California Spotted Owl Passive Acoustic Monitoring Program: Final Annual Report (2021–2023)

Jason M. Winiarski[1], Sheila A. Whitmore[1], Jonathan P. Eiseman[1], Erin C. Netoskie[1], H. Anu Kramer[1], Kevin G. Kelly[1], Connor M. Wood[2], Kate A. McGinn[1], Stefan Kahl[2], Holger Klinck[2], and M. Zachariah Peery[1]

[1] *Department of Forest and Wildlife Ecology, University of Wisconsin - Madison*
[2] *K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Cornell University*

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Executive Summary

The California spotted owl (*Strix occidentalis occidentalis*) is associated with mature forests and has resided at the center of forest management planning for several decades in the Sierra Nevada. In 2021, population monitoring transitioned from intensive demographic surveys in local study areas to passive acoustic surveys conducted across much of the Sierra Nevada bioregion. Here, we report patterns in California spotted owl site occupancy rates (i.e., the probability of owls occurring at a survey site) for the first three years of surveys, 2021–2023. Key accomplishments and findings include:

- Autonomous recording units (ARUs) were deployed for about 5 weeks each during the breeding season over nearly 2.5 million hectares across 7 national forests, spanning nearly all suitable California spotted owl habitat on the west slope of the Sierra Nevada. In 2023, this effort included 1,324 ARUs deployed in 624 400-ha grid cells, which was a slight reduction from 2021 and 2022 because of inclement weather and access issues.
- In 2023, the probability of detecting an owl over a 5-week survey period, if present, was 94.5% when only one night of detections was required to assign occupancy to a survey cell, and 98.6% when at least two nights of detections were required.
- California spotted owls were widespread across the Sierra Nevada (see Figure 3) and were detected on all 7 surveyed national forests. They were most common at low-to-middle elevations.
- At the national forest level, California spotted owl site occupancy (proportion of sites occupied after correcting for imperfect detection, ψ) ranged from ranged from 0.167 in the Lassen National Forest to 0.644 in the Stanislaus National Forest in 2023 when only a single night of detections was required to assign occupancy to a survey cell. Occupancy ranged from 0.100 in the Lassen National Forest to 0.537 in the Stanislaus National Forest when two or more nights of detections were required (see Table 5).
- Strict-criteria site occupancy across the Sierra Nevada bioregion in 2023 ($\psi = 0.264$; 95% CRI: 0.228–0.299) did not differ significantly from 2021 ($\psi = 0.294$; 95% CRI: 0.262–0.327) and 2022 ($\psi = 0.283$; 95% CRI: 0.252–0.316) estimates, whereas individual forest occupancy rates varied more between years (see Table 5 and Figure 10).
- California spotted owl site occupancy rates declined strongly and consistently in relation to the amount of a cell burned at high-severity from 1 to 36 years prior to surveys (see Figure 9). While the adverse effects of severe fire were observed across the full range of time scales considered, the relatively weak relationship 1-year post fire was likely the result of owls remaining within severely burned areas immediately after a fire, then either dying or dispersing in subsequent years.
- Naïve barred owl site occupancy was very low (0.6% of surveyed cells in 2023) owing to a successful lethal removal study, with ≤ 9 occupied cells in each year. Barred owls were detected in 4 cells on 3 forests in 2023: Plumas, Tahoe, and Sequoia (see Figure 6).

Collectively, these results indicate it is feasible to monitor (1) population trends and (2) effects of wildfire and barred owls for California spotted owl populations in the Sierra Nevada with passive acoustic surveys. Results are currently being reviewed to determine if the existing ARU network can provide sufficient sample size to evaluate the effects of forest management actions on California spotted owl populations. Finally, additional years of surveys will help refine observed trends and inform management planning.

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Cover photo: California spotted owl (*Strix occidentalis occidentalis*) by Danny Hofstadter

1 Background

The California spotted owl (*Strix occidentalis occidentalis*) is a territorial species associated with mature and old-growth forest that has resided at the center of forest management planning for several decades in the Sierra Nevada. California spotted owls are threatened, or potentially threatened, by a suite of anthropogenic and environmental factors. First, increasingly large, severe fires are causing localized losses of forest cover driving potentially decadal population declines in those areas (Jones et al. 2016, Jones et al. 2021). Second, historical harvesting of large trees appears to have caused population declines in some but not all areas (Conner et al. 2013, Tempel et al. 2014b, Roberts et al. 2017). Third, the barred owl (*S. varia*), 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. 2020). The invasion motivated a lethal removal experiment in 2018 that, as of 2021, reduced barred owl densities 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*).

Concern over the status of California spotted owls has key implications for forest management activities intended to reduce forest fuels and curb increasingly large and severe wildfires. While reducing severe wildfire activity could reduce losses of suitable spotted owl habitat, fuels management activities have the potential to simplify the complex forest structure that spotted owls use for nesting and roosting. Accordingly, there is an acute need to monitor the effects of fuels management on California spotted owls, particularly as natural resource agencies attempt to increase the pace and scale of forest restoration activities across the Sierra Nevada.

Since the late 1980's and early 1990's, California spotted owl populations have been monitored via four local demographic study areas in the Sierra Nevada (Tempel et al. 2016, Jones et al. 2018). These studies, while providing important insights regarding population trends and factors affecting populations at local scales, were not designed to monitor the subspecies at a bioregional scale. Accordingly, trends in spotted owl populations across the Sierra Nevada are unknown, as are the relative impacts of environmental stressors and management activities (e.g., fuels reduction treatments) on the overall population.

Passive acoustic monitoring (PAM) is becoming an increasingly common approach for population assessments because it can enable broader and more continuous coverage than conventional, in-person surveys (Shonfield and Bayne 2017, Darras et al. 2018, 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, support 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. 2019). As a result, there is great potential for PAM to support population trend assessments at greater spatial scales than has previously been possible. Accordingly, in 2021 we initiated a PAM program to begin monitoring the subspecies across all seven national forests on the west side of the Sierra Nevada (Kelly et al. 2023).

2 Objectives

Here we report the results of the first three years (2021–2023) of passive acoustic monitoring for both California spotted owls and barred owls in the Sierra Nevada. Our primary objectives were to estimate site occupancy probability for California spotted owls and understand how site occupancy varies geographically (e.g., among national forests), and as a function of wildfire history. A secondary objective is to assess whether barred owl site occupancy remains low in the Sierra Nevada following the initiation of the lethal removal study in 2018.

3 Methods

3.1 Study area

The Sierra Nevada is the dominant physiographic feature of eastern California, nearly spanning the entire length of the state. Our PAM program spans mixed-conifer forest on the west slope of the Sierra Nevada where most of the suitable spotted owl habitat occurs (Verner et al. 1992), and includes coverage in all seven National Forests (Figure 1). We subdivided the western slope into 8,087 400-ha hexagonal grid cells, which are approximately the size of a spotted owl territory in this region (Tempel et al. 2014a). We excluded cells from our complete set of candidate cells if they intersected highways, were >50% water, or lacked road access. In practice, this also excluded particularly steep and wilderness areas, though they ultimately comprised a very small proportion of the candidate cells (<5%). We also avoided surveying adjacent cells to reduce the possibility of double-counting owl territories (Wood et al. 2019).

3.2 Passive acoustic surveys

We deployed one to four, but generally two, ARUs (SwiftOne recorder, K. Lisa Yang Center for Conservation Bioacoustics) in each grid cell at acoustically advantageous locations (e.g., ridgetops), with a minimum spacing of 500 m (Figure 1). 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 from 20:00–06:00 PDT at a sample range of 32 kHz, 16-bit resolution, and gain of +33 dB. Deployments began in early April and lasted through early August, with any given grid cell surveyed for approximately five weeks continuously.

3.3 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 "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 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. Based on analyses conducted by Kelly et al. (2023), we selected thresholds of 0.989 for spotted owls and 0.970 for barred owls, which yielded a reasonable balance between false-positive and false-negative detections. We then manually confirmed all putative BirdNET-derived owl observations above species-specific prediction score thresholds for two reasons. First, false-positive detections (i.e., 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 broadcast 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.

