

Passive acoustic monitoring indicates Barred Owls are established in northern coastal California and management intervention is warranted

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ABSTRACT

Barred Owls (*Strix varia*) have recently expanded westward from eastern North America, contributing to substantial declines in Northern Spotted Owls (*Strix occidentalis caurina*). Passive acoustic monitoring (PAM) represents a potentially powerful approach for tracking range expansions like the Barred Owl's, but further methods development is needed to ensure that PAM-informed occupancy models meaningfully reflect population processes. Focusing on the leading edge of the Barred Owl range expansion in coastal California, we used a combination of PAM data, GPS-tagging, and active surveys to (1) estimate breeding home range size, (2) identify patterns of vocal activity that reflect resident occupancy, and (3) estimate resident occupancy rates. Mean breeding season home range size (452 ha) was reasonably consistent with the size of cells (400 ha) sampled with autonomous recording units (ARUs). Nevertheless, false-positive acoustic detections of Barred Owls frequently occurred within cells not containing an activity center such that site occupancy estimates derived using all detected vocalizations (0.61) were unlikely to be representative of resident occupancy. However, the proportion of survey nights with confirmed vocalizations (VN) and the number of ARUs within a sampling cell with confirmed vocalizations (VU) were indicative of Barred Owl residency. Moreover, the false positive error rate could be reduced for occupancy analyses by establishing thresholds of VN and VU to define detections, although doing so increased false negative error rates in some cases. Using different thresholds of VN and VU, we estimated resident occupancy to be 0.29–0.44, which indicates that Barred Owls have become established in the region but also that timely lethal removals could still help prevent the extirpation of Northern Spotted Owls. Our findings provide a scalable framework for monitoring Barred Owl populations throughout their expanded range and, more broadly, a basis for converting site occupancy to resident occupancy in PAM programs.

Keywords: autonomous recording units, Barred Owl, bioacoustics, occupancy, passive acoustic monitoring, range expansion, Spotted Owl, *Strix varia*, *Strix occidentalis*

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LAY SUMMARY

- The range of the Barred Owl has expanded to overlap that of the Northern Spotted Owl, and Barred Owls have contributed to the Northern Spotted Owl population declines.
- Monitoring Barred Owl populations is critical for Northern Spotted Owl and western forest ecosystem conservation.
- Passive acoustic monitoring is increasingly being used to estimate occupancy rates of Barred Owls, but how well these estimates reflect actual population status has not been well studied.
- We compared passive acoustic survey results to active, in-person survey results in Coastal California to identify Barred Owl vocal activity patterns that most reflect the actual presence of resident Barred Owls.
- We set thresholds in measures of vocal activity to refine our estimate of Barred Owl occupancy, and found the occupancy rate of Barred Owls in our study area to be between 0.29 and 0.44.
- Our occupancy estimate indicates that management intervention in the form of lethal removal could prevent further Northern Spotted Owl population decline in this region.

El monitoreo acústico pasivo indica que *Strix varia* está establecida en el norte de la costa de California y se justifica la intervención de manejo

RESUMEN

Strix varia se ha expandido recientemente hacia el oeste desde el este de América del Norte, contribuyendo a una disminución sustancial de *Strix occidentalis caurina*. El monitoreo acústico pasivo (MAP) representa un enfoque potencialmente poderoso para seguir las expansiones de rango como la de *S. varia*, pero se necesita un mayor desarrollo de los métodos para garantizar que los modelos de ocupación informados por el MAP reflejen adecuadamente los procesos poblacionales. Haciendo foco en el borde de la expansión del rango de *S. varia* en la costa de California, utilizamos una combinación de datos de MAP, etiquetado GPS y censos activos para (1) estimar el tamaño del área de hogar reproductiva, (2) identificar patrones de actividad vocal que reflejen la ocupación residente, y (3) estimar las tasas de ocupación residente. El tamaño promedio del área de hogar durante la temporada reproductiva (452 ha) fue razonablemente consistente con el tamaño de las celdas (400 ha) muestreadas con unidades de grabación autónomas (UGAs). No obstante, las detecciones acústicas falsas positivas de *S. varia* ocurrieron con frecuencia dentro de celdas que no contenían un centro de actividad, por lo que es poco probable que las estimaciones de ocupación del sitio derivadas del uso de todas las vocalizaciones detectadas (0.61) representen la ocupación residente. Sin embargo, la proporción de noches de censo con vocalizaciones confirmadas (VN) y el número de UGAs dentro de una celda de muestreo con vocalizaciones confirmadas (VU) fueron indicativas de la condición de residencia de *S. varia*. Además, la tasa de errores falsos positivos podría reducirse para los análisis de ocupación estableciendo umbrales de VN y VU para definir las detecciones, aunque hacer esto aumentó las tasas de errores falsos negativos en algunos casos. Usando diferentes umbrales de VN y VU, estimamos que la ocupación residente fue de 0.29–0.44, lo que indica que *S. varia* se ha establecido en la región, pero también que las eliminaciones letales oportunas aún podrían ayudar a prevenir la extirpación de *S. o. caurina*. Nuestros hallazgos proporcionan un marco escalable para monitorear las poblaciones de *S. varia* a lo largo de su rango expandido y, más ampliamente, la base para convertir la ocupación de sitio en ocupación residente en los programas de MAP.

Palabras clave: bioacústica, expansión de rango, monitoreo acústico pasivo, ocupación, *Strix varia*, *Strix occidentalis*, unidades de grabación autónomas

INTRODUCTION

Environmental change has led to shifts in species' ranges across the globe (Dornelas *et al.* 2014), with land use and climate change allowing certain species to overcome barriers to dispersal and expand their ranges into new ecosystems (Hansen *et al.* 2001). Biotic interactions between species undergoing range expansion and native species in colonized ecosystems can have significant deleterious effects on biodiversity, the structure of biological communities, and ecosystem processes (Holt 2003, Carey *et al.* 2012). With species range expansions increasingly occurring in continental systems comes the need to monitor the progress of these expansions and their ecological impact at broad geographic scales (McGeoch and Latombe 2016). Yet, surveying rapidly expanding species poses special challenges given the dynamic nature of their distributions in space and time.

