



Original Articles

Long-term monitoring in transition: Resolving spatial mismatch and integrating multistate occupancy data

Matthew J. Weldy^{a,b,*}, Damon B. Lesmeister^{a,b,c}, Charles B. Yackulic^d, Cara L. Appel^{a,c}, Chris McCafferty^a, J. David Wiens^e

^a Pacific Northwest Research Station, USDA Forest Service, Corvallis, OR 97331, USA

^b Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA

^c Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, OR 97331, USA

^d U.S. Geological Survey, Southwest Biological Science Center, Flagstaff, AZ, 86001, USA

^e U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, OR 97330, USA

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ABSTRACT

The success of long-term wildlife monitoring programs can be influenced by many factors and study designs often represent compromises between spatial scales and costs. Adaptive monitoring programs can iteratively manage this tension by adopting new cost-efficient technologies, which can provide projects the opportunity to reallocate costs to address new hypotheses, adapt to changing ecological conditions, or adjust sampling scale or resolution. If there is interest in longer time series of monitoring data, methodological transitions may necessitate integrated models to link newer data with historical data. However, data integration can be difficult if spatial or temporal scales are mismatched. Here, we develop an integrated multistate site-occupancy model and resolve sample unit spatial mismatch to link datasets from two northern spotted owl (*Strix occidentalis caurina*) monitoring schemes that broadly overlapped during a methodological transition. The first dataset was obtained from a decades-long spotted owl monitoring program using call-playback and mark-resight surveys on historical territories of varying size and shape. This monitoring program has recently transitioned to passive acoustic monitoring of randomly selected 5-km² hexagons over larger spatial extents. Both monitoring datasets overlapped with areas in which barred owl (*Strix varia*), an invasive competitor that has played an important role in northern spotted owl declines, were being removed experimentally. Reconciling spatial mismatch substantially increased the representation of the call-playback dataset and integrating the two datasets increased precision of spotted owl use and paired occupancy estimates relative to single dataset estimates. Estimates of spotted owl pair occupancy across the study area were lower than previous territory-based estimates based on call-playback surveys. Our integrated model further showed that a concurrent barred owl removal experiment increased landscape use and site occupancy by pairs of spotted owls. Our empirical application of an integrated modelling approach demonstrates a useful analytical framework for long-term monitoring efforts undergoing methodological transitions (e.g. mark-recapture to non-invasive population monitoring). This framework allows monitoring programs to maintain continuity of monitoring objectives across methodological transitions, rigorously incorporate previous findings, and adaptively respond to changing ecological conditions.

1. Introduction

Long-term population monitoring is often important for conservation and management (Hughes et al., 2017). The most successful monitoring programs incorporate robust experimental design, sustained collection of high-quality data, and the ongoing development and testing of hypotheses based on research findings. However, in practice the

implementation of long-term monitoring programs often represents tradeoffs among implementation costs, the spatiotemporal scale of sampling, and the resolution of data. Adaptive monitoring programs can iteratively manage these tradeoffs by adopting new cost-efficient technologies (e.g., remote sensing, camera traps, bioacoustics). In turn, efficiencies gained in adopting new technologies allows projects to reallocate costs to address new hypotheses, adapt to changing ecological

* Corresponding author.

E-mail address: MatthewJWeldy@gmail.com (M.J. Weldy).

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conditions, or adjust the spatiotemporal density, scale, or resolution of sampling, while maintaining the integrity of core monitoring objectives (Lindenmayer and Likens, 2009). As monitoring methods evolve it can be challenging to maintain the integrity of long-term datasets because new data may be incompatible with historical data. However, careful analytical approaches can sometimes resolve incongruities like mismatched sampling scales (Gotway and Young, 2002; Pacifici et al., 2019; Fletcher et al., 2019), variable information content (Riecke et al., 2019; Tehrani et al., 2022), differences in relative data size (Richardson et al., 2010), and shifts in the spatiotemporal or mechanistic relationships among new, and historical data (Saunders et al., 2019; Zipkin et al., 2019; Zipkin et al., 2021).

The northern spotted owl (*Strix occidentalis caurina*; hereafter spotted owl) was listed as threatened in 1990 under the U.S. Endangered Species Act (U. S. Fish and Wildlife Service, 1990) and by 2020 warranted uplisting to endangered status because of continued population decline and persistent threats (U. S. Fish and Wildlife Service, 2020). Spotted owls have been central to long standing conservation conflict in the U.S. Pacific Northwest between the relative economic values of old forests and their preservation (Gutiérrez, 2020), which in turn has spurred several decades of population monitoring using mark-resight methods (Franklin et al., 2021) and numerous important scientific advances in the field of conservation biology (Noon and Franklin, 2002). As old-forest obligates spotted owls have been integrally coupled with forest management and conservation in the Pacific Northwest (Forsman et al., 1984; Anthony et al., 2006; Forsman et al., 2011; Lesmeister et al., 2018; Sovern et al., 2019). Within the range of spotted owls, the Northwest Forest Plan has guided forest management on 10 million ha of federally administered lands with balanced objectives that included protecting and recovering habitat of imperiled old-forest species and monitoring biodiversity (Spies et al., 2019).

The Northwest Forest Plan's Effectiveness Monitoring Program was, in part, based on the long-term monitoring of spotted owl populations under a two-phase approach (Lint et al., 1999). The first phase of spotted owl population monitoring relied on mark-resight data and models to estimate trends in vital rates across multiple long-term demographic study areas. Historical territories used by spotted owls were surveyed annually with call-playback surveys, and territorial spotted owls were marked and subsequently resighted to estimate vital rates and population growth at 5-year intervals in a meta-analysis framework (Franklin

et al., 1996; Franklin et al., 2021). In parallel these mark-resight data have been progressively applied in analyses of territory occupancy (Olson et al., 2005; Kroll et al., 2010; Dugger et al., 2011; Yackulic et al., 2014; Rockweit et al., 2022). Loss and fragmentation of old-growth forests have been historical causes of population declines of spotted owls, and in recent decades barred owls (*Strix varia*) have become an additional range-wide threat, that has prompted the initiation of barred owl removal experiments to benefit spotted owls (Diller et al., 2016; Wiens et al., 2021).

