California Spotted Owl Passive Acoustic Monitoring Program: Final Annual Report (2021–2022)

Jason M. Winiarski[1], Kevin G. Kelly[1], Sheila A. Whitmore[1], Jonathan P. Eiseman[1], Erin C. Netoskie[1], H. Anu Kramer[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 two years of surveys, 2021 and 2022. 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 Mountains. In 2021, this effort included 1,488 recording units deployed in 764 400-ha grid cells. In 2022, this effort was increased to 1,606 units in 773 grid cells.
- The probability of detecting an owl over a 5-week survey period, if present, was 96.5% when only one night of detections was required to assign occupancy to a survey cell, and 99.1% when at least two nights of detections were required.
- California spotted owls were widespread across the Sierra Nevada (see Figure 2) and were detected on all 7 surveyed forests. They were most common at low to middle elevations with the highest occupancy rates occurring near the Stanislaus-Sierra boundary.
- California spotted owl site occupancy (proportion of sites occupied after correcting for imperfect detection) ranged from 0.243 on the Lassen National Forest in 2022 to 0.617 on the Stanislaus National Forest in 2021 when only a single night of detections was required to assign occupancy to a survey cell (see Table 5). Occupancy rates were approximately 34% lower when two nights of detections were required.
- Site occupancy across the region did not differ significantly between 2021 (0.426) and 2022 (0.400), whereas individual forest occupancy rates varied more between years (see Table 5 and Figure 9).
- 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 35 years prior to surveys (see Figure 8) – with 1-year post-fire effects largely occurring in response to the Caldor and Dixie fires. 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.
- Naïve barred owl site occupancy was very low owing to a successful lethal removal study, with only 9 occupied cells in 2021 and 3 occupied cells in 2022. Barred owls were detected on 4 forests: Lassen, Tahoe, Eldorado, and Sequoia (see Figure 5).

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 two years (2021 and 2022) 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 6,236 400-ha hexagonal grid cells, which are approximately the size of a spotted owl territory in this region (Tempel et al. 2014a). Our total sampling area of 2,449,400 ha (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, 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 grid 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 three, 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 21–35+ 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 1984–2021 were assigned to the 21–35+ 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 in 2021 and 2022 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 two 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 (in hours; summed across ARUs within a cell) and date:

$$logit(p_{ij}) = \alpha_0 + \alpha_1 \times ARU_{hours} + \alpha_2 \times date_{ij} + \alpha_3 \times date_{ij}^2$$

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):

$$\begin{aligned} logit(\psi_i) = & \beta_0 + \beta_{forest[i]} + \beta_1 \times elevation_i + \beta_2 \times elevation_i^2 + \beta_3 \times northing_i + \beta_4 \times northing_i^2 + \\ & \beta_5 \times high.severity.1yr_i + \beta_6 \times high.severity.2-5yrs_i + \beta_7 \times high.severity.6-10yrs_i + \\ & \beta_8 \times high.severity.11-20yrs_i + \beta_9 \times high.severity.21-35yrs_i + \beta_{10} \times year_i \end{aligned}$$

We also allowed ψ to vary by national forest with a random intercept to account for forest-level variation (models with a random cell-level intercept did not converge). To provide Sierra Nevada-wide and forest-specific annual trends in occupancy, we built additional liberal and strict models. To estimate Sierra Nevada-wide site occupancy rates in 2021 and 2022, we used a model that only contained a fixed effect of year and a national forest random intercept for occupancy. To estimate site occupancy trends for each national forest, we included a year by national forest interaction. 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

4.1 Passive acoustic survey effort

In 2021, we deployed 1,488 ARUs in 764 surveyed grid cells, with an average of 1.95 ARUs deployed per cell (Table 1). We increased our survey effort slightly in 2022, deploying 1,606 ARUs in 773 cells, with an average of 2.08 ARUs deployed per cell. We monitored 835 unique cells across years, of which 84% (n = 702) were monitored in both 2021 and 2022. Surveys were initiated approximately one month earlier (earliest ARU recording = 7 April) and concluded month later (latest ARU recording = 8 August) in 2022 than 2021. In total, we recorded >490,000 and >512,000 hours of audio data in 2021 and 2022, respectively. Deployments spanned almost all of the suitable California spotted owl habitat on the west slope of the Sierra Nevada ecosystem (Figure 2).

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 ≥ 0.989) across the Sierra Nevada region and in each national forest (Table 2, Figure 2). Our manual review yielded 17,324 confirmed spotted owl detections in 2021, and 16,062 confirmed detections in 2022. Of these detections, the vast majority were male four-note vocalizations (77.8%; Figure 3). Naïve occupancy of spotted owls was lowest in Lassen National Forest (0.283 in 2021; 0.237 in 2022) and highest in Stanislaus National Forest (0.606 in 2021; 0.505 in 2022). Within occupied cells, most detections came from males only (51.6%–82.4% of occupied cells), followed by pairs (14.7%–42.1%), females only (0%–7.5%), unknown sex owls only (0%–6.5%), and juveniles (0%–2.78%; Figure 4).

Barred owls were only detected in four national forests: Lassen, Tahoe, Eldorado, and Sequoia (Table 3, Figure 5). There were also fewer confirmed detections compared with spotted owls (n = 1,174 in 2021; n = 572 in 2022) and lower naïve occupancy, which did not exceed 0.043. Only three cells had barred owl detections in 2022, yielding a naïve occupancy rate of 0.004.

