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RESEARCH ARTICLE

Early detection of rapid Barred Owl population growth within the range of the California Spotted Owl advises the Precautionary Principle

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ABSTRACT

Biological invasions are most practical to manage when invasive species population densities are low. Despite a potentially narrow window of opportunity for efficient management, managers tend to delay intervention because the cost of prompt action is often high and resources are limited. The Barred Owl (*Strix varia*) invaded and colonized the entire range of the Northern Spotted Owl (*S. occidentalis caurina*), but insufficient population data contributed to delays in action until the Barred Owl posed an existential threat to the Spotted Owl. The leading edge of the Barred Owl expansion has since reached the Sierra Nevada, the core range of the California Spotted Owl (*S. o. occidentalis*). We conducted passive acoustic surveys within 400-ha grid cells across ~6,200 km^2 in the northern Sierra Nevada and detected a 2.6-fold increase in Barred Owl site occupancy between 2017 and 2018, from 0.082 (85% confidence interval: 0.045–0.12) to 0.21 (0.14–0.28). The probability of Barred Owl site colonization increased with the amount of older forest, suggesting that Barred Owls are first occupying the preferred habitat of Spotted Owls. GPS-tagged Barred Owls (n = 10) generally displayed seasonal and interannual site fidelity over territories averaging 411 ha (range: 150–513 ha), suggesting that our occupancy estimates were not substantially upwardly biased by "double counting" individuals whose territories spanned multiple grid cells. Given the Barred Owl's demonstrated threat to the Northern Spotted Owl, we believe our findings advise the Precautionary Principle, which posits that management actions such as invasive species removal should be taken despite uncertainties about, for example, true rates of population growth if the cost of inaction is high. In this case, initiating Barred Owl removals in the Sierra Nevada before the population grows further will likely make such action more cost-effective and more humane than if it is delayed. It could also prevent the extirpation of the California Spotted Owl from its core range.

Keywords: Barred Owl, bioacoustics, biological invasion, California Spotted Owl, multi-season occupancy estimation, passive acoustic monitoring, Sierra Nevada, *Strix occidentalis occidentalis*, *Strix varia*

Detección temprana de crecimiento poblacional rápido de *Strix varia* adentro del rango de *S. occidentalis occidentalis* aconseja el Principio Precautorio

RESUMEN

Las invasiones biológicas son más prácticas de manejar cuando las densidades poblacionales de la especie invasora son bajas. A pesar de una ventana de oportunidad potencialmente estrecha para un manejo eficiente, los gestores tienden de demorar la intervención debido a que el costo de una acción rápida es usualmente alto y los recursos son limitados. *Strix varia* invadió y colonizó el rango completo de *S. occidentalis caurina*, pero los datos poblacionales insuficientes contribuyeron a retrasar la acción hasta que *S. varia* planteó una amenaza de existencia para *S. o. caurina*. La vanguardia de la expansión de *S. varia* ha llegado desde entonces hasta la Sierra Nevada, el área núcleo de *S. o. occidentalis*. Realizamos muestreos acústicos pasivos dentro de celdas de 400 ha en una cuadrícula de ~6,200 km^2 en el norte de la Sierra Nevada y detectamos un aumento de 2.6 veces en la ocupación de sitios por parte de *S. varia* entre 2017 y 2018, desde 0.082 (85% intervalo de confianza [0.045–0.12]) hasta 0.21 [0.14–0.28]. La probabilidad de colonización de sitios de *S. varia* aumentó con la cantidad de bosque más viejo, sugiriendo que *S. varia* está ocupando primero el hábitat preferido de *S. occidentalis*. Los individuos marcados con GPS de *S. varia* (n = 10) generalmente mostraron fidelidad de sitio estacional e interanual sobre territorios con un tamaño promedio de 411 ha (rango: 150–513 ha), sugiriendo que nuestras estimaciones de ocupación no estuvieron sesgadas sustancialmente hacia arriba por un "doble conteo" de individuos cuyos territorios abarcaron múltiples celdas de la cuadrícula. Dado que *S. varia* demostró ser una amenaza para *S. o. caurina*, creemos que nuestros hallazgos aconsejan el Principio Precautorio, el cual postula que las acciones de manejo como la remoción de una especie invasora deberían hacerse a pesar de las incertidumbres sobre, por ejemplo, las verdaderas tasas de crecimiento poblacional, si el costo de la inacción es alto. En este caso, el inicio de la remoción de *S. varia* en la Sierra Nevada antes que la población crezca más, hará que esta acción sea probablemente más costo-efectiva y más humana, que si se demora. También podría prevenir la extirpación de *S. o. occidentalis* de su área núcleo.