In the transition to the second phase of population monitoring for spotted owls, a grid of 5-km² hexagonal cells were overlaid across the spotted owl's geographical range and hexagons were randomly selected to be surveyed using autonomous recording units. A site-occupancy analytical framework has been proposed to track populations and inform future distribution and habitat models (Lesmeister et al., 2021). In 2018, both mark-resight methods and passive acoustic monitoring were conducted simultaneously in the Coast Range of Oregon, USA, where owl populations have been monitored since the 1990 s. One challenge of this transition for monitoring spotted owls has been developing analytical methods capable of integrating mark-resight data generated from long-term demographic studies with new passive acoustic monitoring (i.e., bioacoustics) data to robustly incorporate previous findings, evaluate consistency among disparate datasets, and ensure the integrity of long-term data throughout and beyond the transition period (Newman et al., 2017; Runge et al., 2018; Zipkin and Saunders, 2018; Abrahams, 2019; Mangewa et al., 2019; Williams et al., 2020; Yackulic et al., 2020; Yackulic et al., 2022).

Here we present an integrated multistate site-occupancy modeling approach with applicability to other population monitoring programs that are considering a transition to protocols that use non-invasive survey methods, or for programs that seek to incorporate multiple datasets (e.g., Zipkin and Saunders, 2018). Our integrated modelling approach combined two spatially overlapping site-occupancy datasets collected with different survey methods (territory, bioacoustics) at different spatial scales to detect presence of spotted owls and track population status over time. Our primary objective was to develop an analytical approach to link northern spotted owl monitoring data across a methodological transition, and to provide more precise estimates (relative to single dataset models) of spotted owl site occupancy and detection probabilities that draw on the strengths of the component

Table 1

Description, summary information, and predictions for variables used in multistate site-occupancy models for northern spotted owls *Strix occidentalis caurina*, using data collected during 2018 in the Oregon Coast Range, USA. Variables were used in linear models for the probability of a site being used by spotted owls regardless of state (ψ), the probability of a pair occupying a site with known non-paired use (R), the probability of detecting occupancy if the true state is used by non-paired owls (p_1), the probability of detecting occupancy if the true state is occupied by a pair (p_2), and the probability of detecting a pair given occupancy has been detected (δ). We predicted positive (+) or negative (−) associations with parameter effects.

Covariate	Description	Summary	Prediction
Removal	Indicator variable for a hexagon in the control or treatment area of barred owl removal experiment.	Control (0), n = 463 Treatment (1), n = 91	+
Territory	Indicator variable for a hexagon overlapping a historical territory.	Overlapping (1), n = 517 Not overlapping (0), n = 37	−
Noise	Continuous average weekly hexagon-specific background noise measured in decibels relative to full scale (dBFS).	$\bar{X}$: −106.43 dBFS σ : 6.91 dBFS [−120.58 – −82.37] dBFS	−
Recording time	Continuous average time-, and hexagon-specific recording time.	$\bar{X}$: 3,033.54 min σ : 792 min [60 – 3,360] min	+
Area surveyed	Non-stochastic offset for variable area sampled in change of support calculation.	$\bar{X}$: 0.12 σ : 0.25 [0 – 1]	+
Previous detection	Indicator variable for whether an owl was previously detected on a site.	Previously detected (1) Not previously detected (0)	+

datasets for integrated parameter estimates. In linking different types of monitoring data, we demonstrate a shared model data integration approach (Pacifi et al., 2019) to resolve differences in field methods and spatial resolutions among datasets (i.e. a *change of support* problem; Mugglin et al., 2000, Gelfand et al., 2001; Gotway and Young, 2002, 2007).

A secondary objective was to evaluate the effectiveness of the integrated model structure to detect previously observed effects from component data considered in isolation or with alternative data. Specifically, our case study spatially overlapped with a concurrent before-after control-impact experiment that determined lethal removal of barred owls could improve declining population trends of spotted owls (Wiens et al., 2021). This spatial overlap with the removal experiment provided an opportunity to test if our integrated modeling approach could also detect an effect of barred owl removal on spotted owls. We hypothesized that the expected small population size of spotted owls (Franklin et al., 2021) would result in a low site occupancy rate for the study area and that occupancy estimates would be higher at sites within the barred owl removal area (Table 1). Moreover, previous analyses using bioacoustic data have established the importance of accounting for background noise and cumulative recording time in detection rates of spotted owls (Duchac et al., 2020). Thus, we predicted that increases in background noise would reduce detection probabilities and that

increases in weekly recording time would increase detection probabilities in the integrated model, similar to previous findings based on bioacoustic data alone.

2. Materials and methods

2.1. Study area

Our study took place during March – September 2018 in the Coast Range of Oregon, United States (43.7 – 45°N, 124.1 – 123.3°W; Fig. 1). Most lands of the study area were federally administered and part of a 3,922 km² long-term study area where spotted owls were monitored under the Northwest Forest Plan (Lint et al., 1999). For the barred owl removal experiment, the study area was divided into similar removal (treatment) and non-removal (control) areas to measure the response of spotted owls to barred owl removal during 2015 – 2020 (Wiens et al., 2021). Thus, barred owls were being actively removed prior to and during our focal sampling period in 2018.

