilities such that some form of survey would be recommended across the entire landscape. The habitat and historical occupancy model, which excluded burned areas, had a higher pseudo R2 value (0.858 vs. 0.285) and lower error (10-fold cross validation error of 0.03 vs. 0.12). Thus, in areas with primarily unburned forest and no historical occupancy data, the predictive power of the first prioritization model is limited.

While the predictive power of the habitat-only prioritization model may be low in some areas, it could be applied to any project area occurring in the mixed conifer zone of the Sierra Nevada (Figure 6A). For example, a project manager might decide to perform active-only surveys in areas with a predicted occupancy ≥0.6 to eliminate the extra step of conducting passive acoustic surveys in areas likely to be occupied by spotted owls. As an example of how the habitat-only prioritization model might increase survey efficiency across a portion of our ARU study area, 43% of that area would fall into this high occupancy category with a predicted occupancy ≥0.6 (Figure 6B). Assuming that ARUs would not be needed in those areas, 61 of 126 ARU deployments could be eliminated (Figure 6B). Alternatively, where precise nest or roost locations are unnecessary, a manager may decide to simply assume occupancy in areas above a certain threshold of predicted occupancy (e.g., >0.8), thereby eliminating the

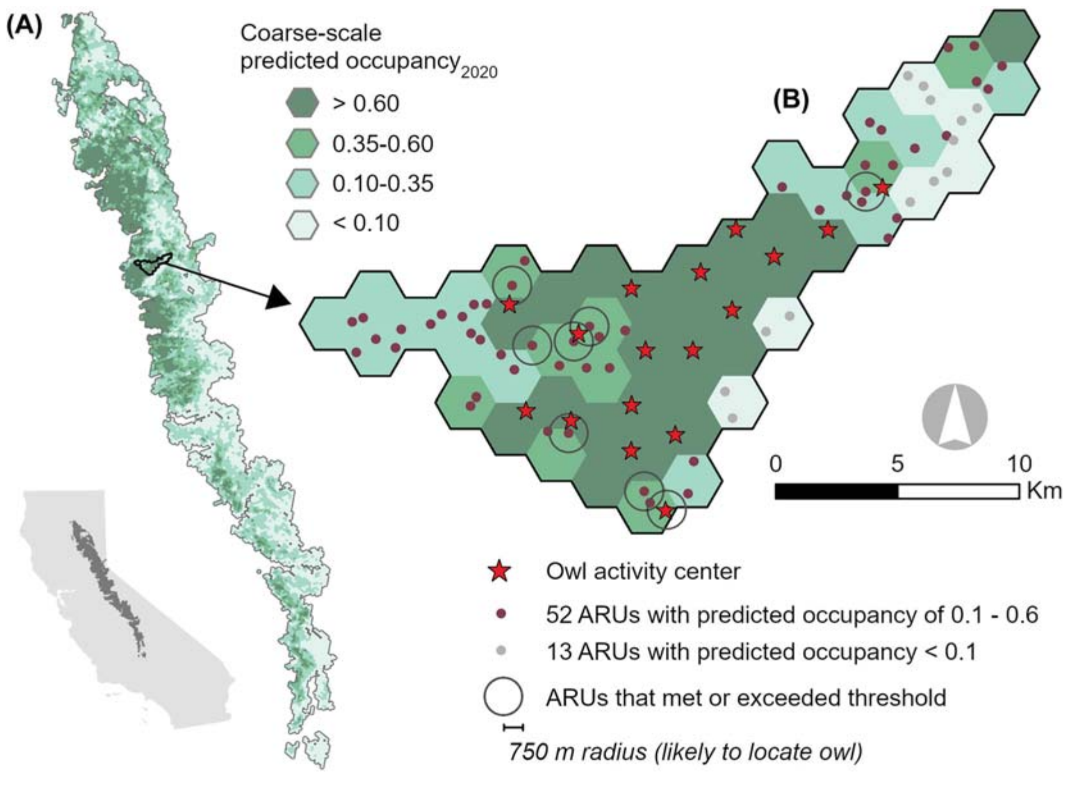

FIGURE 6 A) predicted California spotted owl occupancy based on canopy height estimates across the Sierra mixed conifer zone, California, USA, 2020. These predictions are also shown in the B) autonomous recording unit (ARU) study area on the Eldorado National Forest, California, USA, 2020. The locations of ARUs flagged for follow-up based on the 3-week, 2 detection-night threshold are also shown with a radius of 750 m.

