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Detecting small changes in populations at landscape scales: a bioacoustic site-occupancy framework

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ABSTRACT

Occupancy modeling based on detection/non-detection data has become a common approach for monitoring changes in the populations of both sensitive and invasive species, with emerging bioacoustic technology enhancing opportunities for implementing such programs at landscape-scales. Statistical power, however, to detect small but biologically meaningful changes in site occupancy as part of landscape-scale monitoring is typically low, with large – yet hereto unknown – sampling efforts likely required for rigorous inference. Therefore, we (i) assessed sampling levels and detection probabilities needed to detect small changes in site occupancy driven by both intrinsic trends and management effects, and (ii) evaluated the feasibility of using bioacoustics to simultaneously monitor a common but declining species and a rare but increasing invasive competitor within a site occupancy framework. Simulation-based power analyses indicated that detection/non-detection data collected at large numbers of sites (500–1500) can yield high statistical power (> 80%) to detect ≥2% annual declines in site occupancy within 10 years, but depended on the number of visits per site, initial occupancy rates, and detection probabilities. Statistical power to detect ≥30% declines in local survival rates in 10 years was also high. Based on ~6-night passive-acoustic surveys, site occupancy and detection probabilities were 0.43 and 0.50, respectively, for the common but declining species (the spotted owl), and 0.09 and 0.67, respectively, for the rare but increasing competitor (the barred owl). Simulations parameterized with these empirically-derived rates indicated that 2% annual declines in spotted owl site occupancy could be detected with high statistical power in 10 years with 1,000 sites surveyed three times per season (year) or 1500 sites surveyed two times per season. Statistical power to detect 4% annual increases in site occupancy for expanding barred owl populations with this sampling scheme was also high. Thus, our study yielded the novel finding that passive-acoustic monitoring can be used to detect small but potentially biologically meaningful changes in site occupancy for multiple species with very different population dynamics with high confidence. More broadly, as computational improvements bring acoustic-based whole-community identification into the realm of possibility, our approach will allow managers to rapidly assess the statistical power attainable for each species: systematic and statistically robust monitoring of entire faunal communities within a unified framework at a landscape scale may become a reality.

1. Introduction

Estimating population trends and understanding the factors responsible for changes in abundance are key components of monitoring programs for species of conservation concern (Marsh and Trenham, 2008). Trend estimates can have important implications for assigning protected status to declining species (IUCN, 2012), while the globally pervasive phenomena of increasing range shifts (Dornelas et al., 2014)

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has made tracking and understanding the expansion of non-native species a critical conservation task (Gutiérrez et al., 2007; Phillips et al., 2007). In both cases, understanding the drivers of population change is essential to implementing effective conservation strategies, whether they are designed to facilitate the recovery of endangered species, avert further declines of threatened species, or control invasive species (Caughley and Sinclair, 1994; Peery et al., 2004; Russell et al., 2017). Population changes over time have typically been quantified using costly and labor-intensive abundance estimation and demographic approaches (e.g., capture-recapture). However, the more recent development of site occupancy modeling approaches has facilitated the implementation of population monitoring programs based on detection/non-detection data while taking into account imperfect detection (MacKenzie et al., 2002, 2003; Tyre et al., 2003). A key consideration for designing and implementing occupancy-based monitoring programs involves determining what level of sampling effort will yield sufficient statistical power to detect biologically meaningful changes in site occupancy and thus support robust inferences (Mackenzie and Royle, 2005).

Despite the common application of occupancy approaches to monitor populations, statistical power to detect temporal trends and management effects on site occupancy is low under typical sampling designs and efforts (Rhodes et al., 2006; Popescu et al., 2012). Gains in statistical power within an occupancy framework can be achieved by increasing the number of sites sampled, the duration of the monitoring program, the number of visits per site (secondary sampling periods) in each primary sampling period, and detection probability (1 – the false negative rate; Rhodes et al., 2006; Popescu et al., 2012; Steenweg et al., 2016). However, the sampling effort required to achieve “acceptable” statistical power (typically 0.80) to detect small changes with a viable sampling design incorporating imperfect detection has not been established (Popescu et al., 2012; for large declines see Rhodes et al., 2006).

Recent advances in passive-acoustic recording technologies have the potential to increase the feasibility of detecting small changes in site occupancy as part of landscape-scale population monitoring for acoustically active species (Kalan et al., 2015; Shonfield and Bayne, 2017; Shonfield et al., 2018; Hill et al., 2018). Autonomous recording units (ARUs) passively record sound for long periods of times (days to months) and the resulting acoustic data can be analyzed to produce the detection/non-detection information at the core of occupancy modeling approaches (MacKenzie et al., 2002, 2003; Campos-Cerqueira and Aide, 2016). ARUs reduce the need for trained observers and potentially per-survey costs, which could allow for more frequent and spatially extensive surveys than traditional observer-based approaches (Borker et al., 2015; Shonfield et al., 2018; Hill et al., 2018). As a result, ARUs have been used to survey a broad range of marine and terrestrial species (Delport et al., 2002; Hartwig, 2005; Walters et al., 2012; Penone et al., 2013; Helble et al., 2013). Furthermore, the performance of ARUs compared to trained human observers in avian studies has been evaluated in a wide range of habitats and although the two approaches have different advantages and disadvantages, inferences regarding parameters of interest are generally comparable (Zwart et al., 2014). While bioacoustic approaches are rapidly gaining momentum as a research tool, their capacity to detect small population changes with high statistical power as part of a landscape-scale monitoring program has not yet been evaluated (Rhodes et al., 2006).

Both site-specific sampling considerations and acoustic data processing procedures can influence detection probabilities and thus the statistical power of an acoustics-based monitoring program (e.g., Helble et al., 2013). From a sampling perspective, deploying more units for longer secondary sampling periods can increase detection probabilities (Hagens et al., 2018) and thus increase statistical power for detecting changes in occupancy (Popescu et al., 2012). The effects of acoustic analyses stem from the fundamental task of extracting target signals, typically focal species vocalizations, from massive amounts of raw audio data: if too few of the vocalizations that have been recorded are successfully extracted, detection will likely decrease. There are generally two stages of extraction: identifying potential target signals, or regions of interest (ROI), and classifying those regions of time as either true focal species vocalizations (i.e., detections) or non-detections (i.e., false alarms). Optimizing the identification process entails balancing the proportion of all true target signals that are correctly identified as ROI (i.e., recall; measured using a library of known calls) and the proportion of ROI that truly represent focal species vocalizations (i.e., precision) (Mellinger et al., 2016). Choices that increase recall – such as setting a low threshold for what constitutes a ROI – may increase detection, but also tend to decrease precision and thus increase the amount of processing time required to classify ROI. Managing trade-offs during both acoustic analyses and sampling considerations that may affect detection have important consequences for population monitoring programs given the sensitivity of statistical power to detection probabilities within a site occupancy framework (Popescu et al., 2012).

Here, we evaluated the extent to which acoustic detection/non-detection data analyzed within a dynamic occupancy modeling framework can be used to monitor populations at broad temporal and spatial scales as an alternative to more labor-intensive demographic or observer-based occupancy approaches. Dynamic occupancy models have become a widely-used tool for monitoring populations because they incorporate the processes of site colonization and extinction through time (MacKenzie et al., 2003; Martin et al., 2010; Ahumada et al., 2013; Comer et al., 2018). We first explored sampling efforts and detection probabilities needed to detect population trends and potential effects of landscape management activities with high statistical power. We then used California spotted owls (*Strix occidentalis occidentalis*) and barred owls (*S. varia*) in the Sierra Nevada, USA as a case study to evaluate the extent to which changes site occupancy for the two species with different population dynamics can be monitored with passive-acoustic surveys.

Spotted owls and barred owls are ideal model organisms for assessing passive-acoustic surveys as a tool to monitor populations because they both use vocalizations for pair bonding and territory maintenance activities (Ganey, 1990; Van Lanen et al., 2011). Local spotted owl populations are currently monitored using demographic methods (Franklin et al., 1996), and these studies have provided considerable insights into population dynamics within local study areas (Wiens et al., 2014; Tempel et al., 2016; Jones et al., 2018). However, spotted owls reside at the epicenter of landscape-scale forest management debates, and are threatened by factors that transcend demographic study areas and are difficult to manage, particularly impacts of the invasive barred owl (Wiens et al., 2014). As a result of their westerly range expansion over the last several decades, barred owls are now sympatric with northern spotted owls (*S. o. caurina*) (Livezey, 2009) and are colonizing the range of the California spotted owl in the Sierra Nevada (Keane, 2017). Barred owls are competitively dominant to spotted owls and are believed to pose an existential threat to both subspecies (Gutiérrez et al., 2007; Wiens et al., 2014). Therefore, a cost-effective monitoring program with the statistical power to detect small population changes in both spotted owls and barred owls at landscape scales and to detect population responses of both species to management activities would be an important conservation achievement. More broadly, as species range shifts and action ecosystem management become more prevalent (Dornelas et al., 2014; Suding et al., 2015), the framework for such a program would provide a foundation upon which other studies could be developed to provide insight into the population dynamics and responses to management of both threatened and invasive species at previously unattainable spatial scales.

2. Methods

2.1. Estimating statistical power for a site occupancy monitoring program

Using simulations, we estimated statistical power to detect both

Table 1
Input parameter values for simulation-based analyses conducted to estimate statistical power to detect (i) management effects on local survival and (ii) trends in occupancy based on a 10-year monitoring program employing a dynamic occupancy study design.