2.2. Survey data

We used two spatially overlapping site-occupancy datasets collected in 2018 for the integrated analysis. The first dataset (hereafter

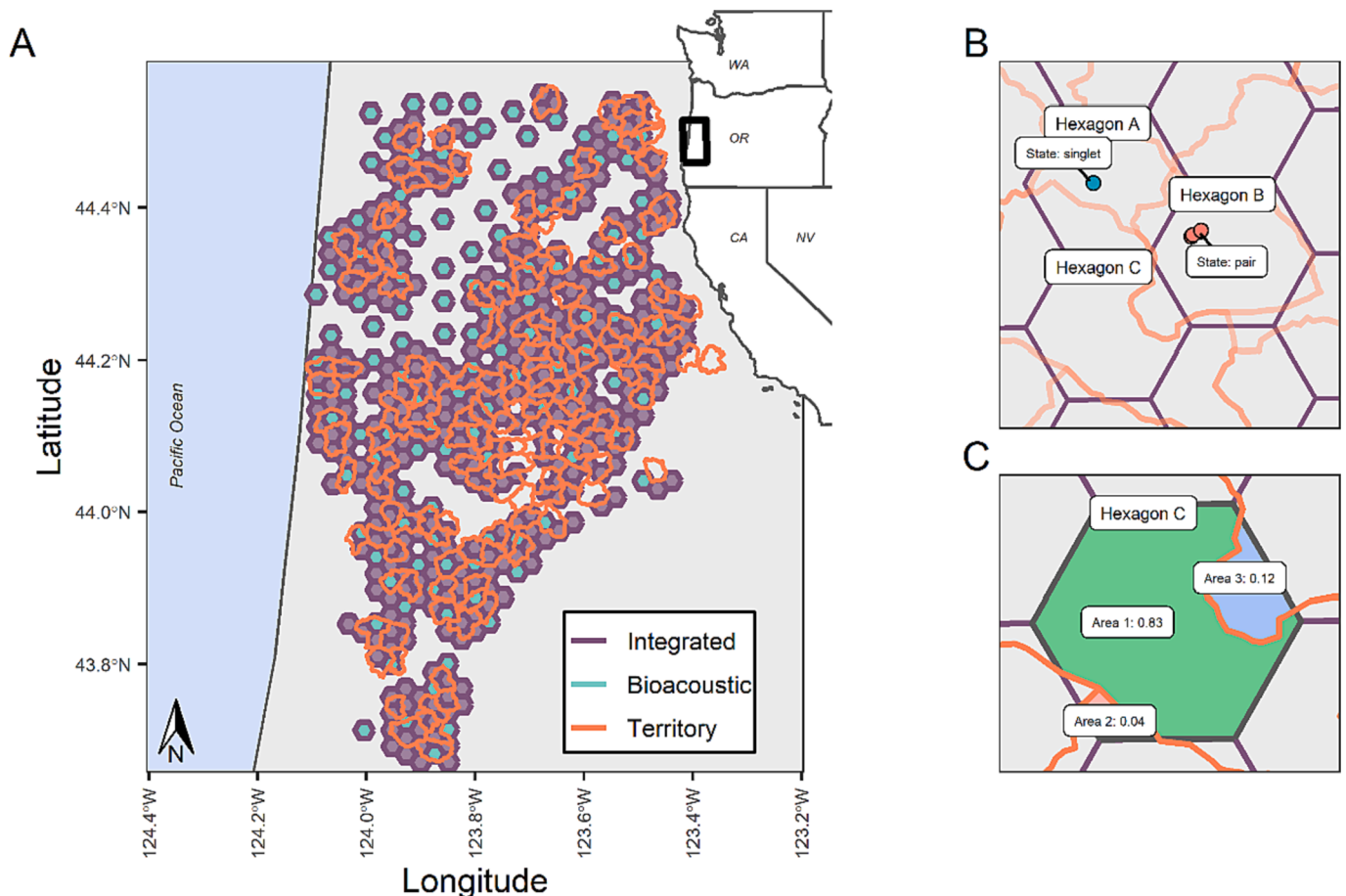


Fig. 1. Study area and demonstration of change of support spatial recasting in an integrated multistate site-occupancy analysis for northern spotted owls *Strix occidentalis caurina*, using data collected during 2018 in the Oregon Coast Range, USA. A) Map of the study area displaying the spatial extent of the integrated bioacoustic (hexagons with teal fill) and historical territory (orange outlines) datasets as well as the spatial union of these two datasets defining the study area of the integrated analysis (hexagons with purple outline; hexagons from the integrated union that do not overlap bioacoustic hexagons also have a purple fill). B) To resolve a modifiable areal unit problem resulting from data collection on different scales, territory observed state detections were recast, using the true spatial locations of detections, to the hexagon scale of the bioacoustics data. C) Demonstration of the area surveyed calculation used as a non-stochastic offset in the linear complementary log-log models for detection of non-paired (p_1) and paired owls (p_2). The area surveyed offset term was defined as the log of the proportion of total of area surveyed at each hexagon on each occasion by all overlapping territory survey areas. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

bioacoustic data) was collected during eight weeks of daily surveys in 119 hexagons in the study area (Fig. 1). Hexagons were part of a larger uniform grid of 5-km² hexagons established across the range of the spotted owl (Lesmeister et al., 2021). Hexagons selected for bioacoustics monitoring contained $\geq 50\%$ forest-capable lands and $\geq 25\%$ federal ownership. We defined forest-capable lands as those areas capable of developing closed-canopy forests (Davis et al., 2011). Each hexagon was surveyed with five autonomous recording units (ARUs), which recorded eight hours of audio each day (two hours before to two hours after sunrise, and 1 h before to 3 h after sunset) for up to eight weeks. We processed the audio data with a convolutional neural network (PNW-Cnet) that output prediction scores (range 0 – 1) of spotted owl call presence for every 12 s of audio data (Ruff et al., 2021). Ruff et al. (2022) provides a description of the call types included in the most recent version of the convolutional neural network (see Ruff et al., 2020; Ruff et al., 2021 for call types included in previous versions of the convolutional neural network). Audio segments classified as potentially containing spotted owl calls (scores ≥ 0.25) were validated manually and summarized into eight weekly occasions for occupancy analyses. We then subset these validated audio segments to those containing 4-note spotted owl call(s) and these segments were then further classified into male and female types using logistic regression (Dale et al., 2022). We developed multistate site-occupancy detection histories from these classifications, where the detection history for each site consisted of 40 survey occasions (eight survey weeks • five ARUs). Detection histories contained information on three observed states: 1) no observed calls, 2) observed male or uncertain sex assignment 4-note call, and 3) observed female 4-note call. The observed state value at each site- and ARU-specific occasion was the maximum state value detected during the weekly occasion. In interpreting results, we assumed that when female 4-note calls were detected it represented the detection of a probable pair because all hexagons where female spotted owls were detected also had detections of male spotted owls at the same ARU in the same week, in the same week at a different ARU within the same hexagon, or in a different