Barred Owls (*Strix varia*) are a prominent example of a species undergoing an extensive range expansion with substantial adverse ecological effects. Native to the eastern United States, Barred Owls have been expanding westward across North America over the last century, likely facilitated by habitat corridors created in the Great Plains through post-colonial land use changes including fire exclusion and tree planting (Livezey 2009a, Livezey 2009b). Barred Owl populations in their expanded range have undergone rapid population growth and now occur at high densities throughout many forested areas of the Pacific Northwest (Gutiérrez *et al.* 2007, Yackulic *et al.* 2012). Barred Owls inhabit the entire range of the federally threatened Northern Spotted Owl (*S. occidentalis caurina*) and their range has continued to expand through California's coastal region as far south as the San Francisco Bay Area (Dark *et al.* 1998, Jennings *et al.* 2011). Barred Owls have contributed to substantial declines in Northern Spotted Owl populations and likely pose an existential threat to this subspecies, largely through competitive interactions (Kelly *et al.* 2003, Dugger *et al.* 2016, Yackulic *et al.* 2019). Furthermore, as apex generalist predators capable of achieving high densities, Barred Owls potentially threaten

a host of other sensitive taxa, such as frogs, salamanders, and trout, through direct predation (Hamer *et al.* 2001, Wiens *et al.* 2014, Holm *et al.* 2016, Kryshak *et al.* 2022), and may alter biotic forest ecosystem interactions by causing prey switching in sympatric predators or disrupting prey-driven plant and fungus dispersal (Holm *et al.* 2016). Cost-effective yet rigorous monitoring programs over broad spatial scales are needed to understand how Barred Owl populations are expanding in space and time, and to ultimately help target and assess the success of management interventions aimed at reducing Barred Owl populations and limiting their spread (Long and Wolfe 2019).

Passive acoustic monitoring (PAM), or the systematic deployment of autonomous recording units (ARUs) over periods of multiple days or weeks to monitor species populations, lends itself to tracking range expansions of vocally active species such as Barred Owls at broad spatial scales. It can provide large amounts of acoustic data with less effort and with fewer trained observers than traditional active vocal-lure survey methods (Digby *et al.* 2013, Borker *et al.* 2014, Wood *et al.* 2020a), and ARUs can collect data simultaneously at many locations across a wide geographic range. The resulting audio data can then be processed to generate detection/non-detection information for a focal species or group of species, which in turn can be used to estimate occupancy and population change across a landscape (Wood *et al.* 2019a, Abrahams and Geary 2020).

Occupancy models derived from PAM data, however, may not always represent actual population processes (Wood and Peery 2022, Appel *et al.* 2023). A major benefit of PAM is its scalability, or the potential to apply methods to geographic areas of varying size, but this means that ARUs tend to be deployed without knowledge of focal species' habitat use: arbitrarily defined survey grid cells are unlikely to align with the space use of resident animals. Therefore, occupancy rates of grid cells distributed across a landscape, or site occupancy, may not reflect the proportion of the landscape occupied by resident pairs, or resident occupancy (Wood and Peery 2022).

Grid cells may be classified as “occupied” on the basis of a confirmed vocalization from the focal species, yielding estimates of site occupancy (i.e., use of a grid cell). However, the detection of non-resident individuals can yield estimates of site occupancy that are higher than resident occupancy and can be decoupled from changes in population size induced by environmental change, and thus compromise conservation outcomes (Berigan *et al.* 2019). For example, changes in site occupancy can reflect changes in the numbers of transient individuals in an area that are originating elsewhere but do not establish residence in the surveyed area; additionally, population declines could lead to wider-ranging resident individuals being detected redundantly across multiple survey sites. Nuanced analyses of vocal activity patterns have revealed that eliminating the “false positives” generated not by misclassification errors but by non-resident or non-territorial individuals can improve our understanding of occupancy patterns, and ultimately population processes, derived from PAM (Wood *et al.* 2020b, Reid *et al.* 2021).

Vocal activity patterns representing resident occupancy can be identified in Barred Owl PAM-based occupancy estimation by ground-truthing occupancy status via active surveys and GPS-tagging individuals. PAM has been used to estimate Barred Owl site occupancy rates over broad spatial scales in the Pacific Northwest and in the Sierra Nevada, California (Wood *et al.* 2019a, 2020a; Duchac *et al.* 2020), but improved understanding of Barred Owl populations could inform ongoing and future regional-scale management activities such as lethal removal (USFWS 2013). Removal has been used to curb Barred Owl densities in other regions (Diller *et al.* 2016, Wiens *et al.* 2021, Hofstadter *et al.* 2022), and could be adopted at the southern leading edge of the range expansion to “push” populations north and create viable, long-term refuges for Northern Spotted Owls in areas that still contain functional populations (Long and Wolfe 2019).

We developed and refined PAM methods to monitor the Barred Owl population at the southern leading edge of their expansion in coastal California, where little is known about the Barred Owl population status but where biogeographical advantages could make removals particularly effective (Hofstadter *et al.* 2022). We used a combination of PAM data, GPS-tagging, and active surveys to (1) estimate home range size for Barred Owls to inform PAM survey design, (2) identify patterns of vocal activity that best reflect resident occupancy, and (3) estimate Barred Owl resident occupancy rates by correcting site occupancy estimates using vocal activity thresholds. This research has the potential to yield PAM-derived occupancy models which more accurately reflect Barred Owl populations and thus more meaningfully inform Barred Owl management practices at a critical time for conservation action.

METHODS

Study Area

We conducted our study on a mixed-ownership landscape in the coastal redwood region of California during the spring and summer of 2020 and 2021. This region is characterized by low elevation (0–900 m), high topographic variability, mesic conditions, and moderate temperatures; forests are dominated by coast redwood (*Sequoia sempervirens*), tanoak (*Notholithocarpus densiflorus*), Douglas-fir (*Pseudotsuga*

menziesii), and coast live oak (*Quercus agrifolia*; USFWS 2011). Fieldwork was conducted in two main locations: north-west Mendocino County—Redwood Forest Foundation Inc.’s (RFFI’s) Usal Redwood Forest (Figure 1A)—and west-central Mendocino County—California Department of Forestry and Fire Protection’s (CalFire’s) Jackson Demonstration State Forest (JDSF) and The Conservation Fund’s (TCF’s) Big River property (Figure 1C). Additional areas used for GPS-tagging of owls were California State Parks and Mendocino Redwood Company (MRC) lands in Mendocino County along with TCF’s Buckeye Forest property in Sonoma County. The Conservation Fund and RFFI are land conservation-focused organizations, MRC manages land for commercial timber production, California State Parks is primarily concerned with conservation and recreation, and the main activities promoted on JDSF are research, recreation, and sustainable timber harvest.