Parameter	Scenario	Values
Management and trend analyses		
Detection probability	General	0.4, 0.8
	Spotted owl	0.5
	Barred owl	0.67
Sites per year	All	500, 1000, 1500
Visits per site	All	2, 3
Annual variation (CV) in colonization	General	0.01
	Spotted owl	0.01
	Barred owl	0
Annual variation (CV) in survival	All	0.04
Management analysis		
Initial occupancy	General	0.375
	Spotted owl	0.43
	Barred owl	0.09
Proportion of sites treated	All	0.5
Proportional reduction in survival	All	0.1, 0.3, 0.5
Trend analysis		
Initial occupancy	General	0.375, 0.667
	Spotted owl	0.43
	Barred owl	0.09
Annual change in occupancy	General	-0.02, -0.04
	Spotted owl	-0.02, -0.04
	Barred owl	0.04

temporal trends in site occupancy as well as effects of generic, hypothetical management activities (e.g. fuel reduction treatments to reduce fire risk in the Sierra Nevada, USA; Collins et al., 2011) on site occupancy. Specifically, we simulated site occupancy datasets using random but known properties, and ran dynamic occupancy using several different parameterizations to evaluate statistical power. We did so for a range of different plausible (i) initial site occupancy rates (ii) detection probabilities, (iii) levels of sampling effort (number of sites sampled, number of visits/site, and study duration), and (iv) effect sizes (rates of yearly changes in occupancy and overall management impacts on site occupancy) (Table 1). We simulated multi-season detection/non-detection datasets following a robust sampling design with multiple secondary sampling periods (visits) in each primary sampling period (e.g., year) as is typically done for many species (Kendall et al., 1997). Simulated datasets were an expression of site occupancy dynamics as a state process based on (i) the probability of an occupied site continuing to be occupied from one season to the next (i.e., site survival), and (ii) the probability of a site unoccupied in time t becoming occupied in time $t+1$ (i.e., site colonization). We simulated occupancy dynamics for sites occupied in year t using local (site) survival rather than site extinction (i.e., site survival = 1 − site extinction), following (Popescu et al., 2012), as survival is a demographic parameter commonly used in management and conservation applications. We simulated local survival and colonization events for each site using Bernoulli trials. Conditional on the true site occupancy state, we simulated the observed occupancy state in each secondary sampling period based the probability of detection (Royle and Kéry, 2007). We simulated 300 data sets for each combination of initial occupancy, detection probability, sampling effort, and effect size using program R 2.13 (R Core Development Team, 2014), and quantified statistical power as described below (see Appendix 1 for R code).

2.1.1. Simulation scenarios

Under equilibrium, the probability that site i is occupied can be expressed as:

$$\psi_i = \frac{\gamma_i}{\gamma_i + \varepsilon_i}$$

where ε_i and γ_i are site-specific probabilities of extinction and colonization, respectively. When simulating datasets to evaluate temporal trends in occupancy, we set ψ_1 to 0.375 or 0.667 to evaluate the ability to detect site occupancy trends in uncommon and common species, respectively. Under equilibrium, $\psi_i = 0.375$ yields $\varepsilon_i = 0.20$ (i.e., local survival = 0.80) and $\gamma_i = 0.12$, and $\psi_i = 0.667$ yields $\varepsilon_i = 0.20$ (i.e., local survival = 0.80) and $\gamma_i = 0.40$. We simulated 2% and 4% annual declines in site occupancy which reflected 17% and 31% total declines, respectively, over a 10-year monitoring program. Detecting of declines of these magnitudes can have important policy implications (IUCN, 2012), and provide opportunities to arrest declines before they significantly threaten population and species viability. We limited analyses to a 10-year monitoring program given that longer programs (e.g., 20 years) are less likely to garner support during project development. In addition, we ran sets of simulations with 0% reduction in local survival and colonization to estimate the Type I error rates, as these rates may be sensitive to different model parameterizations (Popescu et al., 2012).

Directly projecting temporal trends in occupancy rates in simulated datasets was not possible given that occupancy histories were generated using a dynamic occupancy approach where occupied sites became unoccupied according to ε and unoccupied sites became occupied according to γ. Therefore, we simulated annual increases in extinction rates (decrease in local survival) and decreases in colonization rates that were expected to yield 2% and 4% annual declines in occupancy. Simple recursive calculations indicated that for an initial occupancy of $\psi_i = 0.375$, an annual increase of 2.3% in extinction coupled with an annual decrease of 2.3% in colonization led to a 2% annual decline in the mean annual change in site occupancy ($\hat{\lambda}_t$) over a 10-year simulation. For $\psi_i = 0.667$, the yearly extinction and colonization rates changed 3.2% annually to achieve the same decline. To achieve a 4% decline in the mean annual change in site occupancy ($\hat{\lambda}_t$) with an initial occupancy of $\psi_i = 0.375$, we used an annual increase of 4.2% in extinction coupled with an annual decline of 4.2% in colonization; for $\psi_i = 0.667$, the yearly rates of change in extinction and colonization were 5.9%. However, annual variation in site occupancy occurs in natural populations and will reduce power to detect changes in occupancy. Therefore, we allowed local survival and colonization in each year to vary by adding a normally distributed random value with mean = 0 and standard deviation (SD) = 0.04 and 0.01, respectively, which represented the approximate level of variation in these parameters for spotted owls (Tempel et al., 2016).

We estimated statistical power assuming 500, 1000, or 1500 sites were surveyed per year with either 2 or 3 visits per site in each year of the study. We focused on large numbers of sampling sites because of our emphasis on landscape-scale monitoring of widely distributed species. We limited our exploration to a relatively small number of visits per year given the inevitable constraints associated with visiting many dispersed sites on multiple occasions. Finally, we estimated statistical power assuming detection probability was 0.40 or 0.80 to bracket a reasonable range of values that could affect the ability of a monitoring program to assess population trends. Variation in several not-simulated factors could affect detection, including focal species' intrinsic vocalization rates, number of ARUs deployed and duration of deployment, choices affecting the precision—recall trade-off made during the target signal extraction phase of acoustic analyses, and other hardware and software features, but were beyond the scope of these simulations.

When estimating statistical power to detect management effects on local survival, we modeled occupancy histories assuming a true equilibrium occupancy state in $t = 1$, where $\psi_1 = 0.375$. Thus, in our case, $\varepsilon_i = 0.20$ (i.e., local survival = 0.80) and $\gamma_i = 0.12$ in the absence of

management. We simulated 10-year occupancy datasets with 10, 30 and 50% reductions in local survival and, for simplicity, assumed management actions did not affect site colonization. This represents a generic case in which management actions are detrimental to a focal species while perhaps successful by other metrics (e.g., Fraser et al., 2017; Wood et al., 2018), or an invasive species removal program (Hauser and McCarthy, 2009). However, as described below (2.1.2), we were also equally capable of detecting management-driven increases in occupancy (Popescu et al., 2012), representing the success of a conservation-oriented management action. For each management effect size, we estimated statistical power assuming 50% of the sites were actively managed over the life of a 10-year study period. We simulated management effects in a staggered manner, where an equal number of sites was subject to active management each year under two scenarios: 25% or 50% of all sites managed, because management activities are unlikely be conducted at large numbers of sites in a given year. Any given site i was only subject to management once and the management effect persisted at those sites until the end of the study. As with the population trends analysis, we simulated data sets assuming 500, 1000 or 1500 sites were surveyed per year, 2 or 3 visits per site each year, and that detection probability was 0.4 or 0.8.

2.1.2. Testing hypotheses with simulated data

Package *unmarked 0.9–2* (Fiske and Chandler, 2011) only fits dynamic occupancy models parameterized with the initial site occupancy rate, extinction, and colonization, and does thus not directly allow for the testing of trends in site occupancy rates over time. Therefore, we fit initial occupancy, colonization, and extinction models to each simulated dataset and estimated derived annual occupancy rates ($\widehat{\psi}_t$) recursively (MacKenzie et al., 2003; Tempel and Gutiérrez, 2013). We then estimated annual rates of change in occupancy as $\widehat{\lambda}_t = \widehat{\psi}_{t+1}/\widehat{\psi}_t$ and the geometric mean of the rate of change as $\widehat{\overline{\lambda}}_t = (\prod_{t=1}^{n} \widehat{\lambda}_t)^{\frac{1}{n}}$. We estimated sampling variance associated with $\widehat{\overline{\lambda}}_t$ using the delta method (Powell, 2007) based on 25 non-parametric bootstraps of the occupancy model fitted in package *unmarked*. We decided to run 25 bootstraps per simulation because fitting the occupancy models was time-prohibitive for large number of sites ($n = 1500$), and because the outputs for $n = 100$ and $n = 500$ bootstraps for a range of models did not yield different results outputs for $n = 25$ bootstraps. When testing for temporal trends in site occupancy, we compared $\widehat{\overline{\lambda}}_t$ to 1 (i.e., stationarity) and inferred significance if the upper 95% confidence limit for $\widehat{\overline{\lambda}}_t$ was < 1 (Tempel and Gutiérrez, 2013). We calculated statistical power as the proportion of simulations (out of 300) which met our significance criterion. By only considering tests to be statistically significant when $\widehat{\overline{\lambda}}_t < 1$, we effectively conducted a one-tailed test. By effectively setting $\alpha = 0.05$, we provided estimates of power to detect overall changes in occupancy at the landscape level, thus allowing for the possibility of testing of increases in occupancy as part of the actual monitoring program.

We tested for management effects on local survival rates using BACI-structured dynamic occupancy models following the framework developed by Popescu et al. (2012), a process facilitated by the ability to fit occupancy models to a large number of simulated datasets in the package *unmarked*. Using the *colext* function, we first indicated Control and Impact (i.e., management) sites with a site-specific variable, SiteMgmt = 'Control' and 'Impact', respectively. Next, we allowed site survival and colonization to vary across seasons (years) using seasonal site-specific variables, Season = "1", "2," … "N". Thus, the SiteMgmt factor had only two levels, whereas the Season variable had as many levels as there were seasons in the study ($n = 10$). We then indicated site–season combinations that represented impact sites after management application with a seasonal site-specific variable, SeasonSiteMgmt. This variable had level Control for the three subsets of the data set that were not subject to management (i.e., Control–Before, Control–After, and Impact–Before), and level Impact for the subset that were subject to management (i.e., Impact–After). SeasonSiteMgmt provided flexibility to fit models where management actions were conducted for in different years across sites. To test for a management effect, a model representing the (alternative) hypothesis of a management effect on site survival was represented as [ε(SiteMgmt + Season + SeasonSiteMgmt)] and compared to the null model of no management effect expressed as [ε(SiteMgmt + Season)]. While site colonization was held constant in the simulated dataset, we used the most general colonization model when testing for changes in site extinction [γ(SiteMgmt + Season SeasonSiteMgmt)] given that changes in colonization are of management interest and should be evaluated as part of an actual monitoring program (Ringold et al., 1996).