Palabras clave: bio-acústica, estimación de ocupación multi-estacional, invasión biológica, monitoreo acústico pasivo, Sierra Nevada, *Strix occidentalis occidentalis*, *Strix varia*

INTRODUCTION

Populations of invasive species typically follow a pattern of logistic growth in which they remain at relatively low densities for several or even many generations (i.e. exhibit a lag phase), then undergo rapid growth, and finally stabilize near carrying capacity (Crooks and Soulé 1999). An invasive species in the lag phase can be difficult to distinguish from other non-indigenous species that are simply persisting at low densities with negligible ecological effects (Simberloff 2011, Boltovskoy et al. 2018). Managers often delay management intervention until there is strong evidence that a species is likely to be an environmental threat because the cost of intervention is usually high and resources are limited. This "wait and see" approach is risky because once the growth phase has begun, the window of opportunity for cost-effective invasive species management can be small (Baxter et al. 2008).

In the case of the Barred Owl (*Strix varia*) and the endangered Northern Spotted Owl *(S. occidentalis caurina*), the delays in managing an invasive species have led to a conservation crisis (Gutiérrez et al. 2007). The Barred Owl invaded the range of the Northern Spotted Owl over 60 yr ago (Livezey 2009a, 2009b), but progress of that expansion appeared to be slow until there was a rapid increase ~20 yr ago (Yackulic et al. 2012, 2014). Yet Barred Owl population estimates were based on detections arising from vocal lure surveys targeting Spotted Owls, and heterospecific vocalizations affect both Spotted Owl and Barred Owl response rates and thus led to biased survey results (Crozier et al. 2006, Van Lanen et al. 2011, Wiens et al. 2011). That bias contributed to uncertainty about both the effects Barred Owls had on Spotted Owls and their true population growth rates (Courtney et al. 2004, Buchanan et al. 2007). That uncertainty, the social cost of lethal owl removals, lengthy permitting processes, and other factors contributed to a decades-long period of unchecked growth of the Pacific Northwest Barred Owl population that has greatly increased the likelihood that Barred Owls will displace the Northern Spotted Owl through competitive exclusion (Wiens et al. 2014, Diller et al. 2016, Yackulic et al. 2019) and cause widespread trophic cascades (Holm et al. 2016). Local-scale removal experiments are currently underway to assess the feasibility of curbing Barred Owl populations (Diller et al. 2016, Wiens et al. 2018), but doing so across the Pacific Northwest would require very substantial resources and social capital (Livezey 2010).

The leading edge of the Barred Owl range expansion has since reached the core range of the California Spotted Owl (*S. o. occidentalis*) in the Sierra Nevada ecoregion (Keane 2017). To avoid the response biases associated with single-species vocal lure surveys, we implemented landscape-scale passive acoustic surveys of the owl community across the northern Sierra Nevada as a tool for proactively monitoring the Barred Owl invasion (Wood et al. 2019a, 2019b). Subsequently, we found that Barred Owl site occupancy in 2017 was low (Wood et al. 2019b) and similar to lag-phase densities that occurred in the Pacific Northwest prior to rapid population growth (Yackulic et al. 2019).

In this study we used our landscape-scale multi-species passive acoustic monitoring to estimate interannual changes in Barred Owl site occupancy. A substantial increase in Barred Owl site occupancy in the Sierra Nevada would suggest that the population is entering the growth phase, whereas stasis or only slight growth would indicate that the population either remains in the lag phase or perhaps may not flourish in the Sierra Nevada as it has in the Pacific Northwest. We also tested for associations between environmental variables and both site colonization and occupancy. Finally, we GPS-tagged Barred Owls to characterize patterns of space use to assess the extent to which acoustic detections represented unique, stable territories rather than transient individuals. Collectively, we hoped to provide information that would help inform proactive, empirically grounded management of Barred Owls in the Sierra Nevada.

METHODS

Passive Acoustic Surveys and Bioacoustic Analyses

We conducted passive acoustic surveys across >6,000 km^2 of the Lassen and Plumas National Forests in the northern Sierra Nevada, California, from May to August in 2017 and 2018. We randomly selected 400-ha hexagonal grid cells (hereafter "sites") from a grid of ~1,500 cells overlaid upon the California Spotted Owl's range in these 2 national forests. Sites approximated the size of Spotted and Barred owl territories in this region based on Tempel et al. (2016; see also below) and were noncontiguous to reduce non-independence among sites. We surveyed 167 sites in both 2017 and 2018 (~10% of the landscape) and an additional

179 sites in 2018 (i.e. 346 sites total across ~22% of the landscape). Each survey (i.e. secondary sampling period) entailed one 5- to 7-night deployment of 2 or 3 autonomous recording units (ARUs; Swift Recorder, Cornell Lab of Ornithology, Ithaca, New York, USA) located without knowledge of owl occupancy. In situ testing indicated that the ARUs had an effective sampling distance of ~250 m, so they were placed at least 500 m apart and at least 250 m from grid cell boundaries in areas that had safe and efficient access (i.e. generally <200 m from minor roads) and were acoustically advantageous (e.g., ridgelines rather than gullies). Sites were surveyed 1–3 times per season. ARUs had one omni-directional microphone and recorded continuously from 2000 hours to 0600 hours, inclusive, with a gain of +38 dB and a sample rate of 32 kHz.