Owl Capture, GPS-tagging, and Tracking

Based on location data from previous survey efforts (M. Stephens personal communication), we captured adult Barred Owls during the spring of 2020 and 2021 using an owl decoy and a speaker broadcasting Barred Owl calls to lure owls into breakaway mist nets. We typically captured one adult owl per territorial pair and attached a GPS tag (Lotek Wireless Inc. model PinPoint VHF 240, Newmarket, Ontario, Canada) using a backpack harness (Forsman 1983). Tags were equipped with both VHF and GPS capabilities, allowing for the real-time tracking of owls along with the remote download of collected GPS data via a receiver (Lotek Wireless Inc. model Pinpoint VHF Commander). We programmed the GPS tags to collect 4–8 GPS locations per night (when owls are most active) along with one location every other day during the typical roosting period. Once breeding status was determined for tagged owls (see below), we reprogrammed tags remotely to collect just one location per night to ensure the battery lasted through the end of the breeding season (~August 31st). Any GPS locations collected beyond August 31st were classified as nonbreeding season locations.

Throughout the 2020 and 2021 breeding seasons, we located tagged Barred Owls using VHF radio telemetry to download GPS location data for home range estimation and to locate Barred Owl activity centers for our occupancy analysis. We tracked owls approximately once every two weeks. We used GPS location data and behavioral observations to determine the nesting status of tagged owls and confirmed all nest locations through visual observation. In addition to the location of nest trees, we noted visual observations of roosting adults and the presence of fledglings during surveys and defined the locations of these observations as Barred Owl activity centers.

ARU Deployment and Bioacoustics Analysis

During April–July of 2020, we deployed ARUs (Swift recorder, K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology) across the study area. We divided the entire 450 km² study area into 110 400-ha hexagonal grid cells (the approximate size of Barred Owl territories; Wood *et al.* 2019a). Thirty-five cells in the study area were dropped from the analysis due to lack of road access or the presence of logging activity, leaving 75 surveyed cells. We placed three ARUs within each cell (225 total locations; Figure 1), ensuring that

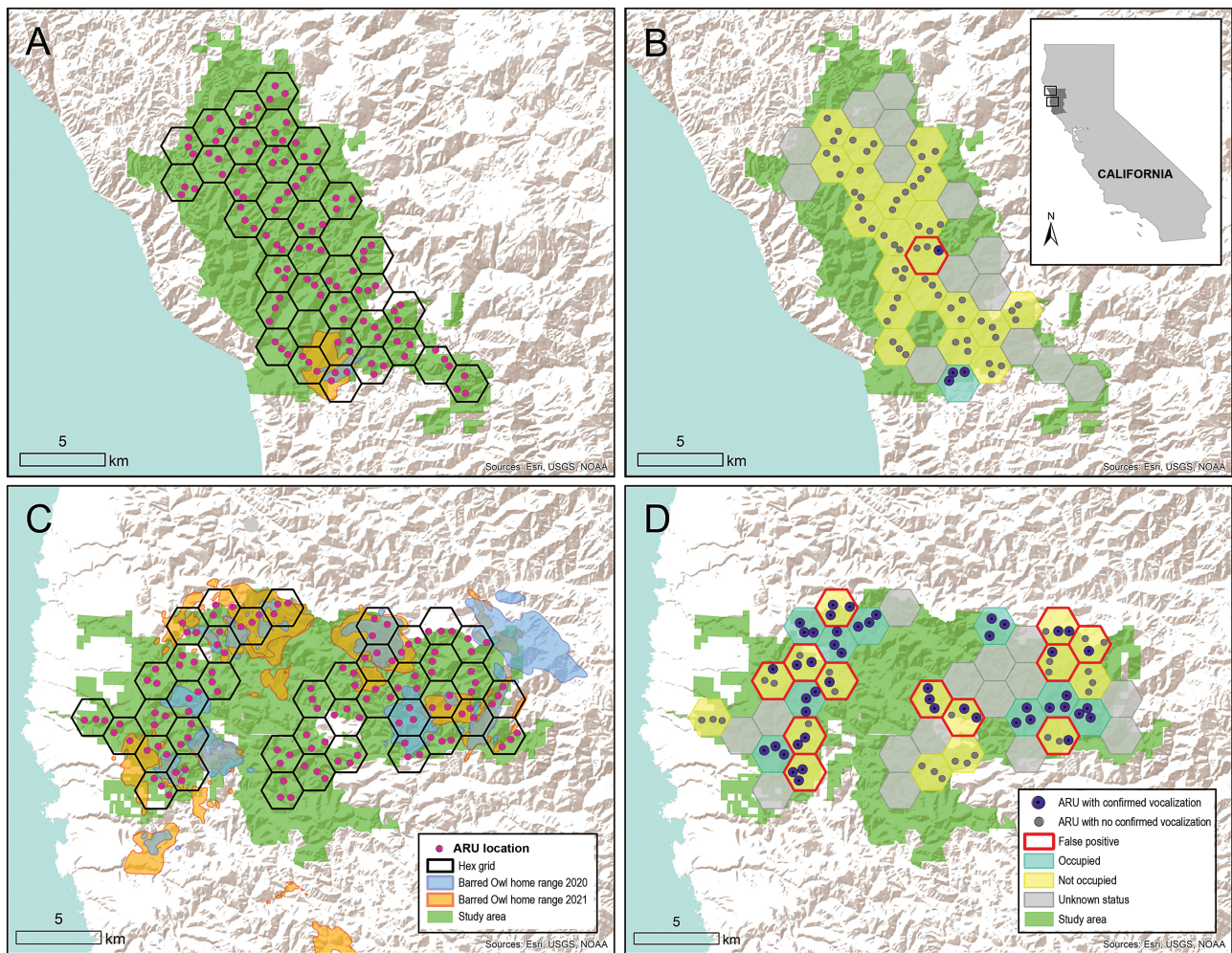


Figure 1. Study areas sampled by passive acoustic monitoring in (A and B) northwest Mendocino County and (C and D) west central Mendocino County. Panels (A) and (C) show all cells and autonomous recording unit (ARU) deployment locations overlain on 95% fixed-kernel density estimate (KDE) breeding season home ranges for GPS-tagged adult Barred Owls. Panels (B) and (D) show ARUs that received at least one confirmed vocalization over the entire 2020 survey season in cells for which Barred Owl residency status was known. Cells classified as unoccupied, but which received a confirmed vocalization at at least one ARU were considered false positive errors.

ARUs were ≥ 500 m apart and at least 250 m from the cell edge because in situ testing indicated that this ARU model typically had an effective sampling distance of ~ 250 m (and as high as ~ 350 m). ARUs were deployed in each location for 5–8 consecutive nights (typically six nights) on 2–3 occasions each separated by one month. ARUs were typically deployed at high points of topographic relief to increase their effective sampling range and within ~ 200 m of roads or ATV trails for efficiency of deployment and retrieval. ARU deployment locations remained consistent among sampling occasions. ARUs were programmed to record continuously 1700–1000 local time each night (sunset and sunrise were 1945–2045 and 0545–0645, respectively, during our study) with a single omni-directional microphone at a sample rate of 32 kHz, a bit depth of 16, and a gain of +38 dB.

