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Estimating population size for California spotted owls and barred owls across the Sierra Nevada ecosystem with bioacoustics

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ABSTRACT

Monitoring population size at ecosystem scales is difficult for most species of conservation concern. While assessing site occupancy at broad scales has proven feasible, rigorous tracking of changes in population size over time has not – even though it can provide a stronger basis for assessing population status and conservation-decision making. Therefore, we demonstrate how relatively low-intensity, ecosystem-scale passive acoustic monitoring (PAM) can be linked to local-density monitoring to estimate the population size of native California spotted owls (*Strix occidentalis occidentalis*) and invasive barred owls (*S. varia*) across the western Sierra Nevada, California. Based on a PAM sampling grid with 400 ha cells (the approximate home range size of these species), we estimated site occupancy to be between 0.42 (SE = 0.02) and 0.30 (SE = 0.02) for California spotted owls using relatively liberal and strict criteria, respectively, for considering a cell occupied. PAM-based site occupancy estimates within local-scale density monitoring study areas (range = 0.41–0.78 and 0.28–0.76 for liberal and strict criteria, respectively) were strongly and positively correlated with local density (range = 0.08–0.31 owl/km^2) for this species. In contrast, ecosystem-wide site occupancy of barred owls was very low based on PAM (0.034, SE < 0.01), as were densities within local monitoring studies (range = 0–0.005 owls/km^2). By scaling ecosystem-wide site occupancy estimates to densities estimated with local monitoring studies, we estimated that, depending on occupancy criteria, 2,218 (SE = 278) or 2,328 (SE = 489) California spotted owls occurred in the Sierra Nevada ecosystem in 2021. Thus, while California spotted owls are a rare subspecies, they were well-distributed across the Sierra Nevada. Because there were so few barred owl detections, we could not estimate ecosystem-scale abundance, which reflects the success of prior experimental removals in the region. In conclusion, our study provides a generalizable framework for estimating population size for territorial species with PAM at ecosystem scales when local-scale estimates of density are available. Thus, we demonstrate that this approach can provide novel and valuable insights into monitoring populations to aid species conservation.

1. Introduction

Population monitoring is integral to biodiversity conservation, but monitoring cryptic or rare species over broad spatial scales and long time periods is challenging. Passive acoustic monitoring (PAM) is becoming an increasingly common approach because it can enable broader and more continuous coverage than conventional, in-person surveys (Darras et al., 2018; Shonfield and Bayne, 2017; Sugai et al., 2019). PAM involves deploying autonomous recording units (ARUs) to record acoustically active species and extracting target signals from the audio data. Animal sounds identified in PAM data can then be readily adapted to detection/non-detection data that can, in turn, inform

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occupancy modeling. The large sample sizes enabled by large-scale PAM projects can yield high statistical power to detect even small changes in occupancy over space and time (Wood et al., 2019b). As a result, there is great potential for PAM to support population trend assessments at greater spatial scales than have previously been possible. Nevertheless, PAM-based estimates of occupancy may not reflect population metrics that are of interest to conservation if ARU sampling is not guided by knowledge of target species' use of any particular area (Wood and Peery, 2022).

For many species, human surveyors either establish or visit what they believe to be biologically meaningful locations, such as historically active breeding areas, to estimate "territory occupancy" as the proportion of potentially occupied territories. For territorial species, territory occupancy can scale directly to population abundance (Conner et al., 2016; Tempel and Gutiérrez, 2013). In contrast, PAM designs often involve deploying ARUs in a randomized subset of grid cells within a larger, grid-based sampling frame without knowing the actual location of resident or territorial individuals. Under this design, "site occupancy" represents the presence of an acoustically active individual of the target species at a survey site (i.e., grid cell). Yet not all observed individuals are necessarily residents of surveyed sites, causing "ecological false positives" which can lead to estimates of site occupancy that exceed territory occupancy rates and are subsequently less closely linked to population size (Berigan et al., 2019; Wood and Peery, 2022). Therefore, ecological false positives can obscure environmental and anthropogenic effects on populations because individuals may visit sites that no not support residents (Berigan et al., 2019).

At least two techniques can be used to mitigate the effects of ecological false positives on inferences about population processes. First, survey sites (e.g., grid cells) can be separated by distances such that it is unlikely territorial individuals will be detected in more than one grid cell. However, this approach reduces sample sizes and thus statistical power to detect changes in occupancy – as well as site-level location information that could be important for management. Second, metrics of acoustic activity (e.g., the count, timing, and types of vocalizations detected as well as identity of vocalizing individuals) can be used to filter out observations less likely to be indicative of residency (Reid et al., 2021) such that only sites at which resident individuals are present are treated as occupied. Criteria can be developed to determine which biological indicators truly constitute site occupancy (i.e., criteria applied to sites by season level) and/or individual detections (i.e., criteria applied to site by sampling period level). However, acoustic-based metrics are not a perfect way to eliminate ecological false positives because resident and non-residents can produce similar levels of vocal activity (Reid et al., 2021; Watson et al., 2023). Thus, there is a need to bridge spatially limited survey approaches that yield estimates of abundance or density and spatially extensive PAM approaches that yield more abstract estimates of site occupancy (Weldy et al., 2023).

We present an approach for combining ecosystem-scale PAM data (tens of thousands of km^2) with local-scale monitoring data (tens to hundreds of km^2) to strengthen PAM-based approaches for monitoring populations and estimate abundance. Under this approach, estimates of population density are obtained from local-scale monitoring programs; then, in conjunction with ecosystem-scale PAM monitoring data, direct relationships are developed between population density and site occupancy in areas of overlapping coverage to derive ecosystem-scale estimates of population size. Importantly, concerns posed by ecological false positives (Berigan et al., 2019; Wood and Peery, 2022) will be reduced if the relationship between site occupancy and density are consistent across space and time. Accordingly, we demonstrate how combining PAM and local-scale territory occupancy data can be used to estimate population size for territorial species at ecosystem scales in a manner that circumvents some of the aforementioned challenges posed by ecological false positives.