We collected 49,800 hr of audio in 2017 and 145,600 hr in 2018. We applied a sliding window template detector to our audio data to identify Barred Owl 2-phrased hoots (i.e. territorial "who cooks for you?" calls) using Raven Pro 2.0 (Cornell Lab of Ornithology Bioacoustics Research Program, Ithaca, New York, USA) and manually reviewed all potential detections. We determined site occupancy based on the presence of a manually confirmed Barred Owl territorial vocalization recorded at any of the ARUs deployed at a site, and optimized the template such that it had >0.98 probability of correctly identifying at least one Barred Owl vocalization in a bout of calling (tested against 386 calls in 23 bouts; see Wood et al. [2019b] for further detail). The template detector occasionally identified the vocalizations of hybrid Spotted × Barred owls (hereafter "hybrids"). We counted hybrids as Barred Owls but post hoc testing indicated that the template frequently did not detect hybrid vocalizations.

Occupancy Modeling

We converted the bioacoustic data to Barred Owl detection histories in a multi-season occupancy framework (MacKenzie et al. 2003), which allowed us to model (1) $p_{i,t}$, the probability of detecting an owl given that one is present on survey *i* of year *t*; (2) ψ_t, the probability that a site is occupied in year *t*; and (3) γ_t, the probability that an unoccupied site will be colonized in year *t*. This formulation also allows for estimation of site extinction probability.

In the first of 2 sets of models, we used data from the 167 sites that were surveyed in both years to estimate detection, occupancy, and colonization. In competing models, we allowed detection to be constant (*p*(.)), vary among secondary sampling periods within year (*p*(Time)), vary among years (*p*(Year)), and vary with time and year. We allowed occupancy to be both constant and vary between years, whereas colonization was held constant given we could only estimate the parameter in 2018.

In the second set of models, we used all the sites (n_{2017} = 167, n_{2018} = 346) to test for associations between detection, occupancy, and colonization and covariates related to vegetation cover type and topography at the site level. To do so, we calculated the proportion of each 400-ha cell (i.e. "site") composed of open forest (canopy cover [CC] < 40%), young forest (CC ≥ 40% and Quadratic Mean Diameter [QMD] < 31cm), medium forest (CC ≥ 40% and QMD 31–61 cm), old forest (CC ≥ 40% and QMD ≥ 61 cm) based on Gradient Nearest Neighbor data (www.lemma.forestry.oregonstate.edu/data/structure-maps), and montane riparian forest derived from 2016 National Land Cover Database data (www.mrlc.gov/national-land-cover-database-nlcd-2016). We also considered the average slope and elevation within sites (USGS Digital Elevation Model).

For both sets of models, we first determined the detection structure, then occupancy, and then colonization, by comparing univariate models and using the structure (i.e. covariate, if any) of the top-ranked model in subsequent steps. We ranked models with Akaike's information criterion with a correction for small sample size (AIC_c); we considered models with ΔAIC_c < 2 to have substantial support from the data (Burnham and Anderson 2010). We used packages *xlsx* and *RMark* in program R (R Core Development Team 2014) for these analyses.

GPS Tagging and Owl Site Fidelity

We measured the dispersion of sites occupied by Barred Owls in both years using the average nearest-neighbor ratio in ArcGIS 10.3 (ESRI, Redlands, California, USA). To determine whether the Barred Owls we detected with ARUs were site-faithful or more nomadic, we marked 10 individuals with GPS tags. Between May and August of both years we used visual and vocal lures to attract Barred Owls at locations where we had previously detected owls, captured them with dho-gaza nets, and applied Argos-enabled GPS backpack tags (Lotek Wireless, Newmarket, Ontario, Canada). We programmed tags to record 4–5 nighttime locations per week and one additional location at noon every 2 weeks April–August, and then to record one nighttime location per week September–March. Genetically pure Barred Owls in the invading population sometimes have plumage that is visually intermediate between Spotted Owls and Barred Owls of the eastern North American population (J. Dumbacher personal communication), making visual identification difficult. Three of the individuals we marked had intermediate plumage, but without knowing their pedigrees we could not ascertain whether they were hybrids or atypical Barred Owls.

We calculated Barred Owl home range size using a 95% kernel density estimator (KDE) and also calculated 10–90% KDEs in intervals of 10%. In Oregon, Barred Owl territories, or the core areas of their ranges that are actively defended, averaged 22% of the size of their home ranges (Wiens et al. 2014), so we treated the size of the KDE percentile that best matched that proportion as an estimate of territory size. We used packages *adehabitatHR*, *foreign*, *maptools*, *rgeos*, *rgdal*, and *xlsx* in program R, and ArcGIS for these analyses.