Maximum likelihood methods are used to estimate parameters for initial occupancy, detection, extinction and colonization; as such, likelihood ratio tests (LRT) are useful for testing hypotheses regarding the relative level of support for certain parameters using nested models (MacKenzie et al., 2005; Royle and Dorazio, 2008). Nesting means that a less general model (associated with the null hypothesis H_0) can be obtained by restricting some parameters of a more complex model (associated with the alternative hypothesis H_a). The likelihood ratio is:

$$\Lambda = \frac{L(\theta_0|y)}{L(\theta_A|y)}$$

The likelihood ratio statistic is then computed as $-2\log(\Lambda)$, and if the null is true, it asymptotically follows a chi-squared distribution, $\chi^2(v)$, where degrees of freedom v is the difference in the number of parameters to be estimated under H_A and H_0 (Royle and Dorazio, 2008). If H_0 rejection occurs, it suggests that the more general model better describe the ecological process, and thus the additional effects have a significant impact on estimating model parameters. We calculated statistical power as the proportion of simulations (out of 300) for which H_0 was rejected.

2.2. Monitoring spotted owls and barred owls with passive-acoustic surveys

2.2.1. Fieldwork and bioacoustics

We conducted passive-acoustic surveys for spotted owls and barred owls using ARUs deployed in the northern Sierra Nevada, USA, from May through August of 2017, a period that combined safe site access and relatively high owl vocal activity (Ganey, 1990). Seventy-four hexagonal grid cells 400-ha in size (i.e., sites), the approximate size of spotted owl territories in that region (Tempel et al., 2016) and likely somewhat larger than barred owl territories (Wiens et al., 2014), were each surveyed twice. Sites were randomly located in the Lassen and Plumas National Forests, but were non-contiguous to minimize non-independence among sites (Fig. 1). Each survey consisted of a 5- to 7-night deployment of 2 or 3 ARUs, and surveys were separated by at least one month. ARUs were deployed within each cell without knowledge of spotted owl occupancy history. ARUs (Swift recorder, Bioacoustics Research Program, Cornell Lab of Ornithology) had one omni-directional microphone and were programmed to record continuously at a sample rate of 32 kHz, bit depth of 16, and gain of +38 dB to an internal SD card.

We used the Template Detector feature of Raven 2.0 (Bioacoustics Research Program, Cornell Lab of Ornithology, 2017) to extract target signals from the acoustic data, in this case spotted owl and barred owl territorial vocalizations. Briefly, the template detector identifies regions of interest (ROI) by matching patterns in the data to user-defined templates (Mellinger and Clark, 2000), in our case high-quality recordings of territorial calls we collected within and outside our study area (Fig. 2). Because occupancy data requires only one true positive detection (see 2.2.2), we optimized our templates to identify at least one vocalization from any given bout of calling bout-level recall was high for both species ($R_{B\text{-}spotted\ owl} = 0.96$; $R_{B\text{-}barred\ owl} = 0.94$; Fig. 3; see

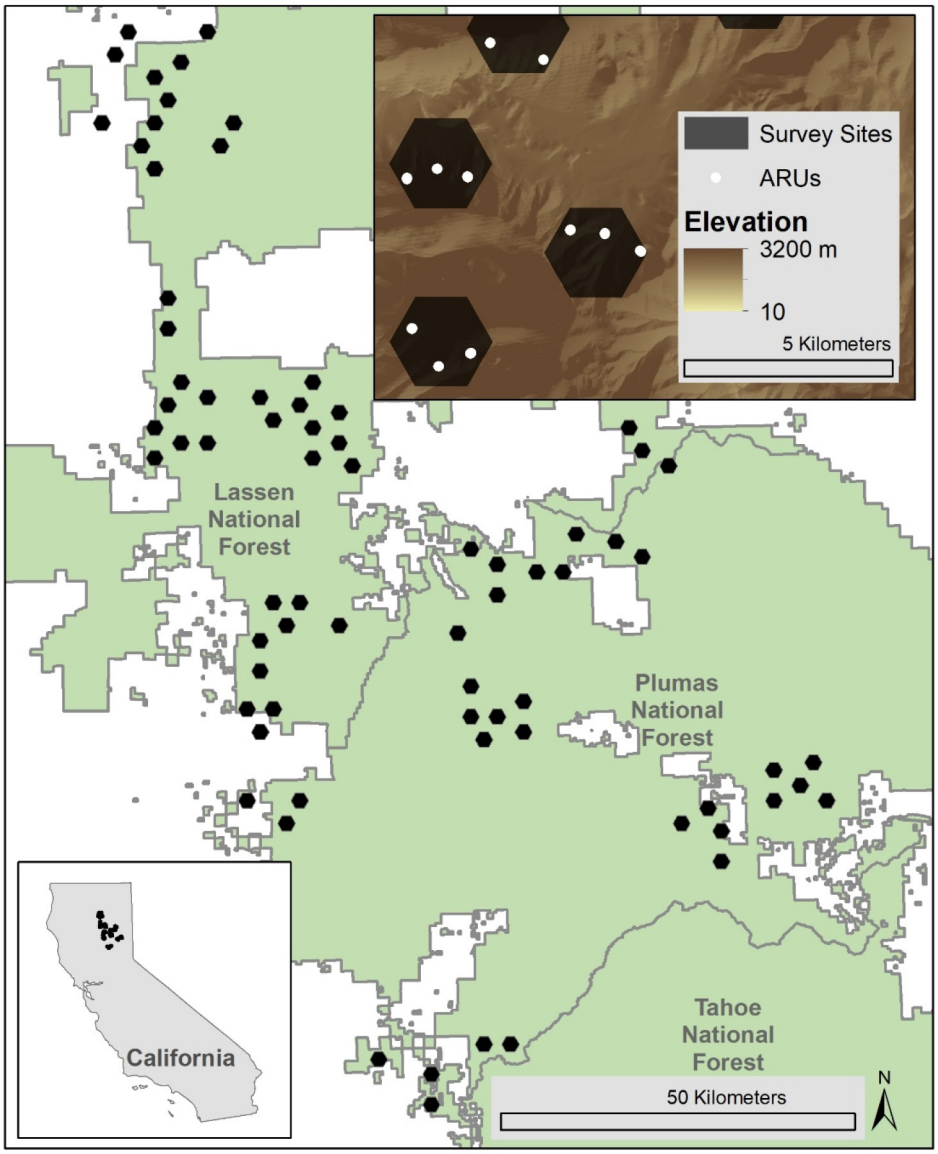

Fig. 1. The Lassen and Plumas National Forests in the northern Sierra Nevada, in California, USA, with sampling sites shown in black at three spatial scales.

Appendix 2 for a complete description of the template detector development process). Therefore, we were confident that detection was not substantially influenced by missed vocalizations. We applied both species' templates to all acoustic data collected from 20:00 to 06:00 local time at the 74 survey sites to identify spotted owl and barred owl vocalizations.

2.2.2. Occupancy modeling

For each species we registered a detection for a site during a given secondary sampling period if any of the ARUs deployed there recorded a focal species vocalization on at least one night. Possible detection histories were thus coded as 0-0, 1-1, 0-1, and 1-0. We used single-species, single-season occupancy models without site covariates (i.e., uniform occupancy and detection) to estimate the initial occupancy and detection probabilities needed to parameterize simulation-based power analyses for spotted owl and barred owls. We did not test more complex models because including site covariates in the simulations would have vastly increased their complexity. These analyses were conducted using the package *unmarked* (Fiske and Chandler, 2011) in program R (R Core Development Team, 2014).

2.2.3. Statistical power analyses

We estimated the statistical power to detect both temporal trends in and impacts of management on site occupancy for spotted owls and barred owls using estimates of occupancy and detection probabilities derived from the analyses described above (2.2.2). Specifically, we treated estimates of site occupancy as initial occupancy rates and assumed that estimated detection probabilities would be constant through the simulated 10-year monitoring program. Following the procedures described above (2.1.2), we estimated statistical power to detect a simulated 2% annual decrease in spotted owl occupancy over 10 years, which is consistent with current estimates (Jones et al. 2018), from $\psi_1 = 0.43$, by specifying a 2.4% annual increase in extinction and 2.4% annual decrease in colonization from initial values of 0.80 and 0.15, respectively, which yielded the current, acoustic-based estimate of occupancy under the assumption of equilibrium (see 2.2.2). We estimated statistical power to detect a simulated 4% annual increase in barred owl occupancy over 10 years from $\psi_1 = 0.09$, by specifying a 1% annual decrease in extinction and a 11% annual increase in colonization from initial values of 0.90 and 0.01, respectively, which yielded the current, acoustic-based estimate occupancy (see 2.2.2). Our rationale for testing for *increases* in barred owl site occupancy was to determine sampling