3.4 Environmental covariates

We quantified environmental covariates that might influence occupancy for each grid cell using program R (R Core Team 2023). The elevational range of bird species varies depending on latitudinal position in the Sierra Nevada (Saracco et al. 2011, Siegel et al. 2011, Brunk et al. 2023). Therefore, we calculated average elevation within each cell and the northing spatial coordinate (California Albers projection) of its centroid using the `rgee` and `sf` packages (Aybar et al. 2023, Pebesma et al. 2023). To control for the effect of geographic location within the Sierra Nevada on elevation, we modeled the linear relationship between latitude (converted to northing in California Albers projection) and elevation (elevation ~ northing), and used the elevation residuals in our occupancy model to examine the effects of elevation and latitude separately.

To assess the effects of fire history and severity on occupancy, we obtained annual fire footprints and fire severity rasters from the Monitoring Trend in Burn Severity program (MTBS; https://www.mtbs.gov/). The MTBS database contains wildfires $\geq$ 1000 acres beginning in 1984. We used MTBS fire perimeters to identify the most recent fire intersecting a cell and to calculate time since fire (if a cell burned). We used time since fire to assign each cell to one of four time categories representing early fire regeneration stages: one year post-fire, 2–4 years, 5–10 years, 11–20 years, and 21–36+ years (Brunk et al. 2023). Finally, we used the `landscapemetrics` package (Hesselbarth et al. 2023) to calculate the proportion of a cell burned by high severity fire corresponding with the time category of the most recent fire. Cells that did not burn between 1984–2022 were assigned to the 21–36+ category, and the proportion burned at high severity was set to zero. For cells with multiple fires in the same year or across years, we used the largest fire or the most recent fire to calculate fire covariates.

3.5 Occupancy modeling

We estimated site occupancy rates for spotted owls from 2021–2023 using single-season occupancy models (MacKenzie et al. 2002) applied to detection/non-detection data derived from manually validated observations generated by BirdNET. We fit the three years of data using a "stacked" approach, where each site-year combination is treated as a unique "site" (Fuller et al. 2016). Entire grid cells within a given year were considered sites, such that multiple ARUs therein could contribute owl observations to its occupancy status. Following Kelly et al. (2023), we conducted two separate sets of occupancy analyses for California spotted owls representing two acoustic-based detection criteria: one-night (i.e., a single confirmed owl observation constituted a detection) and two-night (i.e., detections were only considered when there were confirmed owl observations on at least two nights) thresholds for determining occupancy status. The one-night threshold represents the "liberal" or more relaxed definition of occupancy, while the two-night threshold represents a "strict" or more conservative definition of occupancy (Kelly et al. 2023). For both analyses, our season entailed 18 week-long secondary sampling periods starting 7 April and ending 8 August. We did not model barred owl occupancy because of low numbers of detections across the Sierra Nevada (see Section 4.2).

To evaluate the effects of wildfire and other environmental variables on spotted owl occupancy, we constructed a single global occupancy model for the liberal and strict detection criteria. We considered each cell and year combination as a site i, and each week of nightly audio recordings as a temporal replicate j. We assumed that detection and occupancy would vary based on survey characteristics during each temporal replicate and site-level environmental conditions. We modeled the detection process p as a function of ARU survey effort (log-scaled hours; summed across ARUs within a cell), date, and year (categorical effect):

$$logit(p_{ij}) = \alpha_0 + \alpha_1 \times effort_{ij} + \alpha_2 \times date_{ij} + \alpha_3 \times date_{ij}^2 + \alpha_4 \times year_{ij}$$

We modeled the occurrence process ψ as a function of residual elevation, latitude (northing), the percent of a cell burned by high severity fire in different time since burn categories, and year (categorical effect):

$$\begin{aligned} logit(\psi_i) = &\beta_0 + \beta_{forest[i]} + \beta_1 \times elevation_i + \beta_2 \times elevation_i^2 + \beta_3 \times northing_i + \beta_4 \times northing_i^2 + \\ &\beta_5 \times high.severity.1yr_i + \beta_6 \times high.severity.2-4yrs_i + \beta_7 \times high.severity.5-10yrs_i + \\ &\beta_8 \times high.severity.11-20yrs_i + \beta_9 \times high.severity.21-36yrs_i + \beta_{10} \times year_i \end{aligned}$$

To estimate Sierra Nevada-wide site occupancy rates from 2021–2023, we used a model that only contained a fixed effect of year. To estimate site occupancy for each national forest, we included a year by national forest interaction. For both of these models, we included the same detection predictors used in the global occupancy model. Continuous predictors in all models were standardized with a mean of zero and standard deviation of one.

Models were fit in a Bayesian framework using the Stan interface package `ubms` in R (Kellner et al. 2022). For each model, we used default priors and ran four chains for 1500 iterations each, with a warmup of 750 iterations. We assessed model convergence using the Rhat metric, visually inspecting traceplots, and by checking for a sufficient number of effective samples for each parameter (>400). We conducted additional model checking with residual plots and goodness-of-fit tests (Kellner et al. 2022). To assess uncertainty in model output, we present 95% credible intervals.

4 Results

We note that there are slight differences in the results presented below compared to the 2021–2022 version of the report (e.g., number of surveyed cells/ARUs deployed in 2021 and 2022, precision of occupancy estimates) due to a correction in USFS cell assignment/querying, and different occupancy model parameterizations.

4.1 Passive acoustic survey effort

Record snowpack in the Sierra Nevada hindered our ability to deploy ARUs early in the season, at higher elevations, and at some previously surveyed cells, resulting in lower survey effort in 2023 than in previous years (Figure 2). In addition, ARU failures due to a SD card formatting issue reduced survey effort to just a few days for 86 ARUs in the southern Sierra Nevada study region (i.e., Stanislaus, Sierra, and Sequoia national forests). In 2023, we deployed 1,324 ARUs in 624 grid cells, with an average of 2.12 ARUs deployed per cell (Table 1). From 2021–2023 we monitored 837 unique cells, of which 67% (n = 560) were monitored in all three years. Surveys were initiated 13 days later (earliest ARU recording = 20 April) and concluded about one week earlier (latest ARU recording = 30 July) in 2023 than 2022. In total, we recorded 425,700 hours of audio data in 2023, which was lower than previous years (490,823 and 515,322 hours in 2021 and 2022, respectively). Deployments spanned almost all suitable California spotted owl habitat on the west slope of the Sierra Nevada ecosystem (Figure 3).

4.2 California spotted owl and barred owl detections in passively recorded audio

We obtained spotted owl detections (i.e., 3-second audio clips with a BirdNET confidence score $\geq$ 0.989) across the Sierra Nevada region and in each national forest (Table 2, Figure 3). Our manual review yielded 9,730 confirmed spotted owl detections in 2023, 43.7% and 44.5% lower than the number of detections in 2021 and 2022, respectively. Across all years, the vast majority of detections in 2023 were male four-note vocalizations (83.9%; Figure 4). Within occupied cells, most detections came from males only (51.7%–82.4% of occupied cells), followed by pairs (14.7%–42.1%), unknown sex owls only (0%–8.9%), females only (0%–7.5%), and juveniles (0%–2.9%; Figure 5). Naïve occupancy of spotted owls in 2023 was lowest in Lassen National Forest (0.161) and highest in Stanislaus National Forest (0.587).

In 2023, barred owls were only detected in three national forests: Plumas, Tahoe, and Sequoia (Table 3, Figure 6). There were also fewer confirmed barred owl detections compared with spotted owls (n = 271) and lower naïve occupancy, which did not exceed 0.015 at the forest-level. Only four cells had barred owl detections in 2023, yielding a naïve occupancy rate of 0.006 across the entire study area.