week at the same ARU. Mated females (especially when nesting) are known to be less vocally active than males (Forsman et al., 1984).

The second dataset (hereafter territory data) was collected during 12 weeks at 175 historical spotted owl territories, where each territory represented the cumulative area used by individually marked spotted owls from 1993 to 2018 (Franklin et al., 2021). Territories ranged in size from 3.57 km² to 15.66 km² and spatially overlapped between one and five hexagons used for bioacoustics monitoring (Fig. 1). We surveyed each territory in the study area at least two times during March – August to locate territorial spotted owls by either walking in to known owl locations during daytime, or by using night time roadside call-playback surveys where an observer played recorded owl calls and listened for ≥ 10 min for a territorial defense response from a resident owl (Franklin et al., 1996). Call-playback surveys were designed to detect presence of owls at historically occupied territories and walk-in surveys were completed to establish the presence of mated pairs and their nesting status. Latitude and longitude coordinates were recorded for all detections.

3. Change of support

Data from the two survey methods partially overlapped spatially but were sampled at different spatial resolutions (Fig. 1C; Gotway and Young, 2002). To reconcile the differing spatial scales, both data sources were treated as outcomes of the same occupancy distribution and variability in spatial sampling coverage was accounted for using a non-stochastic and additive offset (Jelinski and Wu, 1996; Pacifici et al., 2019). Previous analyses of territory occupancy aggregated detections of color-marked owls into site detection histories within historical territories (Dugger et al., 2016; Franklin et al., 2021; Yackulic et al., 2019; Rockweit et al., 2022). We used spatial locations of spotted owl detections during territory-based surveys to recast to the 5-km² hexagon grid used for bioacoustics monitoring (Fig. 1). We then developed territory-based site detection histories for each overlapping hexagon.

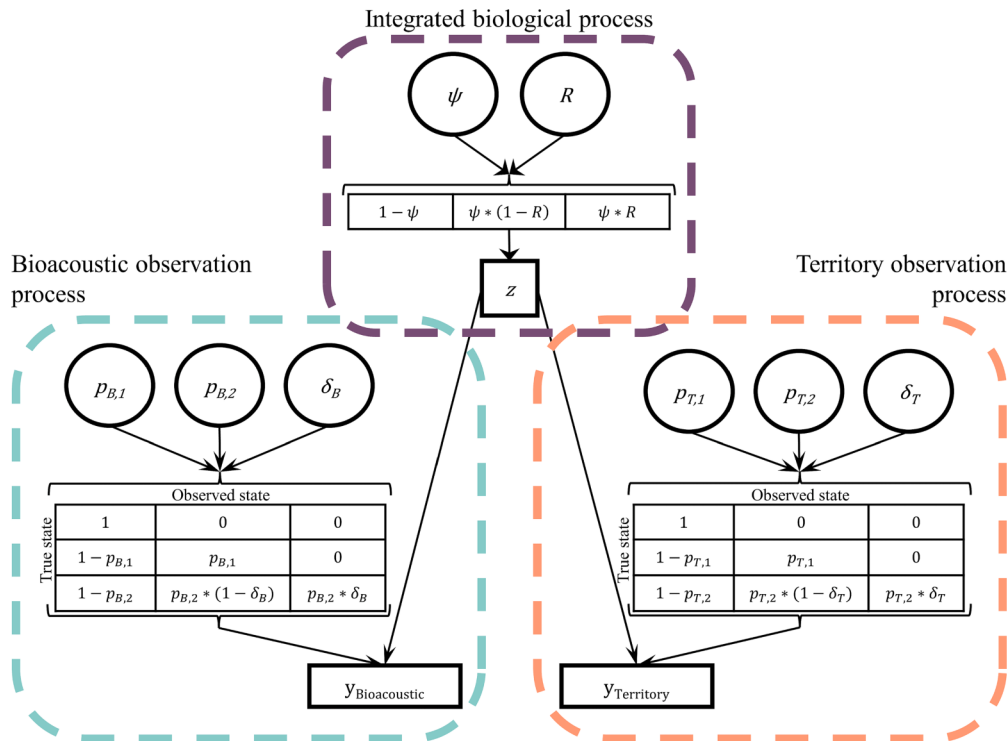


Fig. 2. Directed, acyclic graph (DAG) of an integrated multistate site-occupancy model used to link two spatially overlapping monitoring schemes for northern spotted owls (*Strix occidentalis caurina*) in the Oregon Coast Range, USA, 2018. Bold squares represent data sources, or estimated latent states, circles represent parameters, tables are matrices of conditional observation probabilities, and arrows represent conditional dependence.

Similar to Zipkin et al. (2017), we assigned observed states (no owls detected, non-paired owl detected, owl pair detected) from each territory-based survey occasion to hexagons using non-detections or the spatial coordinates of spotted owl detections.