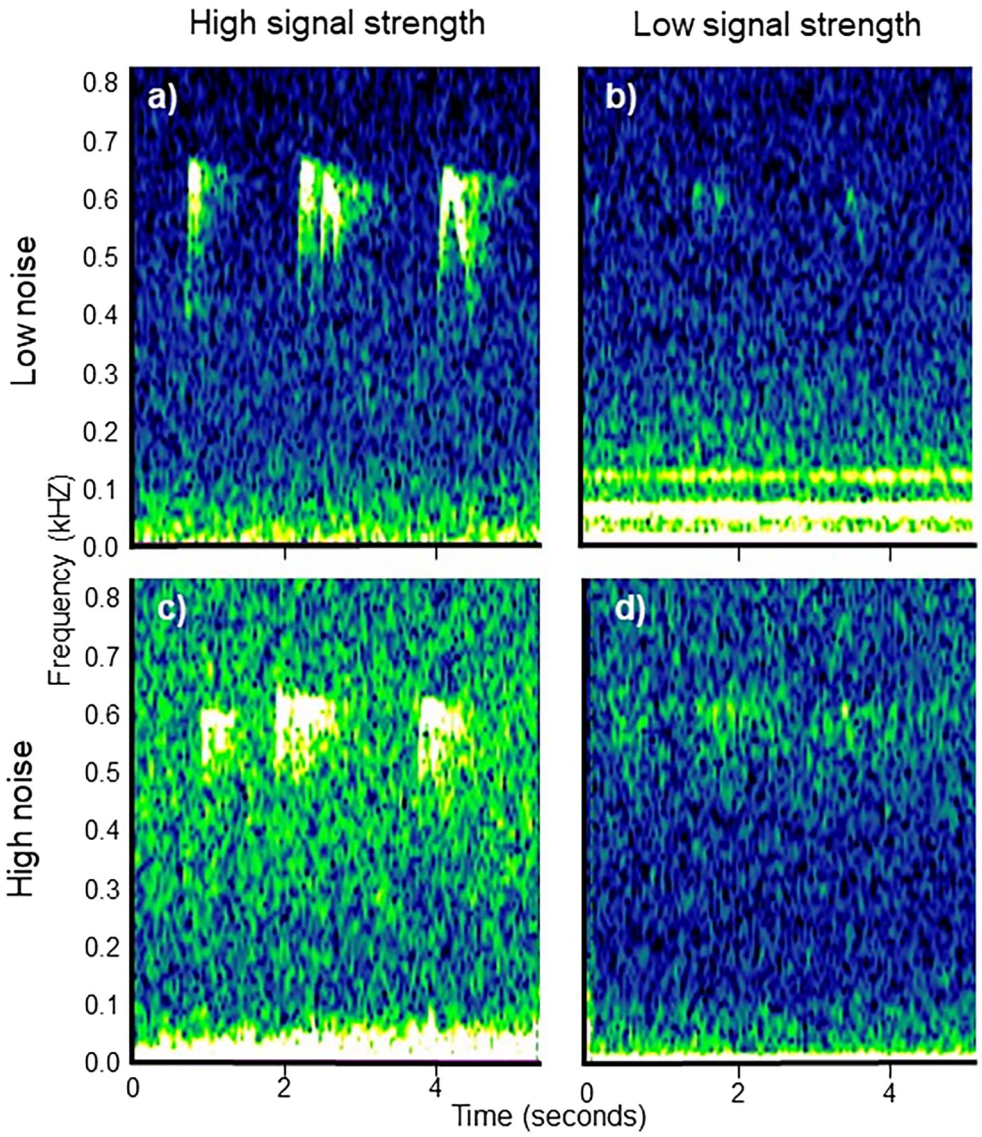

Fig. 2. Spectrograms of spotted owl vocalizations with high (a, c) and low (b, d) signal strength, and high (c, d) and low (a, b) noise. These vocalizations were all identified by the spotted owl template group; signal (a) is qualitatively similar to the merged spotted owl template vocalization (Hann window, 3 dB bandwidth = 21.2 Hz, 4096-sample DFT).

effort needed to detect population growth in the absence of management intervention. We also estimated statistical power to detect 0, 10, 30, and 50% reductions in site survival for both owl species. Though this framework was designed to detect management-driven declines, it also had the capability to detect increases in occupancy (Popescu et al., 2012). We did not simulate yearly variation in local survival and colonization for barred owls because the models failed to converge when additional variation was added, likely because of the low initial occupancy rate. Our rationale for testing for reductions in site survival for barred owls was to determine sampling needs to detect the effects of management actions, should they be employed, to limit the abundance and spread of this invading species under a BACI experimental design. For all analyses, we simulated monitoring programs with 500, 1000, or 1500 sites, and with 2 or 3 sampling periods to provide a real-world example of the range of possibilities simulated in Section 2.1 Detection probability was 0.50 for spotted owls and 0.67 for barred owls.

3. Results

3.1. Statistical power

3.1.1. Power to detect trends

Statistical power to detect 4% annual declines (31% total declines over a 10-year period) in site occupancy was high, always exceeding 0.80 when detection probability was 0.4 and always exceeding 0.90 when detection probability was 0.8 (data not shown). Statistical power to detect 2% annual declines in site occupancy (17% total decline over a 10-year period) increased as a function of the number of sites surveyed, numbers of visits, detection probability, and initial occupancy (Fig. 4a). Statistical power to detect 2% declines was particularly sensitive to initial site occupancy with, for example, power increasing from 0.37 to 0.78 when initial occupancy was increased from 0.38 to 0.67 with 500 sites visited 3 times each and a detection probability of 0.40. Indeed, statistical power to detect a 2% annual decline in site occupancy did not reach 0.80 when initial occupancy was 0.375 and detection probability was 0.4 (Fig. 4a); moreover, power to detect a 2% annual decline when initial site occupancy was 0.375 required 1500 sites visited 3 times each

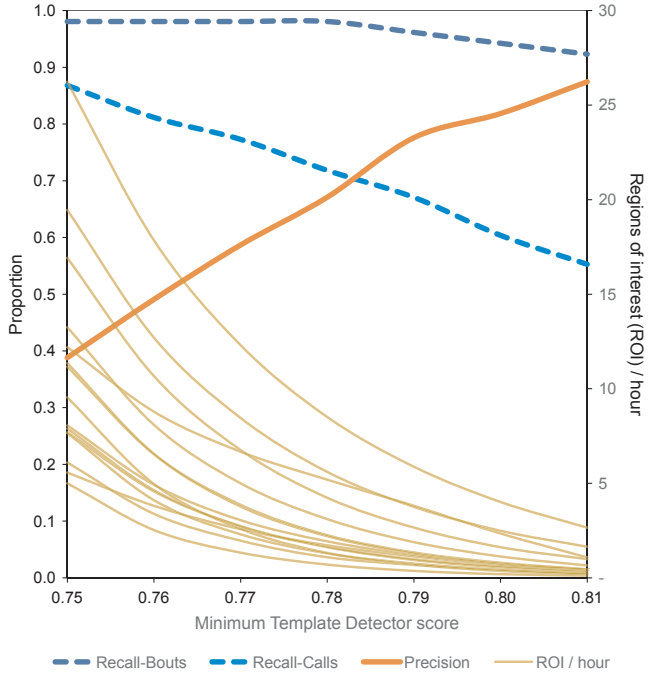

Fig. 3. Performance of the spotted owl template at different minimum Template Detector scores. Recall (dashed blue lines) decreased as precision (orange line) increased; bout-level recall (dark blue), or the proportion of bouts of calling in which at least one vocalization was correctly identified, was higher than call-level recall (light blue). The number of potential signals of interest per hour (dark yellow lines, each of which represents survey sites from a different time/place in the study) decreased as precision increased. We evaluated all potential signals of interest (i.e., instances that matched the spotted owl template) with a score of 0.80 or greater.

even when detection probability was 0.80 (Fig. 4b). Statistical power to detect 2% annual declines in site occupancy was > 0.80 and often > 0.90 with an initial site occupancy of 0.67, except when surveys were limited to 500 sites visited twice and detection probability was 0.40 (Fig. 4a and b). In all cases the simulated declines matched the declines predicted by the dynamic occupancy models, denoting good model fit.

3.1.2. Power to detect management effects

As expected, statistical power to detect hypothetical management effects, manifested as reductions in local survival at managed sites, increased with the number of sites surveyed, numbers of visits, and detection probabilities (Fig. 4c and d). Statistical power to detect management effects was very high (0.91–1.00) when local survival was reduced at sites subject to management by 50% for all combinations of the number of sites surveyed, numbers of visits, detection probabilities, and proportion of sites subject to management (data not shown). Statistical power to detect a 30% reduction in local survival was also high (> 0.80) for all sampling schemes considered, except when only 25% of sites were subject to management, the number of sites surveyed was small ($n = 500$) and detection probability (p) was low ($p = 0.40$; Fig. 4c). In contrast, statistical power to detect 10% reductions in local survival was low, reaching a maximum of 0.68 when 1500 sites were surveyed 3 times each and detection probability was 0.8 (Fig. 4d). In some cases, increasing the number of sites from 500 to 1000 or from 1000 to 1500 resulted in considerable increases in statistical power (e.g., 0.20–0.27), but gains were small when the number of visits per site was increased from 2 to 3 (Fig. 4c and d). For all sampling schemes considered, the proportion of simulated data sets yielding statistically significant effects of management even when no management impacts on local survival were simulated (nominal Type I error rate) was approximately 0.05.

3.2. Surveying spotted and barred owls

3.2.1. Occupancy and detection estimates

We deployed 2–3 ARUs per site (approximately 50% of the sites had 2 ARUs and 50% had 3 ARUs) for an average of 5.7 nights per survey at the 74 sampling sites. Spotted owl vocalizations were identified in the data at 24 sites (naïve occupancy = 0.32), and barred owl vocalizations were identified in the data at 6 sites (naïve occupancy = 0.081). Recall decreased as precision increased for spotted owls (Fig. 3), but bout-level recall remained very high for both species (Table A1). There was substantial variation in the rate of ROI per hour, and as expected that rate declined as precision increased (Fig. 3).