4.3 California spotted owl detection and occupancy

Survey effort (ARU hours) was an important predictor of detection probability in both the liberal and strict occupancy models, with spotted owls detected more consistently with increasing effort (Table 4, Figure 7). The linear and quadratic effects of date were uncertain for the liberal model. There was some evidence for a non-linear effect of date for the strict model (Figure 7), but 95% credible intervals for this parameter overlapped zero, likely because of fewer ARU deployments early and late in the season. For the liberal and strict models, mean detection probabilities in a week-long sampling period in 2023 were 0.443 (95% CRI: 0.414–0.471) and 0.581 (95% CRI: 0.564–0.614), translating to a 94.5% and 98.6% chance of detecting a spotted owl if it was present at a site during a typical 5-week ARU survey. This was lower than in previous years, though the 95% CRIs slightly overlapped zero (liberal $\beta_{year(2023)}$ = -0.16, 95% CRI: -0.31–0.00, strict $\beta_{year(2023)}$ = -0.17, 95% CRI: -0.36–0.01).

Spotted owls were predicted to occur most often at low-to-middle elevations (after correcting for location within the Sierra Nevada) and the middle of the Sierra Nevada range near the Stanislaus/Sierra National Forest boundary, although this non-linear relationship with latitude was uncertain for the liberal and strict models (Table 4, Figure 8). The percent of a cell burned by high severity fire negatively affected occupancy across all time categories for both the liberal and strict models, and had the largest effects for the 2–4 year and 5–10 year time categories (Table 4, Figure 9).

Spotted owls were well distributed across the Sierra Nevada, with a mean occupancy probability of 0.414 in 2021 (95% CRI: 0.380–0.449), 0.388 in 2022 (95% CRI: 0.355–0.423), and 0.379 in 2023 (95% CRI: 0.340–0.419) for the liberal model (Table 5 and Figure 10). Mean occupancy probabilities for the strict model were 0.294 in 2021 (95% CRI: 0.262–0.327), 0.283 in 2022 (95% CRI: 0.252–0.316), and 0.264 in 2023 (95% CRI: 0.228–0.299). Occupancy probabilities varied widely across forests, with the lowest liberal mean occupancy in Lassen National Forest (ψ_{2023} = 0.167; 95% CRI: 0.101–0.251) and highest liberal mean occupancy in Stanislaus National Forest (ψ_{2023} = 0.624; 95% CRI: 0.524–0.722). Occupancy patterns were similar but lower in Lassen National Forest (ψ_{2023} = 0.100; 95% CRI: 0.048–0.172) and Stanislaus National Forest (ψ_{2023} = 0.537; 95% CRI: 0.406–0.665) from the strict model. There was no significant difference in Sierra Nevada-wide occupancy from 2021–2023, but there was a positive effect of year (2022) in the Sierra for the strict occupancy model with a year × forest interaction ($\beta_{year2022:Sierra}$ = 0.924; 95% CRI: 0.174–1.659).

5 Discussion

Our results demonstrate that California spotted owls can be monitored effectively across a large portion of the Sierra Nevada bioregion using passive acoustic surveys. Importantly, seasonal detection probabilities were very high and estimates of site occupancy were reasonably stable over the three years surveys were conducted (liberal = 0.379–0.414; strict = 0.264–0.294), as would be expected if occupancy tracks population size, which varies little inter-annually (Blakesley et al. 2010). While detection probability is high, we note that most detected vocalizations came from males as they are louder and easier to detect than females (especially breeding females) and juveniles (Reid et al. 2022); however, many of the sites occupied by males are also likely occupied by females (Tempel et al. 2014b) and presumably involved breeding. Further, Sierra Nevada-wide estimates of site occupancy were reasonably precise, with standard deviations of posterior distributions ranging from 0.018–0.020 for the liberal model and 0.016–0.018 for the strict model from 2021–2023. National forest-specific estimates of occupancy fluctuated more among the three years, with pronounced declines observed on the Sierra and Sequoia National Forests from 2022 to 2023 (Table 5, Figure 10). It is unclear at this time whether these large drops in estimated occupancy reflect population declines or are the result of temporary (1-year) declines in detection probability that we were unable to account for. Nevertheless, in general, forest-level occupancy estimates were estimated with reasonable precision, suggesting that monitoring California spotted owls at the scale of individual forests may also be feasible with longer-term surveys. Thus, while it remains premature to estimate trends in occupancy, the first three years of surveys indicate that PAM monitoring of California spotted owls is logistically feasible and that it is possible to detect ecologically meaningful changes in populations.

Occupancy declined substantially at sites with a relatively a high proportion of severe wildfire in the past 36 years, which is generally consistent with numerous studies using territory occupancy information derived from call-based surveys (e.g., Jones et al. 2016, 2021; Tempel et al. 2022; McGinn et al. *in review*). While the adverse effects of severe fire were observed across the full range of time scales considered, the relatively weak relationship 1-year post fire was likely the result of owls remaining in the fire footprint immediately after a fire, then either dying or dispersing in subsequent years.

While California spotted owls are a rare species in the Sierra Nevada, our results indicate that they nevertheless remain well distributed across the region (Figure 3). Thus, we suspect that this core population of California spotted owls–which has been proposed for listing as a Threatened species by the US Fish and Wildlife Service–is recoverable. However, the strong, long-term, and adverse effects of large severe fires, which are increasing in the Sierra Nevada poses a major threat to California spotted owls. Indeed, our analyses, in conjunction with previous studies (Jones et al. 2016, Jones et al. 2021) and current work (McGinn et al., *in review*) indicate that these megafires are increasingly creating gaps in the distribution of California spotted owls in the Sierra Nevada – and have the potential to fragment the species into smaller, less viable populations. We suggest that fuels management activities that curb the frequency and intensity of large severe fires will benefit California spotted owls, as suggested by previous modeling studies (Tempel et al. 2015, Jones et al. 2022) – so long as they minimize impacts to key habitat elements.

Our results also reflect the enduring success of the barred owl lethal removal study, which was initiated in 2018 and fully implemented in 2019, with 76 removals of barred owls and hybrids during this period (Hofstadter et al. 2022). Prior to removals, barred owl modeled site occupancy based on acoustic surveys was 0.19 in 2018 and declined to 0.03 in 2020 as a result of removals (Hofstadter et al. 2022). Naïve estimates of barred owl site occupancy from 2021–2023 did not exceed 0.012, indicating that barred owls continue to remain at very low densities across the Sierra Nevada bioregion. Indeed, 3–4 national forests in each year had no barred owl detections, despite high detection probabilities (Kelly et al. 2023). Low barred owl site occupancy was maintained with 15 or fewer barred owl removals in each year from 2020–2023 (53 removals total; Berigan, *unpublished data*). Accordingly, low-level lethal removals appear to be a viable means for preventing the extirpation of California spotted owls from the Sierra Nevada, so long as the PAM, which provides barred owl locational information as well as a means to monitor removal success, is maintained.

A key future direction for the PAM program involves understanding the extent to which it can be used to monitor the effects of fuels management on California spotted owls. This effort will include an assessment of how well survey sites are stratified across the range of different forest management activities that have been implemented recently as well as planned forest management activities. This assessment will be used to develop a statistical power analysis to estimate the probability of detecting fuels management effects as a function of sample size and study duration. Should it be deemed necessary, strategies to augment sampling in treated areas and increase statistical power will be assessed.

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8 Tables

Table 1: Autonomous recording unit (ARU) survey effort and timing in the Sierra Nevada region, 2021–2023.

Year	Survey period	Cells surveyed	ARUs deployed	ARU hours
2021	May 03–July 19	758	1,476	490,823
2022	April 07–August 08	778	1,615	515,322
2023	April 20–July 30	624	1,324	425,700

Table 2: California spotted owl detections and naïve occupancy by national forest, 2021–2023.