4. Analysis

We developed an integrated multistate site-occupancy model (Nichols et al., 2007; Royle and Link, 2005) with a shared biological process and two separated observation processes (Fig. 2). The probability of being in one of three latent states z was defined with a multinomial distribution using a conditional approach with two parameters which were allowed to vary among sites, i : ψ , the probability of a site being used by a spotted owl regardless of state, and R the probability of occupancy by a pair given the site is used (see Appendix 1 for a mathematical description of the model). Specifically, the three states were State 1: not used by spotted owl ($1 - \psi_i$), State 2: used by spotted owls but not a pair ($\psi_i^*(1 - R_i)$), and State 3: occupied by a pair of spotted owls ($\psi_i^*R_i$). These parameter definitions, or similar variants, have been used previously for spotted owls (Kroll et al., 2016; Wood et al., 2020; Rockweit et al., 2022). We modeled variation in ψ_i and R_i using logit link functions and additive effects of an intercept, a site-specific effect of barred owl removals, and a site-specific effect for a site overlapping a historical territory (Table 1).

For both datasets the observation process was defined by three detection probabilities relating the observed state at i for time t to the latent state z . The conditional probabilities for these relations were defined by a matrix M where rows represented the latent ("true") states ($z = 1$ unused, $z = 2$ used by a non-pair, and $z = 3$ pair occupancy) and columns represented different observations: unobserved, observed male or uncertain sex assignment 4-note call, and observed female 4-note call. We assumed errors in state assignment can only occur down the rank order of true biological states. Detection probabilities p_1 , p_2 , and δ vary by i and t . Detection probabilities were defined

$p_{1,i,t}$ = probability of detecting use at i , during t ,
given $z_i = 1$,

$p_{2,i,t}$ = probability of detecting use at i , during t ,
given $z_i = 2$,

$\delta_{i,t}$ = probability of detecting a pair after occupancy has been detected at i ,
given $z_i = 3$.

For the bioacoustic observation process, we modeled variation in $p_{1,i,t}$, $p_{2,i,t}$, and $\delta_{i,t}$ on the logit scale as an additive function of an intercept, and two centered and scaled continuous effects. For the territory observation process, we modeled variation in $p_{1,i,t}$, $p_{2,i,t}$, and $\delta_{i,t}$ on the complementary log-log (cloglog) scale as an additive function of an intercept, and an offset *Area surveyed* to account for the proportion of total area for hexagon i surveyed during t ; both $p_{2,i,t}$ and $\delta_{i,t}$ included an additional additive categorical offset for *Previous detection* on a site. The *Area surveyed* non-stochastic offset term was defined as the log of the total proportion of area surveyed for each i at t , by all overlapping territory survey areas. For example, if hexagon C was overlapped by three territories in variable proportions (area 1: 0.83, area 2: 0.04, area 3: 0.12), and both area 1 and area 3 were surveyed on the first occasion, then for hexagon C the total area surveyed during the first occasion would be $0.83 + 0.12 = 0.95$ (Fig. 1C). We assume that the territory polygons used in the calculation of the Area surveyed offset adequately represented the territories surveyed during 2018. Violation of this assumption could potentially bias detection probabilities.

We derived estimates of ψ and ψ_{pair} (calculated as ψ^*R) for the larger Coast Range demographic study area as a weighted mean across all treatment combinations of the *Removal* and *Territory* covariates at their relative representation across the expanded area. The study area overlapped 1,691 hexagons. Representation across the *Removal* and *Territory*

treatments were: 1,174 hexagons not overlapping removal areas or historical territories, 426 hexagons not overlapping removal areas but overlapping historical territories, and 91 hexagons overlapping both removal areas and historical territories. In our study there were no hexagons overlapping a removal area but not overlapping historical territories.

To evaluate the effects of data integration on parameter precision of the biological state process, and the relative contribution of the bioacoustic and territory data to the posterior estimates of the integrated model, we fit two analog, non-integrated multistate site-occupancy models to the bioacoustic and territory data separately (hereafter singular models). These two singular models were hierarchically identical to the integrated model; however, each had only one observation process corresponding to the dataset. We calculated coefficients of variation (CV) for each biological process parameter and used these to evaluate the effects of data integration on parameter precision. We used Bhattacharyya distance (D_b) as a dissimilarity measure to assess the contribution of the bioacoustics and territory data relative to the integrated biological process parameters (Appendix 2; Bhattacharyya, 1943; Coleman and Andrews, 1979).

We conducted all analyses in R version 4.0.2 (R Core Team, 2020) using the nimble package version 0.10.1 (de Valpine et al., 2017). We used diffuse priors for all parameters and evaluated the sensitivity of our estimates to prior selection by considering two prior sets: Normal (μ , τ) for complementary log-log scale parameters where $\mu = 0$ and $\tau = 0.1$ and $\mu = 0$ and $\tau = 0.01$, and Normal (μ , τ) for logit scale parameters where $\mu = 0$ and $\tau = 0.368$ and Uniform (a , b) where $a = -5.0$ and $b = 5.0$. Each model was estimated with three independent 25,000-iteration chains following a 25,000-iteration burn-in period. We assessed model convergence by visual examination of trace plots and monitored the Brooks–Gelman–Rubin convergence diagnostic to ensure $\hat{R} < 1.03$ (Brooks and Gelman, 1998). We described the posterior distributions for each parameter by their mean and 95% credible interval (hereafter CI) and assessed the strength of individual effects or the magnitude of difference between estimates based on the degree to which the CI for the estimate did or did not overlap zero.

5. Results

We recorded 195,287 hr of audio data over the survey season. The spatial union of the bioacoustic and territory-based survey datasets intersected 554 hexagons and the change of support procedures increased the number of sampled units by the territory data from 175 territories to 517 hexagons with a maximum of five territories overlapping a single hexagon. After the change of support procedures, hexagon-specific survey area coverage offset was highly variable and ranged 0 – 1 (Table 1). Naïve occupancy of the integrated sites (the proportion of sites with detections without factoring in detectability) was low for all datasets (bioacoustic: 0.04; territory: 0.06; integrated: 0.08) and much lower for naïve pair occupancy (bioacoustic: 0.007; territory: 0.03; integrated: 0.03).

