Biological Conservation 311 (2025) 111442

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Rapid implementation and adaptive design of a large-scale monitoring program for a declining species

Michaela L. Gustafson [a], Kate McGinn [b,c], Jeffrey A. Heys [d], Sarah C. Sawyer [e], Connor M. Wood [a,*]

[a] K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA
[b] Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, Madison, WI, USA
[c] USDA Forest Service, Rocky Mountain Research Station, Albuquerque, NM, USA
[d] USDA Forest Service, San Diego, CA, USA
[e] USDA Forest Service, Vallejo, CA, USA

ARTICLE INFO

Keywords:
Bioacoustics
Passive acoustic monitoring
Spotted owl
Habitat selection
Neighborhood effects

ABSTRACT

Passive acoustic monitoring (PAM) has proven effective as a means of monitoring species at broad spatial scales, but implementing a monitoring effort with limited information may require an iterative approach to survey design. We illustrate this challenge using the Southern California, USA population of the California Spotted Owl (*Strix occidentalis occidentalis*), which has declined >50 % over the past 30 years and faces multiple ongoing threats. Monitoring goals were: assessing the owl's distribution and locating individuals to facilitate regulatory compliance. Using a preexisting PAM design developed for this species, we deployed >200 recording units across the region, then used machine learning and manual verification to identify owl vocalizations. We also used known owl territory locations and remote sensing data to create a map of core owl habitat (nesting/roosting areas). We fit a set of occupancy models and found that: occupancy was low (0.20–0.298) and that both occupancy and detection were positively related to core habitat. To refine our design, we conceptualized the focal species' space use in terms of spatial home range, acoustic home range, and territory, interpreted our results and newly available movement data with this lens to determine the appropriate survey grid resolution. The new design should increase detection and baseline occupancy, improving statistical power and better meeting monitoring goals. Rapidly adapting monitoring programs to suit the target species and its home ecosystem may be necessary to effectively inform conservation action.

1. Introduction

Passive acoustic monitoring (PAM) has proven effective as a means of monitoring species at broad spatial scales (Kelly et al., 2023; Chronister et al., 2024) and for facilitating rapid conservation interventions (Wood et al., 2019a; Hofstadter et al., 2022). The emergence of real-time acoustic monitoring devices, as opposed to conventional autonomous recording units (ARUs) that store audio onboard for subsequent analysis, has made daily updates on rapidly progressing conservation challenges attainable (Bota et al., 2024; Wood et al., 2024). Yet the application of PAM – or other autonomous sensors like camera traps – to time-sensitive conservation issues faces another challenge: rapidly identifying appropriate study designs. Power analyses are a critical means of quantifying the potential performance of alternative monitoring designs (Southwell et al., 2019; Wood et al., 2019b; Banner et al., 2019), and analyses that explicitly include the cost of different designs are particularly valuable (Smart et al., 2022). But in some cases, even the basic factors needed to conduct a power analysis, such as realistic values for population- and survey parameters and appropriate sampling units, may be unknown. In such cases, multiple iterations of pilot study efforts may be necessary to identify the most suitable monitoring design.

Co-development of a design featuring a monitoring "wish list" developed by managers and corresponding survey techniques developed by researchers can clarify what types of information may be both needed and attainable (Stojanovic et al., 2024). For example, if the evaluation of planned management activities or expected disturbances (e.g., large fires, or increasing drought) is an important goal, situation-specific power analyses may be warranted (Popescu et al., 2012; Wood, 2022).

---

* Corresponding author at: 159 Sapsucker Woods Rd, Ithaca, NY, USA.
E-mail address: cmw289@cornell.edu (C.M. Wood).

https://doi.org/10.1016/j.biocon.2025.111442
Received 12 February 2025; Received in revised form 15 July 2025; Accepted 13 August 2025

If PAM is being considered as a more scalable addition to long-term observer-based monitoring, formal evaluation of detection probabilities achievable using both bioacoustics and human surveyors are often conducted (Holderried et al., 2024). For questions about the distribution of a species, particularly one that is thought to be rare, the spatial distribution of sampling locations can evolve over time (Benedetti et al., 2017), but substantive changes to the definition of eligible sampling units (e.g., survey grid resolution, habitat-based selection stratification, etc.) cannot continue indefinitely without creating gaps in valuable time-series data. Thus, rapid, critical evaluation of candidate designs' ability to meet objectives and their feasibility is important to balance appropriately informed monitoring design development with the increasingly time-sensitive need for reliable population monitoring data.

The California Spotted Owl (*Strix occidentalis occidentalis*; CSO) has been the subject of increasingly extensive PAM since 2017, but the expansion of current efforts into a new ecoregion, specifically at the species' southern range boundary where the population is most at-risk, is challenged by substantially different biogeography. The U.S. Fish and Wildlife Service (USFWS) recognizes two distinct population segments (DPS) for the CSO: the Sierra Nevada and the Coastal-Southern California (U.S. Fish and Wildlife Service, 2023). The Sierra Nevada, USA, represents the core of the CSO's range and the owl has been monitored intensively there (albeit at local scales) for several decades via vocal lure surveys (Jones et al., 2018); PAM began there in 2017. After a pilot season and a simulation-based power analysis informed by initial field data (Wood et al., 2019b), the monitoring program was eventually extended to encompass the entire Sierra Nevada ecosystem by 2021 (Kelly et al., 2023). Much less is known about the Southern California DPS. The San Bernardino and San Gabriel Mountains (CA) are thought to be population strongholds, but individuals have been sighted as far north as Carmel Valley, CA and as far south as the Sierra San Pedro Mártir, MX (de León Girón et al., 2024). Monitoring efforts have been less consistent and much less extensive than in the Sierra Nevada, but the available data are concerning. The population is estimated to have declined by over 50 % in the past 30 years, a decline driven in part by changing disturbance regimes (e.g., fire and drought, Tempel et al., 2022) and, likely by acute thermal stress associated with climate change (McGinn et al., 2023). The population is at risk of collapse (Barry et al., 2025). These findings informed the U.S. Fish and Wildlife Service's proposal to list the Coastal-Southern California population segment as “Endangered” under the Endangered Species Act in early 2023 (U.S. Fish and Wildlife Service, 2023).

As an at-risk species, CSO receives extensive habitat protections, but such protections have often conflicted with forest management objectives across the species' range (Ganey et al., 2017). Yet forest management practices that limit the occurrence of large, severe fire can ultimately benefit the CSO if implemented strategically and with the benefit of detailed data about the species' distribution (Jones et al., 2021). Indeed, forest management practices throughout this population segment's range may be necessary to prevent its extirpation due altered fire regimes and increased drought susceptibility. ESA listing would further necessitate a better understanding of where CSO actually occur, to evaluate how habitat protections are applied to individuals, rather than populations. Thus, comprehensive population data about the CSO across Southern California recently became an urgent priority for managers, with two “wish-list” monitoring goals (Stojanovic et al., 2024) emerging: 1) obtain a regional understanding of a population undergoing a potentially critical decline (Tempel et al., 2022; Barry et al., 2025), and 2) locate as many individuals as possible to proactively facilitate regulatory compliance.

In early 2024, less than a year after the initial USFWS proposal to list the Coastal-Southern California population segment as Endangered, we applied the PAM design used to obtain ecosystem-scale monitoring data for the Sierra Nevada population of CSO to Southern California. Biogeographic differences between ecosystems are small enough to support the CSO in both places, but large enough that the pre-existing monitoring design could be inefficient – most notably the Sierra Nevada has extensive conifer forests while vegetation and topography in Southern California are more complex and varied such that CSO habitat is more disjunct therein. The monitoring goals described above led to two project objectives: 1) rapidly conduct passive acoustic surveys for the CSO across Southern California during the 2024 breeding season, and 2) develop a new, Southern California-specific monitoring design based on our pilot data. Our iterative, adaptive approach to monitoring design may help realize the potential passive acoustic surveys offer for ecosystem-scale population assessments at a time when rapid ecological change is unfolding at ecosystem scales.