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 6). The linear and quadratic effects of date were uncertain for the liberal model, but spotted owls were detected more often later in the season for the strict model. There was some evidence for a non-linear effect of date for the strict model (Figure 6), 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 were 0.488 (95% CRI: 0.468–0.505) and 0.622 (95% CRI: 0.603–0.641), translating to a 96.5% and 99.1% chance of detecting a spotted owl if it was present at a site during a typical 5-week ARU survey.

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 model (Table 4, Figure 7). Occupancy was similar in 2021 and 2022 for both detection criteria models. 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 8).

Spotted owls were well distributed across the Sierra Nevada, with a mean occupancy probability of 0.426 in 2021 (95% CRI: 0.315–0.552) and 0.400 in 2022 for the liberal model (95% CRI: 0.291–0.524; Table 5 and Figure 9). Mean occupancy probabilities for the strict model were 0.304 in 2021 (95% CRI: 0.193–0.429) and 0.290 in 2022 (95% CRI: 0.188–0.411). Occupancy probabilities varied widely across forests, with the lowest liberal mean occupancy of 0.243 (95% CRI: 0.172–0.323) in Lassen National Forest in 2022 and highest liberal mean occupancy of 0.617 (95% CRI: 0.517–0.712) in Stanislaus National Forest in 2021. Occupancy patterns were similar but lower for the strict model (Lassen National Forest mean occupancy in 2022 = 0.117 [95% CRI: 0.065–0.179]; Stanislaus National Forest mean occupancy in 2021 = 0.503 [95% CRI: 0.401–0.602]). There was no significant difference in Sierra Nevada-wide occupancy between 2021 and 2022, but there was a positive effect of year for the strict occupancy model with a year × forest interaction ($\beta_{year:Sierra}$ = 0.922; 95% CRI: 0.517–0.712).

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 two years surveys were conducted (liberal = 0.426 and 0.400; strict = 0.304 and 0.290), 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 0.057–0.059 for the liberal model and 0.055–0.057 for the strict model in 2021 and 2022, respectively. National forest-specific estimates fluctuated more between the two years (Table 5, Figure 9), but were also estimated with reasonable precision. Thus, monitoring California spotted owls at the scale of individual forests may also be feasible with longer term surveys. Thus, while it is premature to estimate trends in occupancy, the first two 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 35 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*). Consistent with this finding, the Eldorado and Lassen National Forests, which were burned by the Caldor and Dixie fires following 2021 surveys, exhibited the greatest proportional declines in site occupancy between 2021 and 2022. 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 2). 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 in 2021 and 2022 as part of this study were only 0.012 and 0.004, respectively, indicating that barred owls continue to remain at very low densities across the Sierra Nevada bioregion. Indeed, three 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 to 2022 (39 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, 2021–2022.

Year	Survey period	Cells surveyed	ARUs deployed	ARU hours
2021	May 03–July 19	764	1,488	494,768
2022	April 07–August 08	773	1,606	512,161

Table 2: California spotted owl detections and naïve occupancy by national forest, 2021–2022.

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
Plumas	2021	1,015	106	40	146	0.274
	2022	1,092	102	41	143	0.287
Tahoe	2021	4,105	62	55	117	0.470
	2022	2,498	53	47	100	0.470
Eldorado	2021	1,856	48	55	103	0.534
	2022	1,727	60	46	106	0.434
Stanislaus	2021	4,551	37	57	94	0.606
	2022	4,398	48	49	97	0.505
Sierra	2021	958	79	36	115	0.313
	2022	2,544	84	44	128	0.344
Sequoia	2021	3,667	38	31	69	0.449
	2022	2,989	47	38	85	0.447
All forests	2021	17,324	456	308	764	0.403
	2022	16,062	481	292	773	0.378

* Naïve occupancy is defined as the proportion of surveyed cells with at least one spotted owl observation.

Table 3: Barred owl detections and naïve occupancy by national forest, 2021–2022.

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
Plumas	2021	0	146	0	146	0.000
	2022	0	143	0	143	0.000
Tahoe	2021	1,110	112	5	117	0.043
	2022	443	99	1	100	0.010
Eldorado	2021	1	102	1	103	0.010
	2022	0	106	0	106	0.000
Stanislaus	2021	0	94	0	94	0.000
	2022	0	97	0	97	0.000
Sierra	2021	0	115	0	115	0.000
	2022	0	128	0	128	0.000
Sequoia	2021	16	68	1	69	0.014
	2022	98	84	1	85	0.012
All forests	2021	1,174	755	9	764	0.012
	2022	572	770	3	773	0.004

* Naïve occupancy is defined as the proportion of surveyed cells with at least one spotted owl observation.