For the bioacoustic surveys, the mean weekly ARU-specific estimate of p_1 was 0.04 (CI: 0.02 – 0.06), p_2 was 0.15 (CI: 0.11 – 0.19), and δ was 0.20 (CI: 0.10 – 0.32; Fig. 3). Derived weekly hexagon-scale detection probabilities, calculated as $1 - (1 - p)^5$, were $p_1 = 0.17$ (CI: 0.09 – 0.26), $p_2 = 0.55$ (CI: 0.44 – 0.66), and $\delta = 0.66$ (CI: 0.42 – 0.86). The odds of detection for p_1 , p_2 , and δ were 0.68 times lower for each standard deviation increase ($\sigma_{\text{Noise}} = 6.91$ dBFS) in the level of background noise relative to full scale and 1.46 times higher for each standard deviation increase ($\sigma_{\text{Recording Time}} = 792.92$ min) in recording time (Fig. 3; Table 2). For the territory surveys, the mean probability of p_1 was 0.18 (CI: 0.09 – 0.31), the mean probability of p_2 was 0.45 (CI: 0.27 – 0.64), and the mean probability of δ was 0.83 (CI: 0.63 – 0.96; Fig. 3). There was no evidence for a change in the probability of detection for p_2 and δ after previous detection on sites (Table 2).

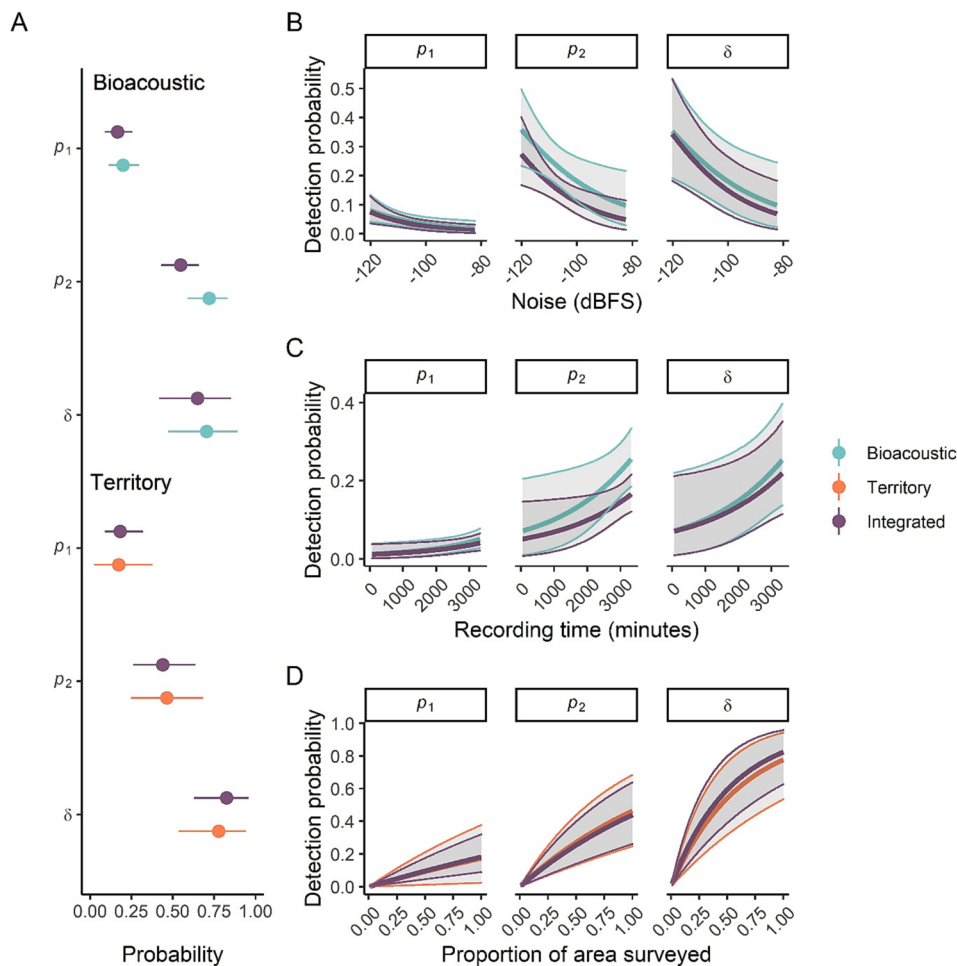


Fig. 3. Mean and 95% credible interval detection probability estimates for a northern spotted owl *Strix occidentalis caurina* multistate site-occupancy analysis, using data collected during 2018 in the Oregon Coast Range, USA. Comparisons are among estimates from models fit to bioacoustics and historical territory data alone and an integrated model fit using both bioacoustics and territory datasets. A) Weekly hexagon-scale estimates for the probability of detecting use given the true state non-paired use (p_1), the probability of detecting use given the true state is paired occupancy (p_2), and the probability of detecting a pair occupancy given that use has been detected (δ). B) Detection probabilities (p_1 and p_2) relative to the average amount of background noise (dBFS). C) Detection probabilities (p_1 and p_2) relative to the recording time (minutes). D) Detection probabilities (p_1 and p_2) relative to the proportion of area surveyed.

Table 2

Posterior means, lower (LCL) and upper (UCL) 95% credible intervals, for parameters of the integrated multistate site-occupancy model for northern spotted owls *Strix occidentalis caurina* using data collected during 2018 in the Oregon Coast Range, USA.