RESULTS

Change in Barred Owl Occupancy

Based on sites surveyed in both years (n = 167), detection and occupancy probabilities differed between years (p(Year) ψ(Year) γ(.); $\Delta AIC_c = 0$, ω = 0.31; Appendix Table 1). Detection was greater in 2017 than in 2018 ($p_{2017} = 0.83$, 85% confidence interval [CI]: 0.60–0.98; $p_{2018} = 0.37$, CI: 0.26–0.47). Site occupancy increased by a factor of 2.6 from 0.082 (CI: 0.045–0.12) to 0.21 (CI: 0.14–0.28) between the 2 years, an increase of 163% (Figure 1A). The 85% confidence intervals of those estimates did not overlap (Arnold 2010). Site colonization in 2018 was 0.18 (CI: 0.12–0.24) and the derived estimate of site extinction in 2018 was 0.44 (CI: 0.15–0.73). The null model indicating constant detection (P = 0.39; CI: 0.29–0.49) and occupancy (ψ = 0.19; CI: 0.13–0.24) across years also received substantial support ($\Delta AIC_c = 0.33$, $w_i = 0.26$; Appendix Table 1). The support for uniformity in occupancy between years was likely driven by the low value of p in that model relative to p_{2017} in the top-ranked model.

Based on our expanded sites (n = 346; Figure 2B), the most-supported multi-season occupancy model was p(Medium Forest) ψ(Year + Slope) γ(Old Forest) (w_i = 0.37; Appendix Table 2). According to this model, detection increased with the amount of medium forest ($\beta_{\text{Medium Forest}} = 6.52$; CI: 4.28–8.77), occupancy was lower in territories with steeper slopes ($\beta_{\text{Slope}} = -0.64$; CI: −0.085 to −0.075), and colonization increased with the amount of old forest ($\beta_{\text{Old Forest}} = 5.34$; CI: 4.61–6.06; Figure 1B–D; Appendix Table 2).

On the basis of vocal characteristics, we identified hybrid individuals on at least 2 sites, one of which was also occupied by a Barred Owl. However, as noted above, the template detector was not optimized to identify hybrid vocalizations so it is likely that some or even many sites occupied by hybrids were not identified. Therefore, we likely underestimated the combined Barred Owl and Barred × Spotted owl hybrid population in the northern Sierra Nevada.

Territory Size, Distribution of Territories, and Site Fidelity

In 2017, occupied sites (i.e. grid cells in which a confirmed Barred Owl vocalization was recorded) were significantly clustered (nearest-neighbor ratio = 0.55,

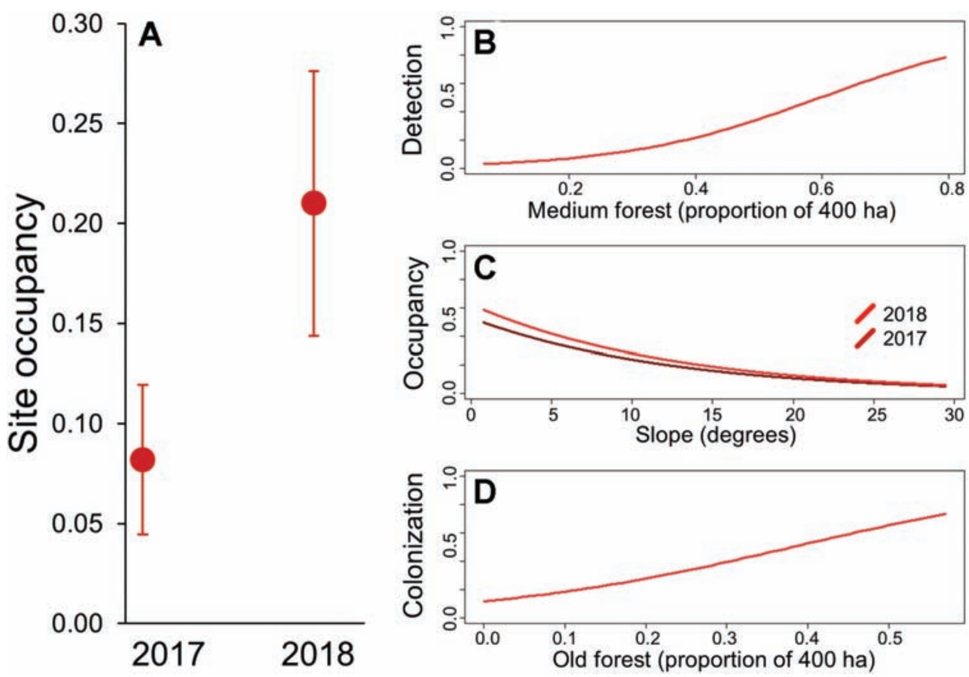

FIGURE 1. Barred Owl population change and habitat associations. (**A**) Barred Owl population change between 2017 and 2018 estimated by the top multi-season occupancy model based on 167 core sites surveyed in both years (Appendix Table 1); error bars are 85% confidence intervals. Relationships between Barred Owl (**B**) detection, (**C**) occupancy, and (**D**) colonization estimated by the top multi-season occupancy model based on 167 sites in 2017 and 346 sites in 2018 (Appendix Table 2).