National forest	Year	Detections	Unoccupied cells	Occupied cells	Surveyed cells	Naïve occupancy*
Lassen	2021	1,172	86	34	120	0.283
	2022	814	87	27	114	0.237
	2023	158	78	15	93	0.161
Plumas	2021	1,069	107	40	147	0.272
	2022	1,092	103	41	144	0.285
	2023	1,573	86	45	131	0.344
Tahoe	2021	4,121	63	56	119	0.471
	2022	3,970	54	49	103	0.476
	2023	1,608	39	48	87	0.552
Eldorado	2021	1,856	48	55	103	0.534
	2022	1,728	60	47	107	0.439
	2023	2,571	57	43	100	0.430
Stanislaus	2021	4,549	36	57	93	0.613
	2022	4,398	48	49	97	0.505
	2023	2,485	26	37	63	0.587
Sierra	2021	954	78	35	113	0.310
	2022	2,544	84	44	128	0.344
	2023	486	62	18	80	0.225
Sequoia	2021	3,566	34	29	63	0.460
	2022	2,989	47	38	85	0.447
	2023	849	52	18	70	0.257
All forests	2021	17,287	452	306	758	0.404
	2022	17,535	483	295	778	0.379
	2023	9,730	400	224	624	0.359

* Naïve occupancy is defined as the proportion of surveyed cells with at least one spotted owl observation (without accounting for imperfect detection). For example, naïve occupancy of 0.359 across all forests in 2023 corresponds with 35.9% of cells being occupied.

Table 3: Barred owl detections and naïve occupancy by national forest, 2021–2023.

National forest	Year	Detections	Unoccupied cells	Occupied cells	Surveyed cells	Naïve occupancy*
Lassen	2021	47	118	2	120	0.017
	2022	31	113	1	114	0.009
	2023	0	93	0	93	0.000
Plumas	2021	0	147	0	147	0.000
	2022	0	144	0	144	0.000
	2023	12	129	2	131	0.015
Tahoe	2021	1,110	114	5	119	0.042
	2022	443	102	1	103	0.010
	2023	2	86	1	87	0.011
Eldorado	2021	1	102	1	103	0.010
	2022	0	107	0	107	0.000
	2023	0	100	0	100	0.000
Stanislaus	2021	0	93	0	93	0.000
	2022	0	97	0	97	0.000
	2023	0	63	0	63	0.000
Sierra	2021	0	113	0	113	0.000
	2022	0	128	0	128	0.000
	2023	0	80	0	80	0.000
Sequoia	2021	16	62	1	63	0.016
	2022	98	84	1	85	0.012
	2023	257	69	1	70	0.014
All forests	2021	1,174	749	9	758	0.012
	2022	572	775	3	778	0.004
	2023	271	620	4	624	0.006

* Naïve occupancy is defined as the proportion of surveyed cells with at least one barred owl observation (without accounting for imperfect detection). For example, naïve occupancy of 0.006 across all forests in 2023 corresponds with 0.6% of cells being occupied.

Table 4: Mean, standard deviation (SD), and 95% credible intervals (and whether they overlap zero) of parameter estimates from California spotted owl occupancy models fit to ARU data from 2021–2023. Models were fit under liberal (i.e., one-night threshold) and strict (i.e., two-night threshold) detection criteria. The intercept baseline for each model is for the year 2021, and σ represents forest-level variability in occupancy.

Detection criteria	Submodel	Parameter	Mean	SD	2.5%	97.5%	Overlap 0?
Liberal	*Detection*	Intercept	-0.07	0.05	-0.18	0.03	TRUE
		Date	0.21	0.19	-0.15	0.57	TRUE
		Date^{2}[*]	-0.19	0.19	-0.56	0.18	TRUE
		ARU hours	0.54	0.04	0.47	0.61	FALSE
		Year (2022)	0.06	0.07	-0.09	0.20	TRUE
		Year (2023)	-0.16	0.08	-0.31	0.00	TRUE
	Occupancy	Intercept[†]	-0.57	0.23	-1.06	-0.11	FALSE
		Elevation	-0.45	0.06	-0.57	-0.33	FALSE
		Elevation^{2}[‡]	-0.58	0.07	-0.71	-0.45	FALSE
		Northing	-0.22	0.18	-0.59	0.11	TRUE
		Northing^{2}	-0.52	0.13	-0.78	-0.29	FALSE
		% High severity (1 yr)	-0.22	0.06	-0.35	-0.12	FALSE
		% High severity (2-4 yrs)	-0.68	0.09	-0.86	-0.51	FALSE
		% High severity (5-10 yrs)	-0.54	0.07	-0.70	-0.40	FALSE
		% High severity (11-20 yrs)	-0.20	0.06	-0.32	-0.09	FALSE
		% High severity (21-36 yrs)	-0.22	0.06	-0.33	-0.11	FALSE
		Year (2022)	-0.01	0.12	-0.24	0.21	TRUE
		Year (2023)	0.04	0.13	-0.23	0.30	TRUE
		σ_{Forest}	0.54	0.23	0.25	1.09	FALSE
Strict	*Detection*	Intercept	0.50	0.06	0.38	0.62	FALSE
		Date	0.47	0.22	0.05	0.90	FALSE
		Date^{2}	-0.43	0.22	-0.85	0.01	TRUE
		ARU hours	0.57	0.04	0.49	0.65	FALSE
		Year (2022)	0.02	0.09	-0.15	0.19	TRUE
		Year (2023)	-0.17	0.09	-0.36	0.01	TRUE
	Occupancy	Intercept	-1.17	0.32	-1.76	-0.47	FALSE
		Elevation	-0.50	0.07	-0.63	-0.37	FALSE
		Elevation^{2}	-0.61	0.07	-0.75	-0.47	FALSE
		Northing	-0.23	0.20	-0.63	0.15	TRUE
		Northing^{2}	-0.70	0.14	-0.99	-0.42	FALSE
		% High severity (1 yr)	-0.26	0.07	-0.40	-0.14	FALSE
		% High severity (2-4 yrs)	-0.72	0.11	-0.95	-0.51	FALSE
		% High severity (5-10 yrs)	-0.65	0.10	-0.85	-0.47	FALSE
		% High severity (11-20 yrs)	-0.21	0.07	-0.37	-0.09	FALSE
		% High severity (21-36 yrs)	-0.23	0.07	-0.37	-0.11	FALSE
		Year (2022)	0.04	0.12	-0.20	0.28	TRUE
		Year (2023)	0.00	0.14	-0.27	0.26	TRUE
		σ_{Forest}	0.73	0.29	0.36	1.43	FALSE

[*] Date^{2} quadratic effect allows for a curved or peaked relationship between detection probability and date.
[†] Elevation^{2}: quadratic effect of elevation (after controlling for latitude).
[‡] Northing^{2}: quadratic effect of northing (latitude in California Albers projection).

Table 5: California spotted owl occupancy ψ (i.e., proportion of cells that are occupied after accounting for imperfect detection) by forest and year from the liberal and strict detection criteria occupancy models. Mean, standard deviation, and 95% credible intervals of ψ are shown. Estimates for specific forests were derived from occupancy models including a year by forest interaction; Sierra Nevada-wide estimates were derived from occupancy models including a year (fixed effect) and forest random effect.

Detection criteria	National forest	Year	Mean	SD	2.5%	97.5%
Liberal	Lassen	2021	0.294	0.041	0.213	0.376
		2022	0.243	0.039	0.172	0.325
		2023	0.167	0.038	0.101	0.251
	Plumas	2021	0.288	0.037	0.219	0.361
		2022	0.293	0.039	0.218	0.372
		2023	0.352	0.043	0.272	0.439
	Tahoe	2021	0.483	0.044	0.396	0.571
		2022	0.486	0.050	0.389	0.580
		2023	0.566	0.054	0.460	0.673
	Eldorado	2021	0.517	0.042	0.435	0.598
		2022	0.454	0.047	0.363	0.545
		2023	0.447	0.048	0.350	0.539
	Stanislaus	2021	0.624	0.050	0.524	0.722
		2022	0.517	0.052	0.417	0.617
		2023	0.644	0.065	0.512	0.763
	Sierra	2021	0.324	0.043	0.243	0.411
		2022	0.347	0.042	0.268	0.429
		2023	0.251	0.051	0.159	0.358
	Sequoia	2021	0.467	0.061	0.345	0.585
		2022	0.452	0.054	0.346	0.560
		2023	0.287	0.056	0.184	0.403
	All forests	2021	0.414	0.018	0.380	0.449
		2022	0.388	0.018	0.355	0.423
		2023	0.379	0.020	0.340	0.419
Strict	Lassen	2021	0.202	0.036	0.135	0.275
		2022	0.116	0.029	0.065	0.179
		2023	0.100	0.031	0.048	0.172
	Plumas	2021	0.178	0.031	0.122	0.245
		2022	0.202	0.033	0.140	0.270
		2023	0.245	0.037	0.177	0.318
	Tahoe	2021	0.356	0.044	0.273	0.441
		2022	0.313	0.046	0.226	0.406
		2023	0.382	0.052	0.282	0.485
	Eldorado	2021	0.378	0.041	0.301	0.457
		2022	0.294	0.040	0.219	0.376
		2023	0.323	0.044	0.240	0.411
	Stanislaus	2021	0.507	0.052	0.408	0.610
		2022	0.454	0.051	0.354	0.555
		2023	0.537	0.065	0.406	0.665
	Sierra	2021	0.185	0.035	0.122	0.257
		2022	0.279	0.039	0.207	0.357
		2023	0.121	0.038	0.058	0.202
	Sequoia	2021	0.366	0.059	0.253	0.479
		2022	0.410	0.054	0.306	0.521
		2023	0.203	0.050	0.119	0.307
	All forests	2021	0.294	0.017	0.262	0.327
		2022	0.283	0.016	0.252	0.316
		2023	0.264	0.018	0.228	0.299