Both local-scale territory occupancy data and ecosystem-scale PAM data exist for the Sierra Nevada population of the California spotted owl (*Strix occidentalis occidentalis*), an old forest-associated species. Whereas this subspecies of spotted owl has been proposed as threatened species by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service, 2023), there has never been an estimate of their population size in this large mountain range. Therefore, such an estimation is particularly valuable because the Sierra Nevada constitutes the primary population of this subspecies given that the central coastal and southern California population is highly fragmented and composed primarily of small, declining subpopulations (Barry et al., Under Review; Tempel et al., 2022) that may not be viable. We also estimate PAM-based site occupancy for barred owls (*S. varia*) across the Sierra Nevada - a direct competitor that poses an existential threat to spotted owls (Wiens et al., 2021) – two years after a lethal removal study in the Sierra Nevada (Hofstadter et al., 2022). Although estimates of Sierra Nevada-wide spotted owl occupancy and population size were previously considered unattainable (Peery et al., 2017), we demonstrate that combining local-scale population data with ecosystem-wide PAM data facilitates the estimation of total population size and site occupancy. Thus, our approach constitutes a strategy not only suitable for spotted owl conservation in this ecosystem, but also many other species for which both PAM and local-scale population data are available.

2. Methods

2.1. Study species

The spotted owl is a territorial species associated with mature and old-growth forest that faces several threats in the Sierra Nevada, which is the core range of the California subspecies. First, increasingly large, severe fires are causing localized losses of forest cover and driving potentially decadal population declines in those areas (Jones et al., 2021; Jones et al., 2016). Second, historical harvesting of large trees has caused population declines in some (Conner et al., 2016, 2013; Jones et al., 2018; Tempel et al., 2016) but not all areas (Hobart et al., 2019; Roberts et al., 2017). Third, the barred owl, a competitively dominant invasive species, which is in the process of driving northern spotted owls (*S. o. caurina*) extinct (Franklin et al., 2021; Wiens et al., 2021), has invaded the range of the California spotted owl and recently entered a rapid growth phase in the northern Sierra Nevada (Wood et al., 2019a). The invasion motivated a lethal removal experiment to assess whether barred owl occupancy could be reduced across the Sierra Nevada (Hofstadter et al., 2022). Fourth, although population-level effects are unknown, the California spotted owl is widely exposed to environmental toxicity via anticoagulant rodenticides (Hofstadter et al., 2021). Fifth, rising temperatures driven by climate change will subject California spotted owls to increasing thermal stress (Weathers et al., 2001), which has potential implications for adult survival and reproduction (McGinn et al., in Review).

The California spotted owl faces an array of threats and may soon receive formal protection under the Endangered Species Act. Yet the relative sizes of the native spotted owl and the invasive barred owl populations in the Sierra Nevada are unknown. Despite decades of research, the broad geographic range and secretive nocturnal habits of spotted owls have precluded any spatially comprehensive population assessment. Thus, estimating population size of these species will aid future conservation efforts.

2.2. Study areas and survey design

The Sierra Nevada is the dominant physiographic feature of eastern California, nearly spanning the length of the state. Within this vast ecosystem, we conducted ecosystem-scale PAM surveys and density estimation within four local-scale monitoring studies. Our PAM program spanned the west-slope Sierran mixed-conifer forest, including coverage in all seven National Forests, three of the four National Parks, and some private lands (Fig. 1) because the eastern slope of the Sierra Nevada had

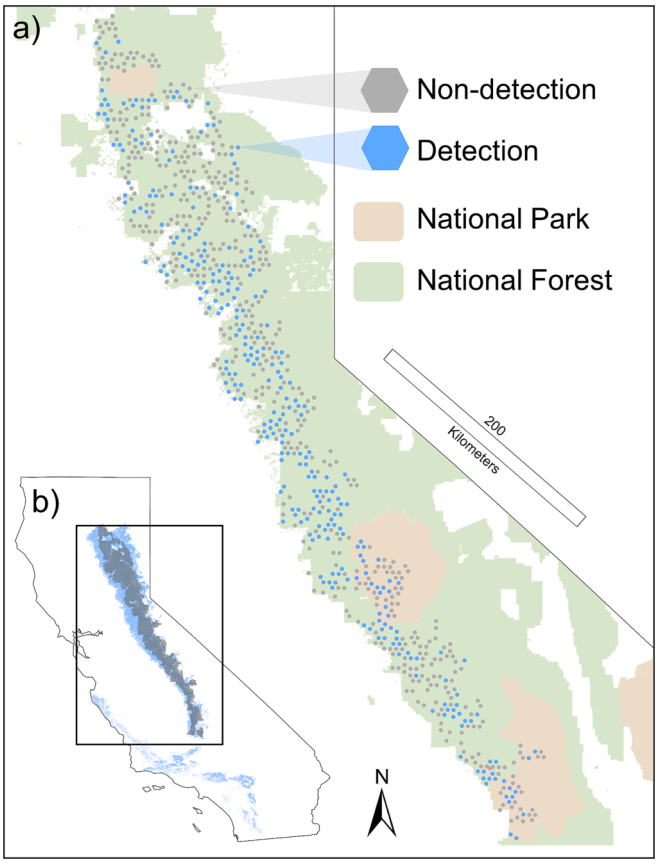

Fig. 1. PAM survey cells and California spotted owl detections. a) PAM surveys were conducted in 851 400-ha hexagonal cells distributed across seven National Forests (green) and three National Parks (brown). California spotted owls were detected (blue) across the Sierra Nevada. b) PAM surveys (grey) occurred across most of the California spotted owls presumed suitable habitat in the Sierra Nevada (light blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