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 and 2022. 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	-0.05	0.04	-0.13	0.02	TRUE
		Date	0.22	0.24	-0.25	0.68	TRUE
		$Date^{2*}$	-0.14	0.24	-0.59	0.33	TRUE
		ARU hours	0.52	0.04	0.44	0.59	FALSE
	Occupancy	Intercept	-0.53	0.20	-0.92	-0.10	FALSE
		Elevation	-0.41	0.07	-0.55	-0.27	FALSE
		$Elevation^{2\dagger}$	-0.66	0.08	-0.81	-0.51	FALSE
		Northing	-0.31	0.17	-0.67	0.02	TRUE
		$Northing^{2\ddagger}$	-0.43	0.13	-0.70	-0.19	FALSE
		% High severity (1 yr)	-0.25	0.07	-0.39	-0.12	FALSE
		% High severity (2-4 yrs)	-0.57	0.13	-0.83	-0.34	FALSE
		% High severity (5-10 yrs)	-0.56	0.09	-0.75	-0.39	FALSE
		% High severity (11-20 yrs)	-0.30	0.09	-0.49	-0.15	FALSE
		% High severity (21-35 yrs)	-0.22	0.07	-0.37	-0.09	FALSE
		Year (2022)	0.03	0.12	-0.20	0.26	TRUE
		σ_{Forest}	0.48	0.21	0.20	1.02	FALSE
Strict	*Detection*	Intercept	0.50	0.04	0.42	0.58	FALSE
		Date	0.55	0.28	0.01	1.09	FALSE
		$Date^2$	-0.44	0.28	-0.97	0.09	TRUE
		ARU hours	0.55	0.04	0.47	0.64	FALSE
	Occupancy	Intercept	-1.17	0.30	-1.77	-0.54	FALSE
		Elevation	-0.44	0.07	-0.59	-0.30	FALSE
		$Elevation^2$	-0.66	0.08	-0.83	-0.50	FALSE
		Northing	-0.40	0.20	-0.80	-0.02	FALSE
		$Northing^2$	-0.64	0.16	-0.98	-0.34	FALSE
		% High severity (1 yr)	-0.30	0.08	-0.46	-0.15	FALSE
		% High severity (2-4 yrs)	-0.65	0.16	-0.99	-0.36	FALSE
		% High severity (5-10 yrs)	-0.65	0.12	-0.90	-0.44	FALSE
		% High severity (11-20 yrs)	-0.32	0.11	-0.56	-0.14	FALSE
		% High severity (21-35 yrs)	-0.19	0.07	-0.34	-0.06	FALSE
		Year (2022)	0.08	0.12	-0.17	0.32	TRUE
		σ_{Forest}	0.67	0.28	0.29	1.39	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 estimates (mean, standard deviation, and 95% credible intervals) by forest and year from the liberal and strict detection criteria occupancy models. 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	0.297	0.042	0.217	0.384
		2022	0.243	0.039	0.172	0.323
	Plumas	2021	0.289	0.037	0.221	0.365
		2022	0.300	0.038	0.227	0.376
	Tahoe	2021	0.482	0.045	0.394	0.570
		2022	0.484	0.051	0.385	0.582
	Eldorado	2021	0.522	0.043	0.436	0.605
		2022	0.453	0.046	0.364	0.547
	Stanislaus	2021	0.617	0.050	0.517	0.712
		2022	0.515	0.051	0.414	0.611
	Sierra	2021	0.327	0.043	0.245	0.412
		2022	0.348	0.043	0.267	0.434
	Sequoia	2021	0.459	0.060	0.347	0.579
		2022	0.454	0.055	0.344	0.563
	All forests	2021	0.426	0.059	0.315	0.552
		2022	0.400	0.057	0.291	0.524
Strict	Lassen	2021	0.205	0.035	0.140	0.278
		2022	0.117	0.029	0.065	0.179
	Plumas	2021	0.179	0.030	0.123	0.242
		2022	0.204	0.035	0.142	0.278
	Tahoe	2021	0.354	0.043	0.275	0.437
		2022	0.312	0.046	0.225	0.407
	Eldorado	2021	0.379	0.042	0.296	0.460
		2022	0.297	0.041	0.219	0.380
	Stanislaus	2021	0.503	0.051	0.401	0.602
		2022	0.456	0.051	0.358	0.556
	Sierra	2021	0.184	0.035	0.121	0.257
		2022	0.280	0.038	0.205	0.357
	Sequoia	2021	0.367	0.056	0.261	0.480
		2022	0.410	0.052	0.312	0.516
	All forests	2021	0.304	0.057	0.193	0.429
		2022	0.290	0.055	0.188	0.411

9 Figures

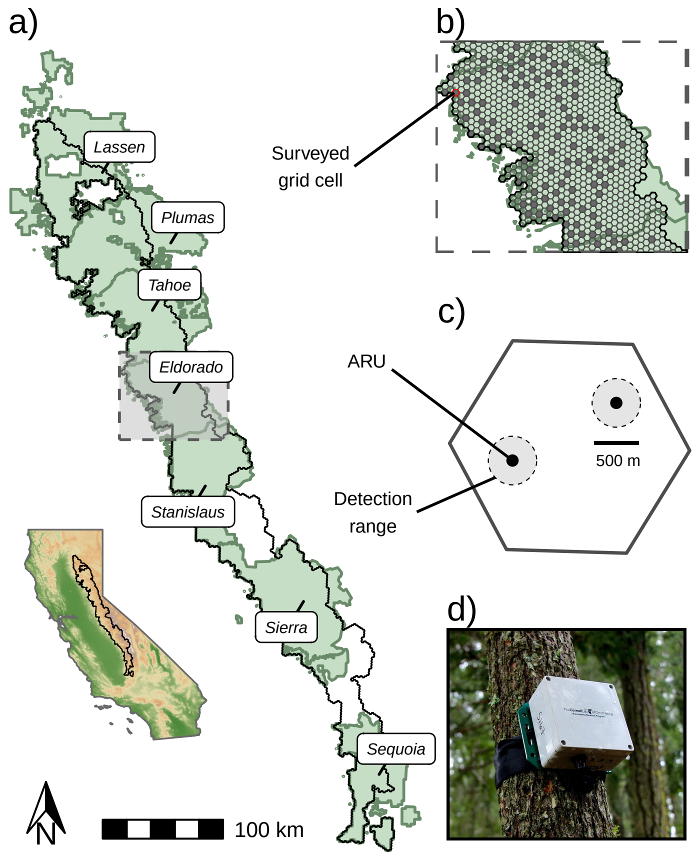

Figure 1: California spotted owl passive acoustic monitoring study area and design. The study area (a) encompassed suitable spotted owl habitat across seven US National Forests in the Sierra Nevada region of California. We subdivided the study area into a grid of 400 ha hexagonal cells (n = 7,489), which are approximately the size of a spotted owl territory in this region (b). Within each surveyed cell (c), we deployed 1–3 (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).