Dataset	Parameter	Covariate	Mean	LCL	UCL	Scale
Both	ψ	Intercept	-1.56	-2.62	-0.57	Logit
		Removal	0.38	-0.52	1.28	Logit
		Territory	0.16	-0.92	1.33	Logit
	R	Intercept	-1.32	-3.17	0.49	Logit
		Removal	1.96	0.29	4.05	Logit
		Territory	0.43	-1.52	2.38	Logit
Bioacoustic	p_1	Intercept	-3.34	-4.02	-2.80	Logit
	p_2	Intercept	-1.76	-2.12	-1.43	Logit
	δ	Intercept	-1.43	-2.18	-0.74	Logit
	p_1, p_2, δ	Noise	-0.39	-0.69	-0.11	Logit
	p_1, p_2, δ	Recording time	0.38	0.03	0.79	Logit
	p_1, p_2, δ	Proportion of area surveyed	0.11	-0.53	0.76	Logit
Territory	p_1	Intercept	-1.67	-2.39	-0.99	Complementary log-log
	p_2	Intercept	-0.54	-1.17	0.02	Complementary log-log
	δ	Intercept	0.60	0.00	1.17	Complementary log-log
	p_2, δ	Previous detection	0.11	-0.53	0.76	Complementary log-log

The mean estimate of ψ was 0.18 (CI: 0.07 – 0.36), R was 0.24 (CI: 0.04 – 0.62), and ψ_{pair} was 0.04 (CI: 0.01 – 0.12; Fig. 4). Mean ψ was higher on sites where barred owls were removed but 23.6% of the CI for the removal effect overlapped zero (Table 2) indicating relatively weak, but positive effects of removals on spotted owl use regardless of pair state. We found no evidence that ψ was higher on historical territories. The odds of conditional pair occupancy (R) were 7.01 times greater on sites where barred owls were removed, and 1.5 times greater on historical spotted owl territories (Table 2). This is despite some overlap in the CIs of R on non-removal and removal sites (Fig. 4). Credible intervals

of derived ψ_{pair} estimates overlapped by 15% relative to non-removal sites, indicating some evidence for a meaningful difference in ψ_{pair} between non-removal and removal sites (Fig. 4). At the scale of the Oregon Coast Range demographic study area mean estimates of ψ were 0.19 (CI: 0.11 – 0.32) and ψ_{pair} were 0.05 (CI: 0.02 – 0.11).

The percentage decrease in CVs for the integrated biological process parameter estimates relative to the singular estimates ranged from -6.19% to 123.61% and was variable among comparisons (Table 3). Bhattacharyya distance was variable among comparisons for the integrated biological process estimates relative to the singular estimates, but

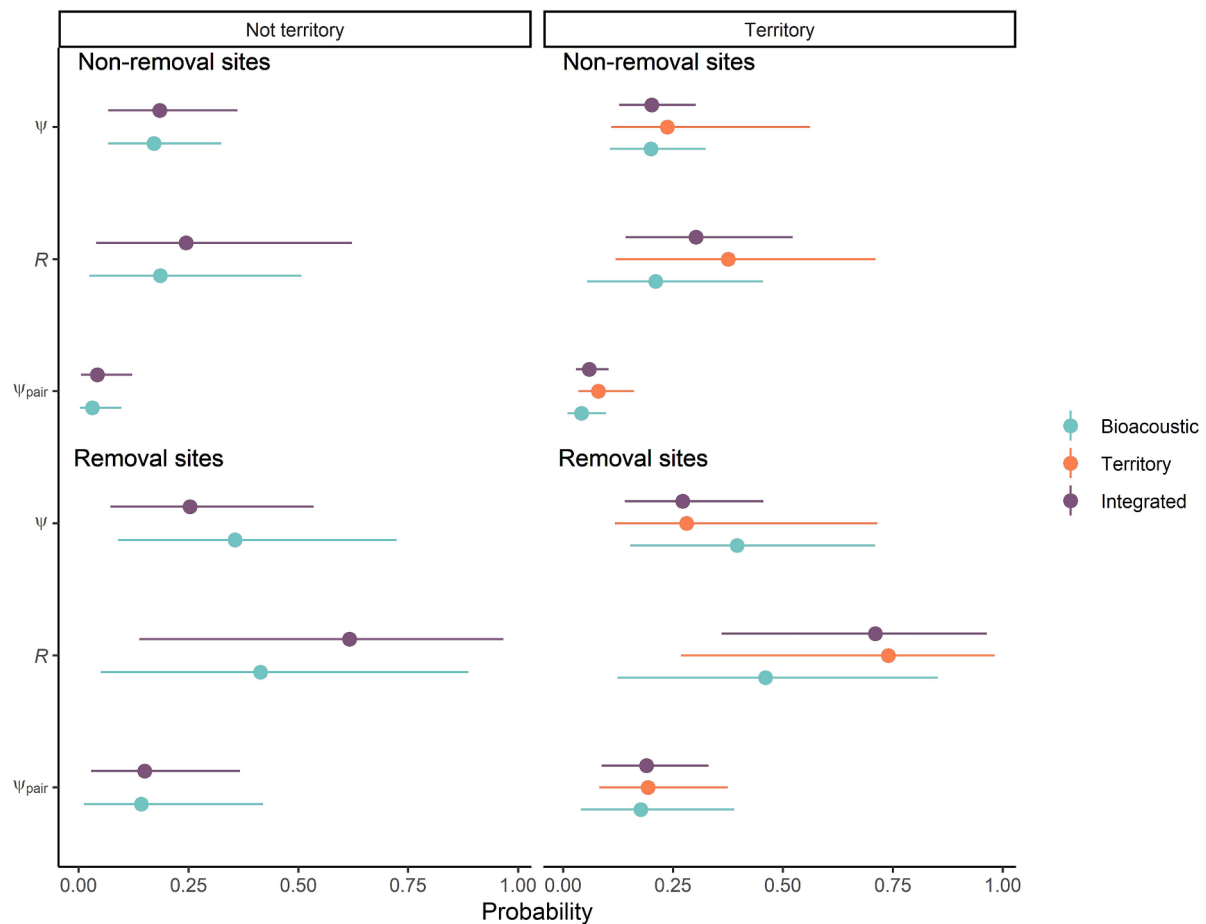


Fig. 4. Comparison of mean and 95% credible interval biological process probability estimates between sites with and without barred owl removal for a multistate site-occupancy analysis for northern spotted owls *Strix occidentalis caurina*, using data collected during 2018 in the Oregon Coast Range, USA. The left panel shows estimates on sites not overlapping historical territories and the right panel shows sites overlapping historical territories. Comparisons are among estimates from models fit to bioacoustics and historical territory data alone and an integrated model fit using both bioacoustics and territory datasets. ψ is the probability of a site being used by spotted owls regardless of pair state, R is the probability of a spotted owl pair occupying a site with known spotted owl use, and ψ_{pair} is the derived ($\psi_{pair} = \psi \cdot R$) unconditional probability of pair occupancy.