very few owls (Verner et al., 1992). We subdivided this western slope area into 6,236 4 km^2 hexagonal grid cells, which are approximately the size of a spotted owl territory in this region. Our total sampling area of 24,494 km^2 (320–2,890 m asl) covered 57% of the California spotted owl's habitat in the Sierra Nevada ecosystem. Candidate cells were excluded if they: intersected highways, were > 50% water, lacked road access in National Forests, or lacked road or trail access (<4 km from a road or trail) in National Parks. In practice, this also excluded particularly steep and wilderness areas, though they ultimately comprised a very small proportion of the candidate grid cells (<5%). In 2021, we surveyed 851 non-adjacent grid cells (13.6% of the total area) to reduce the possibility of double-counting owl territories (Wood et al., 2019b).

We deployed one to three, but generally two, ARUs (SwiftOne recorder, K. Lisa Yang Center for Conservation Bioacoustics) in each grid cell at acoustically advantageous locations such as ridgetops, with a minimum spacing of 500 m. If a cell overlapped an accessible spotted owl Protected Activity Center (121 ha areas of high-quality habitat around historic spotted owl nest and roost sites) we attempted to deploy at least one ARU inside that Protective Activity Center polygon. Otherwise, deployments were made without specific knowledge of owl occupancy. ARUs had a single omni-directional microphone with −25 dB sensitivity; we programmed them to record 20:00 – 06:00 PDT at a sample range of 32 kHz, 16-bit resolution, and gain of + 33 dB. Deployments began in early-May and lasted through early July, with any given grid cell surveyed for approximately five weeks continuously.

The four local-scale spotted owl monitoring study areas spanned the length of the Sierra Nevada (Fig. 2). From north to south, the Lassen (1,254 km^2; 1,200–2,100 m asl), Eldorado (818 km^2; 300–2,500 m asl), and Sierra (693 km^2; 300–2,900 m asl), Sequoia–Kings Canyon (343 km^2; 425–3,050 m asl) study areas consisted predominantly of land managed by the U.S. Forest Service, with some private lands largely managed for commercial forest products whereas the Sequoia–Kings Canyon study area occurred entirely within two national parks of the same name. All active, historical, and potential spotted owl territories in these study areas have been monitored annually from as early as 1986 to 2021 (Conner et al., 2013; Tempel et al., 2016) using standard call-based spotted owl survey methods (Forsman, 1983). Call-based spotted owl surveys, in which human surveyors imitate or broadcast spotted owl calls, can yield high seasonal detection probabilities for territories (>0.95) (Wood et al., 2018) such that local spotted owl populations are effectively censused. Thus, we refer to them as "density monitoring study areas" because abundance within a fixed area was estimated annually over time.

Fig. 1.

2.3. Identifying target vocalizations in passively recorded audio

To identify spotted owl and barred owl vocalizations in the passively recorded audio, we used the BirdNET algorithm, a deep convolutional neural network originally designed to identify nearly 1,000 species of North America and European birds (Kahl et al., 2021). We developed a customized version of BirdNET that was overfit to the species and audio characteristics of our PAM program; tests against independent validation data indicated that it could readily identify target vocalizations for two species: the spotted owl's "four-note", "contact call", "crow bark", "monkey hoot", and juvenile begging, and the barred owl's "eight-note" (or "who cooks for you") and "hoo-aw" calls. BirdNET's core output is a unitless numeric prediction score, ranging from 0 to 1, for each call type in each 3-second interval of audio data. BirdNET was trained to predict each owl call type individually as well as spotted and barred owl vocalizations generally. Any vocalization above a final species-specific threshold (reported in the results section) was flagged and manually validated. BirdNET's prediction score is not a probability but rather an indication of confidence in the identification with larger numbers indicating greater confidence.

We manually confirmed all putative BirdNET-derived owl observations above species-specific prediction score thresholds for two reasons. First, false positive detections (inferring presence when no individuals occur in the survey area) can inflate occupancy estimates and obscure the effects of environmental factors on occupancy (Berigan et al., 2019). Such false positives can occur because sounds can be misclassified as a spotted owl or barred owl, including calls broadcasted as part of owl surveys. Second, accurate presence data are important to inform forest management activities that could affect spotted owl habitat quality and to locate barred owls for lethal removal.

When selecting specific prediction thresholds above which to manually validate predictions, we considered the trade-off between the effort associated with manual review (to eliminate false positives) and the probability of not detecting territorial owls present within survey cells. Lower (more liberal) prediction thresholds could increase the number of owl calls that are correctly identified; in other words, recall, the proportion of target signals that are recorded and correctly identified as such would likely increase. However, lowering the prediction threshold would also inevitably lead to larger, and potentially intractable, numbers of predictions requiring manual review; in other words, precision, the proportion of predictions that were correct, would decrease. Conversely, higher (more stringent) prediction thresholds would reduce the number of predictions requiring review but could reduce the probability of detecting territorial owls (and thus result in lower detection probabilities estimated as part of the occupancy analyses described below). Thus, in the case of higher prediction thresholds, recall would decrease but precision would increase. Therefore, to