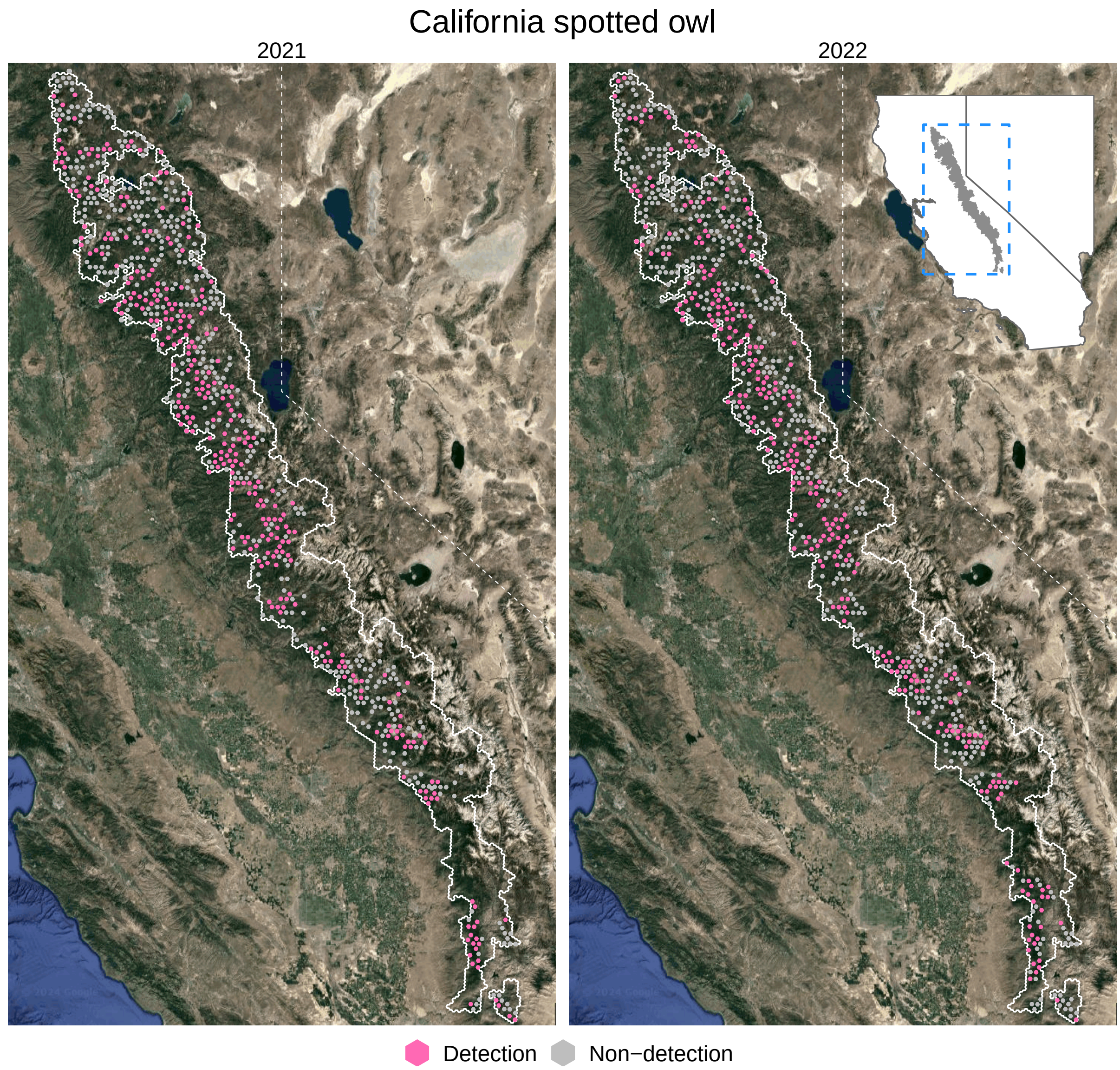

Figure 2: Grid cells with California spotted owl detections (pink hexagons) and non-detections (gray hexagons) in the Sierra Nevada study region (solid white line), 2021–2022.