To detect and classify Barred Owl vocalizations in the audio data, we used a sliding window template detector in Raven Pro 2.0 (Cornell Lab of Ornithology 2017). This template targeted the first phrase of a typical Barred Owl 2-phrase (8-note) call (Odom and Mennill 2010) and was developed by Wood *et al.* (2019a) using identical hardware and recording settings. We selected template detector

settings that yielded an estimated recall—or proportion of true target signals correctly identified as such—of 0.66 for individual calls and 0.95 for bouts of calling (many territorial vocalizations clustered in time). A bout-level recall of 0.95 means that if a Barred Owl vocalization bout occurred, there was generally only a $\sim 5\%$ chance that the detector failed to identify any of the vocalizations. The detector had a precision—or proportion of detector results that contain a true vocalization—of 0.52. We manually validated all detector results, and these confirmed Barred Owl territorial vocalizations are henceforth referred to as “confirmed vocalizations.”

Barred Owl Occurrence

We assessed Barred Owl occurrence across the study area with 15-min Barred Owl-focused active broadcast surveys during the breeding season of 2020 and used these data to confirm the apparent absence of Barred Owls in areas where we did not locate an activity center. From March to July of that year, a Northern Spotted Owl survey crew also conducted regular 10-min Spotted Owl-focused broadcast

surveys across the study area, surveying predetermined locations 1–7 times over the course of the season (M. Stephens personal communication). Spotted Owl-focused broadcast surveys frequently elicit responses from Barred Owls, though with a single-visit detection probability 18% lower than Barred Owl-focused surveys (0.48 vs. 0.66; [Wiens et al. 2011](#)). Collectively, these surveys allowed us to classify a portion of the landscape as occupied or unoccupied by a resident Barred Owl pair.

Statistical Analyses

KDE home range estimation

We removed GPS points from our analysis with fewer than four satellites and horizontal dilution of precision > 10. We used the *ks* package ([Duong 2022](#)) in program R 4.1.2 ([R Core Team 2021](#)) to calculate the 95% fixed-kernel density estimate (KDE) for each tagged owl using a plug-in approach to bandwidth selection ([Gitzen et al. 2006](#)). We generated estimates for the breeding season (March 1st to August 31st), the nonbreeding season (September 1st to February 28th), and the full year (March 1st to February 28th), and considered these estimates to represent the breeding season, nonbreeding season, and year-round home ranges of each individual, respectively. We then calculated the overall mean home range size for each period. We calculated female and male home range means for the breeding season and compared them with independent 2-sample *t*-tests, using a square-root transformation of the response to improve the normality of the distributions. We did not calculate separate female or male mean home ranges for the nonbreeding or year-round periods as we considered our male sample size ($n = 2$) for both periods to be insufficient for drawing conclusions. We excluded home range estimates for individuals with fewer than 50 breeding season or nonbreeding season location observations for each respective calculation, and with fewer than 50 locations from either period in the year-round calculation ([Seaman et al. 1999](#)).

Defining Barred Owl activity centers and minimizing false positive and false negative error in the acoustic data

Though we eliminated the possibility of misclassifications by manually validating all detector results, we sought to estimate the rate of false positives arising from confirmed Barred Owl vocalizations in survey cells that we determined to be unoccupied based on multiple forms of in-person surveys. Such events could be explained by the temporary presence of transient individuals or by wide-ranging individuals vocalizing far away from their activity center.

We first determined the resident occupancy status of PAM survey cells based on active surveys and GPS data. We classified a cell as “occupied” if it contained a Barred Owl activity center, “unoccupied” if it did not contain an activity center from these surveys, and “unknown” if data from the cell was insufficient to determine occupancy status. Barred Owl activity centers were defined as nests, roosts, or fledgling locations observed during nest search surveys from March to July 2020. We considered roosts to be indicative of an activity center when the roosting owl we observed was GPS-tagged and known to be a resident of the area based on GPS data. We assigned a single activity center to each Barred Owl territorial pair, and we prioritized the nest location in assigning the activity center. An adult roost location was used to represent the activity center only if no nest was observed, and

a fledgling location was used only if no nest or adult roost was observed. We did not observe more than one nest, adult roost, or fledgling location in areas where that location type was used to represent the activity center, which eliminated the need to make subjective decisions about which of multiple potential activity centers in an owl territory to use.

In the PAM grid cells without GPS tag data, we used detection/non-detection data from broadcast surveys to corroborate the absence of a Barred Owl activity center. A cell was considered to lack an activity center if we received no Barred Owl detection from either: (1) at least one Barred Owl-focused broadcast survey in two separate locations in the cell, or (2) at least five Spotted Owl broadcast surveys in each of at least three separate locations in the cell. Cells in which Barred Owls were detected during broadcast surveys despite the absence of a known activity center, as well as those with insufficient surveys, were treated as “unknown.”

To estimate the false positive error rate, we calculated the proportion of unoccupied cells that received at least one confirmed vocalization during the passive acoustic sampling season; to estimate the false negative error rate, we calculated the proportion of occupied cells that did not receive a confirmed vocalization over the sampling season.

Acoustic metrics of Barred Owl vocal activity

Increasing the minimum score above which all detector-based putative detections are reviewed is the simplest way to reduce false positives, but doing so often also increases false negatives. To test whether we could reduce false positives without increasing false negatives, we created three statistics describing Barred Owl vocal activity over the entire survey season and related them to true grid cell residency status (occupied or unoccupied). Our metrics were (1) the proportion of survey nights with at least one confirmed vocalization (“vocalization nights”; VN), (2) the number of confirmed vocalizations per hour (“call rate”; CR), and (3) the number of ARUs in the cell with at least one confirmed vocalization (“vocalization units”; VU). Higher values of these metrics are likely to be indicative of resident owl pairs because a resident pair will call more frequently and more consistently across multiple nights throughout their activity center compared to an individual owl simply passing through the area ([Wood et al. 2019b](#)). We used logistic regression to determine which of these metrics best explained the resident occupancy status (occupied/unoccupied) of Barred Owls in the cells where status was known across the survey season. We evaluated model fit using Akaike’s Information Criterion corrected for small sample size (AIC_c) using the R package *MuMIn* ([Bartoń 2022](#)) and considered models with $\Delta AIC_c < 2$ to be competitive ([Burnham and Anderson 2002](#)). To determine thresholds in well-supported variables where tradeoffs between false positives and false negatives were optimized, we identified vocal activity metric values at which false positive or false negative error rates changed and calculated the error rates for each of those values. From there, we selected the thresholds which resulted in minimization of both types of error.