2. Methods

2.1. Monitoring design and study area

The CSO monitoring design we applied was developed for use in lands managed by the USDA Forest Service (USFS) in the Sierra Nevada (Wood et al., 2019b; Kelly et al., 2023). In the Sierra Nevada, USFS-managed lands that lie within Spotted Owl habitat as defined by a 2013 USGS habitat map (USGS Gap Analysis Program, 2013) and USFS habitat maps (J. Keane, pers. comm.) are predominantly mixed conifer forest, with some deciduous and coniferous forests at the lowest elevations (~600 m a.s.l.) and some subalpine forests at the highest elevations (~2000 m a.s.l.). A ~ 25,000 km^2 area of relatively contiguous habitat (of varying quality) was then subdivided into 400 ha hexagonal grid cells. That grid resolution was chosen because 400 ha is the approximate size of a CSO territory in that region (Tempel et al., 2016) and the monitoring program was designed for an occupancy framework wherein occupied grid cells serve as proxies for owl territories. Occupancy, in turn, is related to abundance for this territorial species (Tempel and Gutiérrez, 2013) such that large-scale occupancy-based monitoring can be used to infer population size (Kelly et al., 2023).

The mountains of Southern California, the Transverse and Peninsular Ranges, are quite different. Despite spanning a slightly shorter elevational gradient than the Sierra Nevada (both begin at ~200 m a.s.l.; the Southern California highpoint is 3500 m a.s.l. while the Sierra Nevada high point is just over 4400 m a.s.l.), there is far more floristic diversity in Southern California. Coastal sage (south and west slopes) and desert (east slope) cover the lowest elevations (200-500 m a.s.l.), followed by chaparral (500–1000 m a.s.l.); CSO are found at intermediate elevations (1000–1700 m) where there is a mix of chaparral, oak, and conifer species depending on slope and aspect, and in the contiguous conifer forests found at higher elevations ~1700-2600 m.

Despite these differences, because we had limited time to devise a new monitoring design, we used a survey site selection criteria in Southern California that was only lightly modified from the Sierra Nevada design: we overlaid USFS-managed lands with a hexagonal grid of 400 ha cells and considered a cell eligible for sampling if it: *i*) intersected a road or hiking trail; *ii*) contained ≥15 % CSO habitat as defined by the same 2013 USGS habitat layer (USGS Gap Analysis Program, 2013) (Fig. 1); and *iii*) not contiguous with another surveyed grid cell, with the initial selection determined randomly (Fig. 1). Thus, the study area was determined by first-order selection, or the geographic range of the species (sensu (Johnson, 1980)), without further biological detail. The minimum habitat threshold (i.e., ≥20 ha of “habitat”) was determined qualitatively in consultation with local biologists in order to balance the inclusion of areas with small pockets of high-quality habitat (typically found at the lower elevational limits of the species' distribution, and not a salient aspect of the Sierra Nevada-based design) against the exclusion of areas in which the species is unlikely to be present (in order to make the best use of limited crew time for ARU deployments). Of the initial 7600 km^2 project area (USFS-managed lands), 6224 km^2 (n = 1556 grid cells) were eligible to be surveyed (because they intersected a road or hiking trail and contained ≥15 % CSO habitat), and up to approximately 1430 km^2 (358 grid cells) could be surveyed (i.e.,

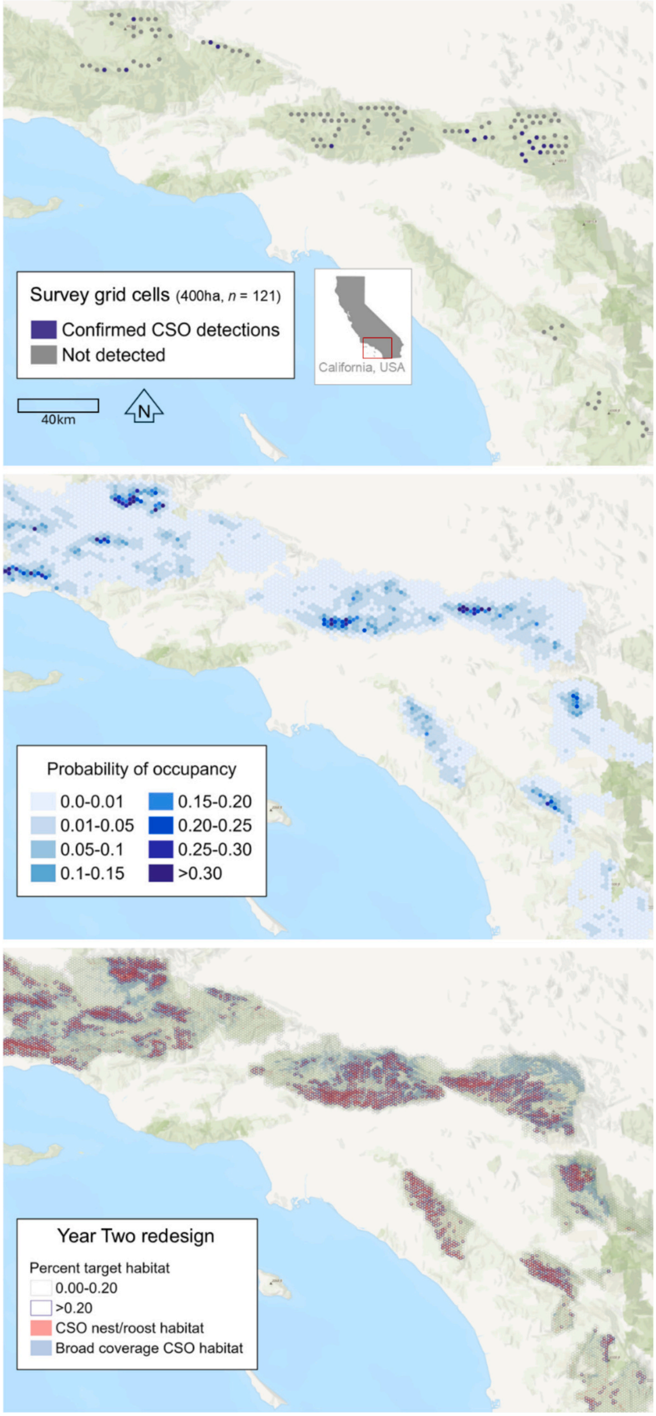

Fig. 1. The distribution of our year one surveys including naïve occupancy of the California Spotted Owl (top panel); predicted occupancy based on our top model of site occupancy (with just one confirmed true positive owl observation required for a grid cell to be considered occupied, the "one-night criterion") (middle panel); the general owl habitat model (blue) (USGS Gap Analysis Program, 2013), our model of owl nest/roost habitat (red), and the revised survey grid for year two. Two key differences between the year one design we implemented and the planned year two design are: 1) a focus on nest/roost habitat rather than generalized "habitat" (nest/roost as well as foraging), and 2) switching the survey grid resolution from 400 ha to 150 ha, a change that reflects the substantially smaller estimated territory size of the Spotted Owl in Southern California compared to the Sierra Nevada, the ecosystem for which the 400 ha grid was designed (Wood et al., 2019b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

because only ∼23 % of the cells in a hexagonal tessellation can be selected while maintaining non-contiguity).

2.2. *Passive acoustic surveys and processing audio*

Passive acoustic surveys consisted of the deployment of one or two ARUs (SwiftOne recorder, K. Lisa Yang Center for Conservation Bioacoustics) per grid cell deployed $\geq$500 m apart and $\geq$ 250 m from the cell perimeter (in situ testing suggests that these ARUs can reliably detect the target species out to 250 m). Within the randomly selected grid cells, deployment locations were left to the discretion of the field crew based on their evaluation of safe access and sound propagation (i.e., to maximize the effective listening radius of the ARUs) as the first and second priorities, respectively. Surveys began 17-April and ended 25-June 2024, with any given ARU deployed for five weeks. ARUs recorded 18:00–23:59, 0:00–9:00 (local time) daily at a sample rate of 32 kHz and gain of +33 dB via one omnidirectional microphone.

We analyzed the audio we collected with the BirdNET algorithm, a convolutional neural network able to identify animals by sound alone (Kahl et al., 2021). We used a customized version that had been overfit to our audio characteristics (ARU, sample rate, gain, and background soundscape) and study species (additional manual annotations of birds from Californian montane conifer forests were added to the training data, most notably extensive passive recordings of CSO), but BirdNET is freely available on GitHub (https://github.com/kahst/BirdNET-Analyzer). BirdNET evaluates 3-s snippets of audio and generates a unitless "confidence score" to express its confidence in each prediction. Scores are species- and hardware-specific, but because our entire workflow was identical to that used in the Sierra Nevada we could make use of the confidence score threshold established there (Kelly et al., 2023; Kramer et al., 2024). While the Sierra Nevada project workflow entailed a manual review of all predictions with a score $\geq$ 0.989 recorded 20 h00 – 06 h00 (local time), we relaxed our review process such that all predictions with a score $\geq$ 0.96 recorded 19 h00 – 07 h00 (local time). Reducing the score threshold and allowing more hours of audio increased the quantity of predictions to be reviewed – and the lower score threshold was qualitatively determined based on the quantity of predictions we could review in the time allotted for that task. Our goal was to insure against potential regional differences in vocal activity rates among CSO populations that could influence detectability. Consequently, we spent slightly more time reviewing detector predictions than if we had simply replicated the bioacoustic workflow of the pre-existing survey design. However, this allowed us to be more confident that no birds were recorded but not detected due to a too-stringent score threshold and thus avoid a situation in which detection probabilities were avoidably suppressed by user-imposed limits to detector performance. We also cross-referenced our data against vocal lure surveys that occurred in our study area and censored the entire night of survey effort any time a survey occurred within 1.5 km of an ARU, thus ensuring that our data truly reflected natural CSO vocal activity.