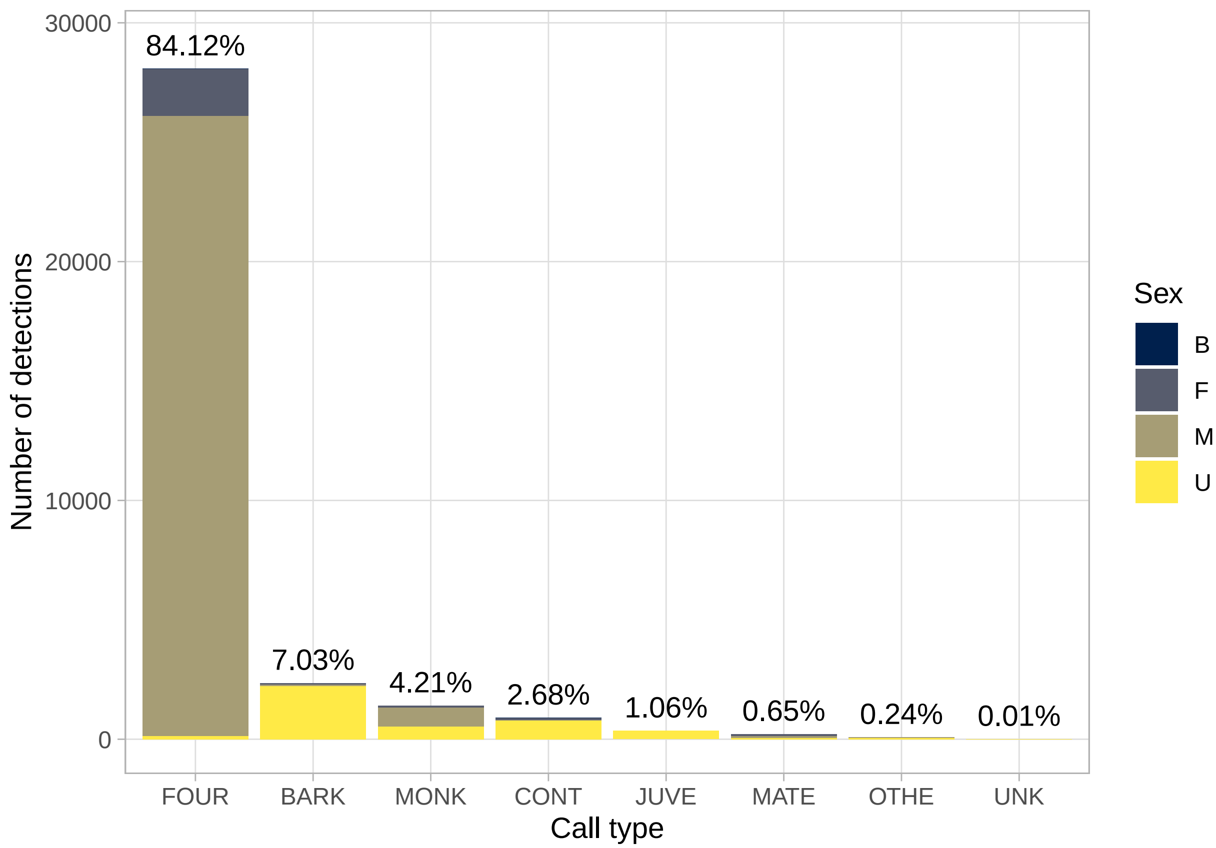

Figure 3: California spotted owl vocalizations in confirmed detections by call type (FOUR = four-note; BARK = bark; MONK = monkey call; CONT = contact call; JUVE = juvenile begging, MATE = mating call; OTHE = other, UNK = unknown) and sex (B = both; F = female; M = male; U = unknown), 2021–2022. Percentage of detections by call type is provided above each bar.