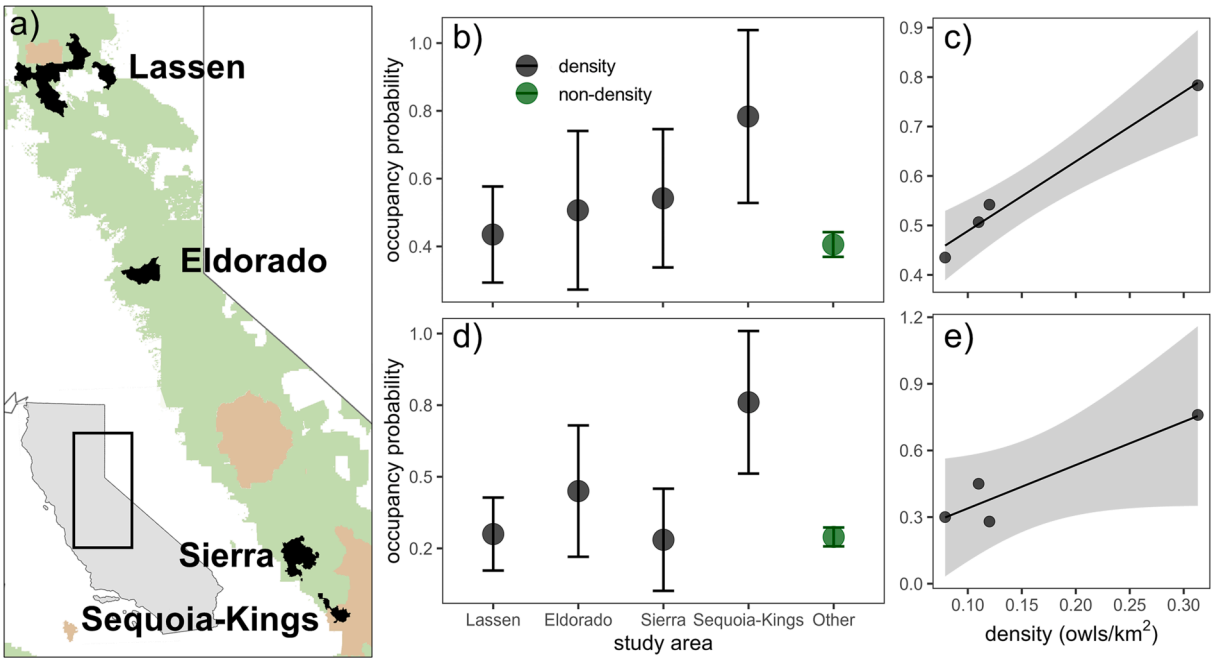

Fig. 2. Acoustic-based site occupancy probabilities for the four local-scale density monitoring study areas (gray points) and all grid cells (n = 744) outside those areas (green points). Green indicates National Forests and brown indicates National Parks. The Lassen, Eldorado, Sierra, and Sequoia-Kings density monitoring study areas a) cover a nearly comprehensive latitudinal gradient for the Sierra Nevada. We report b) liberal estimates of occupancy and c) their relationship with density (owls/km^2) in black. We also report liberal and strict estimates of occupancy for sites outside density monitoring study areas, or the "non-density" study area, in dark green. Finally, we report d) strict estimates for occupancy and e) their relationship with density. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

evaluate these tradeoffs and select prediction thresholds for spotted owls, we leveraged information from PAM grid cells known to contain residents of either species to calculate two key statistics across a range of BirdNET prediction scores (0.969, 0.979, 0.989, and 0.999 for spotted owls, and 0.960, 0.970, 0.980, and 0.990 for barred owls). We calculated (*i*) the number of BirdNET predictions requiring manual review, and (*ii*) the proportion of those cells containing a territorial owl that had a confirmed vocalization at or above that threshold. For each species, we selected prediction score thresholds that yielded high probabilities of observing territorial individuals while only requiring that a tractable number of predictions be manually reviewed. For spotted owls, we drew on data from 17 PAM-surveyed grid cells in the Eldorado density monitoring area that contained nesting or roosting spotted owls in 2021. For barred owls, the number of PAM cells with territorial barred owls for this test was small given recent barred owl removals in the region (Hofstadter et al., 2022); we used information from two grid cells known to contain territorial barred owls.

When conducting our manual review of predictions above the selected thresholds, we removed false positives from our dataset caused by spotted owl and barred owl surveys with two methods. First, we manually reviewed the audio data associated with all potential observations and eliminated any potential observations that were not clearly a spotted owl. This included recognized recorded or mimicked spotted owl vocalizations by surveyors, as well as other acoustic indications that linked a given potential observation to a surveyor (e.g., human voices and repetitive calling sequences indicative of playback surveys). Second, we obtained spatial data from all known organizations conducting spotted owl surveys in the Sierra Nevada in 2021 and eliminated any potential observations that occurred within 1.5 km of a human surveyor on the same night. While this second precaution may have eliminated some true observations of spotted owls, we prioritized eliminating false positives over false negatives given the ability to model detection probability as part of occupancy modeling.

2.4. Estimating owl site occupancy

We estimated site occupancy rates for spotted owls and barred owls using single-season occupancy models (MacKenzie et al., 2002) applied to detection histories derived from manually validated observations generated by BirdNET. Entire grid cells were considered survey sites such that either or both ARUs therein could contribute owl observations to its occupancy status. For both species, we attempted to conduct two separate sets of occupancy analyses for each species representing two acoustic-based detection criteria. The acoustic-based detection criteria were the one-night (a single confirmed owl observation constituted "detected"; i.e., unfiltered) and two-night ("detected" required confirmed owl observations on two or more nights) thresholds for determining the occupancy status of any given site (i.e., grid cell). The one-night threshold represents the liberal, or more relaxed definition of occupancy, while the two-night threshold represents a stricter definition of occupancy. For both analyses, our season entailed eight one-week-long secondary sampling periods starting 10 May and ending 12 July.