Based on single-season occupancy models, in which we assumed uniform occupancy and detection probabilities, we estimated that spotted owl site occupancy and detection probabilities were 0.43 and 0.50, respectively (Standard Errors = 0.10 and 0.11). As detection probabilities apply to secondary sampling periods, our detection estimate translated to a cumulative probability of 0.75 with two secondary sampling periods per season. We estimated that barred owl site occupancy probability was 0.09 (SE = 0.040), indicating that barred owls were approximately five times less abundant than spotted owls in our study area. We estimated that barred owl detection probability was 0.67 (SE = 0.18), which translated to a cumulative probability of 0.89 across two visits.

3.2.2. Statistical power to detect spotted and barred owl occupancy trends

Statistical power to detect a 2% annual decline in site occupancy for spotted owls increased with both the number of sites sampled and the number of visits per site (Fig. 5a). Statistical power ≥ 0.80 was only achieved when 1500 sites were visited 3 times per season. However, statistical power approached this level when 1000 sites were visited 3 times per season or 1500 sites were visited 2 times per season (power = 0.79 and 0.77, respectively). Statistical power for these levels of sampling efforts translated to 0.87 and 0.86, respectively, when we conducted *post-hoc* power analyses for a 12-year monitoring program. Statistical power to detect a 4% annual increase in site occupancy for barred owls increased considerably with the number of sites sampled and, to a lesser degree, the number of visits per site (Fig. 5b). Achieving statistical power ≥ 0.80 required surveying at least 1000 sites 2 times per year.

4. Discussion

One of main challenges when monitoring threatened species over large spatial extents is to detect small but biologically meaningful changes in population size (Rhodes et al., 2006; Steenweg et al., 2016). Such assessments become even more challenging when novel threats, such as the spread of invasive species or effects of landscape management actions (e.g., forestry), have the potential to affect background population dynamics. Our simulation analyses showed that high statistical power (> 80%) to detect small annual declines in site occupancy (2%) and modest reductions in site survival (30%) resulting from management activities can be achieved by collecting detection/non-detection data at large numbers of sampling sites (500–1500). In contrast, previous assessments of statistical power were either limited to sample sizes that yielded low power to detect potentially important changes in species site occupancy rates (Rhodes et al., 2006; Popescu et al., 2012) or assumed that detection was perfect (i.e., 1). Our field effort demonstrated that emerging bioacoustic methods facilitate the ability to cost-efficiently monitor a vocally active species at large spatial scales. The collected data provides a powerful means for monitoring changes in population levels of interest over space and time within a dynamic occupancy modeling framework. Notably, the statistical power analyses conducted for spotted and barred owls were based on estimates of site occupancy and detection probabilities derived directly from acoustic surveys for these species. Thus, our results indicated that

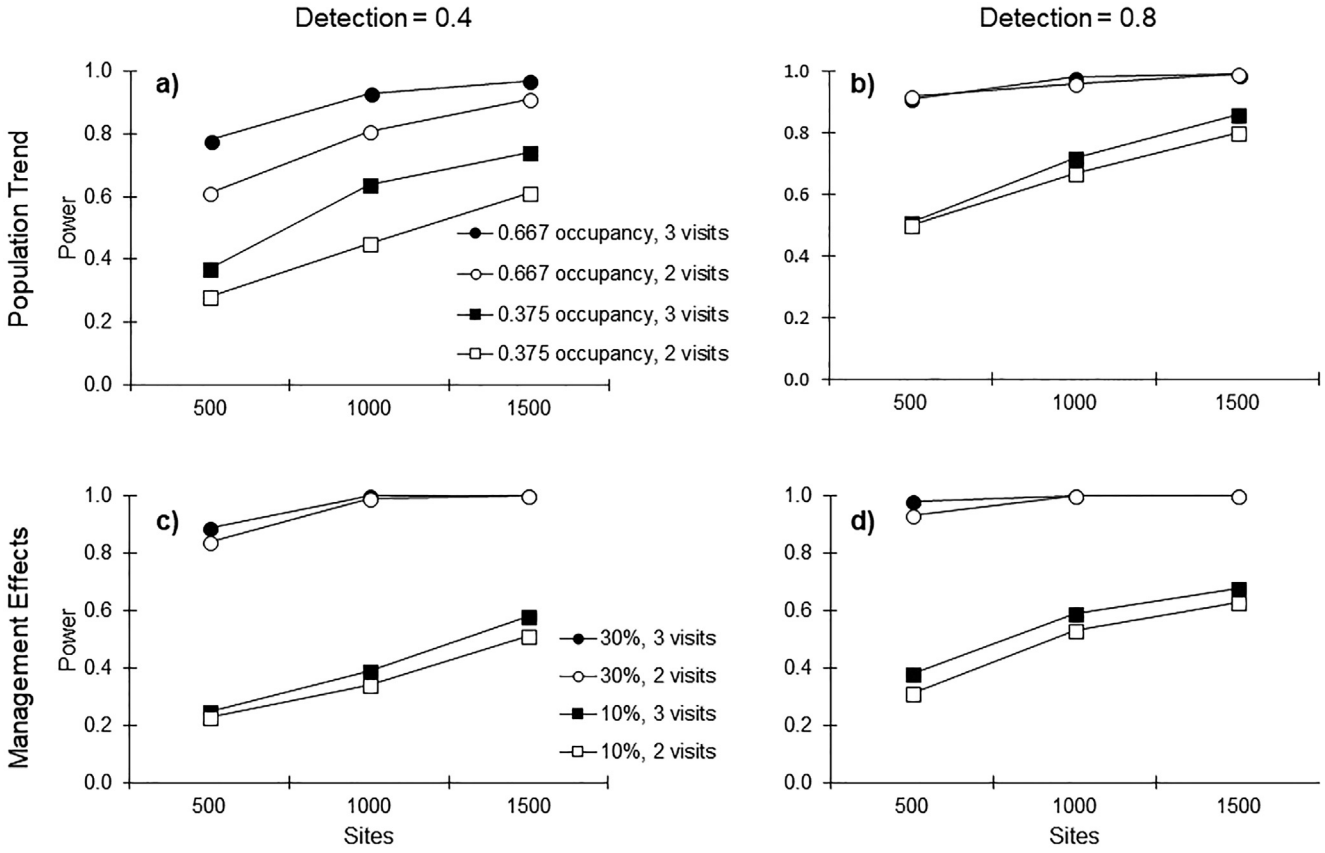

Fig. 4. Statistical power to detect 2% annual declines in site occupancy (a, b) and management effects (c, d) over a 10-year monitoring study as a function of the number of sampling sites, when detection is 0.4 (a, c) and 0.8 (b, d). Occupancy in the legend refers to the initial proportion of sites occupied (a, b); percentages in legends refer to the percent decline in site survival following management (10 or 30%; c, d); visits refer to the number of surveys conducted at each sampling site in each year (2 or 3; a–d).

it is possible to detect small changes in populations – both trends and responses to management – of relatively common, but declining species (Tempel et al., 2016), as well as relatively rare, but invading species using passive-acoustic approaches.

The number of sites needed to detect small annual population declines (from 500 to 1500) may seem ambitiously large in the context of resources typically available to monitor populations and species, but large-scale monitoring programs using human observers to collect detection/non-detection data suitable for occupancy modeling can involve surveys of many more sites (Hines et al., 2014) and the cost of ARUs is rapidly decreasing (Hill et al., 2018). Passive-acoustic surveys can readily be scaled up to the levels we simulated: while we only surveyed 74 sites on two occasions for the occupancy analyses presented here, we are currently surveying 350 sites three times each as part of a larger-scale pilot study. Processing this volume of data (~168,000 h of nighttime audio data, compared to the ~33,700 h

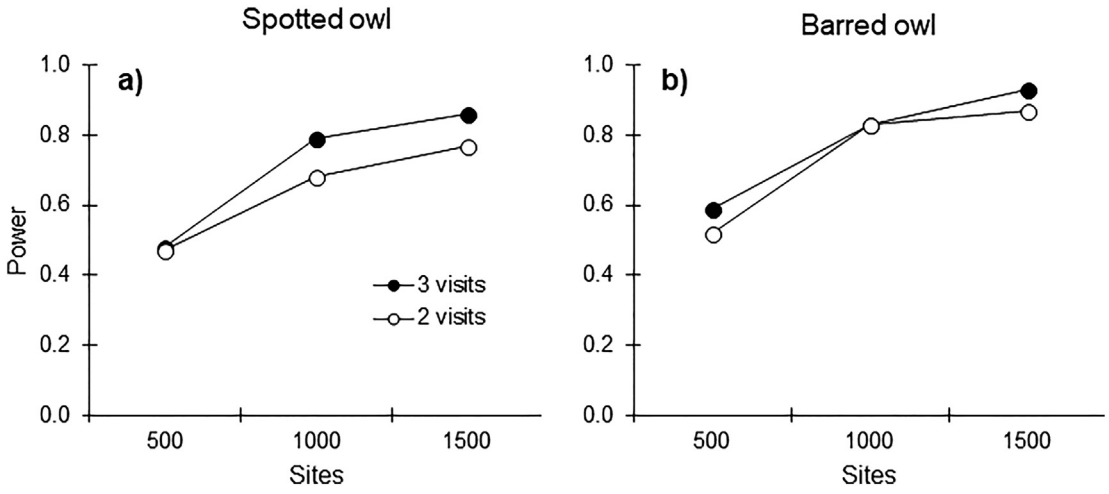

Fig. 5. Statistical power to detect 2% annual declines in site occupancy for spotted owls (a) and 4% annual increases in site occupancy for barred owls (b) as a function of the number of sampling sites and surveys per site when detection probability is 0.5 and 0.67, respectively, over a 10-year monitoring study. Initial occupancy was 0.43 for spotted owls and 0.09 for barred owls.

analyzed here) is greatly facilitated by the capacity to extract focal species vocalizations (i.e., identify ROI and classify them as either detections or false alarms) during the field season as the data is collected. Achieving this level of spatial coverage and survey intensity with call-based surveys would entail substantial costs, logistical challenges, and safety concerns. Practically, this demonstrates the efficacy of bioacoustics as a cost-effective approach to landscape-scale surveys (see also: Hill et al., 2018). Ecologically, it broadens the possibilities for monitoring across broad ecological gradients (Mennitt and Fristrup, 2016). Thus, spatially-extensive monitoring programs based on passive-acoustic surveys have the potential to provide considerable insight into the ecological processes that drive spatial and temporal variation in populations, in addition to estimates of temporal trends and management effects.