9 Figures

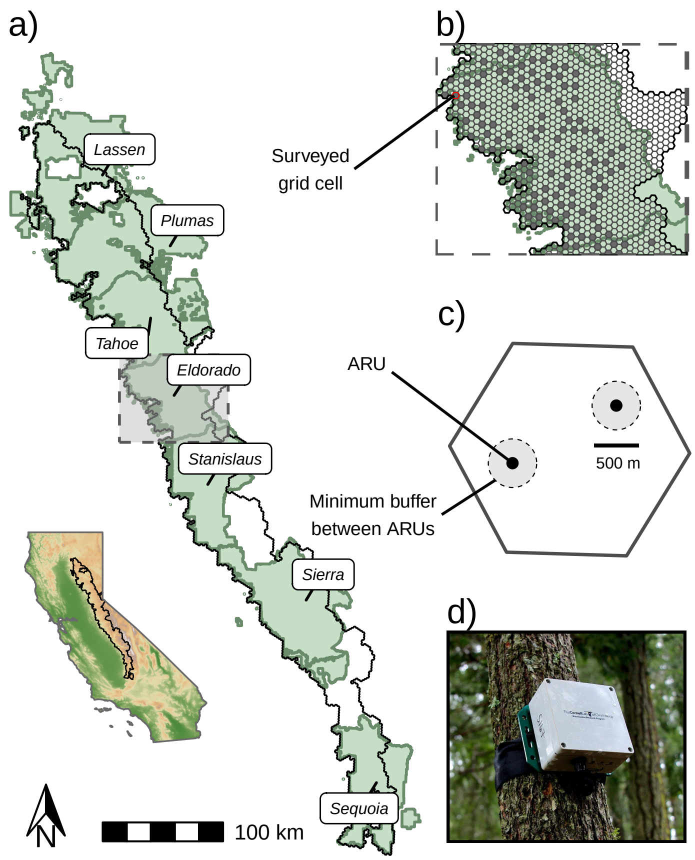

Figure 1: California spotted owl passive acoustic monitoring study area and design. The study area (a) encompassed suitable spotted owl habitat across seven US National Forests in the Sierra Nevada region of California. We subdivided the study area into a grid of 400 ha hexagonal cells (n = 8,087), which are approximately the size of a spotted owl territory in this region (b). Within each surveyed cell (c), we deployed 1–4 (but generally 2) autonomous recording units (ARUs) at least 500 m apart and in acoustically advantageous locations (e.g., ridgetops). When possible, ARUs were attached to small trees to promote sound detection in all directions (d).

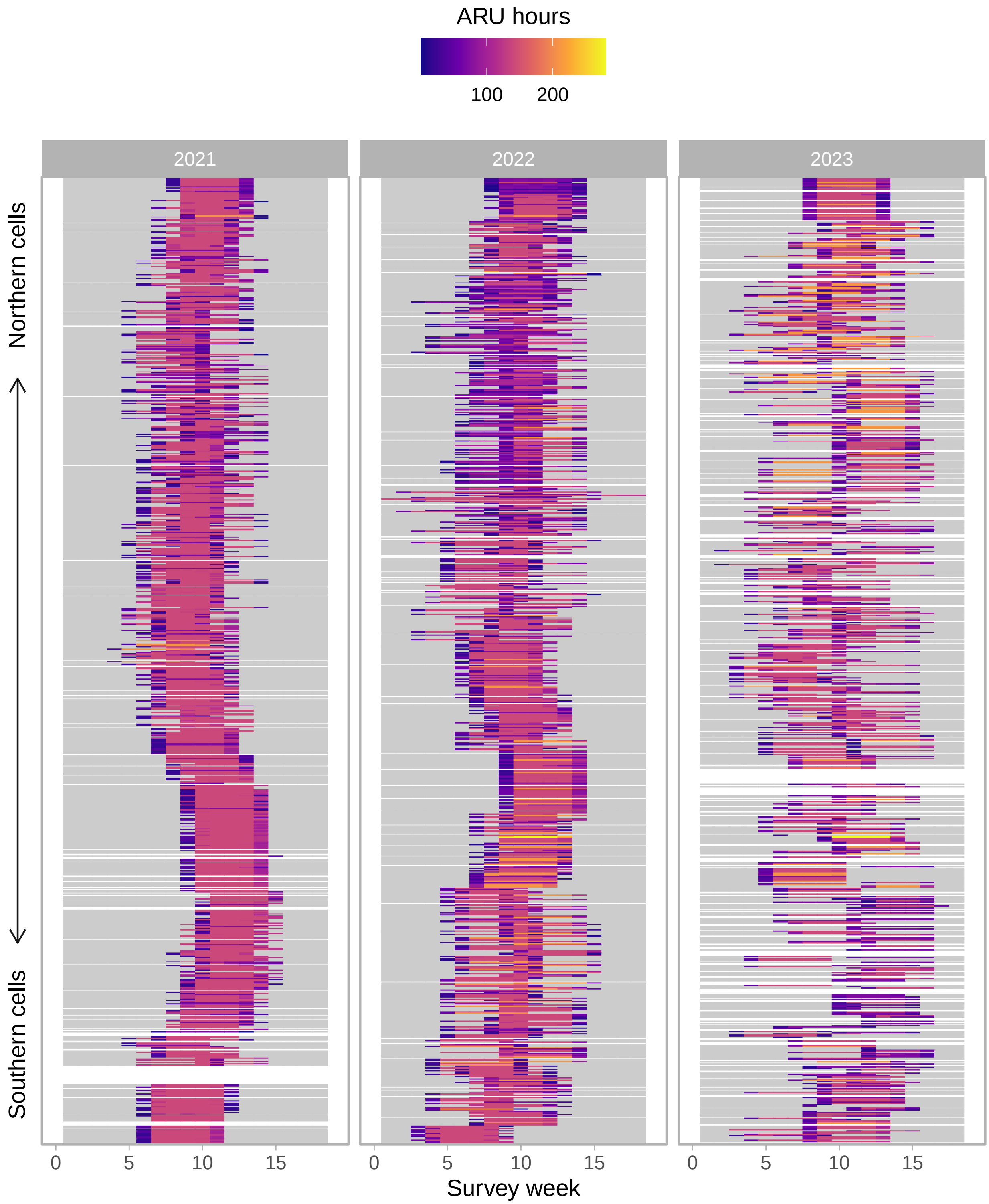

Figure 2: Passive acoustic monitoring effort and timing by hexagonal grid cell in the Sierra Nevada region, 2021–2023. Cells are ordered by latitudinal position, with warmer colors indicating greater survey effort, and gray shading indicating weeks without survey effort. Missing rows show cells that were not surveyed in one or more years.