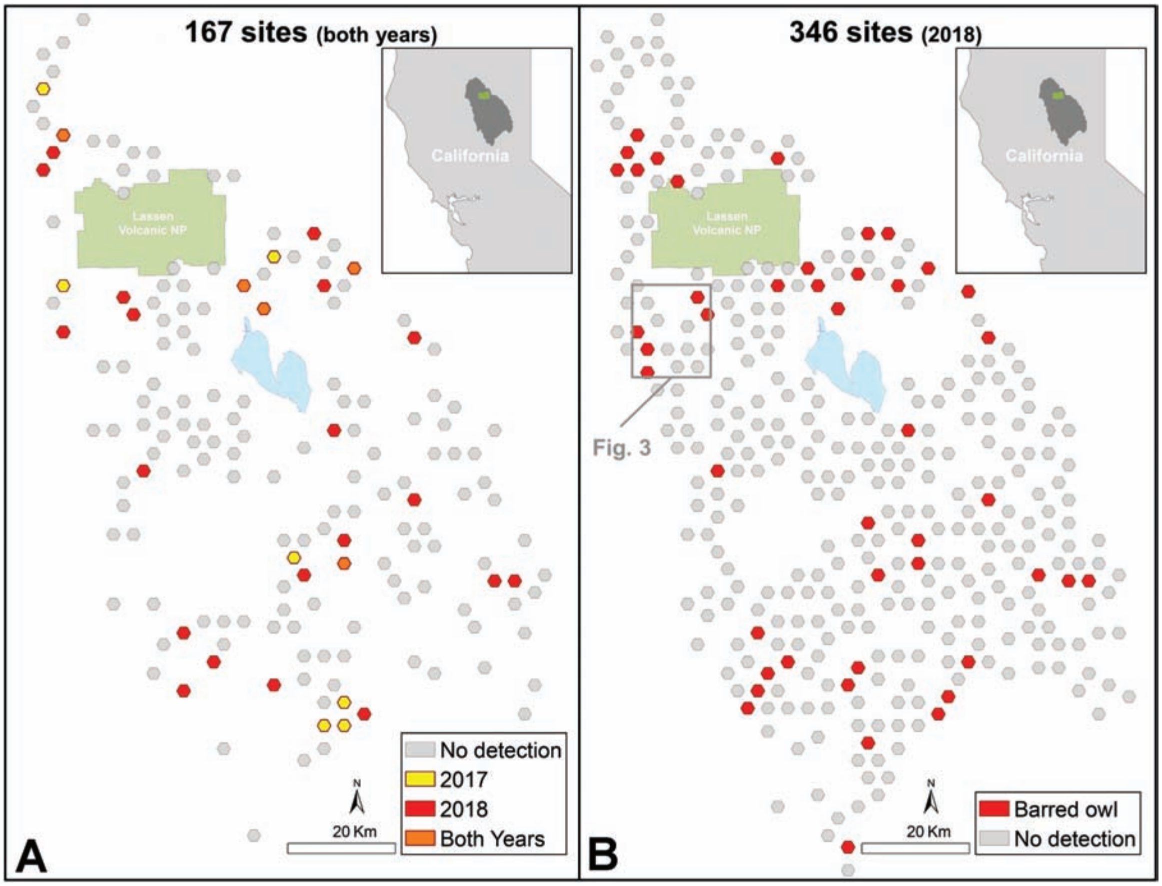

FIGURE 2. Locations of Barred Owl detections determined using passive acoustic surveys in the northern Sierra Nevada, California. (**A**) Sites surveyed in 2017 and 2018; (**B**) all sites in 2018.

$z = -4.46$, $P < 0.001$; Figure 2A) but, in 2018, were more dispersed (nearest-neighbor ratio = 1.14, $z = 1.78$, $P = 0.076$; Figure 2B).

We tracked the 10 putative Barred Owls tagged in 2017 and 2018 for an average of 229 days (range: 52–392), obtaining an average of 39.1 locations (range: 15–72). All 10 individuals had defined home ranges (Figure 3) and all 5 individuals whose GPS tags provided locational data until breeding season following tagging (i.e. until March) exhibited interannual site fidelity. Mean home range (95% KDE) was 2,004 ha (SE = 222, range: 644–3,076 ha) and mean territory size (KDE isopleth closest to 0.22*95% KDE) was 411 ha (SE = 38, range: 150–513 ha). Mean territory size was almost identical to our sampling grid cell sites of 400 ha, which we treated as proxies for owl territories (Figure 3).