4.1. Strategies for increasing statistical power within an acoustic survey framework

As expected, statistical power to detect changes in site occupancy increased with detection probability; developing survey methods and bioacoustic approaches that result in high detectability will thus increase the strength of inferences supported by occupancy-based monitoring programs. Patterns in the intrinsic vocalization rates of the focal species – which are likely an unknown but potentially measurable parameter (e.g., through tagging) – will determine the relative importance of those factors (Hagens et al., 2018). In landscape-scale monitoring efforts, ARUs are generally deployed with little knowledge of focal species occupancy at any given site. Consequently, detection is likely to be sensitive to sampling considerations such as the duration of secondary sampling periods and the number of ARUs deployed per site when vocalization rates are low (but sufficiently high for passive-acoustic monitoring to be a reasonable methodology). Of course, with a fixed budget, increasing both survey duration and the number of units deployed will come at the expense of other aspects of sampling effort, such as the number of surveys per site and the number of sites surveyed. While reducing the number of sites can reduce statistical power to detect changes in site occupancy considerably, in our simulations power was less sensitive to the number of surveys per site (Figs. 4 and 5). Thus, increasing detection probabilities via longer survey periods or deploying more units can be an effective way to increase statistical power without increasing project costs.

Alternatively, managing the precision—recall trade-off (and thus the false alarm rate) can be an effective strategy for increasing detection probabilities. Generally, maximizing recall will minimize the likelihood of the species going undetected during a given secondary sampling period. Increasing recall can be as simple as accepting lower precision and thus spending more effort classifying ROI (i.e., moving left along the x-axis in Fig. 3). Such a strategy, however, can quickly become intractable. For example, increasing recall from 0.60 to 0.67 in our spotted owl training dataset would have increased the rate of ROI/hour from 0.25 to 0.43. Because we had > 37,000 h of data, that modest improvement in recall would have come at a very high cost in terms of time spent classifying ROI. The process of classifying ROI as detections or false alarms can be highly automated (Chambert et al., 2017; Banner et al., 2018), but may be hindered the fact that landscape-scale monitoring results in considerable heterogeneity in the types and quantity of sounds in sampled soundscapes. For example, proximity to human settlement or resource extraction may suppress biological sounds (e.g., reduced “dawn chorus”; (Burivalova et al., 2018), while introducing many others (e.g., barking dogs, vehicles; see the range of ROI/hour in Fig. 3). The magnitude of the precision—recall trade-off can be at least partially mitigated by investing the time to develop high-quality templates and testing their performance across the sampling array.

Implementing landscape-scale monitoring programs employing passive-acoustic surveys entails a range of choices in survey design (e.g., duration of secondary sampling periods) and acoustic analyses (e.g., precision—recall trade-off) which will need to be addressed within the context of project objectives and constrains. Statistical power analyses such as those we conducted can help inform those choices after pilot work provides initial estimates of occupancy and detection. Combining those parameters with the population changes that managers want to detect (e.g., a 2% annual decline, or the effect of management activities that result in changes in local survival) can help refine the survey design. The number of surveyed sites or number of secondary sampling periods could be increased to meet project objectives, or methods of increasing detection could be prioritized.

4.2. Implications for monitoring the invasive barred owl

Spotted owl populations have been monitored throughout its western United States range for several decades using field-intensive demographic studies of marked individuals within study areas that are typically a few hundred km^2 in size (Seamans et al., 1999; Wiens et al., 2014; Tempel et al., 2016). These studies have provided a wealth of information related to population trends, the ecological processes that influence population dynamics, and catalyzed the development of demographic methods that have become the cornerstones of population analyses in ecological research (Noon and Franklin, 2002; Gutiérrez, 2008). However, they have some potential weaknesses. First, the declining status of spotted owl populations throughout their ranges, particularly where barred owls have invaded, has limited the ability to mark owls, thus undermining a fundamental methodological requirement. Second, spotted owl demographic studies only encompass a fraction of the species' range and were non-randomly selected, limiting the ability to draw inferences about population trends and dynamics beyond study area boundaries (Franklin et al., 2004). This is particularly problematic in the face of landscape-scale processes such as forest management and the barred owl invasion. Third, survey methods were designed to locate and identify spotted owls (Franklin et al., 1996); conducting additional surveys to locate barred owls incurs additional costs and reductions to spatial coverage (Wiens et al., 2014). Yet understanding barred owl population trends will be critical for spotted owl conservation (Gutiérrez et al., 2007; Wiens et al., 2014). Passive-acoustic surveys provide an opportunity to monitor spotted owl and barred owl site occupancy at larger spatial scales than demographic studies. In the case of California spotted owls, this potentially includes the entire Sierra Nevada, which harbors the largest population of this subspecies. Assuming an appropriate sampling design, estimates of site occupancy rates can reasonably be inferred for the entire population. Moreover, passive-acoustic surveys allow for the simultaneous monitoring of both owl species, including population trends, responses to management, and interspecific interactions.

A key consideration when using passive-acoustic surveys to monitor spotted and barred owls is the potential for detecting of individuals at more than one sampling site and thus upwardly biasing estimates of occupancy (Berigan et al., 2018). Importantly, this phenomena may occur particularly frequently in declining populations (where occupancy rates are low) and following disturbance events that displace resident individuals (Berigan et al., 2018). The potential for this type of false positive detection in spotted and barred owls is increased in passive-acoustic surveys because the precise location of the detection is uncertain and the identity of the detected individual is unknown. However, several practical measures can be taken to reduce the frequency of false detections and their impacts on estimates of site occupancy. First, sampled sites can be constrained in space such that they are separated by a sufficient distance to reduce the likelihood a site is visited by individuals from more than one pair (e.g., based on GPS tag data). Second, acoustic data can be constrained to include only time periods when false detections are relatively unlikely, in the case of owls around dawn and dusk when they typically are near their activity centers (i.e., nesting and roosting sites). Third, it may be possible to identify individuals based on their vocal characteristics (Delport et al.,

2002; Rognan et al., 2009; Odom et al., 2013). This could allow wide-ranging individuals to be identified and their detections attributed to a single site (Berigan et al., 2018). It could also help address another potential shortcoming of occupancy-based monitoring program: that site occupancy may be less sensitive to population perturbations than demographic measures such as survival and recruitment rates (Rockweit et al., 2017). Vocal identity could be used to test for site turnover and other demographic parameters that are impossible to estimate in traditional occupancy approaches with unmarked individuals. These considerations must be carefully considered and addressed in order to minimize potential biases if landscape-scale acoustic monitoring programs are to achieve their demonstrated potential.

4.3. Conclusions

Passive-acoustic surveys can provide a rigorous approach for monitoring changes in populations of declining or invasive species within a site occupancy framework at broad spatial scales. They also have considerable potential to provide insight to effects of management actions on focal species. Although acoustic monitoring systems do not currently allow robust automatic identification of individuals, the potential for doing so is present if species have individual-specific vocalizations and these are quantified. Thus, passive-acoustic monitoring has the potential not only to capture community dynamics at landscape scales but also to capture demographic change should "vocal signature" become a surrogate for mark-recapture of individuals. Furthermore, refinements in bioacoustic approaches that allow efficient simultaneous identification of multiple species can provide a framework for monitoring entire biological communities (Shonfield et al., 2018; Kahl et al., 2018), not just a few focal species. When this occurs, the framework we present here will allow managers to rapidly assess the statistical power attainable for each species: systematic and statistically robust monitoring of entire faunal communities at a landscape scale within a single unified framework may become a reality.

Authors contributions

MZP conceived the approach with CMW, VP, JJK, RJG, and SCS; MZP, RJG, and JJK secured funding; VP wrote the code for the simulations and conducted them; CMW led the field effort and the acoustic analyses; HK supported the acoustic analyses; all authors contributed to writing the manuscript and give their approval.

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Declarations of interest

None.