need to survey those areas by any method. Thus, the tool can help managers reduce up-front hardware costs and make better use of existing equipment and personnel. Further, a manager might decide that cells with a predicted occupancy <0.1 did not require surveys of any kind (reducing the number of ARUs by an additional 13; Figure 6B). If the above protocol were followed, 53 ARUs (vs. 126 for complete coverage) might have been placed in the remaining area (where the probability of owl occupancy was between 0.1 and 0.6). During the time required for ARU deployment, 3 weeks of acoustic data collection, ARU retrieval, data analysis, and mapping (likely taking ≥1 month), it is likely that many initial active-only surveys would have been completed (at least in accessible areas where roads were clear of snow). These initial active-only surveys would likely have identified owl responses near the 14 occupied activity centers within this area where predicted occupancy is ≥0.6 (at least roughly identifying these activity center locations, though note that this is all speculative; Figure 6B).

Because spotted owl territories generally do not overlap, territory boundaries can be roughly represented by a circle with an area that matches the average spotted owl territory size. In the Sierra Nevada, territory size varies with latitude, and the corresponding radius distances representing a given territory ranged between 0.9 km in the southern Sierra Nevada to 1.4 km in the northern Sierra Nevada (Tempel et al. 2016); this information could be used to determine whether ARUs near identified birds or activity centers need to also be followed up. For example, the radius equating to characteristic territory sizes on the Eldorado National Forest is 1.1 km (Tempel et al. 2016), so a conservative 1-km buffer could be applied to the theoretical Eldorado scenario. Of the 8 ARUs that we flagged for follow-up (using ≥2 detection nights), 2 were within 1 km of an occupied owl activity center within the area covered by active-only surveys (and therefore would likely have been identified as occupied by the time ARU data were processed, and would not need to be followed up), and the remaining 6 ARUs would have been spatially clustered in 3 areas. Thus, this method would limit traditional active-only surveys to less than half of the project area and use ARUs and acoustically assisted active surveys to identify the limited number of additional areas needing follow-up surveys across the rest of the landscape.

While the ultimate predicted occupancy threshold values would be determined by the confidence level required by the specific project, this approach could likely help concentrate acoustically assisted active surveys in areas where they would be most useful, thus prioritizing the survey crew's time. While our models were based on data collected from a single location in the central Sierra Nevada, the general positive relationship between owl occupancy and canopy height and the negative relationship of occupancy with short or open forest area gave us confidence that this model would perform reasonably well throughout the mixed conifer zone of the Sierra Nevada (where coniferous canopy cover is ≥10%; Jones et al. 2018). We emphasize that these models are meant to be used as a tool to assist with project-level surveys and should not be used as a predictor of actual owl occupancy in any area. The recent and continued advances in acoustic monitoring thus provide an opportunity to pair traditional and emerging methods to streamline survey efforts that can increase the pace and scale of land management in the Sierra Nevada and beyond.

Suggested acoustically assisted spotted owl survey protocol

We suggest the following framework for an acoustically assisted survey protocol for the California spotted owl in the mixed conifer zone of the Sierra Nevada, with the intention of meeting a high probability of accurately assessing territory occupancy and locating activity centers in a single year. In the planning phase, predicted occupancy should be estimated across the project area for each 400-ha hexagonal grid cell using Equation 2 when prior occupancy history data are available for ≥3 of the previous 12 years. We recommend ≥3 surveys within the preceding 12 years to ensure a recent and robust historical occupancy calculation. When historical occupancy is not available (or insufficient) or there was a recent disturbance that substantially changed the habitat, the habitat-based site occupancy model described in Equation 1 is most appropriate.