2.3. *Analyzing year one results*

Once we reviewed all eligible CSO BirdNET predictions, we prepared the confirmed CSO observations for use in single-species, single-season occupancy models (MacKenzie et al., 2002) using the package *unmarked* (Fiske and Chandler, 2011) in program R (R Core Development Team, 2020). We divided the survey season into week-long secondary sampling periods, with any given site generally surveyed for five periods. We assembled encounter histories at the scale of the survey grid cell, with observations from both ARUs in a given cell pooled such that the cell can be considered "occupied" if a CSO is identified at either or both ARUs.

We created two sets of encounter histories wherein sites were considered "occupied" if: (1) at least one owl observation occurred, or (2) if owl observations occurred on at least two different nights. The "two-night" criteria is a more conservative approach to defining site occupancy (see (Wood and Peery, 2022)) that reduces the chances of "ecological false positives" wherein an owl is correctly identified at a location (all our owl observations were positively confirmed as such by trained analysts) even though it is not a resident of that area. Studies with marked individuals have revealed that failing to account for the ecological false positives caused by transient individuals inflate occupancy estimates and obscure habitat associations (Berigan et al., 2019). There were no further temporal restrictions (e.g., the two nights could be consecutive in the same secondary sampling period) on our definition of site occupancy for the two-night criteria. The one- and two-night occupancy criteria have been applied to CSO PAM data in the Sierra Nevada where the two-night criterion led to a predictable decrease in estimated occupancy but yielded increased estimated detection (Kelly et al., 2023). Thus, the very simple two-night occupancy definition can substantially influence our understanding of the population and how it is monitored.

With both of our two sets of models (fit with the one-night and two-night occupancy definitions), we used a two-step model selection process to identify the most-supported combination of detection and occupancy covariates. Holding occupancy constant (null), we tested whether detection was uniform or varied with the total hours of survey effort (per sampling period), Julian date (of the sampling period), the amount of "nest or roost habitat" (defined below, quantified here as proportion of a hexagonal survey cell), or the multivariate combinations of these variables (seven models plus the null model of uniform detection). The model with the lowest Akaike's Information Criterion (AIC) was considered to have the most support from the data (Burnham and Anderson, 2010). The most-supported detection structure was carried forward and held constant while we then evaluated whether the probability of site occupancy was uniform or varied with the amount of "nesting habitat", the proportion of a cell that experienced high-severity fire in the previous 10 years ($\geq$75 % canopy mortality as measured by the Composite Burn Index), or both (three models plus the null model of uniform occupancy).

2.4. *Developing a map of spotted owl nest or roost habitat*

Stark contrasts in vegetation on USFS-managed lands in Southern California may be the most salient difference between that region and USFS-managed lands in the Sierra Nevada. In the Sierra Nevada, conifer forests are the dominant ecotype on and are thus relatively contiguous – making a randomized grid a plausible survey design. As noted above, in Southern California, far more plant communities are compressed into a smaller areas, often giving rise to spatially heterogeneous mosaics of habitat. Early in the planning process, concerns arose that a randomized grid could over-sample habitat that owls were unlikely to use (thus wasting resources), under-sample small pockets of valuable habitat (e.g., narrow bands of montane riparian forests extending into a matrix of lower-elevation chaparral) (thus biasing population estimates low), or both. Lacking both *i*) movement data that explicitly compared CSO habitat use between the Sierra Nevada and Southern California, and *ii*) the time to develop a customized survey design prior to the start of the survey season, we moved forward with surveys based on the randomized grid and, in parallel, began planning a design that would be tailored to the unique biogeography of Southern California.

Two factors led us to focus the customized design on nesting and roosting habitat. First, the looming need to locate as many CSO as possible to facilitate regulatory compliance (i.e., monitoring goal 2) while meeting forest restoration goals put a strong incentive on developing a monitoring program capable of locating individuals across the landscape. Focusing survey effort on areas most likely to represent important habitat, such as nest and roost stands, would therefore make the most efficient use of limited resources. Second, the statistical power to detect population trends increases with detection probability (Wood et al., 2019b; Banner et al., 2019), and GPS + audio tag data indicates that CSO vocal activity is concentrated in the core of their territories in the vicinity of nest and roost stands and that the birds are relatively quiet during wider-ranging foraging movements (Reid et al., 2021). Thus, again, targeting core habitat, the areas used for nesting and roosting, would make the most efficient use of limited resources. However, the only available maps of "spotted owl habitat" for Southern California represented first-order habitat selection (their geographic range); identifying the subset of their range used for nesting and roosting represents a focus on third-order selection, or "the useage made of various habitat components within the home range" (Johnson, 1980).

We created a species distribution model (SDM) of CSO nesting or roosting habitat (hereafter we generally use the term "core habitat") by relating nest and roost locations to remotely sensed habitat data. We calculated the mean center of historical nest and roost locations, obtained using methods outlined in prior work (Franklin et al., 2004) in the San Bernardino National Forest. We additionally obtained historical territory centers from the Cleveland National Forest (personal communication K. Winter). We combined these data to obtain a total of 402 "presence" locations. Using the *terra* package (Hijmans et al., 2025) in R (R Core Development Team, 2020), we established 10 random "pseudo-absence" locations for every "presence" location across the extent of southern California, including Ventura, Santa Barbara, San Luis Obispo, San Diego, San Bernardino, Riverside, Orange, Los Angeles, Kern, and Imperial Counties. At each location, we obtained estimates of canopy cover, canopy height, ladder fuel density, and canopy base height from California Forest Observatory (Salo Sciences, 2020). We used a k-fold strategy to reserve 20 % of the data to test model fits. To examine the impacts of habitat characteristics on the probability of occurrence, we fit a series of generalized linear models to the remaining training data specifying a binomial distribution in which presence/pseudo-absence was the response and habitat characteristics were the predictors. We compared models using AIC_c, corrected for small sample size, and we added additional covariates to models until they were no longer competitive; we considered models to be competitive if they were within 2.0 AIC_c units of the top-ranked model (Burnham and Anderson, 2002). We did not include covariates that were correlated with one another ($r > 0.70$) in the same model (Dormann et al., 2013). Using the *predicts* package (Hijmans et al., 2024) and our reserved testing data, we evaluated the top model and determined the threshold at which Cohen's kappa was the highest, which served as our cutoff to distinguish "core habitat." In ArcPro (V2.7.0), we converted the species distribution raster into a shapefile and removed any polygons that were < 1000 m^2, which we deemed too small to support meaningful nesting or roosting habitat. We then created 50 m buffers to account for edge effects and dissolved boundaries between unique shapes. Finally, we searched the literature for information about CSO space use in both Southern California and the Sierra Nevada to determine an appropriate survey grid cell size to apply to the SDM.

3. Results

3.1. *Passive acoustic surveys, initial occupancy and detection estimates*

We deployed 223 ARUs across 121 grid cells (i.e., sites), yielding 83,000 h of audio passively recorded between 19 h00 and 07 h00. Naïve occupancy was 0.149 ($n = 18$ cells with at least one confirmed owl observation; Fig. 1, top panel). Spotted Owls were confirmed in the Los Padres, Angeles, and San Bernardino National Forests, and in all three cases birds were detected that were not recently known to local managers. No CSO were detected via these surveys in the Cleveland National Forest.