Estimating occupancy rates

To estimate the proportion of the entire study area occupied by Barred Owls, we conducted single-species, single-season occupancy analyses ([MacKenzie et al. 2002](#)) using detection/non-detection data derived from passive acoustic surveys

with the R package *RMark* (Laake 2013). These analyses incorporated all 75 PAM cells, not just those for which we were able to determine resident occupancy status with active surveys. We used a simple single-season occupancy model with no site- or observation-level covariates ($p(\cdot)\psi(\cdot)$) and treated each 5–8-night survey occasion as a secondary sampling period (a preliminary analysis revealed that there was no support for a model that included a survey duration detection covariate). We first conducted an occupancy analysis with a traditional site occupancy approach in which encounter histories (composed of 2–3 secondary sampling periods) were based on detections defined as the presence of at least one confirmed vocalization in a cell during a given secondary sampling period. Confirmed vocalizations in this analysis were aggregated across all three ARUs in a cell and across all nights in the survey occasion.

We then conducted additional analyses aimed at approximating resident occupancy in which encounter histories were based on detections defined by the thresholds in vocal activity that were designed to minimize false positives (a grid cell without a resident pair is included) and false negatives (a grid cell occupied by a resident pair of owls is excluded). We applied the vocal activity thresholds at the level of secondary sampling periods. Consider a cell that contains an activity center and was surveyed with three ARUs on three secondary sampling periods, and at least one confirmed vocalization was detected in each period. Under the “traditional” site occupancy approach, the encounter history is 111. If a VN threshold of > 0.1 is applied and the observed VN rate for each secondary sampling period was 0.1, 0.2, and 0.3, the encounter history would be 011. If a VU threshold of > 1 was applied and the observed VU was 2/3, 1/3, and 3/3, the encounter history would be 101.

Our passive acoustic survey approach inherently yielded site occupancy data because it was based on arbitrarily delineated grid cells and ARUs were deployed without knowledge of Barred Owl space use; the goal of these various thresholds was to identify acoustic activity criteria that could produce estimates of site occupancy that are more representative of resident occupancy (Wood and Peery 2022). Therefore, our final step was to compare estimates of detection probability (p) and occupancy (ψ) as generated by different detection criteria.

RESULTS

KDE Home Range Estimation

We estimated the home range size of 37 adult Barred Owls (27 females and 10 males) which collected ≥ 50 GPS locations during the Barred Owl breeding season. Ten adults (8 females and 2 males) collected ≥ 50 locations outside of the breeding season. The mean home range size of all adults during the breeding season was 452 ha (SE = 63, range: 24–1,801 ha, $n = 37$; Figure 2). Female mean breeding season home range size ($\bar{x} = 312$ ha, SE = 47, range: 24–1,204 ha, $n = 27$) was significantly smaller than male mean breeding season home range size ($\bar{x} = 828$ ha, SE = 138, range: 463–1,801 ha, $n = 10$; $t_{35} = -4.68$, $P = 0.00004$). Outside of the breeding season, mean home range size was 1,143 ha (SE = 259, range: 336–2,807 ha, $n = 10$). Year-round mean home range size was 871 ha (SE = 165, range: 338–1,729 ha, $n = 10$). Our estimates of year-round home range size are potentially most reflective of

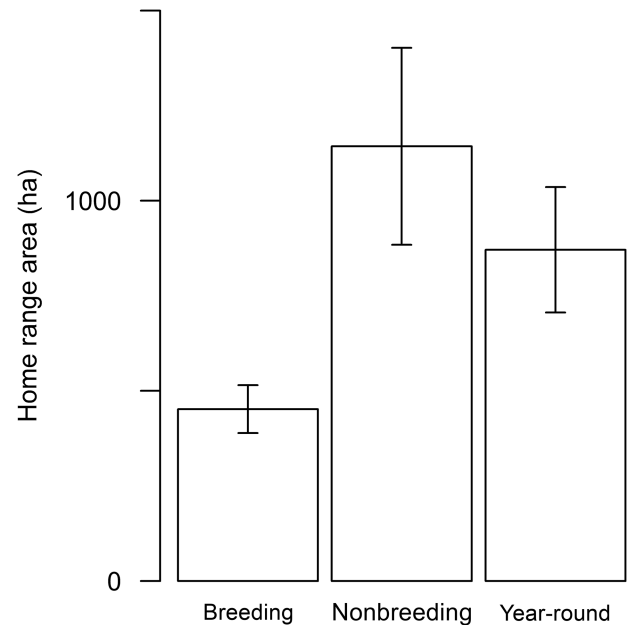


Figure 2. Mean 95% fixed-KDE home ranges based on GPS data for Barred Owls during the breeding season (March 1st to August 31st), nonbreeding season (September 1st to February 28th), and year-round. Error bars show standard error.

the breeding season, with observations collected from March 1st to August 31st accounting for 63% of total year-round location observations.

Active Survey Classification

We were able to determine resident occupancy status for 46 of the 75 cells in our study area. Under our classification scheme, 10 cells were occupied by resident owls, 36 were unoccupied, and the remaining 29 were unknown (Figure 1B and D). Three cells were classified as unoccupied based on Barred Owl-focused surveys alone, 28 cells were classified as unoccupied based on Spotted Owl-focused surveys alone, and 5 cells were classified as unoccupied based on both survey types.

Passive Acoustic Surveys

Barred Owl territorial vocalizations were confirmed in 41 of the 75 surveyed cells and at 89 of the 225 ARU deployment locations. Cells with confirmed vocalizations included 23 of the 46 cells for which residency status was known. The metric VN ranged from 0.016 to 0.43 and CR from 0.0016 to 0.64 when averaged across all ARUs and across secondary sampling periods for the cells which received confirmed vocalizations and for which residency status was known. Six cells received at least one confirmed vocalization at just one ARU, 4 cells at 2 ARUs, and 13 cells at all 3 ARUs. When we considered one confirmed vocalization at at least one ARU in a cell to constitute a detection (i.e., the most basic site occupancy approach), the false positive error rate was 0.36 and the false negative error rate was zero for cells of known residency status (Table 1). In other words, 13 of the 36 cells which were unoccupied by resident owls received at least one confirmed vocalization, and every one of the 10 cells which were occupied by resident owls received at least one confirmed vocalization (Figure 1B and D).

Table 1. False positive and false negative error rates and occupancy estimates for occupancy analyses using different detection definitions. Occupancy (ψ) and detection probability (p) estimates are given with 95% upper and lower confidence limits. VU is the number of ARUs in a cell with confirmed vocalizations, and VN is the proportion of survey nights with confirmed vocalizations.