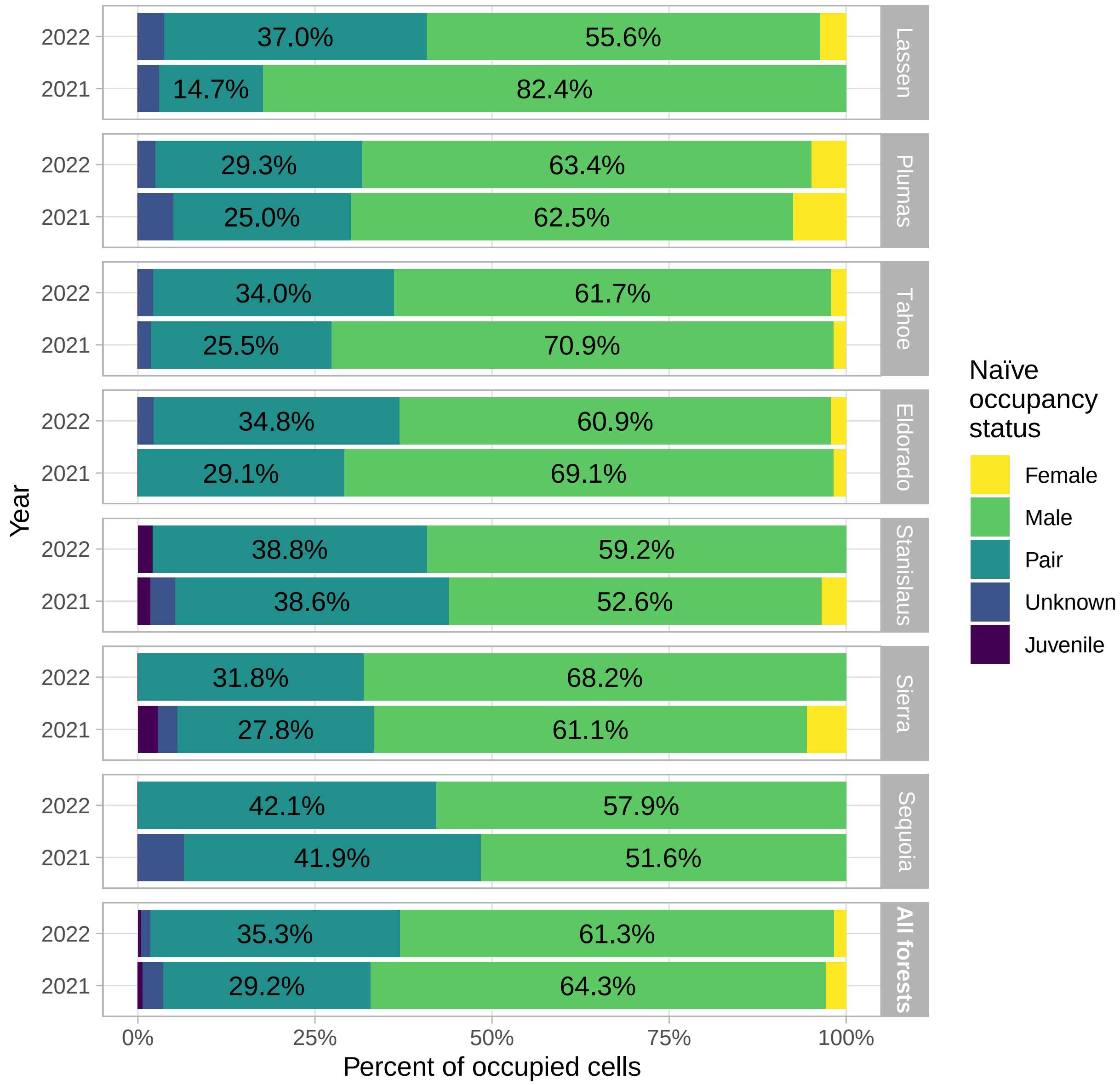

Figure 4: California spotted owl naïve occupancy status (not accounting for imperfect detection) by national forest, 2021–2022. For clarity, percent labels are provided only for the two most frequent naïve occupancy categories (male only and pair). Juvenile status indicates the presence of a pair.

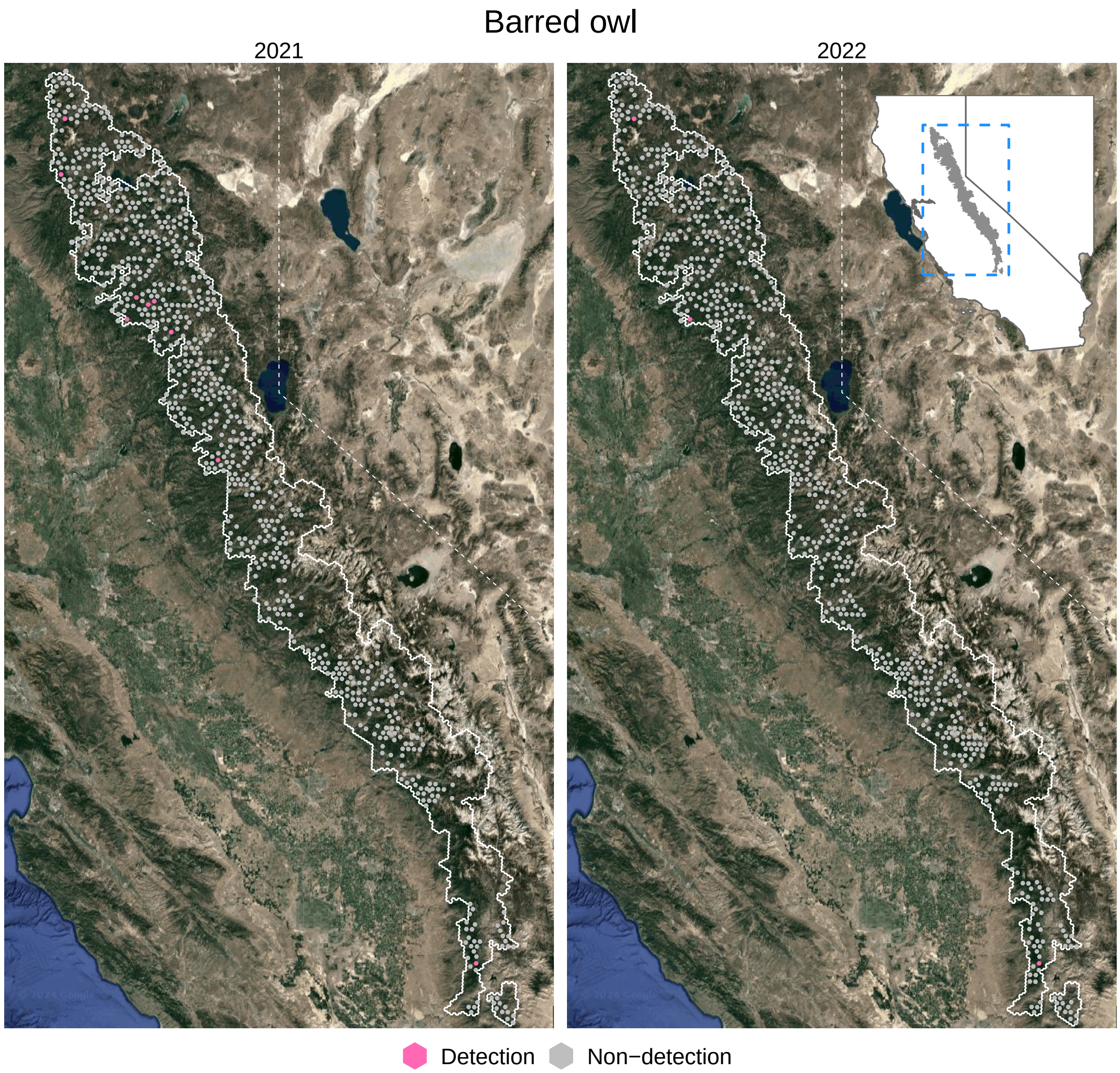

Figure 5: Grid cells with barred owl detections (pink hexagons) and non-detections (gray hexagons) in the Sierra Nevada study region (solid white line), 2021–2022.