With encounter histories generated based on both acoustic-based detection criteria, we constructed several competing full-Sierra Nevada occupancy models in which both detection and occupancy probabilities varied in space and time -with separate model sets evaluated for each of the two criteria. We evaluated model support using Akaike's Information Criterion (AIC) at each stage of analysis and considered models within 2.0 AIC units of the top-ranked model to be competitive (Burnham and Anderson, 2002). First, while holding occupancy constant, we tested for variation in detection probability. We considered survey effort and time separately, and then combined the most-supported variables from each approach into an additive model, which was then compared to the original individual models. In terms of survey effort, detection could be constant or vary as a function of: (*i*) the number of ARUs deployed in a cell (1 vs $\geq$ 2), or (*ii*) the cumulative number of hours ARUs were deployed. In terms of time, detection could also vary: (*i*) among individual secondary sampling periods (p_t), (*ii*)

linearly over time across secondary sampling periods (p_T), or (*iii*) via a non-linear, natural-log trend (p_{lnT}). Once the most supported detection model structure was determined, we evaluated support for models where occupancy was constant, varied by elevation (linearly, log-linearly, and quadratic), and varied by latitude (linearly, log-linearly, and quadratic). If support existed for multiple effects (i.e., ΔAIC of both models < 2.0), these terms were combined and evaluated as additive models.

2.5. Estimating owl abundance

We estimated the abundance of spotted owls and barred owls in the Sierra Nevada ecosystem by (*i*) relating PAM-based estimates of site occupancy (ψ_s) within the four local-scale density monitoring study areas to the density of territorial individuals (D_S) in these areas; and then (*ii*) using these relationships to convert Sierra Nevada-wide PAM-based estimates of site occupancy (ψ_{Sierra}) to a density estimate that applied to the entire ecosystem (D_{Sierra}). We estimated ψ_s based on a single season occupancy model where occupancy was allowed to vary among local-scale study areas (Lassen, Eldorado, Sierra, Sequoia-Kings, and all other grid cells outside of those study areas) – using the best detection model structure from the occupancy described above. We fit a study area effect occupancy model using both one- and two-night detection criteria. We estimated D_S by dividing the number of territorial individuals (N_S) found with our call-based surveys within each of the four density monitoring study areas in 2021 by their respective areas under the assumption that these local populations were effectively censused given the high detection probabilities associated with these surveys (Wood et al. 2018). Note that the number of spotted owls and barred owls in the Lassen study areas was enumerated using 2020 because the > 389 thousand ha Dixie Fire in late summer 2021 required terminating surveys one month earlier than in other years. However, spotted owl populations in the Sierra Nevada typically exhibit little interannual variation (typically < 2%/year (Conner et al., 2013; Tempel et al., 2016)), suggesting that using 2020 abundance data for one local population had little effect on the ecosystem-scale estimate of abundance in 2021. We then calculated four local-scale study area-specific density:occupancy ratios (R_s): $R_s = \frac{D_s}{\psi_s}$ and an area-weighted mean density:occupancy ratio ($\overline{R}$).

Site occupancy across the Sierra Nevada (ψ_{Sierra}) was calculated from our null occupancy model. We assumed that $\overline{R}$ was representative of the (unmeasured) full Sierra Nevada ratio (R_{Sierra}) given the study areas spanned the nearly the entire latitudinal and elevational gradient in the region and incorporated all major land management regimes (national forests, national parks, and private lands). Under this assumption, we solved for Sierra Nevada-wide density as: $D_{Sierra} = \psi_{Sierra} * R_{Sierra}$. We then converted D_{Sierra} to an estimate of the abundance of spotted owls in the Sierra Nevada as follows: $N_{Sierra} = D_{Sierra} * A$, where A was the area (24,856 km^2) encompassed by our entire survey grid in the Sierra Nevada. We applied the density estimate to the entire grid, not just the sampled grid cells because local-scale density was estimated across both sampled and unsampled grid cells in the subset analyses. Standard errors for N_{Sierra} were estimated using Monte Carlo simulations where we randomly generated 1000 values of site occupancy for each local study area using normal distributions parameterized with our point estimates of occupancy and their standard errors – and then computing 1000 values of abundance using the aforementioned calculations.

3. Results

3.1. Identifying target vocalizations in passively recorded audio

We deployed 1,651 ARUs in 851 surveyed grid cells, with an average of 1.94 ARUs per cell in 2021. Deployments spanned almost all suitable California spotted owl habitat on the west slope of the Sierra Nevada ecosystem. The earliest ARU deployment was 3-May, and the final ARU retrieval was 21-July. Thus, we recorded 557,000 h (63.5 years) of audio data, with a mean of 335 h per ARU and 652 h per cell.

The number of BirdNET predictions for either species increased exponentially as the score threshold decreased (Supplemental Table 1). We had substantial but finite capacity to manually review tens of thousands of predictions, and we utilized all expert staff time we allocated for that task based on thresholds of 0.989 for spotted owls and 0.970 for barred owls, which yielded 22,828 and 7,254 predictions, respectively. Our review yielded 18,568 confirmed spotted owl observations and 903 confirmed barred owl observations. After removing 1,807 spotted owl and 136 barred owl predictions that occurred within 1.5 km of call-based owl surveys on the same night, the spotted owl and barred owl precision were 0.813 and 0.124, respectively, at our chosen thresholds.