Both detection and occupancy were consistently positively associated with the amount of core (nest/roost) habitat (Table 1, Fig. 2). Importantly, a broad range of forest conditions were sampled such that the amount of core habitat in a grid cell ranged from 0 to 99 % and was broadly distributed (see the green points in Fig. 2). This, combined with the slopes of their habitat~occupancy curves, suggests that the various

Table 1

Spotted Owl detection and occupancy estimates across Southern California based on the "one-night" and "two-night" occupancy criteria. Under the one-night criterion, a site (400 ha hexagon in which two ARUs were deployed) was considered occupied if at least one owl vocalization was confirmed; under the "two-night" criterion, owl observations on at least two different nights were required for a site to be considered "occupied." When testing for variation in ψ, the most-supported detection structure was used for all models (the most-supported detection model is then listed as the null model in the occupancy component of the table. ΔAIC was calculated separately for the detection and occupancy components of each model. "Habitat" was the proportion of a site composed of nest/roost habitat, "effort" was the total hours of audio recorded in a secondary sampling period, "time" was the Julian date of the start of the secondary sampling period.

Parameter	One-night				Two-night			
	Covariates	AIC	ΔAIC	w	Covariates	AIC	ΔAIC	w
Detection (*p*)	Habitat	233.75	0.00	0.45	Habitat + Effort	152.89	0.00	0.58
	Habitat + Effort	234.85	1.10	0.26	Habitat + Effort + Time	154.01	1.12	0.33
	Habitat + Time	235.64	1.89	0.17	Habitat	157.44	4.55	0.06
	Habitat + Effort + Time	236.49	2.74	0.11	Habitat + Time	159.40	6.51	0.02
	None (null model)	254.83	21.08	0.00	Effort	161.87	8.98	0.01
	Effort	255.86	22.12	0.00	Effort + Time	162.50	9.61	0.00
	Time	256.82	23.07	0.00	None (null model)	167.98	15.09	0.00
	Effort + Time	257.75	24.00	0.00	Time	169.82	16.93	0.00
Occupancy (ψ)	Habitat	231.07	0.00	0.53	Habitat	150.26	0.00	0.46
	Habitat + Fire	232.58	1.51	0.25	Habitat + Fire	151.02	0.77	0.31
	None (null model)	233.75	2.68	0.14	None (null model)	152.89	2.63	0.12
	Fire	234.96	3.88	0.08	Fire	153.14	2.88	0.11

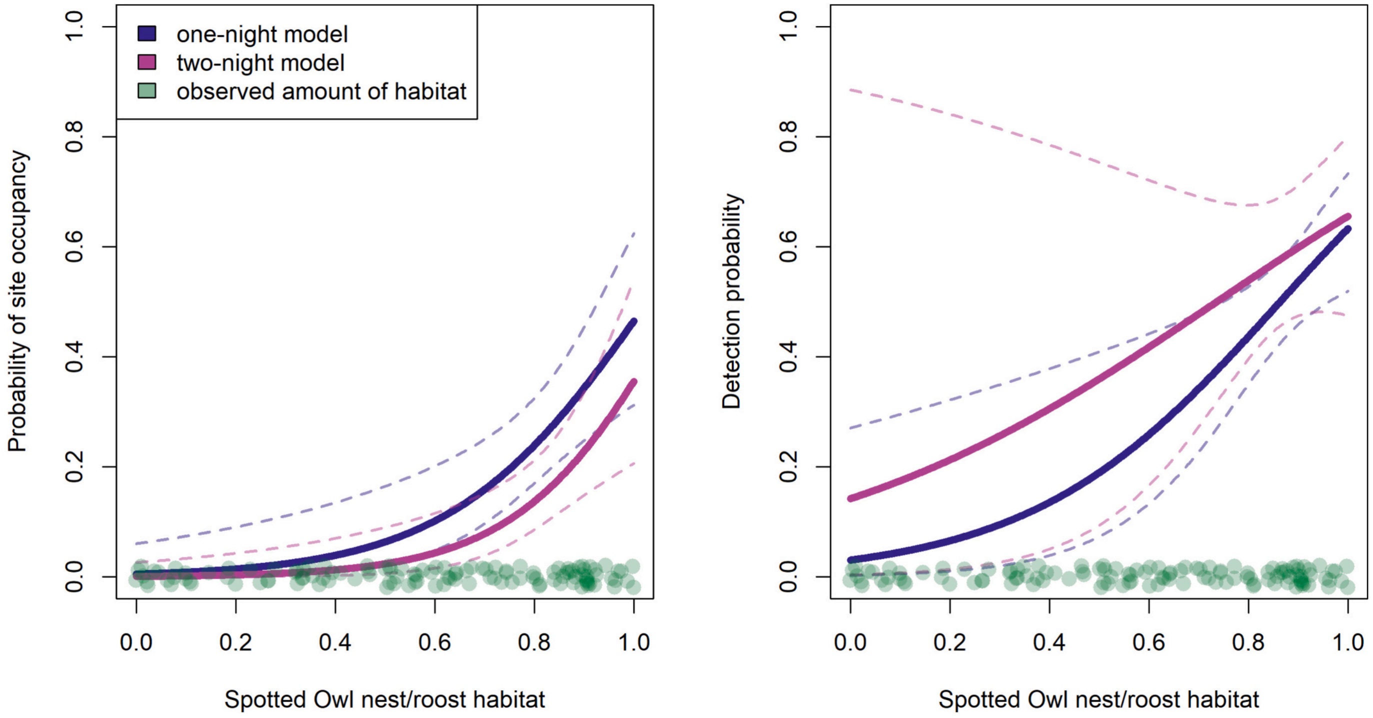

Fig. 2. The probability that Spotted Owl occupied a survey grid cell increased with the amount of nest or roost habitat in that cell (left panel), and the probability detecting an owl given that it was present also increased with the amount of such habitat (right panel). These relationships were consistent whether a confirmed owl observation on one night or two nights was used to classify a site as "occupied" (one-night model [blue line] or two-night model [magenta line]). Fine dashed lines represent the 85 % confidence intervals. See Table 1 for model selection results and Table 2 for model covariates. Survey effort was included in the most-supported two-night model, and full survey effort (i.e., 154 h of audio per secondary sampling period) were used here. Habitat is listed here as the proportion of a 400 ha survey cell (0.2, 0.4, 0.6, and 0.8 correspond with 80, 160, 240, and 320 ha, respectively). Under the current design, a wide range of habitat amounts was sampled (green points); under the proposed design, more high-habitat sites would be surveyed, likely providing greater precision for the estimation of species-habitat relationships at the most salient conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Top models of spotted owl occupancy across Southern California based on one- and two-night occupancy criteria (number of nights on which an owl was observed in order to consider a site "occupied"). Habitat is the proportion of a survey site composed of nest/roost habitat; effort is the total hours of passively recorded audio per secondary sampling period. For the full model selection table, see Table 1.

Occupancy criterion	Detection (*p*)						Occupancy (ψ)			
	Intercept	SE	$\beta_{habitat}$	SE	β_{effort}	SE	Intercept	SE	$\beta_{habitat}$	SE
One-night	−3.450	1.707	3.993	1.942	na	na	−5.229	1.727	5.087	2.048
Two-night	−4.277	2.712	2.438	3.032	0.016	0.006	−6.820	2.224	6.223	2.589

selection criteria in our initial design were not so stringent that our a priori expectations of where birds might be residing did not cause us to fail to sample where they may indeed be.

Under the one-night occupancy criterion, mean estimated occupancy (ψ, derived from the null occupancy model; $\Delta\text{AIC} = 2.68$, Table 1) was 0.298 ($\beta_0 = -0.856$, SE = 0.335). Detection varied with the amount of core habitat in a survey cell ($w = 0.45$), while effort and time were uninformative (Arnold, 2010); site occupancy also varied with habitat ($w = 0.53$), while the fire was uninformative (Table 1). Based on the top model (Table 2), at a site with no core habitat (i.e., habitat = 0), the probability of CSO occupancy (under the one-night occupancy criterion) was 0.005 and the probability of detection if it were occupied was 0.031. In contrast, at a site entirely composed of core habitat (i.e., habitat = 1.0), some of which occurred in the Mountaintop Ranger District of the San Bernardino Forest (Fig. 1), the probability of occupancy was 0.46 and the probability of detection was 0.63.

Under the two-night occupancy criterion, mean estimated occupancy (ψ, derived from the null occupancy model; $\Delta\text{AIC} = 2.63$, Table 1) was 0.20 ($\beta_0 = -1.39$, SE = 0.393). Detection varied with habitat and survey effort ($w = 0.58$), while time was uninformative (Arnold, 2010); and site occupancy varied with habitat ($w = 0.46$), while fire was again uninformative (Table 1). Specifically, detection increased with the total hours of survey effort and with the amount of core habitat, and the probability of site occupancy also increased with habitat (Table 2, Fig. 2). Based on the top model (Table 2) and assuming full survey effort (154 h of audio recorded, which occurred in the vast majority of secondary sampling periods), at a site with no core habit (i.e., habitat = 0), the probability of CSO occupancy (under the two-night occupancy criterion) was 0.001 and the probability of detection if it were occupied was 0.14. Again in contrast, at a site entirely composed of core habitat, the probability of occupancy was 0.35 and the probability of detection was 0.65.