Next, we recommend identifying upper and lower thresholds for predicted occupancy. Cells with a predicted probability of occupancy above the upper threshold would follow the traditional active-only survey protocol (up to

6 surveys separated by 5 calendar days or until an owl is located) that would commence early in the season (Forsman 1983, USFS 1991, Franklin et al. 1996). Cells with a predicted probability of occupancy below the lower threshold would receive neither active-only nor acoustically assisted active surveys. These thresholds would be dependent on what managers deem an acceptable cost of wasted resources expended on active-only surveys in areas where owls may not be present (below the upper threshold), an acceptable risk of failing to observe a spotted owl in the context of the potential risk posed to the species by the proposed forest management activities (below the lower threshold), and other factors. Although active-only survey areas would require 6 surveys, by restricting the survey coverage to only areas with a high likelihood of owl occupancy, the survey effort would be concentrated on areas where owls are most likely to be found, and thus fewer surveys would likely be required because surveys are considered complete as soon as an activity center is located.

For cells between the upper and lower threshold, acoustically assisted active surveys would be conducted. For these surveys, 3 ARUs would be deployed in each 400-ha grid cell in May, spaced ≥500 m apart, and record for 3 weeks. These ARUs should be preferentially placed in good owl habitat (a subjective description that will be necessarily based on the surveyors' knowledge of the species) and away from areas with high levels of ambient noise (e.g., a cascading stream or busy road) to maximize the chances of detecting owls in each cell. Upon retrieval, resultant audio data could be processed using BirdNET-Sierra with the freely available command line interface (https://github.com/kahst/BirdNET-Analyzer; accessed 8 May 2023). Although Raven 1.6.5 can also be configured to run BirdNET-Sierra, minor differences between the 2 processes result in slightly different scores, so the threshold of 0.989 should only be used to filter results from the command line interface version of BirdNET-Sierra to replicate the results of this study. Once this issue is resolved, teams would be able to map putative spotted owl detections within several hours on a consumer-grade laptop because Raven Pro 1.6.5 can implement BirdNET and process 30–50 hours of audio in one hour. As described above, any California spotted owl vocalization (either general or specific) with a BirdNET-Sierra confidence score ≥0.989 during the dusk (2000–2159) or dawn (0400–0559) of the following day would indicate a detection night. The BirdNET scores are sensitive to the nature of the input audio, and the detection-night criteria we developed are a direct result of those scores. Thus, our general approach may be relatively transferrable, but our specific findings may be replicated only if the same algorithm (BirdNET-Sierra) and the same recording equipment (SwiftOne Recorder) and settings (see methods) are used.

Autonomous recording units with ≥2 detection nights could be mapped, along with the total number of detection nights for each ARU (e.g., Figure 2B), which could help crews to locate owls most efficiently by targeting ARUs with the most detection nights for follow-ups and following up clusters of ARUs that met the threshold. Histograms of the total number of detections each night over time for each ARU could also be used to aid crews to prioritize the most recent detections (Figure S3, available in Supporting Information). Any ARUs occurring within an appropriate radius of an identified activity center or owl response discovered by the active-only surveys would not require any additional follow-ups because those owls would already be followed up sufficiently using active-only survey methods. A manager could reference the reported territory radius distances found by Tempel et al. (2016) to determine an appropriate radius distance for the location of their project area.

The remaining ARUs or clusters of ARUs with detections could then be followed up at dusk or dawn (30 minutes before to 30 minutes after sunset or sunrise, respectively). The crew would conduct vocal lure surveys at the ARU with the most detection nights or the most recent detections. If there were no owl response and more ARUs with detections were within the established territory radius (e.g., 1 km for the Eldorado), the crew could move toward those ARUs and continue acoustically assisted active surveys until a response was detected (within reason, considering crew safety and accessibility). Because flagged ARUs require ≥2 nights with detected owl vocalizations, it is likely that an owl activity center was nearby. While this was generally true in our study, owls did not always respond to active survey broadcast calls. Of the 26 acoustically assisted active surveys near occupied activity centers, owls did not respond to 4 (15%). In this study, all owls were detected within 2 surveys and all activity center locations were determined within 3 surveys. Therefore, we recommend dusk or dawn surveys on 3 different dates to determine non-occupancy. Upon hearing an owl response during an acoustically assisted active survey, the crew would proceed (following standard protocol) to track that owl to its nest or roost site to determine the location of the activity center (Forsman 1983, USFS 1991).