We then measured recall at the seasonal level (as opposed to the call level) because we had no need to identify all vocalizations at any given location, but we did want to minimize or eliminate the number of locations at which an owl was recorded but never identified by BirdNET at or above our chosen score threshold. To do so, we calculated the proportion of cells which would be considered occupied at different BirdNET score thresholds and occupancy criteria (liberal one-night or conservative two-night criteria) for the 17 and two PAM grid cells known to contain occupied spotted owls and barred owls, respectively.. We found that a spotted owl territory would be observed 98% and 92% of the time at the one night and two night criteria at our chosen BirdNET score (0.989); barred owl territories (albeit $n = 2$) were always observed across our score thresholds (Supplemental Table 1). These estimates of recall are confounded with other factors, notably bird vocal behavior, that influence detection probability outside of detector recall, but collectively they indicated that we did not fail to observe the target species over the course of the season due to deficiencies in BirdNET at the score thresholds we used. Users of the BirdNET global model, rather than our custom model, are likely to achieve slightly lower performance at the same thresholds. Thus, while call-by-call recall may have been relatively low, our seasonal-level recall, or our ability to observe an animal acoustically during the entire sampling period, was sufficiently high (Wood et al., 2019b).

3.2. Ecosystem-scale estimates of spotted owl and barred owl occupancy

The detection model $p_{t+ARUhours}$ received 81% of the AIC weight using the liberal, one-night criterion and p_t received 100% of the AIC weight for the strict, two-night criterion (Supplemental Table 2). Under either criterion, detection varied among secondary sampling periods (p_t); under the one-night criterion, detection also increased with the number of recording hours in each cell (Table 1). Therefore, these detection models were carried forward to the occupancy modeling phase. The most supported occupancy model was $\psi_{lat+lat2+elev+elev2}$ and received 100% of the AIC weight for both criterion (Supplemental Table 2). Under either criterion, the probability of site occupancy varied nonlinearly with elevation and latitude, such that occupancy probability peaked at mid-elevations and mid-latitudes (Table 1). Based on the null model using the liberal, one-night occupancy criterion, detection probability for spotted owls was 0.50 (SE = 0.01) and site occupancy for the entire Sierra Nevada ecosystem (ψ_{Sierra}) was 0.42 (SE = 0.017). Based on the null model using the strict, two-night occupancy criterion, detection probability was 0.62 (SE = 0.01) and ψ_{Sierra} was 0.30 (SE = 0.02).

Naïve barred owl occupancy with the liberal criterion was just 0.011 (9 of the 851 cells had detections), so we did not apply the strict criterion. Additionally, detection probability could not vary between secondary sampling periods or between the number of ARUs in each cell because there were so few detections and insufficient variation in these factors among cells with detections. The most supported detection model, $p_{T+ARUhours}$, received 47% of the AIC weight and the second-ranked model, $p_{ln(T)+ARUhours}$, received 32% of the AIC weight

Table 1
Site occupancy estimates for spotted owls. For each occupancy criterion (site occupancy defined as a confirmed on at least one night or at least two nights), one model had an AIC model weight of 1.00; β-estimates of model covariates for detection (p) and occupancy (ψ) and their corresponding Upper (UCL) and lower (LCL) confidence intervals are reported (95% CI). All covariates were standardized prior to fitting models, and all models included intercepts, but values are not reported in the table.

Species	Occupancy criterion	Parameter	Covariate	β	LCL	UCL
Spotted Owl	Liberal	p	t[a]	0.76	0.13	1.39
	(one night)	p	ARU_{hours}[b]	0.00	0.00	0.00
		Ψ	lat	15.71	7.11	24.31
		Ψ	lat^2	−16.17	−24.77	−7.57
		Ψ	elev	3.00	1.96	4.04
		Ψ	$elev^2$	−3.33	−4.43	−2.23
	Strict	p	t[a]	−0.37	−1.06	0.32
	(two night)	Ψ	lat	14.36	9.13	19.59
		Ψ	lat^2	−14.80	−23.95	−5.65
		Ψ	elev	2.68	1.56	3.80
		Ψ	$elev^2$	−3.03	−4.19	−1.87
Barred Owl	Liberal	p	T[c]	−7.25	−11.80	−2.70
	(one night)	p	ARU_{hours}	0.09	0.031	0.15
		Ψ	lat	−50.04	−103.65	3.57
		Ψ	lat^2	51.37	−2.94	105.68

[a] Categorical time effect. Median β-estimate for secondary sample period shown.
[b] Values rounded. 95% CI = 0.001–0.003.
[c] Continuous time effect.

(Supplemental Table 3). The top-ranked model was carried to the next modeling stage in which $\psi_{lat+lat2}$ received 52% of the AIC weight (Supplemental Table 3). Detection probability increased with the number of recording hours in each cell and decreased throughout the season, though we could not determine whether this decrease was linear or logarithmic (Table 1). The probability of site occupancy varied non-linearly with latitude, such that occupancy probability peaked at higher and lower latitudes (Table 1). Of the nine cells in which barred owls were detected, eight were in the northern Sierra Nevada (Lassen, Plumas, and Eldorado National Forests) and one was in the southern Sierra Nevada, which created a peak in occupancy at low latitudes. Based on the null model, Sierra-wide detection probability for barred owls was 0.23 (SE = 0.08) and ψ_{Sierra} was 0.03 (SE = 0.02).

3.3. Spotted and barred owl abundance across the Sierra Nevada

Spotted owl site occupancy varied among density monitoring study areas as models with a study area effect outperformed liberal and strict null ecosystem-scale models (Supplemental Table 2; ΔAIC = −0.57 and −4.34, respectively). Based on these top models, study area-specific occupancy estimates ranged from ψ_s = 0.435 to 0.784 for the one-night criteria and ψ_s = 0.283 to 0.760 for the two-night criteria (Table 2, Fig. 2). Occupancy was greatest for the Sequoia-Kings study area and was generally higher within study areas than outside of the study areas compared to nearby surrounding areas (Table 2).