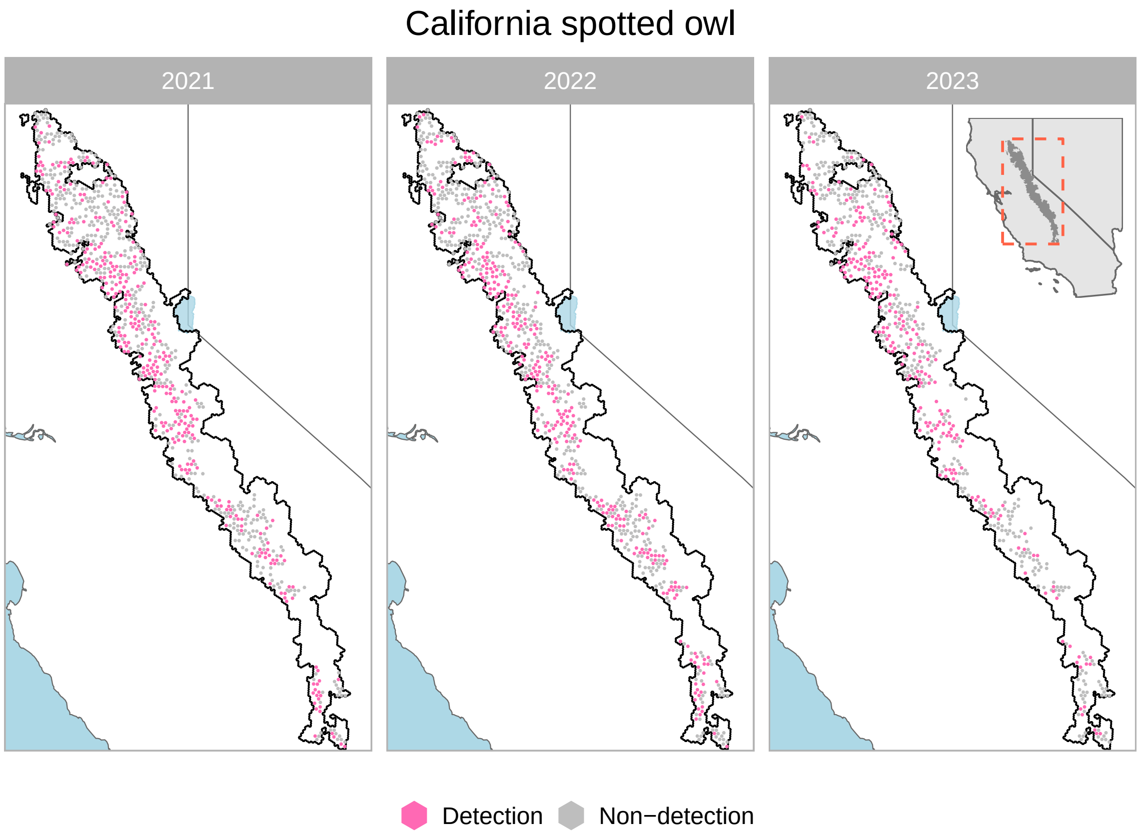

Figure 3: Grid cells with California spotted owl detections (pink hexagons) and non-detections (gray hexagons) in the Sierra Nevada study region (solid black line), 2021–2023.

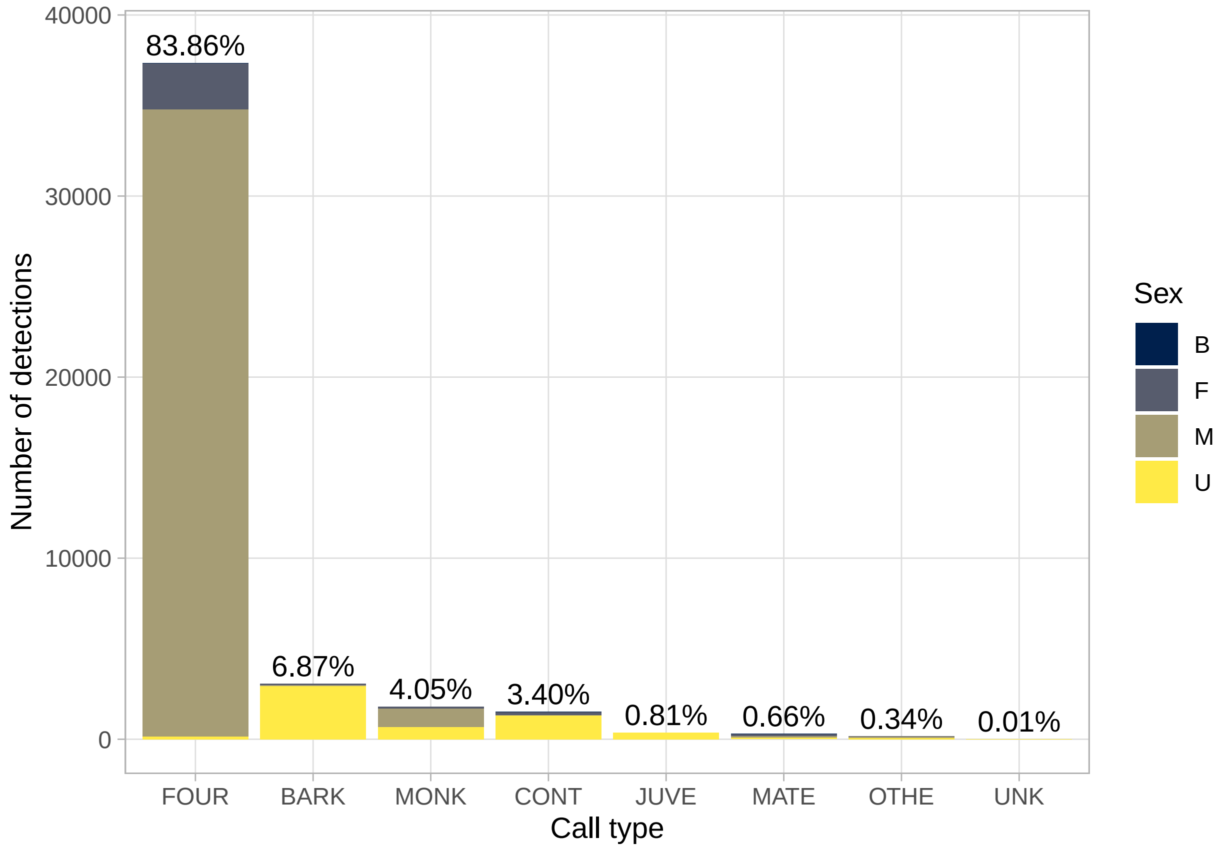

Figure 4: California spotted owl vocalizations in confirmed detections by call type (FOUR = four-note; BARK = bark; MONK = monkey call; CONT = contact call; JUVE = juvenile begging, MATE = mating call; OTHE = other, UNK = unknown) and sex (B = both; F = female; M = male; U = unknown), 2021–2023. Percentage of detections by call type is provided above each bar.