DISCUSSION

Uncertainty about the population status of Barred Owls in the Pacific Northwest and their effects on Spotted Owls contributed to delays in the implementation of decisive conservation action (Courtney et al. 2004, Buchanan et al. 2007, Wiens et al. 2018). By the time the Barred Owl population was unambiguously high and its negative effects on Spotted Owls had been demonstrated with multiple data sources (e.g., Wiens et al. 2014, Yackulic et al. 2014, Dugger et al. 2015), the Barred Owl had already spread across the entire range of the Northern Spotted Owl, was on a trajectory to displace them, and now poses a much more difficult and expensive management dilemma (Wiens et al. 2018, Yackulic et al. 2019). Our study revealed a 2.6-fold increase in Barred Owl site occupancy across the northern Sierra Nevada from 2017 to 2018, which suggests that the growth phase of the invasion there may have recently begun and that efficient regional-scale management may still be possible. Barred Owls colonized areas with more old-forest conditions, which are also positively associated with Spotted Owl territory survival (Jones et al. 2018) and portends prompt interspecific competition. Our 2018 site occupancy estimate of 0.22 for Barred Owls did not fully account for Spotted × Barred owl hybrids, which may constitute up to 40% of "non-Spotted Owls" in the region (J. J. Keane personal communication) and could represent an additional threat to Spotted Owls via hybridization (Keane 2017). The initiation of the growth phase of the Sierra Nevada Barred Owl population could be an imminent threat to California Spotted Owls in the core of their

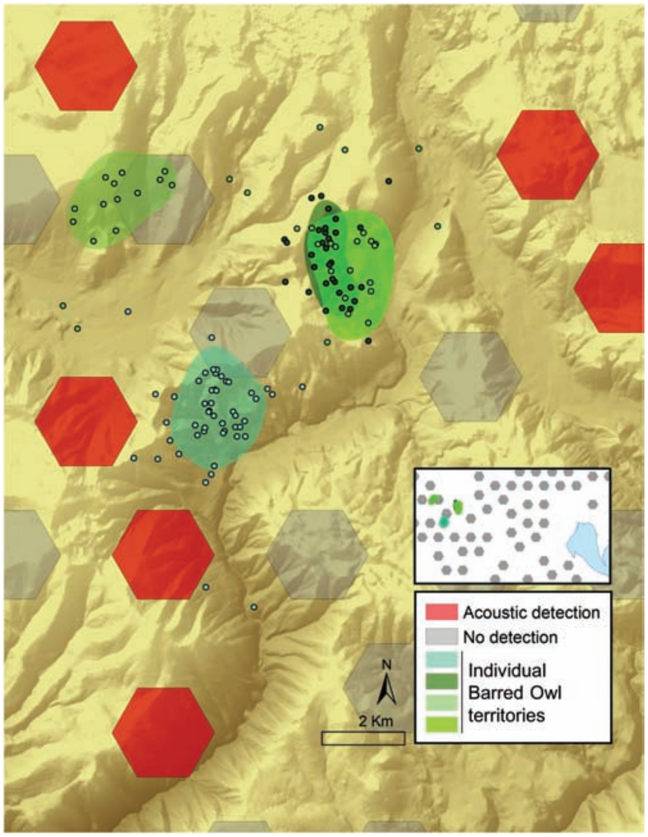

FIGURE 3. Acoustic detections of Barred Owls and locations of GPS-tagged individuals. Locational information includes locations (points) and territories (polygons).

range, yet its early detection presents conservation opportunities that were not available to managers of the northern subspecies.

Although we used only 2 yr of systematic monitoring data to infer rapid population growth, our inference is supported by several lines of evidence, including incidental observations suggesting that Barred Owl population growth was slow but increasing in the Sierra Nevada prior to our study (Keane 2017, J. J. Keane personal communication). This pattern of delayed rapid growth is consistent with an invading population but not with typical interannual variation in forest owl populations in the western United States (Crooks and Soulé 1999, Dugger et al. 2015, Tempel et al. 2016). Habitat associations with occupancy and colonization for Barred Owls in our study area are similar to those documented in the Pacific Northwest and further indicate that potentially intense competition is imminent. Occupancy was lower on steeper slopes in our study area and during the growth phase in the Pacific Northwest (Pearson and Livezey 2003), and colonization was positively associated with older forest in both regions (Yackulic et al. 2012, 2014). We observed clustering of putative Barred Owl territories in 2017 but less so in 2018, which is consistent with an expanding population and possibly dispersal of juveniles from reproductively successful pairs. Our estimated mean Barred Owl territory size closely matched the size of our noncontiguous survey sites, suggesting that detections at different sites represented independent Barred Owl territories and that increases in site occupancy reflected real increases in abundance. The seasonal and interannual site fidelity we observed in GPS-marked individuals suggested that many individuals were residents with established territories rather than vagrant dispersers. However, our GPS data were biased toward resident individuals, who were easier to capture, and may not be completely representative of the overall Barred Owl population because wide-ranging movements can be common along the leading edge of range expansions (Lindström et al. 2013). The relatively high estimate of site extinction (0.44; 7 sites occupied in 2017 had no detections in 2018) despite an overall increase in site occupancy does suggest some degree of transience by Barred Owls in the Sierra Nevada. Wide-ranging individuals can upwardly bias occupancy estimates (Berigan et al. 2019), so we acknowledge that actual Barred Owl territory occupancy may be lower than estimated in both years.