We detected 39 to 99 territorial individuals in the four density study areas (i.e.,N_S) with local densities D_S ranging from 0.079 to 0.313 owl/km^2 (Table 2). Site occupancy was strongly correlated with density based on both the liberal (r = 0.99) and strict thresholds (r = 0.94) – although this relationship was driven by the Sequoia–Kings Canyon study area (Fig. 2). The area-weighted mean density:occupancy ratio ($\overline{R}$) was 0.213 and 0.308 for the one- and two-night criteria, respectively. Based on these local-scale site occupancy and density estimates, we estimated that 2,218 (SE = 278) and 2,328 (SE = 489) territorial spotted owls occurred in the Sierra Nevada based on the liberal and strict thresholds, respectively.

We could not estimate abundance for barred owls because very few individuals occurred in our > 24,800 km^2 PAM study area. In addition to ecosystem-level PAM-based occupancy being extremely low (ψ_{Sierra} = 0.03; see above), there was only one acoustic detection within the boundaries of the density monitoring study areas, which precluded comparisons of density and occupancy estimates across those areas. Further, no barred owls were detected by call-based spotted owl surveys in three of the four density monitoring study areas; only six individuals across five locations were detected in the Lassen study area, the northernmost such study and presumed forefront of the barred owl range expansion from the Cascade ecoregion (Wood et al., 2019a). None of those six individuals occurred in cells surveyed using PAM. Thus, barred owl densities ranged from 0 (three sites) to 0.005 owls/km^2 within (spotted owl) density monitoring study areas.

4. Discussion

The rich and extensive body of literature surrounding the spotted owl contains numerous examples of geographically extensive *meta*-analyses involving multiple local monitoring studies (e.g., Franklin et al., 2021; Jones et al., 2018; Tempel et al., 2016; Wiens et al., 2021)). Moreover, recent work demonstrates how broad-scale PAM and territory occupancy data from local monitoring studies can be integrated to expand the area over which occupancy is inferred and increase the precision of estimates (Weldy et al., 2023). Here we conducted the first systematic, ecosystem-scale population assessment for spotted and barred owls, which has important implications for forest and wildlife management

Table 2
Local-scale spotted owl density monitoring study areas in the Sierra Nevada yielded comprehensive density estimates which we related to site-occupancy estimates (ψ) derived from a subset of the broader PAM project.

Study Area	Number of Owls	Area (km^2)	Density (owls/km^2)	Ψ (one-night)	SE	Ψ (two-night)	SE
Lassen	99	1254	0.079	0.435	0.072	0.302	0.065
Eldorado	39	355	0.110	0.507	0.119	0.445	0.117
Sierra	64	535	0.120	0.542	0.104	0.283	0.091
Sequoia-Kings	57	182	0.313	0.784	0.130	0.760	0.127
Other[a]				0.406	0.019	0.294	0.017

[a] Sites outside the boundaries of local-scale study areas in the Sierra Nevada.

across the state of California. With 1,651 ARUs spanning over six million acres (24,856 km^2) across seven national forests and three national parks, ours is the first study to provide near-total survey coverage of a relevant ecosystem (Fig. 1) as opposed to synthesizing data from smaller (300–1,200 km^2) non-adjacent study areas (e.g., Jones et al., 2018; Tempel et al., 2016; Fig. 2). However, those intense, smaller-scale monitoring efforts were pivotal in providing data to hone our models. By combining occupancy estimates from those smaller, geographically specific studies with our Sierra-wide PAM data, our estimates of 2,218 or 2,328 territorial California spotted owls in the Sierra Nevada ecosystem highlights the potentially at-risk status of this subspecies given the large declines and population rarity observed in the Southern California population (Tempel et al., 2022).

Our finding that barred owl site occupancy across the Sierra Nevada was very low has important implications for the management of both spotted and barred owls. The functional absence of barred owls in 2021, two years after an extensive experimental removal effort (Hofstadter et al., 2022), suggested that only very limited recolonization and *in situ* reproduction had occurred. After our surveys were complete, eight barred owls were lethally removed from seven survey cells, including four of the nine cells in which they were observed via PAM. A lack of recolonization in the Sierra Nevada following barred owl removal is a key contrast between removal efforts within the range of the California spotted owl and those within the range of the northern spotted owl. Moreover, Hofstadter et al. (2022) found that California spotted owls were recolonizing historically active territories within weeks of barred owl removals in 2019, suggesting that the barred owl invasion had driven a decrease in territory occupancy but not yet a decrease in adult survival. Our findings corroborate that conclusion; in the Lassen density monitoring study area, which is the northern most study area closest to the barred owl invasion front, the PAM-based estimate of 2021 spotted owl site occupancy using the one-night occupancy criterion (ψ_{Lassen} = 0.44) was almost identical to a 2018 estimate of site occupancy in that area that also used a one-night occupancy criterion ($\psi_{Lassen\&Plumas}$ = 0.46; Wood et al., 2020).

While California spotted owls are rare, our results also indicate that they nevertheless remain well distributed across the Sierra Nevada (Fig. 1) despite the well documented adverse effects of large, severe wildfire on nesting and foraging habitat and occupancy and demographic rates (Jones et al., 2016; Jones et al., 2021; Rockweit et al., 2017). However, PAM sampling occurred from May to July of 2021, immediately before two "megafires." The Dixie and Caldor Fires burned 4,796 km^2, >50% of that at high severity (≥75% canopy mortality) from July to October of 2021, which likely caused substantial losses of spotted owl habitat in the northern and central Sierra Nevada. Thus, while our population size estimate is likely reasonable for the 2021 breeding season, the current population size may be lower. Nonetheless, declines caused by recent megafires do not obviate the near-certain barred owl-driven declines that have been averted because of experimental removal. Alleviating pressure on the California spotted owl by means of a highly effective ecosystem-scale experimental removal of an invasive competitor better enables the population to endure other pressures. Such pressures include i) large, severe wildfires that are increasingly defining forest dynamics in the Sierra Nevada and across the western U. S. (Cova et al., 2023); ii) rising temperatures that will lead to increased thermal stress in an ecosystem from which key habitat features, namely ancient trees, have been reduced in density (McGinn et al., 2023b; McGinn et al. in Review); and iii) pervasive environmental toxicants display in-utero transmission (Hofstadter et al., 2021). Even threats that pose low individual risks of extinction can have substantial additive effects over time, and synergistic effects can rapidly increase extinction risk (Kimmel et al., 2022). Mitigating one threat among several is insufficient for long-term conservation success, but it is a necessary first step – particularly when that threat has been demonstrated to cause a rapid decline in a population.