MANAGEMENT IMPLICATIONS

When the spatial allocation of ARU survey effort is aided by our tool and acoustically assisted surveys are initiated in May, this approach should meet the objective of locating ≥95% of occupied activity centers on the landscape, even if no prior owl survey information is available. This survey method increases the safety of survey crews by minimizing the need to conduct nighttime surveys and expedites the survey process while reliably locating owls across the landscape. Completing these project-level surveys more rapidly would help to increase the pace and scale of forest management across the Sierra Nevada forest ecosystem, thus improving forest health and reducing the risk of large, high severity fires for human, forest, and wildlife communities.

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CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

ETHICS STATEMENT
Work was conducted in compliance with California Department of Fish and Wildlife Scientific Collecting Permit S-193180001-19324-001-02 and Institutional Animal Care and Use Committee protocol A005367-R01-A01 (granted by University of Wisconsin Madison, Madison, WI, USA).

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available because of privacy or ethical restrictions.

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REFERENCES
Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences 113:11770–11775.

Appel, C. L., D. B. Lesmeister, A. Duarte, R. J. Davis, M. J. Weldy, and T. Levi. 2023. Using passive acoustic monitoring to estimate northern spotted owl landscape use and pair occupancy. Ecosphere 14:e4421.

Berigan, W. J., R. J. Gutiérrez, and D. J. Tempel. 2012. Evaluating the efficacy of protected habitat areas for the California spotted owl using long-term monitoring data. Journal of Forestry 110:299–303.

Berigan, W. J., G. M. Jones, S. A. Whitmore, R. Gutiérrez, and M. Peery. 2019. Cryptic wide-ranging movements lead to upwardly biased occupancy in a territorial species. Journal of Applied Ecology 56:470–480.

Blakesley, J. A., M. E. Seamans, M. M. Conner, A. B. Franklin, G. C. White, R. Gutiérrez, J. E. Hines, J. D. Nichols, T. E. Munton, and D. W. Shaw. 2010. Population dynamics of spotted owls in the Sierra Nevada, California. Wildlife Monographs 174:1–36.

California Forest Observatory [CFO]. 2020. A statewide tree-level forest monitoring system. Salo Sciences, San Francisco, California, USA.

Collins, B. M., S. L. Stephens, J. J. Moghaddas, and J. Battles. 2010. Challenges and approaches in planning fuel treatments across fire-excluded forested landscapes. Journal of Forestry 108:24–31.

Duchac, L. S., D. B. Lesmeister, K. M. Dugger, Z. J. Ruff, and R. J. Davis. 2020. Passive acoustic monitoring effectively detects northern spotted owls and barred owls over a range of forest conditions. Condor 122:duaa017.

Forsman, E. D. 1983. Methods and materials for locating and studying spotted owls. General Technical Report PNW-GTR-162. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.

Forsman, E. D., E. C. Meslow, and H. M. Wight. 1984. Distribution and biology of the spotted owl in Oregon. Wildlife Monographs 87:3–64.

Franklin, A. B., D. R. Anderson, E. D. Forsman, K. Burnham, and F. Wagner. 1996. Methods for collecting and analyzing demographic data on the northern spotted owl. Studies in Avian Biology 17:12–20.

Gutiérrez, R., A. Franklin, and W. LaHaye. 1995. Spotted owl (*Strix occidentalis*). Account 179 *in* A. Poole and F. Gill, editors. The birds of North America. The Philadelphia Academy of Sciences and The American Ornithologists' Union, Washington, D.C., USA.

Hezler, B. C. 2022. Winter surveys for Mexican spotted owls with audio recorders. Western Birds 53:327–334.