Detection definition	False positive error rate	False negative error rate	ψ	LCL	UCL	p	LCL	UCL
Any confirmed vocalization	0.36	0.00	0.61	0.48	0.73	0.70	0.59	0.79
VU = 3	0.08	0.00	0.36	0.14	0.68	0.24	0.10	0.47
VN > 0.08	0.11	0.00	0.44	0.32	0.57	0.65	0.53	0.76
VN > 0.17	0.03	0.30	0.41	0.23	0.62	0.36	0.22	0.54
VN > 0.30	0.00	0.90	0.29	0.11	0.56	0.26	0.11	0.51

Statistical Analyses

Minimizing false positive and false negative error.

Every cell that was occupied by a resident owl received at least one confirmed vocalization at all three ARUs in the cell during at least one secondary sampling period across the survey season; thus, there were no false negative errors associated with the VU metric (Figure 3B). We, therefore, excluded VU as a covariate in our logistic regression analysis. When a logistic regression was fit with either of the remaining explanatory variables, VN or CR, and resident occupancy status as the response, the model with VN was most supported ($\Delta AIC_c = 0$, $w_i = 0.81$; Table 2). We only considered single-covariate models due to high correlation between VN and CR.

Because no false negatives were observed across the range of thresholds considered for VU, we defined a detection by VU = 3 in a given secondary sampling period to minimize the false positive error rate to 0.08 (Table 1; Figure 3B). Setting a threshold of VN > 0.08 to define a detection similarly resulted in a false negative error rate of zero, but a slightly higher false positive error rate of 0.1 (Figure 3A). With a threshold of VN > 0.17, we could achieve a false positive error rate of 0.03, but this resulted in a false negative error rate of 0.3. In other words, 70% of cells which were occupied by resident

owls according to our active survey classification scheme received at least one confirmed vocalization on more than 17% of deployment nights, and those which were unoccupied did not meet this criterion 97% of the time. When we defined a detection by a threshold as high as VN > 0.30, we were able to eliminate false positive error, but the false negative error rate rose to 0.9.

Estimating occupancy rates

In our site occupancy analysis, in which a single confirmed vocalization constituted a detection in a cell during a secondary sampling period, detection probability (p) was 0.70 (95% confidence interval [CI]: 0.59–0.79; Table 1 and Figure 4) and occupancy (ψ) was 0.61 (95% CI: 0.48–0.73). When we defined a detection as a cell with VU = 3, p was 0.24 (95% CI: 0.097–0.47) and ψ was 0.37 (95% CI: 0.14–0.68). When a detection was defined by VN > 0.08, p was 0.65 (95% CI: 0.53–0.76) and ψ was 0.44 (95% CI: 0.32–0.57). When we considered the threshold VN > 0.17 to constitute a detection, p was 0.36 (95% CI: 0.22–0.54) and ψ was 0.41 (CI: 0.23–0.62). When we defined a detection as a cell with VN > 0.30, p was 0.26 (95% CI: 0.11–0.51) and ψ was 0.29 (95% CI: 0.11–0.56).

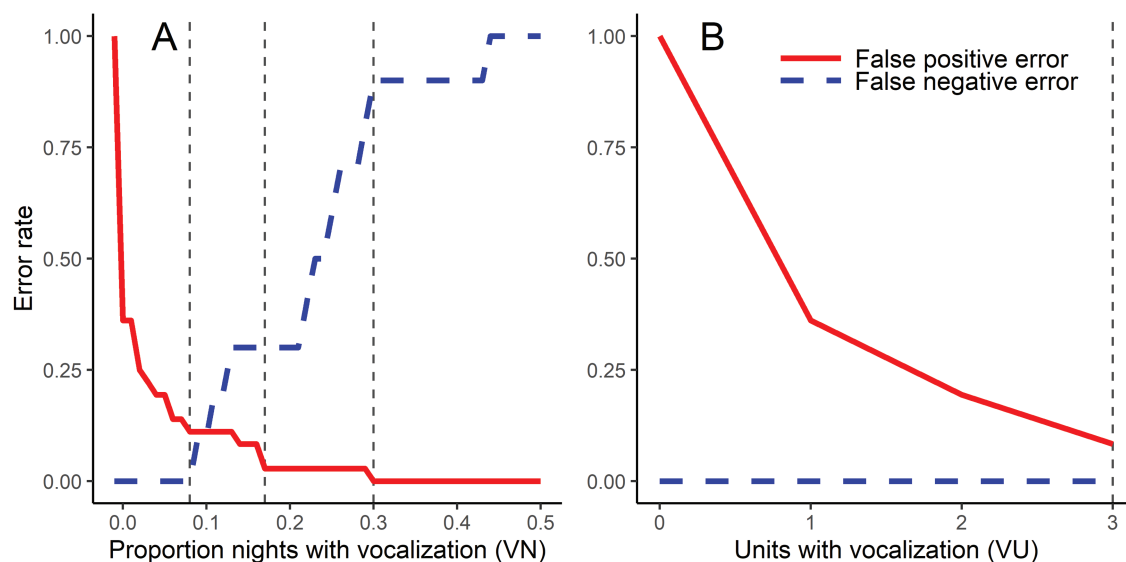


Figure 3. Error curves show tradeoffs in false positive and false negative errors for vocal activity metrics VN (the proportion of nights with at least one confirmed vocalization) and VU (the number of units with at least one confirmed vocalization). In (A), as we used increasing values of VN to define a detection in an occupancy framework, false positive errors decreased while false negative errors increased. In (B), as we used increasing values of VU to define a detection, false positive errors decreased while the false negative error rate remain zero. Dashed vertical lines show thresholds used to define detections (VN > 0.08, VN > 0.17, VN > 0.30, and VU = 3) in occupancy analyses.

Table 2. AIC_c values for logistic regression of vocal activity metrics—the proportion of nights with a recorded vocalization (VN) and call rate—reflective of resident occupancy. k is the number of model parameters and w_i is Akaike weight.

Model covariate	k	ΔAIC_c	w_i
VN ^a	2	0.00	0.811
CR	2	2.91	0.189
Null model	1	22.77	<0.001

^aAIC_c value 27.49.