We believe our estimate of population size for California spotted owls is reasonable for several reasons. Site occupancy was strongly and positively correlated with density under both liberal and strict occupancy criteria within four local-scale density monitoring study areas (r = 0.99 and 0.94, respectively; Fig. 2). Thus, PAM-based site occupancy was predictive of density in our system despite the aforementioned sources of ecological false positives that can decouple site occupancy from density, such as movements of individuals among multiple sampling sites. Limiting passive acoustic sampling to non-adjacent grid cells, coupled with the relatively small area over which spotted owls vocalize (compared to their home range size; (Reid et al., 2022)), may have reduced this form of false detections. Alternatively, ecological false positives may have occurred frequently, but their effects were similar across the range of densities we sampled in local study areas.

Our approach for estimating population size does not require an assumption of equal densities inside versus outside density monitoring study areas so long as density-occupancy *relationships* estimated within local density monitoring study areas apply to the broader sampled with PAM. Thus, differences in densities among public and private lands (Bias and Gutiérrez, 1992; Hobart et al., 2019; Roberts et al., 2017) were not expected to lead to an appreciable bias in our estimate of population size for California spotted owls despite that fact that ARUs were mostly deployed on public lands. We acknowledge that the assumption of stable density-occupancy relationships cannot be tested outside of density monitoring study areas, but the relative consistency we observed in density-occupancy ratios (Fig. 2c and 2e) across the gradient of spotted owl densities in the four density study areas suggests that the assumption was reasonable. Further, site occupancy outside of the local density study areas was similar to site occupancy inside of the local study areas with the lowest occupancy rates (Table 2). However, additional work that evaluates stability in occupancy-density relationships over time is needed to ascertain whether our approach can provide reasonable estimates of temporal trends in regional population size.

Our ecosystem-scale, bioacoustics approach for monitoring spotted owl population size rather than site occupancy presumably reduces the effect of ecological false positives and should therefore, over time, improve our understanding of how the California spotted owl is responding to environmental change. Prompt annual population assessments will enable a more rapidly adaptive approach to ecosystem management, but continued coordination among survey efforts (i.e., PAM and active surveys) will be essential to maintaining data quality. It may be possible to better elucidate habitat relationships by using spotted owls' sex-specific vocalizations to implement multi-state occupancy models that relate pair occupancy to particular habitat features (Appel et al., 2023; Wood et al., 2020). Identification of demographically important vocalizations, notably juvenile begging (McGinn et al., 2023a), could further enhance the classification of survey cells (i.e., from occupied to single/pair to single/pair/successful reproduction) and recover some of the demographic information that is lost when switching from local- to ecosystem-scale monitoring. Perhaps most importantly, tracking abundance over time, rather than occupancy, should provide managers with a more detailed understanding of how sensitive species respond to environmental change we incur deliberately, like forest restoration, and environmental change we have set in motion, like changing fire regimes.

The approach we have demonstrated using data from spotted owl monitoring studies would readily be applied to other species for which similar data are available. Indeed, the rise of bioacoustics as an effective population monitoring tool suggests that there is a growing need to reconcile monitoring data derived from human observers and from passive acoustic surveys (Yip et al., 2017), which may present opportunities to integrate broad-scale bioacoustic data with historical local-scale demographic data (Weldy et al., 2023). Historically, conventional human-based surveys have yielded demographically rich but spatially limited data such that localized censuses are attainable. Passive acoustic monitoring can increasingly offer data about entire biological communities at ecosystem scales (Brunk et al., 2023; Wood et al., 2021),

but the resulting animal observations can be difficult to interpret (Wood and Peery, 2022). We have shown that the two approaches can be synthesized to maximize their complementary strengths – leading to new insights for at-risk populations.

CRediT authorship contribution statement

Kevin G. Kelly: Conceptualization, Investigation, Resources, Project administration, Writing – original draft, Writing – review & editing. **Connor M. Wood:** Methodology, Writing – original draft, Writing – review & editing. **Kate McGinn:** Formal analysis, Methodology, Visualization, Data curation, Writing – original draft, Writing – review & editing. **H. Anu Kramer:** Methodology, Visualization, Writing – review & editing. **Sarah C. Sawyer:** Funding acquisition, Supervision, Writing – review & editing. **Sheila Whitmore:** Investigation, Resources, Project administration, Writing – review & editing. **Dana Reid:** Investigation, Project administration. **Stefan Kahl:** Software, Data curation. **Aimee Reiss:** Investigation, Project administration. **Jonathan Eiseman:** Investigation, Project administration. **William Berigan:** Investigation, Resources, Project administration, Writing – review & editing. **John J. Keane:** Investigation, Project administration. **Paula Shaklee:** Investigation, Project administration. **Lief Gallagher:** Investigation, Project administration. **Thomas E. Munton:** Investigation, Project administration. **Holger Klinck:** Software, Project administration. **R.J. Gutiérrez:** Investigation, Writing – review & editing. **M.Z. Peery:** Conceptualization, Supervision, Project administration, Funding acquisition, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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