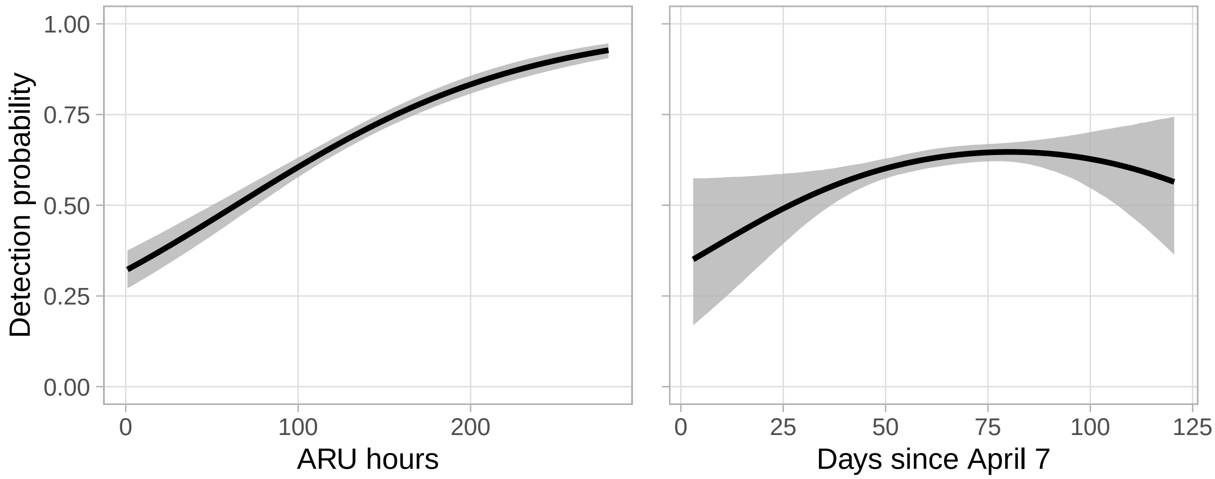

Figure 6: Marginal effects of ARU hours (left panel) and date (right panel) on detection probability from the strict criteria occupancy model. Black lines and shading represent mean and 95% credible intervals, respectively. Predictions were made while all other detection covariates were set to their mean values.

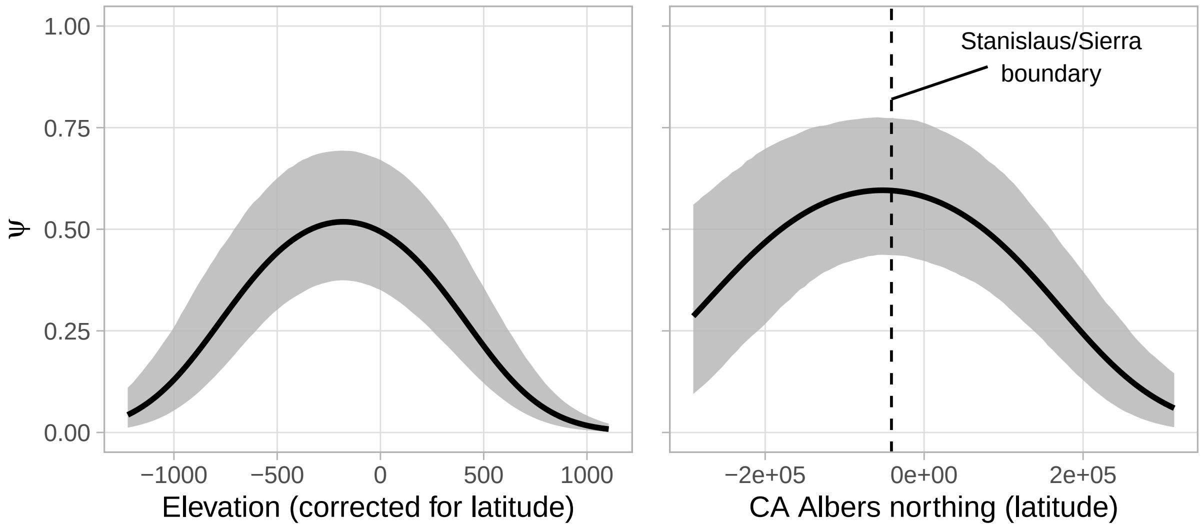

Figure 7: Marginal effects of elevation (controlling for latitude; left panel), and northing (latitude in California Albers projection; right panel) on occupancy probability ψ from the strict criteria model. Black lines and shading represent mean and 95% credible intervals, respectively. Predictions were made while all other occupancy covariates were set to their mean values, and did not include the forest-level random effect.