Uncertainty surrounding the population growth rates of non-indigenous species—and thus whether they may become invasive species—is likely to be a persistent problem, and early detection of such growth is rare. In the case of the Barred Owl in the Sierra Nevada, early detection resulted in part from our implementation of a landscape-scale community-level monitoring program. This passive acoustic approach is more efficient than species-specific surveys for documenting the arrival of non-indigenous species, promptly identifying when they begin to display the rapid population growth that characterizes a nascent invasion, and investigating their effects on native species (Wood et al. 2016, 2019b). Without such multi-species monitoring efforts, the effects of invasive species on native species may only become apparent after population densities make management responses very difficult and expensive. Survey techniques capable of sampling whole communities such as bioacoustics, camera trapping, multi-method trap arrays, and e-DNA may also help alert managers to the arrival of species that are potentially detrimental to native species and initiate conservation responses before such actions become highly expensive and less efficient. Early detection thus enables managers to act based on the "Precautionary Principle," which posits that "when an activity raises threats of harm to human health or the environment, precautionary measures should be taken even if some cause and effect relationships are not fully established scientifically" (Ashford et al. 1998). In essence, early detection of biological invasions allows the type of proactive management paradigm that has been used to mitigate the spread of deadly infectious diseases.

In light of the well-documented effects of Barred Owls on Northern Spotted Owls (e.g., Dugger et al. 2011, 2015; Wiens et al. 2014, Diller et al. 2016, Yackulic et al. 2019), we suggest that the Precautionary Principle be invoked in developing a conservation response to the rapid Barred Owl population growth in the Sierra Nevada. The cost of inaction, which includes the potential extirpation of California Spotted Owls, is high despite the uncertainty in population growth rates associated with 2 yr of survey data (this study) and incidental observations (Keane 2017). We believe that the experimental removal of Barred Owls across the northern Sierra Nevada landscape and potentially in areas farther south in the form of a large-scale Before–After / Control–Impact study constitutes an appropriate conservation response. Removals can be efficient when Barred Owls occur at low densities and their locations are known (Diller et al. 2014, 2016)—as occurs in our study area—but effective removals (lowering densities of Barred Owls sufficiently to allow coexistence with Spotted Owls) are expensive, labor-intensive, and of uncertain efficacy when Barred Owls reach high densities (Wiens et al. 2018).

Most successful invasive species removal programs have occurred on island, lake, or river systems over relatively limited areas with hard dispersal barriers (Simberloff 2003). The Sierra Nevada is not such a system: it is geographically vast (>52,000 km^2) and connected to a large Barred Owl source population. Locating Barred Owls for removal would require both widespread and intensive surveying, but our work indicates that such an approach is tractable, yields high statistical power to detect changes in site occupancy, and provides community-level data (Wood et al. 2019a, 2019b). Only a narrow band of suitable habitat facilitates the dispersal of Barred Owls from the Pacific Northwest to the Sierra Nevada ecosystem (Barrowclough et al. 2005, 2011), so following an initial removal effort, removals concentrated in this restricted dispersal zone could be a cost-effective means of "defending" the Sierra Nevada ecoregion from further colonization. Moreover, the associations we observed between Barred Owl site occupancy and flatter areas and between site colonization and older forest could help prioritize the allocation of removal survey effort. The apparent clustering of Barred Owl territories, likely resulting from Barred Owls using conspecific cues when establishing territories (Seamans and Gutiérrez 2006), may also make initial removals and follow-up surveys more efficient (Diller et al. 2014). While challenging, we believe that maintaining Barred Owls at low population densities within the Sierra Nevada—the core range of the California Spotted Owl—is feasible with swift and efficient management intervention.

Delaying removals, as occurred within the range of the Northern Spotted Owl, bears an ethical cost because allowing a large increase in the Barred Owl population requires more individuals to be killed to reduce the population to a given level. It also raises the prospect that California Spotted Owls will ultimately be consigned to small refuges requiring continual Barred Owl removals in an inhospitable matrix of high Barred Owl density (e.g., Wiens et al. 2018). Thus, our early detection of rapid Barred Owl population growth provides a novel but potentially fleeting opportunity to initiate efficient Barred Owl management and avert significant ecosystem change in the Sierra Nevada, including the extirpation of the California Spotted Owl.