Importantly, that we found no support for an effect of high-severity fire on site occupancy is likely a function of our SDM (see below), which was based on 2020 forest structure data. Thus, fire-driven changes to owl habitat from nearly all recent fires were already incorporated into our core habitat layer.

3.2. A custom Southern California monitoring design

Our SDM indicated that CSO nesting or roosting habitat was best described by canopy height, canopy base height, and ladder fuel density (Table 3). Based on the top model, CSO were more likely to occur where there were higher canopies ($\beta_{CH} = 0.16$, 95 % CI [0.14–0.18]), more ladder fuels ($\beta_{LF} = 0.03$, 95 % CI [0.02–0.04]), and higher canopy base heights ($\beta_{CBH} = 0.25$, 95 % CI [0.08–0.42]). The threshold at which Cohen's kappa was the highest was 0.22 and the area under the receiver operating characteristic curve (AUC) was 0.80, which indicates moderate model performance.

Table 3

AIC model summaries for the spotted owl nest/roost habitat species distribution model (SDM). CH is canopy height, LF is ladder fuel density, CBH is canopy base height, and CC is canopy cover. K is the number of parameters in the model, AIC_c is the Akaike's Information Criterion corrected for small sample size, ΔAIC_c is the difference between a model's AIC_c and the top AIC_c. cumWt is the cumulative model weight, and LL is the log-likelihood of the model.

Model	K	AIC_c	ΔAIC_c	AIC_{cWt}	cumWt	LL
CH + LF + CBH	4	1815.57	0.00	0.97	0.97	−903.78
CH + LF	3	1822.74	7.17	0.03	1.00	−908.37
CH	2	1859.77	44.20	0.00	1.00	−927.89
CC	2	1863.47	47.90	0.00	1.00	−929.74
CBH + LF	3	1893.12	77.54	0.00	1.00	−943.55
CBH	2	1997.93	182.35	0.00	1.00	−996.96
LF	2	2006.73	191.16	0.00	1.00	−1001.36
Null	1	2159.28	343.71	0.00	1.00	−1078.64

An important step was subdividing our new map of CSO core habitat into surveyable units that could appropriately represent owl territories in an occupancy framework. Our primary concern was that if grid cells were too big, a change in population size might not be manifested as a change in occupancy because multiple territories could be encompassed by a single cell (e.g., two territories might need to become locally extinct for a one-unit change in occupancy). We conceptualized three tiers of CSO space use: 1) their spatial home range, or the total area a resident pair might use, 2) their acoustic home range, or the proportion of their spatial home range in which they are vocally active, and 3) their territory, or a central subset of their spatial home range that is actively defended and used exclusively by that pair (Fig. 3). By definition, the acoustic home range and the territory cannot be larger than the spatial home range, and for vocally active species, it is unlikely that the territory could be larger than the acoustic home range, unless the species were defending its territory silently (e.g., with olfactory cues or physical aggression). Reid et al. (2021, 2022) explored the biological drivers of variation in acoustic home ranges and the implications for PAM. These three tiers of space use (spatial home range, acoustic home range, and the territory) are animal-centered constructs. A fourth conceptualization, which is observer-centered is also relevant: the observable acoustic home range. For example, the vocalizations of particularly loud species, such as wolves or howler monkeys, may be audible beyond their actual spatial home ranges. Surveying non-contiguous and appropriately sized grid cells should mitigate the practical effects of observable acoustic home ranges that extend beyond the spatial home range.

The 400 ha grid cell size was originally derived from exhaustive territory mapping in four local-scale focal monitoring across the Sierra Nevada in which half the mean distance between known territories was used as the radius of a circle defining the area of putatively exclusive habitat use for each pair (Tempel et al., 2016). High-resolution GPS tags have revealed that these territories are subsets of the owls' spatial home ranges: across the Sierra Nevada, the mean home range, as represented by the 95 % kernel density estimate (KDE), is 775 ha (1st quartile: 541 ha, 3rd quartile: 853 ha; $n = 24$ CSO) (McGinn et al., 2024). Crudely, the 400 ha territory represented approximately 58 % of the home range. The same GPS tagging effort also included CSO in Southern California (specifically the San Bernardino Mountains; $n = 10$ CSO), and the mean home range (again, the 95 % KDE) was 142 ha (1st quartile: 100 ha, 3rd quartile: 175 ha) (McGinn et al., 2024). Applying the 0.58 territory: home range scalar from the Sierra Nevada yields a Southern California territory size of 82 ha. Importantly, there is a strong latitudinal change in territory size even within the Sierra: in the southern Sierra, territories were calculated to be just 250-300 ha (Tempel et al., 2016). Thus, the decrease from 400 to 82 ha is not as simplistically stark as it seems. Moreover, it is uncertain whether the territory:home range scalar is static across space – it may be that as latitude decreases, territory size decreases more slowly than does the spatial home range.

Another important consideration is that, like an owl's territory, its vocal home range is a subset of the spatial home range (Reid et al., 2021). However, the vocal:spatial home range scalar depends on sex and reproductive status, and, for example, non-breeding male CSO in the Sierra Nevada have an acoustic home range that is almost as big as their spatial home range (Reid et al., 2022). Planning for high vocal:spatial home range birds (i.e., non-breeding males which vocalize throughout their spatial home range) (Reid et al., 2022) by choosing a larger grid size mitigates the possibility of double-counting CSO.

In light of these data, particularly the GPS tag data from McGinn et al. (2024), which were not available when we designed the year one surveys, we selected a survey grid size of 150 ha for the new year two design. Such grid cells would be slightly larger than the mean CSO spatial home range in Southern California (142 ha), and are thus conservative units with which to measure the population of this territorial species in terms of site occupancy insofar as they minimize the possibility of inflating population estimates by double-counting the target species and thus obscuring ongoing declines. This decision reflects a

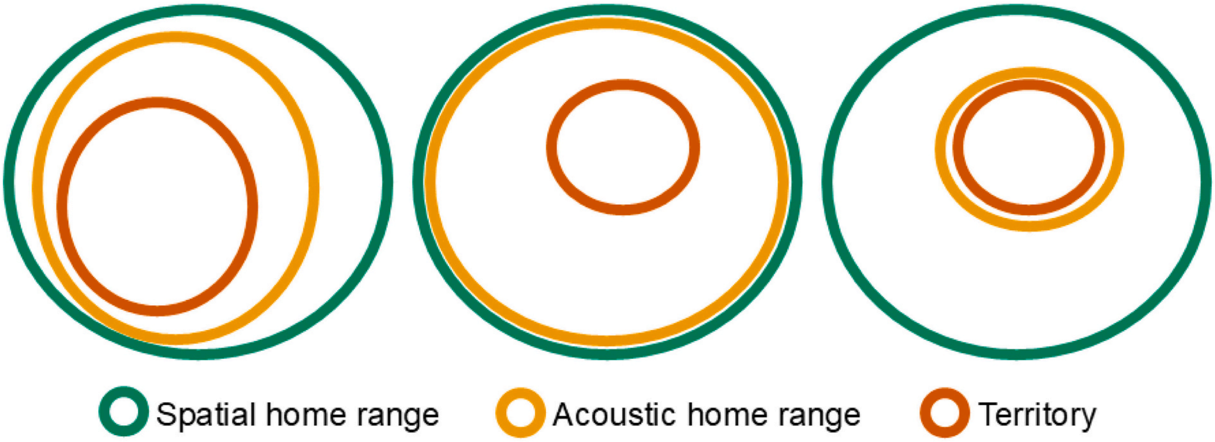

Fig. 3. A conceptual model of three potential combinations of spatial and acoustic ecology for a territorial focal species of a passive acoustic monitoring program. The **spatial home range** is the total area an animal utilizes; the **acoustic home range** is the area in which they are vocally active thus available for detection in a PAM program (meaning that vocal activity of interest in this context may be limited to specific sounds that are detectable in an automated framework; the **territory** is the portion of a spatial home range that is actively defended and used exclusively by that individual, pair, or group. For examples of how the spatial and acoustic home ranges can vary as well as an example of their implications for a monitoring program, see Reid et al. (2021, 2022).

preference for Type II errors (false negatives, failing to find an individual that is truly present) over Type I errors (false positives, incorrectly attributing an animal to a particular survey unit when it actually resides in an adjacent unit). In the context of a steeply declining population (Tempel et al., 2022), Type I errors have a higher consequence, as they could incorrectly indicate recovery and that conservation actions are adequate or unnecessary when either or both policy position would be inaccurate. It has been empirically demonstrated in the CSO literature based on tracking of known individuals and known territories that Type I errors indeed inflate population estimates and obscure habitat associations (Berigan et al., 2019). Nonetheless, Type II errors remain problematic because they undermine both management goals (understanding the distribution of the species and locating individuals to facilitate regulatory compliance) and because as lower occupancy rates are associated with lower statistical power to observe a population trend (Wood et al., 2019b). However, our SDM should enable us to better target survey efforts such that more individuals are located using the year two (150 ha grid resolution) design than with the year one (400 h grid design).