Jones, G. M., R. Gutiérrez, D. J. Tempel, S. A. Whitmore, W. J. Berigan, and M. Z. Peery. 2016. Megafires: an emerging threat to old-forest species. Frontiers in Ecology and the Environment 14:300–306.

Jones, G. M., J. J. Keane, R. Gutiérrez, 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., A. R. Keyser, A. L. Westerling, W. J. Baldwin, J. J. Keane, S. C. Sawyer, J. D. Clare, R. Gutiérrez, and M. Z. Peery. 2022. Forest restoration limits megafires and supports species conservation under climate change. Frontiers in Ecology and the Environment 20:210–216.

Jones, G. M., H. A. Kramer, S. Whitmore, W. Berigan, D. J. Tempel, C. M. Wood, B. K. Hobart, T. Erker, F. A. Atuo, N. R. Pietrunti, et al. 2020. Habitat selection by spotted owls after a megafire reflects their adaptation to historical frequent-fire regimes. Landscape Ecology 35:1199–1213.

Kahl, S., C. M. Wood, M. Eibl, and H. Klinck. 2021. BirdNET: a deep learning solution for avian diversity monitoring. Ecological Informatics 61:101236.

Kelly, K. G., C. M. Wood, K. McGinn, H. A. Kramer, S. C. Sawyer, S. Whitmore, D. Reid, S. Kahl, A. Reiss, and J. Eiseman. 2023. Estimating population size for California spotted owls and barred owls across the Sierra Nevada ecosystem with bioacoustics. Ecological Indicators 154:110851.

Knight, C. A., R. E. Tompkins, J. A. Wang, R. York, M. L. Goulden, and J. J. Battles. 2022. Accurate tracking of forest activity key to multi-jurisdictional management goals: a case study in California. Journal of Environmental Management 302:114083.

Kuchinke, D., J. di Stefano, H. Sitters, R. Loyn, P. Gell, and G. Palmer. 2020. Prescribed burn severity has minimal effect on common bird species in a fire-prone forest ecosystem. Forest Ecology and Management 475:118437.

Mayer, K. E., and W. F. Laudenslayer. 1988. A guide to wildlife habitats of California. California Department of Fish and Game, Sacramento, USA.

Ohmann, J. L., and M. J. Gregory. 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, USA. Canadian Journal of Forest Research 32:725–741.

R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reid, D. S., C. M. Wood, S. A. Whitmore, W. J. Berigan, J. J. Keane, S. C. Sawyer, P. A. Shaklee, H. A. Kramer, K. G. Kelly, and A. Reiss. 2021. Noisy neighbors and reticent residents: distinguishing resident from non-resident individuals to improve passive acoustic monitoring. Global Ecology and Conservation 28:e01710.

Reid, D. S., C. M. Wood, S. A. Whitmore, W. J. Berigan, H. A. Kramer, N. F. Kryshak, J. J. Keane, S. C. Sawyer, R. Gutiérrez, and H. Klinck. 2022. Breeding status shapes territoriality and vocalization patterns in spotted owls. Journal of Avian Biology 2022:e02952.

Rockweit, J. T., A. B. Franklin, and P. C. Carlson. 2017. Differential impacts of wildfire on the population dynamics of an old-forest species. Ecology 98:1574–1582.

Ruff, Z., D. B. Lesmeister, J. Jenkins, and C. M. Sullivan. 2022. Pnw-Cnet v4: automated species identification for passive acoustic monitoring. SoftwareX 23:101473.

Schoennagel, T., J. K. Balch, H. Brenkert-Smith, P. E. Dennison, B. J. Harvey, M. A. Krawchuk, N. Mietkiewicz, P. Morgan, M. A. Moritz, and R. Rasker. 2017. Adapt to more wildfire in western North American forests as climate changes. Proceedings of the National Academy of Sciences 114:4582–4590.

Smith, T. J., and C. M. McKenna. 2013. A comparison of logistic regression pseudo R^2 indices. Multiple Linear Regression Viewpoints 39:17–26.