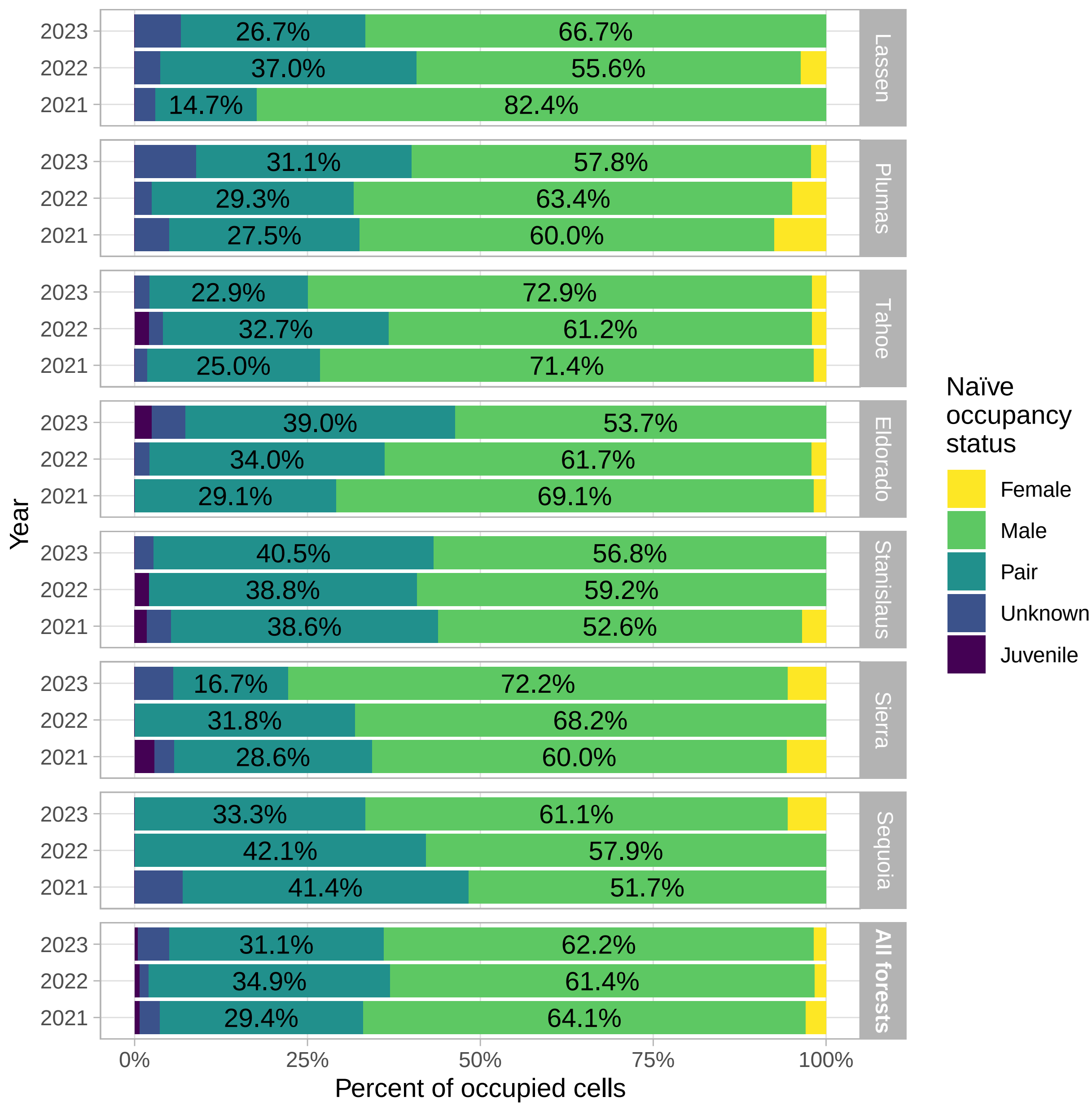

Figure 5: California spotted owl naïve occupancy status (i.e., proportion of cells occupied by spotted owls without accounting for imperfect detection) by national forest, 2021–2023. For clarity, percent labels are provided only for the two most frequent naïve occupancy categories (male only and pair). Juvenile status indicates the presence of a pair.

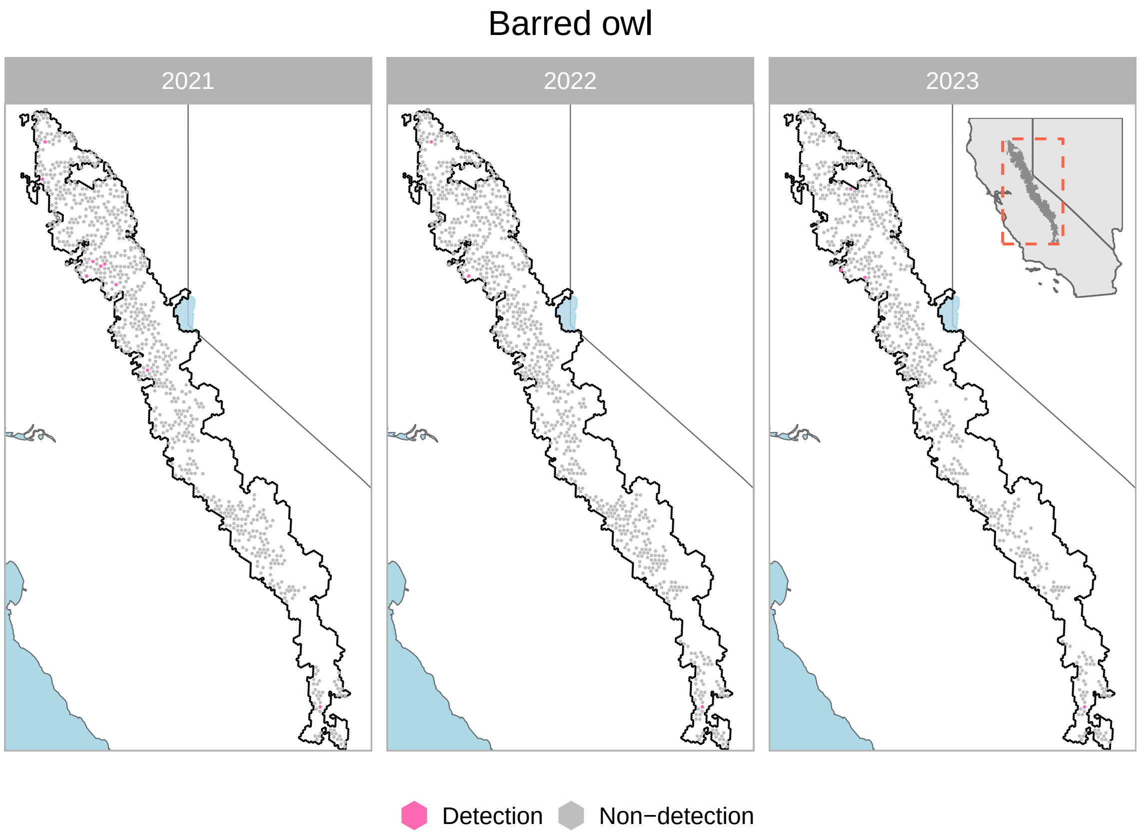

Figure 6: Grid cells with barred owl detections (pink hexagons) and non-detections (gray hexagons) in the Sierra Nevada study region (solid black line), 2021–2023.

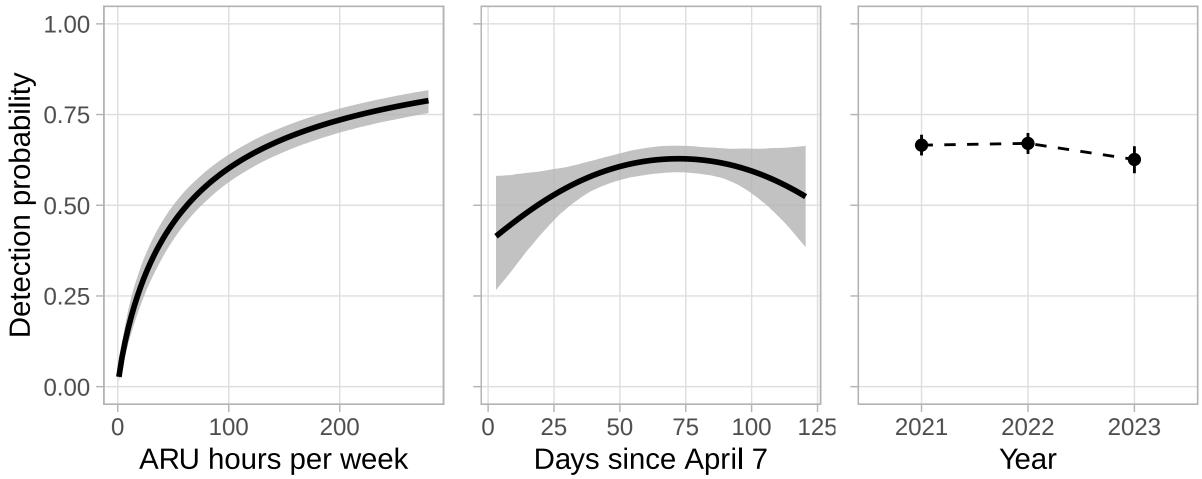

Figure 7: Marginal effects of ARU hours (left panel), date (middle panel), and year (right panel) on detection probability from the strict criteria occupancy model. Mean and 95% credible intervals are shown for each plot. Predictions were made while all other detection covariates were set to their mean values.