After determining the survey grid resolution, we applied several cell selection criteria. First, for logistical and inferential reasons the arbitrary boundaries of the survey grid cannot be informed by actual CSO spatial data (e.g., the locations of specific territories) and thus owl territories could easily lie at the intersection of two or three grid cells. Thus, as before, only non-adjacent survey cells would be eligible for surveys (meaning that a maximum of approximately 24 % of the cells would be eligible to be surveyed). When local managers have a particular interest in surveying a given area that is not part of the larger monitoring effort, targeted supplementary surveys could be employed to meet the monitoring goal of locating as many individuals as possible (e.g., (Kramer et al., 2024)). Second, a cell must have $\geq$30 ha of core habitat (i.e., 20 % of its total area composed of nest/roost habitat) to be eligible to be surveyed (Fig. 1). Thus, the smallest home range from the aforementioned GPS tagging study, 86.5 ha (McGinn et al., 2024), might only partially overlap a grid cell and still be eligible for survey coverage. Setting higher minimum core habitat thresholds would likely increase baseline occupancy but would increasingly impair our ability to make robust inferences about the minimum amount of core habitat necessary for site occupancy. Third, building off our finding that the amount of adjacent core habitat is positively associated with site occupancy at the scale of 400 ha (Fig. 2), we buffered the 150 ha hexagons by 448 m such to create 400 ha polygons, and calculated the amount of core habitat therein. The resulting area could be used to calculate the probability of site occupancy using the relationships we established in our occupancy analysis (Table 2), enabling the implementation of a stratified random design such that areas of higher predicted occupancy could be targeted for surveys in a controlled, systematic manner, potentially even via a two-phase adaptive stratified approach if substantial geographic variation emerges in occupancy rates within areas predicted a priori to have high occupancy rates (Manly, 2004). Finally, fourth, resource and safety constraints are likely to limit eligible cells to those accessible by road or trail.

One ARU would be deployed per 150 ha cell rather than two ARUs per 400 ha cell, such that actual acoustic survey coverage per cell potentially increases slightly. Furthermore, there are not necessarily any additional hardware costs because while the absolute number of survey cells has more than doubled, *i*) the amount of hardware used per cell has been reduced by half, and *ii*) the quantity of cells surveyed can readily be scaled via habitat stratification to match the available resources (e.g., coverage could expand if more ARUs were obtained and more field personnel were hired). Importantly, ARUs will be spaced further apart (as opposed to being deployed in pairs) such that it is likely to take slightly more time and effort to deploy the same quantity of ARUs.

4. Discussion

The Southern California DPS of the California Spotted Owl is the most at-risk population of this subspecies of Spotted Owl (U.S. Fish and Wildlife Service, 2023), but it is substantially understudied relative to the Sierra Nevada DPS. We estimated CSO site occupancy of the Southern California DPS to be 0.298–0.20 (one- or two-night occupancy criterion) amidst an estimated annual decline in territory occupancy of 1.9 % (Tempel et al., 2022). In contrast, site occupancy of the Sierra Nevada DPS as measured by the same monitoring design is much higher (0.42–0.30 based on one- or two-night occupancy criterion (Kelly et al., 2023)) while territory occupancy is declining more slowly (0.8–1.7 % annually (Tempel et al., 2016). Critically, however, the two occupancy estimates are not direct analogs because the 400 ha survey grid resolution is not the best way to assess the CSO population in Southern California, so additional monitoring will be required to develop a truly range-wide population assessment for this subspecies of Spotted Owl. Nonetheless, recent work suggests that the CSO may be functionally extinct in areas of Southern California that were historically occupied (Tempel et al., 2022; Barry et al., 2025), and that habitat loss caused by large, severe fires, more extreme drought- and insect-related tree mortality, and rising temperatures are critical stressors of this population

(Tempel et al., 2022; McGinn et al., 2023). However, the CSO has persisted 400 km south of the Southern California population stronghold in the San Bernardino, with the conifer forests of the Sierra San Pedro Mártir harboring at least some individuals (de León Girón et al., 2024). Forest structure in the Sierra San Pedro Mártir has changed far less than in Southern California such that fire risk is comparatively low, indicating that disturbance regimes and associated forest structure are comparatively faithful to pre-colonial conditions (Stephens et al., 2024). This example of a putatively resilient forest system harboring CSO offers a potential benchmark for successful forest management and owl conservation in Southern California, although, as with the Sierra Nevada, ecological differences between regions may make direct comparisons uninformative. Nonetheless, achieving the goal of resilient forests and a stable CSO population will require effective monitoring of the owl across Southern California to support adaptive management and regulatory compliance.

Our pilot study revealed first and foremost that passive acoustic monitoring of the CSO at regional scales in Southern California can be effective. With a small crew (two field personnel) and a short timeline, we surveyed substantial areas of all four National Forests, locating previously undocumented or not recently observed owls in three of the four forests. Site occupancy was positively associated with the amount of core nest/roost habitat as measured by the SDM we developed (Table 2, Table 3), confirming the value of this habitat map in the context of population monitoring; a more in-depth modeling process would be required to develop a standalone habitat map. The revised grid resolution, 150 ha for future surveys as opposed to 400 ha, should make site occupancy rates more sensitive to change over time because the smaller cells better reflect the spatial ecology of the CSO in this region (McGinn et al., 2024). Systematically allocating survey effort toward areas of high predicted occupancy (Fig. 2) could then inform species conservation efforts that account for mismatches between predicted site quality and observed occupancy (McGinn et al., 2022), including our finding of the importance of neighborhood effects on site occupancy rates. Similarly, developing alternatives to the one- and two-night occupancy criteria, such as defining “detections” for occupancy modeling based on call rates, call times (e.g., dusk only), or pair status might enable more nuanced and biologically-grounded monitoring of this population (Wood et al., 2019c, 2020). Finally, as noted above, the absence of support of an explicit fire effect on occupancy is almost certainly a function of the incorporation of fire-driven changes to forest structure into our core habitat layer; our results should not be interpreted as evidence for CSO site occupancy in Southern California being unresponsive to fire.

Our results offer insights into multiple spatial scales of CSO habitat selection (sensu (Johnson, 1980)) in Southern California. Prior research determined first-order selection by delimiting the geographic range of the CSO in Southern California (USGS Gap Analysis Program, 2013), information we used to determine our survey area. Recent work also provided nuanced insights into fourth-order selection by investigating the influence of fire age and severity on CSO prey captures (McGinn et al., 2024). Our SDM revealed third-order selection by identifying the particular habitat features within owls' home range (namely canopy height, canopy base height, and ladder fuel density as of 2020) that are used for nesting and roosting (Salo Sciences, 2020). These findings are generally corroborated by a recent analysis of long-term territory occupancy data in the San Bernardino and eastern Angeles National Forests, which found a positive effect of large trees on long-term site occupancy rates (Tempel et al., 2022). Intriguingly, there is evidence in our occupancy analysis for second-order selection, or processes determining the home range of individuals (Johnson, 1980). The spatial resolution of our first survey grid, 400 ha, was much larger than the largest Southern California Spotted Owl home range (95 % KDE = 238 ha) observed by (McGinn et al., 2024). Thus, our occupancy model covariates were accounting for habitat that was almost certainly unutilized by a local resident. That the probability of site occupancy increases substantially as the amount of such habitat increases beyond ~240 ha (Fig. 2) suggests substantial neighborhood effects: site occupancy is highest in areas where there is the structural potential for adjacent owl territories. The promotion of sufficient amounts of core habitat areas across multiple contiguous territories may be particularly important to avoid potential negative feedback loops wherein territories are abandoned due to the loss of nearby habitat. Fortunately, our proposed revision to the monitoring design enables systematic prioritization of survey effort toward potentially high-value areas.