DISCUSSION

PAM has been used to track changes in populations and facilitate the management of invasive species, particularly for curbing the adverse ecological effects of the Barred Owl's recent and rapid range expansion (Wood *et al.* 2019a, 2020a, Hofstadter *et al.* 2022). Until this study, the status of Barred Owl populations at the leading edge of their range expansion in coastal California was unknown, as was the potential need for management intervention. We estimated the mean breeding season home range size of Barred Owls in this region to be 452 ha (SE = 63), which was similar to the grid cell size we employed in our PAM sampling grid (400 ha), indicating this to be an appropriate survey cell size for this region. Importantly, we identified metrics of vocal activity (VU = 3, VN > 0.08, VN > 0.17, and VN > 0.30) that either reduced false positive errors without substantial increases in false negative errors or effectively eliminated false positive errors altogether, and thus were more indicative of resident Barred Owl pairs occupying a survey cell. By applying these thresholds in an occupancy analysis, we were able to generate a range of reasonable estimates for the resident occupancy rate of Barred Owls in this region (ψ = 0.29–0.44). We suggest this range of values is a closer approximation of resident occupancy than is achieved by our site occupancy analysis (ψ = 0.61) conducted without applying thresholds. Importantly, our measures of site occupancy and resident occupancy are distinct from territory occupancy, the proportion of historical territories on the landscape which are occupied by a resident individual/pair at a given time, a metric that is commonly used in long-term Spotted Owl monitoring (Reid *et al.* 2021, Wood and Peery 2022). Our work provides a means of reducing the possibility of falsely considering an acoustic survey grid cell occupied when a vocalization of a non-resident individual has merely been detected within the cell, while simultaneously maintaining a reasonably low probability of treating an acoustic survey grid cell as unoccupied when it contains a resident Barred Owl. Accordingly, we suggest that PAM can be used to monitor changes to the population of territorial Barred Owls over space and time and thus inform management actions.

Mean breeding season home range size of Barred Owls in this study (452 ha, SE = 63) was similar to the territory size found in a previous study of GPS-tagged Barred Owls at the Sierra Nevada leading edge of the Barred Owl range expansion (411 ha; SE = 38), though Barred Owls in the Sierra Nevada, where density is low, had substantially larger year-round home ranges (Wood *et al.* 2020a). Breeding season home ranges of Barred Owls estimated with VHF telemetry in a previous study in the Pacific Northwest were also similar, although somewhat larger (mean = 556 ha; SE = 41; Wiens *et al.* 2014). While differences

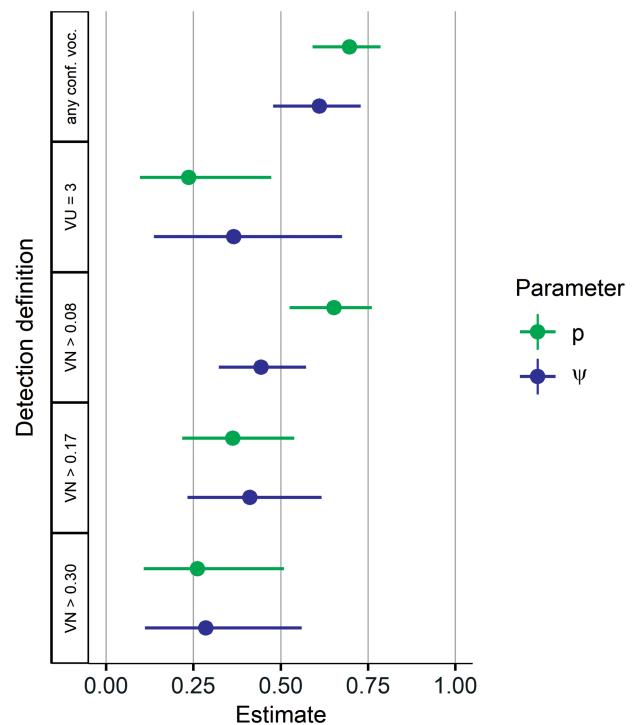


Figure 4. Parameter estimates with 95% confidence intervals for each occupancy analysis conducted based on different detection definitions. Detection definitions are, from top to bottom: (1) any confirmed vocalization, (2) a threshold of VU (the number of ARUs in a cell with confirmed vocalizations) = 3, (3) a threshold of VN (the proportion of survey nights with confirmed vocalizations) > 0.08, (4) a threshold of VN > 0.17, and (5) a threshold of VN > 0.30. Parameters are detection probability (p) and occupancy rate (ψ).

in tracking and statistical methods can challenge comparisons of home range size between studies (Gitzen and Millsap 2003, Gitzen *et al.* 2006, Horne and Garton 2006, Laver and Kelly 2008), these similarities suggest grid cells 400–600 ha in size may be reasonable to monitor Barred Owls during the breeding season across their expanded range—where grid cell sizes could potentially be tailored according to region. While Barred Owl home ranges were comparable in size to grid cells, their position can nevertheless overlap and cause detections in multiple cells (Figure 5), thus causing false positives and estimates of site occupancy that exceed resident occupancy. We noted several instances based on our GPS data (Figures 1 and 5A) in which false positives appeared more likely to result from Barred Owl home ranges overlapping survey cells (rather than from transient individuals), but further investigation into this topic is warranted. Surveying only non-adjacent cells could reduce double-counting in occupancy analyses (Wood *et al.* 2019a), but some home ranges in our study were large enough (1801 ha) that detections in multiple cells would likely remain an issue—highlighting the value of developing thresholds based on vocal activity patterns indicative of residency.

We were able to reduce ecological false positive errors with varying levels of tradeoffs in false negative errors in our Barred Owl occupancy analysis by defining detections using thresholds of both VN (the proportion of nights which received at least one confirmed vocalization) and VU (the number of ARUs in a cell which received at least one confirmed vocalization).