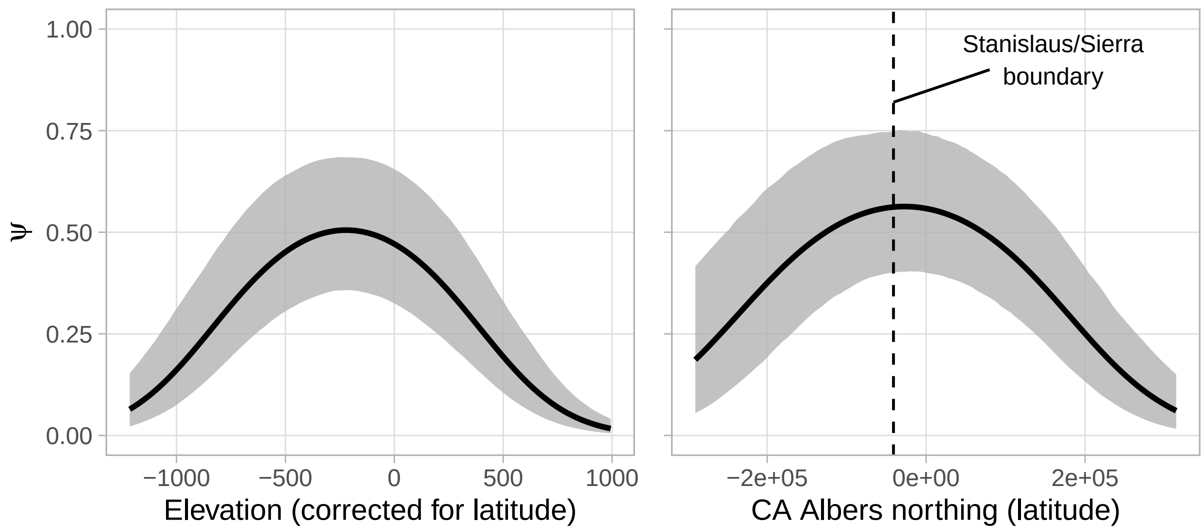

Figure 8: Marginal effects of elevation (controlling for latitude; left panel), and northing (latitude in California Albers projection; right panel) on occupancy probability ψ from the strict criteria model. Black lines and shading represent mean and 95% credible intervals, respectively. Predictions were made while all other occupancy covariates were set to their mean values, and did not include the forest-level random effect.

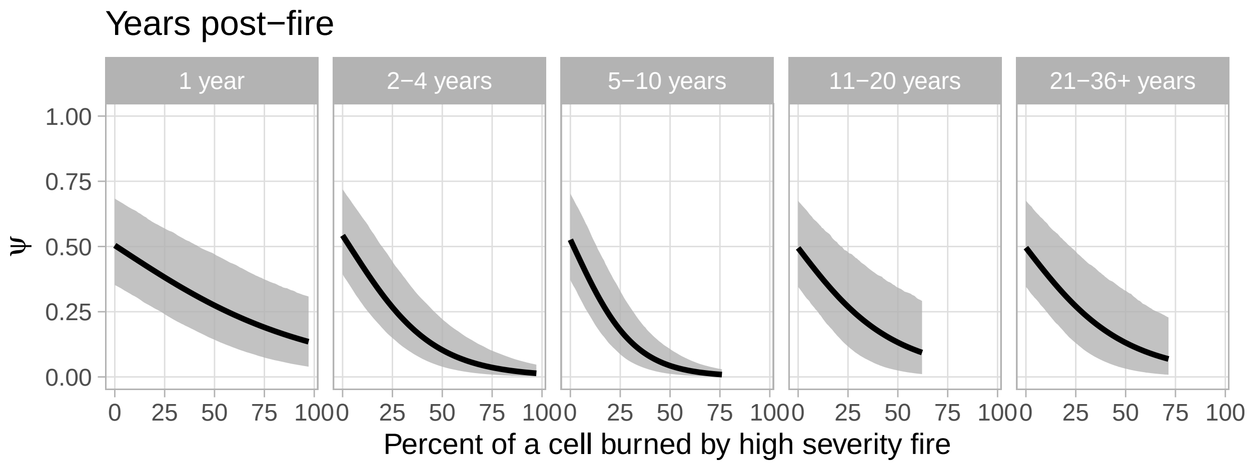

Figure 9: Marginal effects of the percent of a cell that is burned by high severity fire across early forest regeneration stages on occupancy probability ψ from the strict criteria model. Black lines and shading represent mean and 95% credible intervals, respectively. Predictions were made while all other occupancy covariates were set to their mean values, and did not include the forest-level random effect.

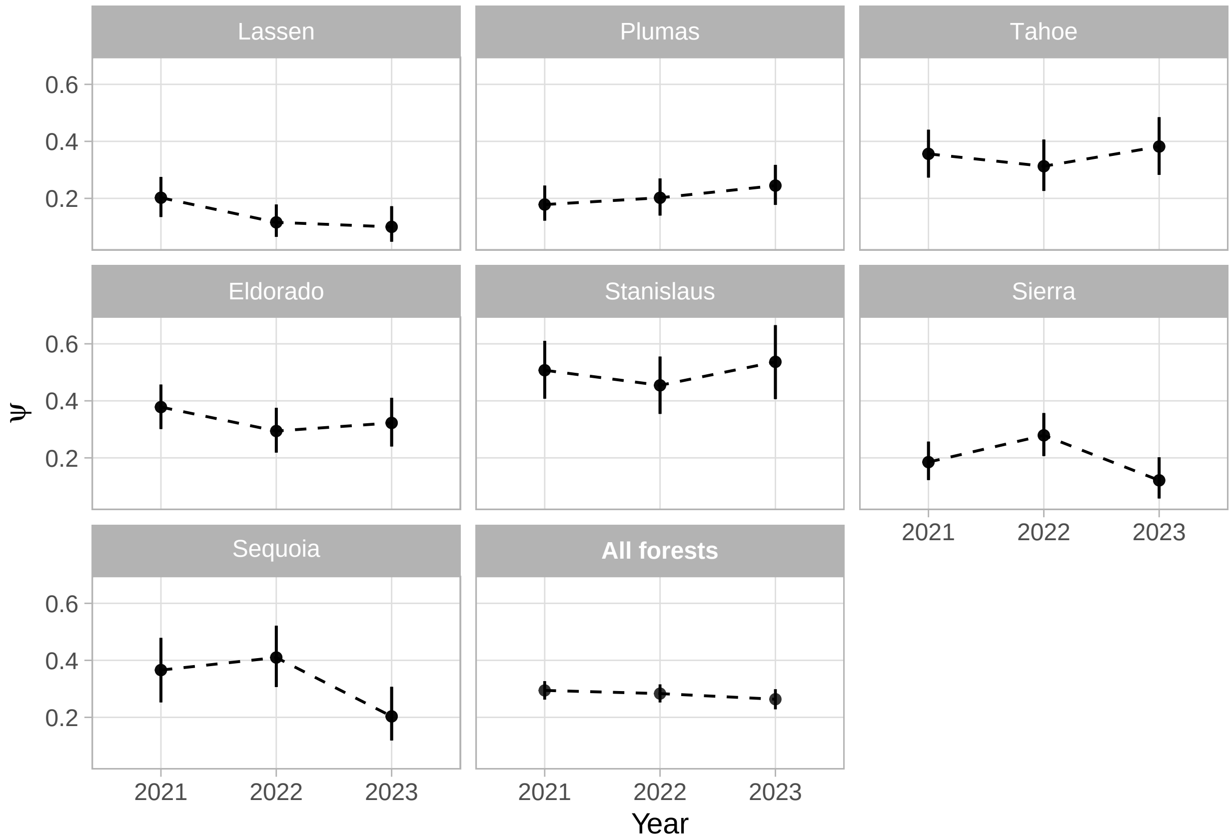

Figure 10: Predicted occupancy probability ψ (i.e., proportion of cells that are occupied after accounting for imperfect detection) by forest and year from the strict criteria occupancy model. Black points and lines represent mean and 95% credible intervals, respectively.