Changing either or both of *i*) the resolution of a monitoring grid and *ii*) the environmental data used to determine grid cells' eligibility for sampling – as we are advocating researchers consider in the context of an adaptive monitoring paradigm – can have profound implications on the inferences that are appropriate to draw from a monitoring plan. For example, our proposed monitoring design features: a grid of 150 ha hexagonal cells overlaid on modeled core habitat, with non-contiguous, accessible cells, potentially selected based on their proximity to additional core habitat, to be surveyed for 5–6 weeks via one ARU. Thus, occupancy estimates are essentially incomparable between the first and second years of this study because the quantity of potentially occupied sites is changing, and the nature of the “site” itself is changing by virtue of changing where the survey grid is overlaid on the landscape. (These considerations are separate from the biologically grounded challenge of defining “occupancy” in a passive acoustic monitoring program (Wood and Peery, 2022), an issue engaged via the one- and two-night occupancy criteria.)

Critically, focusing survey effort more narrowly on high-value habitat should increase occupancy and detection rates, but will not automatically do so if the grid resolution changes. Increasing occupancy (ψ) and detection (p) will increase statistical power to observe a population change (Wood et al., 2019b; Banner et al., 2019), a critical attribute of a monitoring program designed for a declining population, particularly one with low baseline occupancy. In our case, increased statistical power to detect a trend would address both of the management community's monitoring goals to 1) obtain a regional understanding of the population and 2) locate individual owls. Better power to detect a trend is important from a regional population monitoring perspective, including the ideal scenario of delisting due to increasing occupancy and presumed recovery. Designing a monitoring program where baseline occupancy is higher would, by definition, increase the number of birds identified across the landscape, ultimately helping local forest managers to implement fuels reduction treatments while navigating increased regulatory requirements associated with an ESA-Endangered population. However, increased occupancy and detection are not guaranteed. In our case, the average *proportion* of core habitat in any given site is expected to increase dramatically under the new design, yet the maximum *area* of such habitat per cell may decrease because the grid cells are substantially smaller (150 ha instead of 400 ha). The positive effects of core habitat on both parameters (ψ and p) were most evident when the amount of habitat exceeded the size of the proposed 150 ha grid size (Fig. 2). Thus, stratifying grid cell selection based on extra-cell core habitat availability may be necessary to maximize the chances of increasing population parameter estimates in a controlled manner.

The changes described to the monitoring design have inferential costs in addition to their benefits. First, the change in baseline occupancy driven by fundamentally different sampling units between years would render the results incomparable, but it is likely that the long-term benefits outweigh the loss of a first year of data. Second, distributing sampling sites via a more CSO-centric design limits the ability of the monitoring program to provide reliable information about other species. Monitoring of species that co-occur with the CSO via a shared association with the forest structure characteristics identified in our SDM as drivers of nest/roost habitat (i.e., canopy height, canopy base height, and ladder fuel density) may still be viable, and may be valuable insofar as those species may be experiencing similar declines for similar reasons or could serve as indicators of CSO habitat (Bielski et al., 2024). However, the more generalized CSO monitoring design employed in the Sierra Nevada has yielded a wealth of information about the avian community more broadly (Brunk et al., 2025a; McGinn et al., 2025), even including species that are negatively associated with the owl (Brunk et al., 2025b). Indeed, our year one design already yielded some of the first known survey data on the Mexican Whip-poor-will (*Antrostomus arizonae*), one of the least known species in North America (Gustafson and Wood, 2025). A more CSO-focused design in Southern California may preclude, or at least impede, such studies in the future.

Despite the likely loss of inferential capabilities for other species and the potential complexities of multiscale habitat associations, the expected benefits of increasing baseline site occupancy and detection when monitoring an acutely at-risk population may be worthwhile. In the case of the Spotted Owl in Southern California, the revised monitoring design should be better suited to meet both management goals. The tantalizing possibility of resilient forests that harbor Spotted Owls represented by the biogeographically similar Sierra San Pedro Mártir (de León Girón et al., 2024; Stephens et al., 2024) may incentivize sustained yet adaptive monitoring in Southern California to facilitate nimble adaptive management. Unfortunately, our case, an at-risk and declining species facing multiple threats, including climate change and habitat loss, is unlikely to be unique. Our framework for employing PAM to gain preliminary insights into both the ecology of the species (e.g., the novel and unexpected finding of neighborhood effects on site occupancy) and on population parameters that are critical for effective survey design (baseline occupancy and detection estimates) may therefore be broadly informative. Knowledge of focal species spatial ecology is critical to setting an appropriate survey grid resolution, a monitoring design feature with wide-reaching implications. Our hierarchical conceptualization of focal species spatial and acoustic ecology (Fig. 3) may be valuable for other researchers attempting to monitor acoustically active species at broad scales. As a crisis discipline, conservation biology often requires action without complete knowledge (Soulé, 1985), yet making appropriate inferences from passive acoustic monitoring data requires information about focal species spatial and acoustic ecology as they relate to survey hardware, analysis software, and statistical modeling. Thus, rapidly adapting monitoring programs to suit the target species and its home ecosystem is necessary to effectively inform conservation action.

CRediT authorship contribution statement

Michaela L. Gustafson: Writing – review & editing, Writing – original draft, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kate McGinn:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Jeffrey A. Heys:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Sarah C. Sawyer:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Connor M. Wood:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

Acknowledgments

We thank Heather Galloway for assistance deploying ARUs; Kirsten Winter, Kim Boss, Ben Vizzachero, Karen Bagne, and Joe Jordan for logistical support, local expertise, and input on an early draft of this manuscript; Chris Pelkie, Stefan Kahl, and Jay Winiarski for data management and processing support. This work was funded by the USDA Forest Service Washington Office. The development of BirdNET is supported by the German Federal Ministry of Education and Research through the project "BirdNET+" (FKZ 01|S22072). The German Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer Protection contributes through the "DeepBirdDetect" project (FKZ 67KI31040E). In addition, the Deutsche Bundesstiftung Umwelt supports BirdNET through the project "RangerSound" (project 39263/01).

Data availability

Applicable data and code will be made available by request on the corresponding author's Zenodo page upon publication.

References

Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's information criterion. J. Wildl. Manag. 74, 1175–1178.

Banner, K.M., Irvine, K.M., Rodhouse, T.J., Donner, D., Litt, A.R., 2019. Statistical power of dynamic occupancy models to identify temporal change: informing the North American bat monitoring program. Ecol. Indic. 105, 166–176.

Barry, J.M., Jones, G.M., Zuckerberg, B., Tanner, R., Kryshak, N.F., Peery, M.Z., 2025. Rarity of spotted owls in Southern California. Southwest. Nat. 68, 247–256. Southwestern Association of Naturalists.

Benedetti, R., Piersimoni, F., Postiglione, P., 2017. Spatially balanced sampling: a review and a reappraisal. Int. Stat. Rev. 85, 439–454.

Berigan, W.J., Jones, G.M., Whitmore, S.A., Gutiérrez, R.J., Peery, M.Z., 2019. Cryptic wide-ranging movements lead to upwardly biased occupancy in a territorial species. J. Appl. Ecol. 56, 470–480.

Bielski, L., Cansler, C., McGinn, K., Peery, M.Z., Wood, C., 2024. Can the Hermit Warbler (*Setophaga occidentalis*) serve as an old-forest indicator species in the Sierra Nevada? J. Field Ornithol. 95, art4.

Bota, G., Manzano-Rubio, R., Fanlo, H., Franch, N., Brotons, L., Villero, D., Devisscher, S., Pavesi, A., Cavaletti, E., Pérez-Granados, C., 2024. Passive acoustic monitoring and automated detection of the American bullfrog. Biol. Invasions 26, 1269–1279.

Brunk, K.M., et al., 2025a. Bioregional-scale acoustic monitoring can support fire-prone forest restoration planning. Front. Ecol. Environ., e2843 https://doi.org/10.1002/fee.2843.

Brunk, K.M., Kramer, H.A., Peery, M.Z., Kahl, S., Wood, C.M., 2025b. Assessing spatial variability and efficacy of surrogate species at an ecosystem scale. Conserv. Biol., e70058 https://doi.org/10.1111/cobi.70058.

Burnham, K.A., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edition. Springer-Verlag New York, Inc.