State of California and U.S. Department of Agriculture Forest Service [USFS]. 2020. Agreement for shared stewardship of California's forests and rangelands.

Steel, Z. L., G. M. Jones, B. M. Collins, R. Green, A. Koltunov, K. L. Purcell, S. C. Sawyer, M. R. Slaton, S. L. Stephens, and P. Stine. 2023. Mega-disturbances cause rapid decline of mature conifer forest habitat in California. Ecological Applications 33:e2763.

Stephens, S. L., L. N. Kobziar, B. M. Collins, R. Davis, P. Z. Fulé, W. Gaines, J. Ganey, J. M. Guldin, P. F. Hessburg, K. Hiers, et al. 2019. Is fire "for the birds"? How two rare species influence fire management across the US. Frontiers in Ecology and the Environment 17:391–399.

Stevens, J. T., B. M. Collins, J. D. Miller, M. P. North, and S. L. Stephens. 2017. Changing spatial patterns of stand-replacing fire in California conifer forests. Forest Ecology and Management 406:28–36.

Sugai, L. S. M., T. S. F. Silva, J. W. Ribeiro, Jr., and D. Llusia. 2019. Terrestrial passive acoustic monitoring: review and perspectives. BioScience 69:15–25.

Tempel, D. J., and R. J. Gutiérrez. 2013. Relation between occupancy and abundance for a territorial species, the California spotted owl. Conservation Biology 27:1087–1095.

Tempel, D. J., J. J. Keane, R. Gutiérrez, J. D. Wolfe, G. M. Jones, A. Koltunov, C. M. Ramirez, W. J. Berigan, C. V. Gallagher, and T. E. Munton. 2016. Meta-analysis of California spotted owl (*Strix occidentalis occidentalis*) territory occupancy in the Sierra Nevada: habitat associations and their implications for forest management. Condor 118:747–765.

U.S. Department of Agriculture Forest Service [USFS]. 1991. Protocol for surveying for spotted owls in proposed management activity areas and habitat conservation areas. USDA Forest Service, Washington, D.C., USA.

U.S. Fish and Wildlife Service [USFWS]. 2012. Protocol for surveying proposed management activities that may impact northern spotted owls. U.S. Fish and Wildlife Service, Washington, D.C., USA.

U.S. Fish and Wildlife Service [USFWS]. 2023. Endangered and threatened wildlife and plants; California spotted owl; Endangered status for the coastal-Southern California distinct population segment and threatened status with section 4(d) rule for the Sierra Nevada distinct population segment. Federal Register 88:11600–11639.

Usinger, R. L. 1963. Sierra Nevada natural history. University of California Press, Berkeley, USA.

Weldy, M. J., D. B. Lesmeister, C. B. Yackulic, C. L. Appel, C. McCafferty, and J. D. Wiens. 2023. Long-term monitoring in transition: resolving spatial mismatch and integrating multistate occupancy data. Ecological Indicators 146:109815.

Westerling, A. L. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Philosophical Transactions of the Royal Society B 371:20150178.

Wood, C. M., R. J. Gutiérrez, and M. Z. Peery. 2019*a*. Acoustic monitoring reveals a diverse forest owl community, illustrating its potential for basic and applied ecology. Ecology 100:e02764.

Wood, C. M., H. Klinck, M. Gustafson, J. J. Keane, S. C. Sawyer, R. Gutiérrez, and M. Z. Peery. 2021. Using the ecological significance of animal vocalizations to improve inference in acoustic monitoring programs. Conservation Biology 35: 336–345.

Wood, C. M., V. D. Popescu, H. Klinck, J. J. Keane, R. Gutiérrez, S. C. Sawyer, and M. Z. Peery. 2019*b*. Detecting small changes in populations at landscape scales: a bioacoustic site-occupancy framework. Ecological Indicators 98:492–507.

Wood, C. M., S. M. Schmidt, and M. Z. Peery. 2019*c*. Spatiotemporal patterns of the California spotted owl's territorial vocalizations. Western Birds 50:232–242.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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