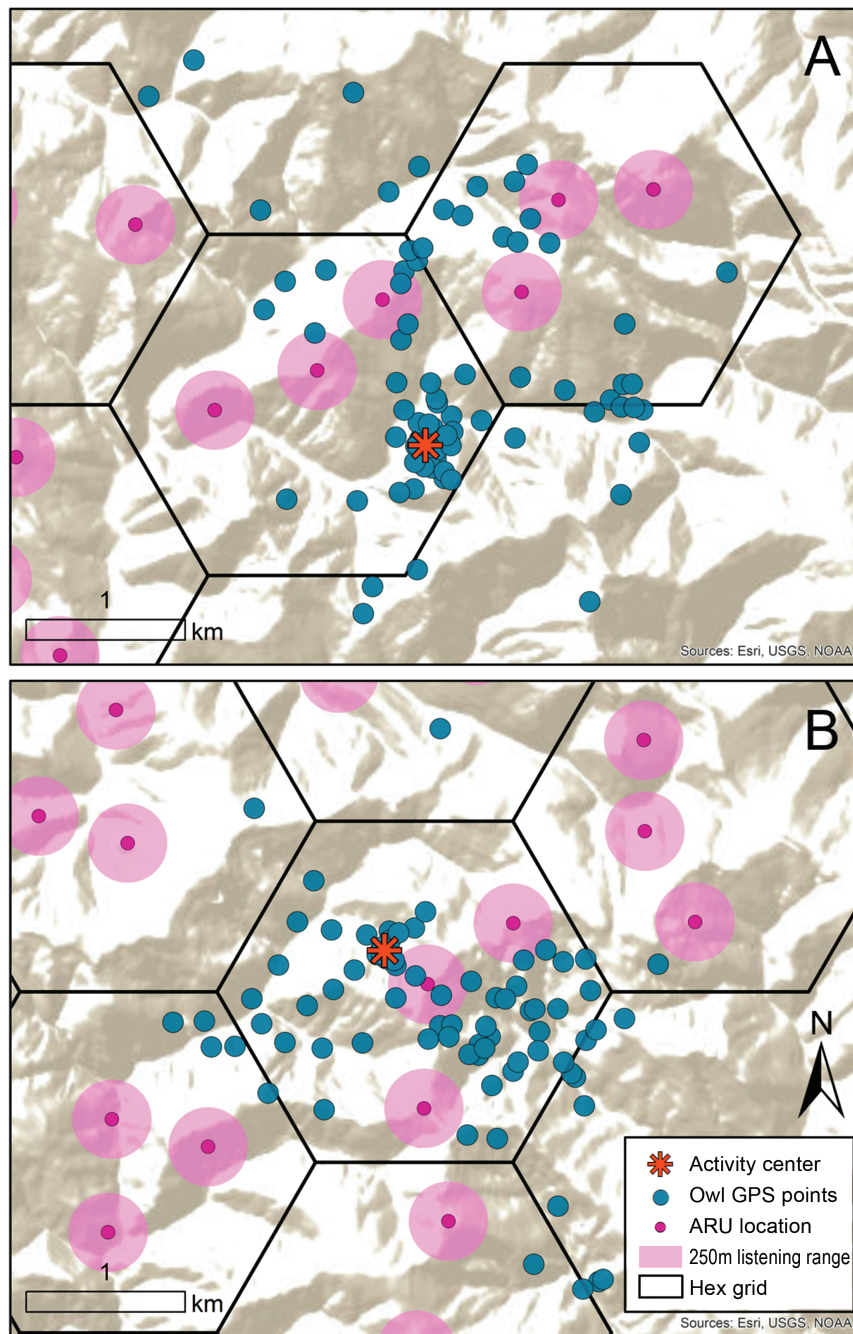


Figure 5. GPS data collected from two adult female Barred Owls in 2020: (A) in some cases, GPS locations spanned multiple cells in ARU hex grid; (B) in others, the majority of breeding season GPS locations occurred within a single cell.

Thus, the characteristics of vocal activity most reflective of actual resident occupancy in Barred Owls were territorial vocalizations across multiple nights and across multiple areas of a given sampling unit. However, some of the criteria considered came at the cost of increasing false negative error rates (see Figure 3A) which, in turn, reduced detection probabilities and increased sampling variation in occupancy estimates (Figure 4). Detection probability remained relatively high, though, for a threshold of $VN > 0.08$ ($p = 0.65$), leading to a relatively precise estimate of occupancy ($\psi = 0.44$, $SE = 0.065$).

Depending on management goals, different vocal activity metric thresholds may be employed to reduce error in the desired manner. The thresholds of $VU = 3$ and $VN > 0.08$ could

be advantageous, for instance, when PAM is being used for the location of Barred Owls for lethal removal, as false negative error would result in missing Barred Owls present on the landscape. The threshold of $VN > 0.08$ may be preferred over a threshold of $VU = 3$ to reduce false positive error without increasing false negative error. Despite the slightly higher false positive error rate of $VN > 0.08$ (0.11 compared to 0.08), the $VU = 3$ threshold resulted in a lower probability of detection and lower precision when it came to the associated occupancy estimate (Table 1). In situations where reducing false positive error is the primary concern, as may be the case for population monitoring, the thresholds of $VN > 0.17$ and $VN > 0.30$ may be more appropriate. In general, researchers and

managers engaged in PAM programs for Barred Owls and other species should (1) treat estimates of site occupancy cautiously, and (2) strive to develop approaches to more closely link occupancy data to population processes.

Management Implications

Our range of resident occupancy estimates ($\psi = 0.29\text{--}0.44$) indicates that Barred Owls have become established in this region of coastal California. This range is higher than a PAM-based estimate of occupancy in the northern Sierra Nevada in 2018 ($\psi = 0.19$) immediately prior to the beginning of lethal removals of Barred Owls in this region (Wood *et al.* 2020a; Hofstadter *et al.* 2022), but lower than an active vocal-lure survey estimate of Barred Owl occupancy in western Oregon in 2011 ($\psi = 0.89$) prior to removal efforts (Wiens *et al.* 2011). While the estimate of occupancy in the Sierra Nevada was not corrected for false detections using vocal activity thresholds, only non-contiguous grid cells were surveyed, thus reducing the likelihood of detecting resident individuals in multiple cells (Wood *et al.* 2020a, Hofstadter *et al.* 2022). Accordingly, we suggest that resident occupancy rates in coastal California are between pre-removal occupancy rates in the Sierra Nevada, where Barred Owl removals reduced occupancy to 0.03 by 2020 followed by rapid Spotted Owl recolonization (Hofstadter *et al.* 2022), and pre-removal occupancy rates in western Oregon where removals have slowed Spotted Owl population decline (Wiens *et al.* 2011, 2021). Therefore, similar removal efforts in coastal California are likely to be a tractable means of managing Barred Owl populations and curbing their ecological impacts. Removals in our study region could help push Barred Owl populations northward, effectively causing a retraction in the Barred Owl invasion front and establishing a refugium where Northern Spotted Owl populations may recover and persist with limited disturbance. The window of opportunity for an efficient removal effort may, however, be quite small as Barred Owl populations are likely to grow rapidly as they have in the Pacific Northwest over the past several decades (Yackulic *et al.* 2012, 2014, Wood *et al.* 2020a). When Barred Owls are allowed to achieve high densities, many years of removals of large numbers of individuals are needed to achieve even modest increases in Spotted Owl populations (Wiens *et al.* 2021). Our study suggests that swift, decisive lethal removals supported by landscape-scale PAM are an appropriate means of Barred Owl management in this region while populations remain relatively low.

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Ethics statement

Work was conducted in compliance with Federal Bird Banding Permit #23685, California state Scientific Collecting Permit S-193180001-19339-001, and IACUC protocol #1041 (San Jose State University).

Conflict of interest statement

The authors declare no conflicts of interest.

Author contributions

MZP, CMW, and JJK conceived of the study; MZP, CMW, JJK, and VO secured the funding; WAW, DFH, NFK, CJZ, KGK, SAW, and VO planned the field work; WAW, DFH, NFK, and CJZ collected the data; WAW led the field work and conducted the analyses; KGK processed the acoustic data; WAW, MZP, and CMW wrote the manuscript.

Data availability

Analyses reported in this article can be reproduced using the data provided by Watson *et al.* (2023).

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