Burnham, K.P., Anderson, D.R., 2010. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York, NY.

Chronister, L.M., Larkin, J.T., Rhinehart, T.A., King, D., Larkin, J.L., Kitzes, J., 2024. Evaluating the predictors of habitat use and successful reproduction in a model bird species using a large-scale automated acoustic array. Ecography 2025 (3), e06940.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46. Wiley Online Library.

Fiske, I., Chandler, R., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43 (10), 1–23.

Franklin, A.B., et al., 2004. Population dynamics of the California spotted owl (*Strix occidentalis occidentalis*): a meta-analysis. In: Ornithological (Monographs:1–54).

Ganey, J.L., Wan, H.Y., Cushman, S.A., Vojta, C.D., 2017. Conflicting perspectives on spotted owls, wildfire, and forest restoration. Fire Ecol. 13, 146–165.

Gustafson, M.L., Wood, C.M., 2025. A first report on Mexican whip-poor-will distribution and detectability across Southern California. Southwest. Nat. 69 (3), 1–4. https://doi.org/10.1894/0038-4909-69.3.7.

Hijmans, R.J., Phillips, S., Barbosa, M., Brunsdon, C., Rowlingson, B., 2024, November 23. Predicts: spatial prediction tools. Available from. https://cran.r-project.org/web/packages/predicts/index.html.

Hijmans, R.J., Barbosa, M., Bivand, R., Brown, A., Chirico, M., Cordano, E., Dyba, K., Pebesma, E., Rowlingson, B., Sumner, M.D., 2025. February 10. terra: Spatial Data Analysis. Available from. https://cran.r-project.org/web/packages/terra/index.html.

Hofstadter, D.F., et al., 2022. Arresting the spread of invasive species in continental systems. Front. Ecol. Environ. 20, 278–284.

Holderried, P., Duschmalé, H., Günther, D., Isenberg, L., Coppes, J., 2024. Essential steps for establishing a large-scale passive acoustic monitoring for an elusive forest bird species: the Eurasian woodcock (*Scolopax rusticola*). Ibis 167 (2), 543–561.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71.

Jones, G.M., Keane, J.J., Gutiérrez, R.J., Peery, M.Z., 2018. Declining old-forest species as a legacy of large trees lost. Divers. Distrib. 24, 341–351.

Jones, G.M., Keyser, A.R., Westerling, A.L., Baldwin, W.J., Keane, J.J., Sawyer, S.C., Clare, J.D., Gutiérrez, R., Peery, M.Z., 2021. Forest restoration limits megafires and supports species conservation under climate change. Front. Ecol. Environ. 20 (4), 210–216.

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

Kelly, K.G., et al., 2023. Estimating population size for California spotted owls and barred owls across the Sierra Nevada ecosystem with bioacoustics. Ecol. Indic. 154, 110851.

Kramer, H.A., et al., 2024. Using bioacoustics to enhance the efficiency of spotted owl surveys and facilitate forest restoration. J. Wildl. Manag. 88, e22533.

de León Girón, G., Gaonamelo, T., RuizCampos, G., Eyes, S.A., Wood, C.M., 2024. Vocalization recordings of the spotted owl (*Strix occidentalis*) in the Sierra San Pedro Mártir, Baja California, Mexico. West. N. Am. Nat. 84.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83, 2248–2255.

Manly, B.F.J., 2004. Two-phase adaptive stratified sampling. In: Thompson, W.L. (Ed.), Sampling Rare or Elusive Species: Concepts, Designs, and Techniques for Estimating Population Parameters, 2nd ed. Island Press, Washington, pp. 123–133.

McGinn, K., Zulla, C., Wright, M., Wilkinson, Z., Dotters, B., Roberts, K., Keane, J., Peery, M.Z., Jones, G.M., 2024. Energetics explain predator occurrence and movement in pyrodiverse landscapes. Landsc. Ecol. 39, 182.

McGinn, K., et al., 2025. Frequent, heterogenous fire supports a forest owl assemblage. Ecol. Appl. 35, e3080.

McGinn, K.A., Atuo, F.A., Jones, G.M., Hobart, B.K., Tempel, D.J., Whitmore, S.A., Berigan, W.J., Gutiérrez, R.J., Peery, M.Z., 2022. Implications of non-ideal occupancy for the measurement of territory quality. Glob. Ecol. Conserv. 35, e02097.

McGinn, K.A., Peery, M.Z., Zulla, C.J., Berigan, W.J., Wilkinson, Z.A., Barry, J.M., Keane, J.J., Zuckerberg, B., 2023. A climate-vulnerable species uses cooler forest microclimates during heat waves. Biol. Conserv. 283, 110132.

Popescu, V.D., De Valpine, P., Tempel, D., Peery, M.Z., 2012. Estimating population impacts via dynamic occupancy analysis of before–after control–impact studies. Ecol. Appl. 22, 1389–1404.

R Core Development Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available from. http://www.R-project.org/.

Reid, D.S., et al., 2021. Noisy neighbors and reticent residents: distinguishing resident from non-resident individuals to improve passive acoustic monitoring. Glob. Ecol. Conserv. 28, e01710.

Reid, D.S., et al., 2022. Breeding status shapes territoriality and vocalization patterns in spotted owls. J. Avian Biol. 2022, e02952.

Salo Sciences, 2020. California Forest Observatory: A Statewide Tree-level Forest Monitoring System. San Francisco, CA, USA. Available from. https://forestobservatory.com.

Smart, A., Southwell, D., Geary, W., Buchan, A., Wintle, B., 2022. Combining financial costs and statistical power to optimize monitoring to detect recoveries of species after megafire. Glob. Ecol. Biogeogr. 31, 2147–2157.

Soulé, M.E., 1985. What is conservation biology? BioScience 35, 727–734.

Southwell, D.M., Einoder, L.D., Lahoz-Monfort, J.J., Fisher, A., Gillespie, G.R., Wintle, B. A., 2019. Spatially explicit power analysis for detecting occupancy trends for multiple species. Ecol. Appl. 29, e01950.

Stephens, S.L., Fossum, C., Collins, B.M., Huerta, H.R., 2024. Early impacts of fire suppression in Jeffrey pine – mixed conifer forests in the Sierra San Pedro Martir, Mexico. For. Ecol. Manag. 564, 122003.

Stojanovic, D., Young, C.m., Stuart, A., Vine, S., Owens, G., Bussolini, L., Hawkins, B., Alves, F., 2024. Designing fit-for-purpose monitoring – a case study of a cryptic songbird. Anim. Conserv. 28 (3), 424–435.

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

Tempel, D.J., 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. Condor 118, 747–765.

Tempel, D.J., Kramer, H.A., Jones, G.M., Gutiérrez, R.J., Sawyer, S.C., Koltunov, A., Slaton, M., Tanner, R., Hobart, B.K., Peery, M.Z., 2022. Population decline in California spotted owls near their southern range boundary. J. Wildl. Manag. 86, e22168.

U.S. Fish and Wildlife Service, 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. Available from. https://www.federalregister.gov/documents/2023/02/23/2023-03526/endangered-and-threatened-wildlife-and-plants-california-spotted-owl-endangered-status-for-the (accessed May 15, 2023).

USGS Gap Analysis Program, 2013. California Spotted Owl Distribution Model [Str_occ_SPOWo]. Available from. http://gapanalysis.usgs.gov/species/data/download/.

Wood, C.M., 2022. Optimizing landscape-scale monitoring programmes to detect the effects of megafires. Divers. Distrib. 28, 479–492.

Wood, C.M., Peery, M.Z., 2022. What does ‘occupancy’ mean in passive acoustic surveys? Ibis 164, 1295–1300.

Wood, C.M., Gutiérrez, R.J., Keane, J.J., Peery, M.Z., 2019a. Early detection of rapid barred owl population growth within the range of the California spotted owl advises the precautionary principle. Condor 122, 1–10.

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

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

Wood, C.M., Klinck, H., Gustafson, M., Keane, J.J., Sawyer, S.C., Gutiérrez, R.J., Peery, M.Z., 2020. Using the ecological significance of animal vocalizations to improve inference in acoustic monitoring programs. Conserv. Biol. 35, 336–345.

Wood, C.M., Günther, F., Rex, A., Hofstadter, D.F., Reers, H., Kahl, S., Peery, M.Z., Klinck, H., 2024. Real-time acoustic monitoring facilitates the proactive management of biological invasions. Biol. Invasions 12. https://doi.org/10.1007/s10530-024-03426-y.