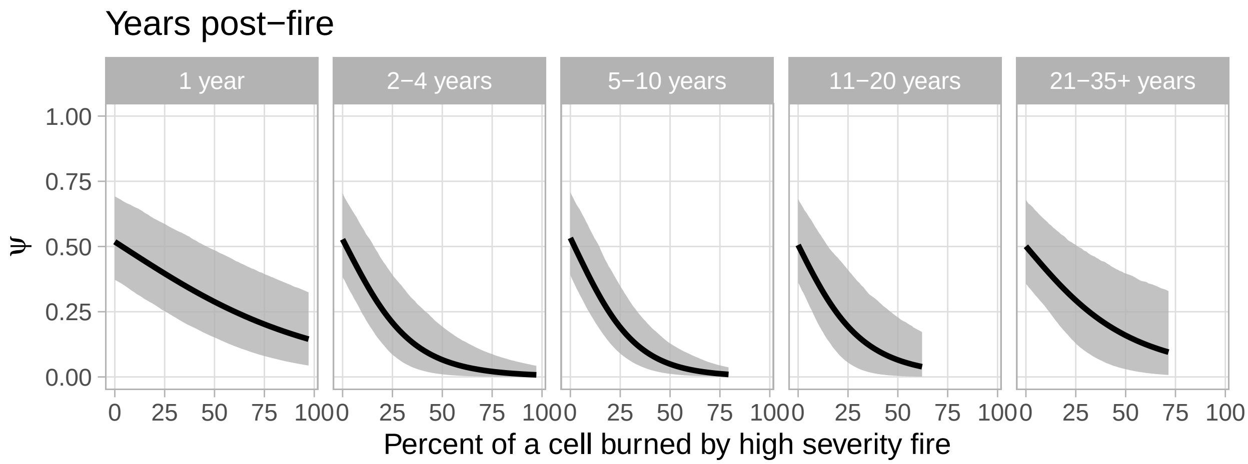

Figure 8: Marginal effects of the percent of a cell that is burned by high severity fire across early forest regeneration stages on occupancy probability ψ from the strict criteria model. Black lines and shading represent mean and 95% credible intervals, respectively. Predictions were made while all other occupancy covariates were set to their mean values, and did not include the forest-level random effect.

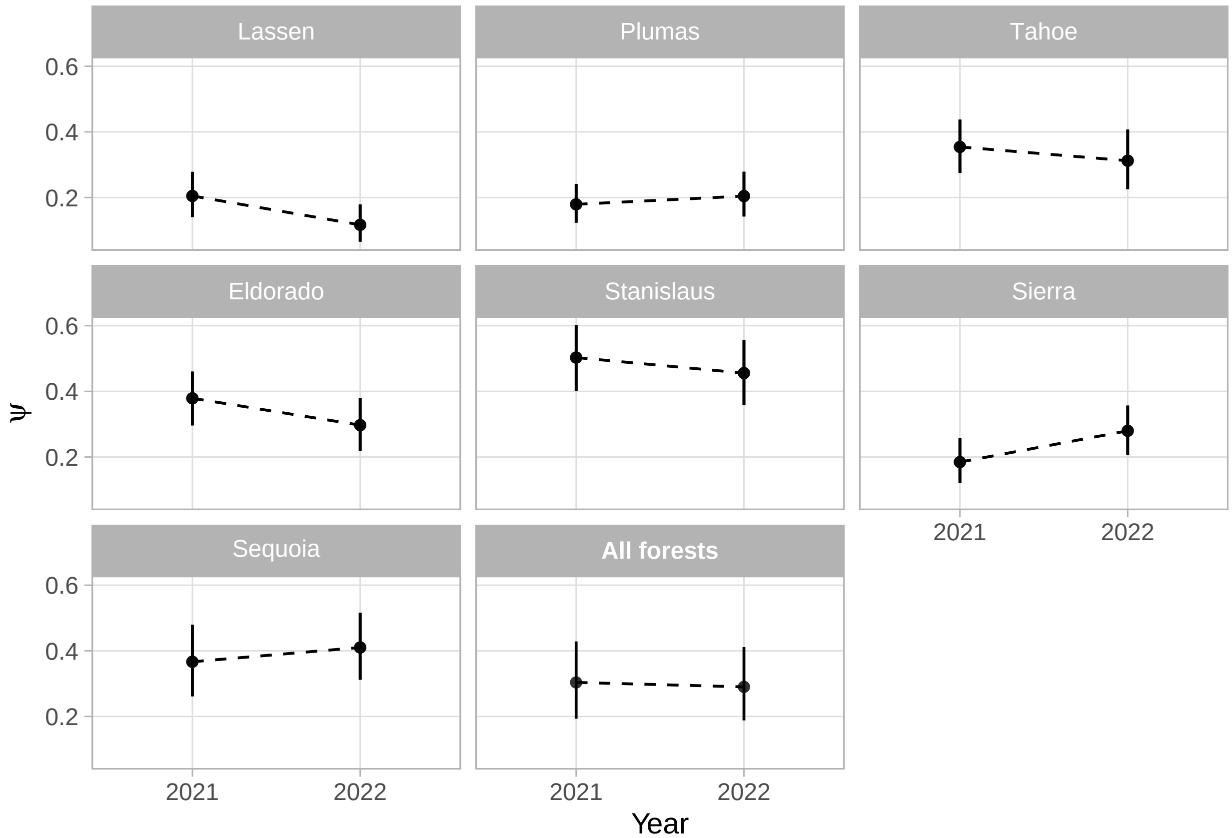

Figure 9: Predicted occupancy probability ψ by forest and year from the strict criteria occupancy model. Black points and lines represent mean and 95% credible intervals, respectively.