Appendix 1: R code for simulating treatment effects on local survival, trends in occupancy, and models fitted with package 'unmarked'

1. R code for simulating occupancy data (detection/non-detection) using treatment impacts in a Before-After Control-Impact framework with treatments implemented in a staggered manner.

```
dataset < - function (phi_T, psi1, nyear, n_sites, site_T, n_vis, phi, sd.phi, r, sd.r, p) {

### The following parameters are given to the function:
### phi_T = decrease in local survival following treatment
### psi1 = initial occupancy
### nyear = number of years or study seasons
### n_sites = number of sites
### n_vis = number of visits per site per year (or season)
### phi = local survival in year 1
### sd.phi = sd of random normal variable introducing a Season effect
### on local survival
### r = colonization in year 1
### sd.r = sd of random normal variable introducing a Season effect
### on colonization
### p = probability of detection

### Define matrix tocc (true territory occupancy state)
tocc < - matrix(rep(0, nyear*n_sites), ncol = nyear)
tocc < - as.data.frame(tocc)
names(tocc) < - paste("t", 1:nyear, sep="")

### Define the matrix obsocc that contains the observations. The first j
### columns will contain observed occupancy states for the first year on
### the 1…j visits, the j + 1 column will contain the observations of
### the first visit in the second year, and so forth.
obsocc < - matrix(rep(0, nyear*n_sites*n_vis), ncol=(nyear*n_vis), dimnames = list(paste("site", 1:n_sites, sep="")), paste("Yr", rep(1:nyear, each = n_vis), "v", 1:n_vis, sep=""))
obsocc < - as.data.frame(obsocc)

### simulate seasonal effects on local survival and colonization(using an
### additive term on the logit scale drawn from N(0,sd.phi) and N(0,sd.r)
### year effects on survival
logit.phi.mean < - qlogis(phi)
year.effect.phi < - rnorm((nyear-1), 0, sd.phi)
phi_year < - plogis(logit.phi.mean + year.effect.phi)

### year effects on colonization
logit.r.mean < - qlogis(r)
year.effect.r < - rnorm((nyear-1), 0, sd.r)
r_year < - plogis(logit.r.mean + year.effect.r)
```

```
### Simulate tocc and obsocc from t = 1 to t = nyear
### First use the Control paramater values for all sites
for(i in 1:n_sites) {
  tocc[i,1] = rbinom(1, 1, psi1)
  obsocc[i,1:n_vis] = rbinom(n_vis, 1, tocc[i,1]*p)

### the first transition (yr1 to yr2) is parameterized with the initial phi
### and r values
  for(t in 2:nyear) {
    if (tocc[i,t-1] == 1) {
      tocc[i,t] <- rbinom(1,1,phi_year[t-1])
    } else if (tocc[i,t-1] == 0){
    tocc[i,t] <- rbinom(1,1,r_year[t-1])
    }
  for(j in 1:n_vis) {
    obsocc[i,((t-1)*n_vis)+j] <- rbinom(1,1,tocc[i,t]*p)
  }
  }
  }

### Then simulate the impact of the experimental treatment on local survival
### in the Treatment subset of matrices tocc and obsocc using a staggered
### treatment; equal number of sites treated per year; last year does not
### receive a treatment
site_T_year = round(site_T/(nyear-2))

### loop through the sites for first treatment year
  for(i in 1:site_T_year) {
    for(tt in 2:nyear) {
      if (tocc[i,tt-1] == 1) {
        tocc[i,tt] <- rbinom(1,1,(phi_year[tt-1]*(1-phi_T)))
      } else {
        tocc[i,tt] <- rbinom(1,1,r_year[tt-1])
      }
      for(j in 1:n_vis) {
        obsocc[i,((tt-1)*n_vis)+j] <- rbinom(1,1,tocc[i,tt]*p)
      }
    }
  }

### apply the treatments for sites for subsequent years (no treatment applied
### in last year)
  for(k in 1:(nyear-3)) {
    for(i in (k*site_T_year+1):((k + 1)*site_T_year)) {
      for(tt in (k + 2):nyear) {
        if (tocc[i,tt-1] == 1) {
          tocc[i,tt] <- rbinom(1,1,(phi_year[tt-1]*(1-phi_T)))
        } else {
          tocc[i,tt] <- rbinom(1,1,r_year[tt-1])
        }
        for(j in 1:n_vis) {
          obsocc[i,((tt-1)*n_vis)+j] <- rbinom(1,1,tocc[i,tt]*p)
        }
      }
    }
  }

### Add a column to observed data for site type (treated or non-treated)
obsocc$Treat = factor(c(rep('Treat', site_T_year*(nyear-2)), rep('Control', n_sites-site_T_year*(nyear-2))))

### Create the matrix of seasonal site covariates Year and Control/Treatment.
### IMPORTANT ###: Occupancy at t = 1 is psi1, so there are (nSeason–1)
### transitions between seasons for modeling colonization and extinction
### The function colext (Fiske and Chandler, 2011) requires the full set of
### parameters (nyear), but the last column of the matrix is unnecessary
### for modeling colonization and extinction. Therefore we fill the last
### column (i.e., last year) with the attribute 'Null'.

### Create a matrix of yearly site covariates containing Year as factor
years <- matrix(rep(seq(1:(nyear-1)), n_sites), ncol = nyear-1, byrow = T,
dimnames = list(paste("site", 1:n_sites, sep="="), paste("Yr", rep(1:(nyear-1)), sep="")))
yrs.Junk <- matrix(rep("Null", n_sites*1), ncol = 1)
years <- cbind(years,yrs.Null)
colnames(years) <- paste("Yr", rep(1:nyear), sep="")
years <- as.data.frame(years)
years <- data.frame(lapply(years, as.factor))

### Create a matrix of SeasonSiteTreat variables (levels "Treat" / "Control")
### start with empty matrix
Control <- matrix(rep(0, n_sites*(nyear-1)), ncol = nyear-1)

### assign Treatment (1) and Control (0) values to each site and year
### combination using code similar to implementing staggered treatments

### loop through the sites for first treatment year
```

```
  for(i in 1:site_T_year) {
    for(tt in 2:(nyear-1)) {
      Control[i,tt] < - 1
    }
  }

### loop through the sites for subsequent treatment years
  for(k in 1:(nyear-3)) {
    for(i in (k*site_T_year+1):((k + 1)*site_T_year)) {
      for(tt in (k + 2):(nyear-1)) {
        Control[i,tt] < - 1
      }
    }
  }

### replace 0 and 1 woth Control and Treatment
Control[Control == 0] < - "CONTROL"
Control[Control == 1] < - "TREAT"

### add value Null for last column of SeasonSiteTreat
trt.Null < - matrix(rep("Null", n_sites*1), ncol = 1)

### combine data into a SeasonSiteTreat dataframe
treat.year < - cbind(Control, trt.Null)
treat.year < - as.data.frame(treat.year)

colnames(treat.year) < - paste("Year", rep(1:nyear), sep = "")

### Combine the observed P/A data, the yearly covariates, treatments (Years)
obsocc1 < - cbind(obsocc, years, treat.year)

### Return observed territory occupancy matrix, i.e. the observations
return(data.frame(obsocc1))
}
```

2. R code for fitting dynamic occupancy models for detection/non-detection data using the R package *unmarked 0.9–2* (Fiske, I., and R. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance, Journal of Statistical Software 43:1–23)

```
library(unmarked)

analysis = function(dataset, nyear, n_vis) {

### Prepare data for 'unmarked', multi-season colext model
### (MacKenzie et al., 2003)

### Matrix for detection/non-detection data
yMat < - PAdata[,1:(nyear*n_vis)]

### Matrix for Year covariate
yearMat < - PAdata[,((nyear*n_vis)+2):((nyear * n_vis)+nyear + 1)]

### Matrix for Treatment/Control yearly covariate
TRTyearMat < - PAdata[,((nyear*n_vis) + nyear + 2):((nyear*n_vis) + 2 * nyear + 1)]

# Combine all the yearly site covariates into a dataframe
yearlies < - data.frame(
  year = matrix(t(yearMat), ncol = 1),
  TRTyear = matrix(t(TRTyearMat), ncol = 1))

# prepare the unmarked multi-year colext dataframe
  oUMF < - unmarkedMultFrame(
    y = yMat,
    siteCovs = PAdata[,"Treat", drop = F],
    yearlySiteCovs = yearlies,
    numPrimary = nyear)

### Run models (the order for parameterizing colext models is: 1st season
### occupancy(psi), colonization(gamma), extinction(epsilon), detection(p))

# Models for testing treatment effect on extinction and colonization
Null.fit < - colext(psi1formula = ~1, gammaformula = ~Treat + year, epslonformula = ~Treat + year, pformula ~ 1, oUMF)
Alt.fit < - colext(~1, ~TRTyear + year + Treat, ~TRTyear + year + Treat, ~1, oUMF)

# Combine the model results to a list
list(Null.fit = Null.fit, Alt.fit = Alt.fit)
}
```

3. R code for simulating occupancy data (detection/non-detection) with a declining trend in occupancy through time.

```
dataset < - function (perc_red, psi1, nyear, n_sites, n_vis, phi, sd.phi, r, sd.r, p) {

### perc_red = percent yearly reduction in local survival and
### colonization across 10 years for a 2% or 4% annual decline
### in occupancy
### psi1 = initial occupancy
### nyear = number of years or study seasons
### n_sites = number of sites
```

```
### n_vis = number of visits per site per year (or season)
### phi = local survival in year 1
### sd.phi = sd of random normal variable introducing a Season effect
### on local survival
### r = colonization in year 1
### sd.r = sd of random normal variable introducing a Season effect
### on colonization
### p = probability of detection

### Define matrix tocc (true territory occupancy state)
tocc < - matrix(rep(0, nyear*n_sites), ncol = nyear)
tocc < - as.data.frame(tocc)
names(tocc) < - paste("t", 1:nyear, sep="")

### Define the matrix obsocc that contains the observations. The first j
### columns will contain observed occupancy states for the first year on
### the 1…j visits, the j + 1 column will contain the observations of
### the first visit in the second year, and so forth.
obsocc < - matrix(rep(0, nyear*n_sites*n_vis), ncol=(nyear*n_vis), dimnames = list(paste("site", 1:n_sites, sep=""), paste("Yr", rep(1:nyear, each = n_vis), "v", 1:n_vis, sep="")))
obsocc < - as.data.frame(obsocc)

# simulate yearly decreases in local survival and colonization
year_phi = rep(0,nyear-1)
year_r = rep(0,nyear-1)

year_phi[1] = phi
year_r[1] = r

for (j in 2:(nyear-1)) {
  year_phi[j] = 1 - ((1-year_phi[j-1]) + (1-year_phi[j-1])*perc_red)
  year_r[j] = year_r[j-1] - year_r[j-1]*perc_red
}

year_phi
year_r

### simulate yearly effects on local survival and colonization using values
### drawn from N(phi, sd.phi) and N(r, sd.r)

year.effect.phi = rep(0,nyear-1)
year.effect.r = rep(0,nyear-1)

for (i in 1:(nyear-1)) {
  year.effect.phi[i] < - rnorm(1, year_phi[i], sd.phi)
  year.effect.r[i] < - rnorm(1, year_r[i], sd.r)
}

year.effect.phi
year.effect.r

### Simulate tocc and obsocc from t = 1 to t = nyear
### First simulate site occupancy and observed data in year 1
for(i in 1:n_sites) {
  tocc[i,1] = rbinom(1, 1, psi1)
  obsocc[i,1:n_vis] = rbinom(n_vis, 1, tocc[i,1]*p)

### the first transition (yr1 to yr2) is parameterized with the initial phi
### and r values; subsequent transitions see a percent decrease in
### colonization and local survival per year
  for(t in 2:nyear) {
    if (tocc[i,t-1] == 1) {
      tocc[i,t] < - rbinom(1,1,year.effect.phi[t-1])
    } else if (tocc[i,t-1] == 0){
      tocc[i,t] < - rbinom(1,1,year.effect.r[t-1])
    }
    for(j in 1:n_vis) {
      obsocc[i,((t-1)*n_vis)+j] < - rbinom(1,1,tocc[i,t]*p)
    }
  }
}

#head(tocc)
#rowSums(tocc)
#head(obsocc)

### Create a matrix of yearly site covariates containing Year as factor
### IMPORTANT ###: Occupancy at t = 1 is psi1, so there are (nSeason–1)
### transitions between seasons for modeling colonization and extinction
### The function colext (Fiske and Chandler, 2011) requires the full set of

### parameters (nyear), but the last column of the matrix is unnecessary
### for modeling colonization and extinction. Therefore we fill the last
### column (i.e., last year) with the attribute 'Null'.

years < - matrix(rep(seq(1:(nyear-1)), n_sites), ncol = nyear-1, byrow = T, dimnames = list(paste("site", 1:n_sites, sep=""), paste("Yr", rep(1:(nyear-1)), sep="")))
yrs.Junk < - matrix(rep("Null", n_sites*1), ncol = 1)
years < - cbind(years,yrs.Null)
colnames(years) < - paste("Yr", rep(1:nyear), sep="")
```

```
years  < - as.data.frame(years)
years  < - data.frame(lapply(years, as.factor))

### Combine the observed P/A data, the yearly covariates
obsocc1  < - cbind(obsocc, years)

### Return observed territory occupancy matrix, i.e. the observations
return(data.frame(obsocc1))
}
```