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Ethics statement: All animal handling was consistent with approved IACUC protocol #1041 (San Jose State University).

Author contributions: CMW led the fieldwork and conducted the analyses; CMW, MZP, and RJG wrote the manuscript; MZP, RJG, and JJK secured funding.

Data depository: Our data is deposited in Zenodo.org. Analyses reported in this article can be reproduced using the data found at https://zenodo.org/record/3249054#.XQkKLLxKhEY

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APPENDIX TABLE 1. Results of multi-season models of Barred Owl site occupancy in the northern Sierra Nevada based on 167 core sites sampled both in 2017 and 2018. *p* represents detection probability that can vary by year (Year) or secondary sampling periods within year (Time), ψ represents the site occupancy probability, and γ represents the site colonization probability. *k* is the number of parameters, AIC_c is Akaike's information criterion corrected for small sample sizes, and w_i is AIC_c model weight.

Model	*k*	AIC_c	ΔAIC_c	w_i	Deviance
p(Year) ψ(Year) γ(.)	5	337.62	0.00	0.31	−216.89
p(.) ψ(.) γ(.)	3	337.96	0.33	0.26	−212.45
p(.) ψ(Year) γ(.)	4	339.10	1.47	0.15	−213.36
p(Year) ψ(.) γ(.)	4	340.00	2.37	0.09	−212.45
p(Time + Year) ψ(Year) γ(.)	7	340.54	2.91	0.07	−218.14
p(Time) ψ(.) γ(.)	5	340.93	3.30	0.06	−213.59
p(Time) ψ(Year) γ(.)	6	341.92	4.30	0.04	−214.67
p(Year + Time) ψ(.) γ(.)	6	343.00	5.38	0.02	−213.59

APPENDIX TABLE 2. Results of multi-season occupancy models exploring associations between Barred Owl site occupancy and vegetation cover classes and topography in the northern Sierra Nevada based on all 346 sites surveyed. We determined the detection (*p*) structure first, then used the top-ranked model (bold) to determine the occupancy (ψ) structure, and repeated that process for colonization (γ). A year term was included for ψ in all models. *k* is the number of parameters, AIC_c is Akaike's information criterion corrected for small sample sizes, and w_i is AIC_c model weight.

Parameter	Model	*k*	AIC_c	ΔAIC_c	w_i	Deviance
p	**Medium Forest**	**5**	**530.04**	**0.00**	**0.47**	**519.92**
	Medium Forest + Year	6	531.20	1.16	0.27	519.03
	Open Forest	5	532.22	2.18	0.16	522.10
	Open Forest + Year	6	533.26	3.22	0.09	521.10
	Slope	5	540.59	10.55	0.00	530.47
	Slope + Year	6	540.77	10.73	0.00	528.60
	Year	5	543.58	13.54	0.00	−366.35
	Elevation + Year	6	544.33	14.29	0.00	532.17
	(.)	4	544.63	14.59	0.00	−363.26
	Old Forest + Year	6	545.40	15.36	0.00	533.23
	Mt. Riparian. Forest + Year	6	545.41	15.37	0.00	533.24
	Young Forest + Year	6	545.62	15.58	0.00	533.45
	Elevation	5	545.99	15.95	0.00	535.87
	Mt. Riparian. Forest	5	546.02	15.98	0.00	535.90
	Old Forest	5	546.56	16.53	0.00	536.45
	Young Forest	5	546.60	16.56	0.00	536.48
ψ	**Year** + **Slope**	**6**	**526.98**	**0.00**	**0.43**	**514.81**
	Year + Old Forest	6	529.02	2.04	0.15	516.86
	Year + Open Forest	6	529.63	2.65	0.11	517.47
	Year	5	530.04	3.06	0.09	519.92
	Year + Young Forest	6	530.44	3.46	0.08	518.27
	Year + Medium Forest	6	530.86	3.88	0.06	518.70
	Year + Mt. Riparian Forest	6	531.87	4.89	0.04	519.70
	Year + Elevation	6	531.89	4.91	0.04	519.72
γ	**Old Forest**	**7**	**525.41**	**0.00**	**0.37**	**511.18**
	(.)	**6**	**526.98**	**1.57**	**0.17**	**514.81**
	Elevation	7	527.87	2.46	0.11	513.65
	Mt. Riparian Forest	7	528.39	2.99	0.08	514.17
	Open Forest	7	528.49	3.09	0.08	514.27
	Medium Forest	7	528.92	3.52	0.06	514.70
	Young Forest	7	528.96	3.55	0.06	514.74
	Slope	7	528.97	3.56	0.06	514.74