4. R code for fitting dynamic occupancy models for detection/non-detection data using the R package *unmarked 0.9–2* (Fiske, I., and R. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance, Journal of Statistical Software 43:1–23), and approximate the variance if the geometric mean of population change (lambda) via Delta Method (Tempel, D.J., Gutiérrez, R.J., 2013. Relation between occupancy and abundance for a territorial species, the California spotted owl. Conservation Biology 27: 1087–1095)

```
library(unmarked)

analysis = function(dataset, nyear, n_vis) {

### prepare the matrix for observed P/A data
yMat  < - PAdata[,1:(nyear*n_vis)]
yearMat  < - PAdata[,((nyear*n_vis)+1):((nyear*n_vis)+nyear)]

### prepare the matrix for yearly covariates (Year)
yearlies  < - data.frame(
  year = matrix(t(yearMat), ncol = 1))

### prepare the unmarked multi-year colext data.frame
oUMF  < - unmarkedMultFrame(
  y = yMat,
  #siteCovs = obsocc1[, c("ActivCenter"), drop = F],
  yearlySiteCovs = yearlies,
  numPrimary = nyear)

### fit the dynamic occupancy model
Model.fit  < - colext(~1, ~year, ~year, ~1, se = T, oUMF)

### use 25 non-parametric bootstraps to estimate standard errors for yearly
### occupancy
Model.fit  < - nonparboot(Model.fit, B = 25)

psis_SEs = cbind(smoothed = smoothed(Model.fit)[2,], SE = Model.fit@smoothed.mean.bsse[2,])
psis_SEs
psis = as.vector(psis_SEs[,1])
SEs = as.vector(psis_SEs[,2])

### evaluate change in occupancy through time
occ_change = rep(0,nyear-1)
for (i in 1:nyear-1) {
  occ_change[i] = psis[i + 1]/psis[i]
}
occ_change

### calculate geometric mean of change in occupancy through time
delta_occ = prod(occ_change)
delta_occ

geom_lambda_occ = delta_occ^(1/9)
geom_lambda_occ

### calculate variance of geometric mean of change in occupancy through time
lambda = psis[nyear]/psis[1]
lambda

sdev1 = SEs[1]*sqrt(nyear)
sdev10 = SEs[nyear]*sqrt(nyear)

var_lambda = (lambda^2) * ((sdev10^2/(psis[nyear]^2)) + (sdev1^2/(psis[1]^2)))
var_lambda

dLamGeom_dLamMean = (lambda^((2-nyear)/(nyear-1)))/(nyear-1)
dLamGeom_dLamMean

var_geom_lambda_occ = var_lambda*(dLamGeom_dLamMean^2)
var_geom_lambda_occ

SD_lambda_occ = sqrt(var_geom_lambda_occ)
SD_lambda_occ

SE_lambda_occ = SD_lambda_occ/sqrt(nyear)
SE_lambda_occ

### calculate 95% confidence interval around the geometric mean of change in
### occupancy through time
upper_lambda_occ = geom_lambda_occ + 1.96*SE_lambda_occ
lower_lambda_occ = geom_lambda_occ - 1.96*SE_lambda_occ

upper_lambda_occ
lower_lambda_occ
```

Table A1
High precision contributes to efficient signal extraction, and high recall at a bout level contributes to high detection. Precision is the proportion of regions of interest (ROI) in the data that represent true focal species vocalizations; $Recall_{Call}$ is the proportion of all true target signals (i.e., focal species vocalizations) that are correctly identified by one of the focal species templates as a region of interest in the data (ROI); $Recall_{Bout}$ is the proportion of all bouts of focal species calling in which at least one vocalization (call) is correctly identified by one of the focal species templates as a ROI (Mellinger et al. 2016). Warping the original, merged template for each species (n = 5 different spotted owls; n = 2 different barred owls) a different number of steps across different amounts of time resulted in different numbers of total templates for each species.

Species (total templates)	Precision	$Recall_{Call}$ (calls)	$Recall_{Bout}$ (bouts)
Spotted owl (17)	0.82	0.60 (N = 568)	0.94 (N = 52)
Barred owl (13)	0.51	0.66 (N = 279)	0.95 (N = 19)
'Sparred' owl (13*)	0.80	0.072 (N = 108)	0.19 (N = 5)

* barred owl templates

```
geom_lambda_occ
list(lambda = geom_lambda_occ, lower.lambda = lower_lambda_occ, upper.lambda = upper_lambda_occ, psis = smoothed(Model.fit)[2,])
}
```

Appendix 2:. Template detector parameters

We used the Template Detector feature of Raven 2.0 (Bioacoustics Research Program, Cornell Lab of Ornithology, 2017) to extract target signals from the acoustic data, in this case spotted owl and barred owl territorial vocalizations. The template detector identifies regions of interest (ROI; i.e., potential target signals) by matching patterns in the data to user-defined templates (Mellinger and Clark, 2000), in our case high-quality recordings of territorial calls we collected within and outside our study area (Fig. 2). To develop the templates, we manually reviewed randomly selected data that spanned the spatial and temporal extent of our study and compiled vocalizations given by spotted owls (n = 568 in 52 bouts of calling) and barred owls (n = 279 in 19 bouts). We then selected in- and out-of-sample vocalizations that had high signal-to-noise ratios (Fig. 2a) to serve as template calls both species.

The spotted owl template was based on the last three notes of the "four-note" territorial call (e.g., Fig. 2a). We merged the calls of seven individuals, four males and three females, to create one average call. The merged template was then warped in time +/−30% in eight steps resulting 17 templates (i.e., −30%, −26.2%, … 0%, +3.8%, …, +30%), which allowed for the identification of vocalizations that were longer or shorter than the original merged template. The loose matching feature was enabled, which blurred and expanded the edges of the notes in the merged, stretched vocalizations to create even more generalized templates. All 17 spotted owl templates were applied to the raw audio data with a frequency buffer of +/−200 Hz, which allowed the template to search high and low enough to detect both female and male calls (merging calls resulted in a template with an intermediate frequency).

The barred owl template was based on the first four notes of the "who cooks for you" territorial call from two different individuals. The calls were merged, stretched +/−15% in six steps, and loose matching was enabled. The template was and applied with a frequency buffer of +/−37 Hz, which we later found was occasionally too narrow a range to capture higher-pitched female vocalizations. Barred x spotted hybrids, or "sparred" owls, make distinctive vocalizations (A. Franklin, pers. comm.), which the barred owl templates could identify despite having been optimized for a different signal (i.e., "who cooks for you").

We prioritized precision when developing our templates because low precision results in a high proportion of ROI that are *not* focal species vocalizations (i.e., "false alarms"). We had > 33,700 h of nighttime audio, so low precision would have made the classification process (manual review) extremely time-consuming (Fig. 3). However, we defined sites as occupied if one or more focal species vocalizations was recorded and identified there, allowing us to miss many vocalizations provided we detected at least one. This meant that low recall of individual vocalizations (R_{Call}) was acceptable if at least one vocalization in each bout of vocalization was correctly identified (R_{Bout}). For our precisions-oriented templates, R_{Bout} was high (> 0.9) for spotted and barred owls (measured with the call libraries; Table A1), meaning that we likely identified most instances of focal species vocalizations, and therefore detection was not substantially influenced by the choices we made during the acoustic analyses.

We applied both species' templates to all acoustic data collected from 20:00 to 06:00 local time at the 74 survey sites to identify spotted owl and barred owl vocalizations. Because occupancy models assume no false positive detections (MacKenzie et al., 2002), two independent observers reviewed all ROI that had been tentatively classified as focal species vocalizations to confirm or reject the purported detection.

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