generally indicated that the posterior distributions for the integrated parameters were more similar to the posterior distributions for the singular bioacoustic parameters (Table 3). However, for the posterior parameter estimates of R on territory sites where comparisons were possible, D_b was similar in magnitude for the integrated parameter estimate relative to the singular bioacoustic parameter estimate (0.10) and the singular territory parameter estimate (0.09) on non-removal sites, but strongly favored similarity in the singular territory parameter estimates (0.01) over the singular bioacoustic parameter estimate (0.25) on removal sites.

Posterior distributions for most coefficients were similar for both prior set specifications (Figure A1). There was some evidence that the posterior estimate for the removal and territory effects on R were sensitive to prior selection. For this parameter the mean of the posterior distribution was slightly higher for prior 2 relative to prior 1.

6. Discussion

Our data integration approach to estimate multistate occupancy and detection probabilities for spotted owls in the Pacific Northwest, USA, resulted in increased precision of estimates relative to identical models fit using detection/non-detection data from territory-based call-playback surveys or bioacoustics surveys alone. We also demonstrated a flexible approach to integrate occupancy data sampled at different spatial resolutions that could be applied in other systems to increase

estimated precision by combining characteristics of different datasets (Abadi et al., 2010; Schaub and Abadi, 2011), resolve inferential differences (Saunders et al., 2019), and reconcile mismatches in spatial or temporal overlap (Zhao et al., 2021). This shared model data integration strategy may be especially effective for population monitoring programs that are undergoing transitions in data collection methods or seeking to combine disparate high-quality spatial or temporal datasets (Pacifi et al., 2017).

Northern spotted owls continue to experience dramatically destabilized and declining populations throughout their geographic range (Dugger et al., 2016; Franklin et al., 2021; Jenkins et al., 2021). Previous meta-analyses assumed that inferences drawn from territory-based monitoring data within long-term demographic study areas were representative of the populations on the larger landscape but testing this assumption has been previously impractical. Here we developed a framework that may be used to better understand these assumptions by expanding the spatial scale of inferences beyond the area defined solely by bioacoustic and territory-based datasets separately. We extrapolated the marginal mean use estimates for landscape use by spotted owls and pair occupancy estimates for all combinations of the *Removal* and *Territory* covariates to the larger landscape. We found that mean estimates from our expanded inferences were similar to our estimates within the study area, but with reduced standard errors of the mean estimates. The distinction between population and finite sample estimates is a source of inferential tension for many ecological studies, classically typified by

Table 3

Coefficients of variation (CV), percentage decrease in coefficients of variation between singular and integrated estimates (% decrease), and Bhattacharyya distance (D_b) relative to the integrated estimates for multistate site-occupancy parameter estimates for northern spotted owls *Strix occidentalis caurina* using data collected during 2018 in the Oregon Coast Range, USA. The treatment column demarcates if barred owls *Strix varia* were lethally removed from the site. The territory column demarcates if sites overlapped historical spotted owl territories.

Treatment	Territory	Parameter	Data	CV	% decrease	D_b
Non-removal	Not in territory	ψ	Bioacoustic	0.39	−6.19	0.01
			Integrated	0.41		
		R	Bioacoustic	0.69	10.12	0.03
			Integrated	0.63		
		ψ_{pair}	Bioacoustic	0.81	14.24	0.03
			Integrated	0.71		
	Territory	ψ	Bioacoustic	0.28	27.53	0.01
			Territory	0.49	123.53	0.23
			Integrated	0.22		
		R	Bioacoustic	0.50	52.74	0.10
			Territory	0.41	24.67	0.09
			Integrated	0.33		
		ψ_{pair}	Bioacoustic	0.56	71.60	0.10
			Territory	0.41	27.97	0.14
			Integrated	0.32		
			Bioacoustic	0.48	−0.59	0.09
			Integrated	0.48		
			Bioacoustic	0.58		
Removal	Not in territory	ψ	Bioacoustic	0.48	−0.59	0.09
			Integrated	0.48		
		R	Bioacoustic	0.58	52.58	0.09
			Integrated	0.38		
		ψ_{pair}	Bioacoustic	0.76	28.99	0.01
			Integrated	0.59		
	Territory	ψ	Bioacoustic	0.36	22.21	0.22
			Territory	0.50	69.68	0.08
			Integrated	0.30		
		R	Bioacoustic	0.42	82.98	0.25
			Territory	0.26	13.64	0.01
			Integrated	0.30		
		ψ_{pair}	Bioacoustic	0.52	57.17	0.04
			Territory	0.39	18.46	0.01
			Integrated	0.33		

small datasets which are assumed to represent larger populations. The framework presented here parallels general approaches to small-area estimation problems and provides a reasonable population scale estimate for the parameters of interest while accounting for uncertainty.

Previous analyses of spotted owl occupancy have found evidence for a decreasing annual trend in the territorial occupancy of pairs across all demographic studies areas, including our study area in the Oregon Coast Range (Dugger et al., 2016; Franklin et al., 2021; Rockweit et al., 2022). During 2016, territorial occupancy of pairs in the Oregon Coast Range was estimated to be 0.19 (CI: 0.14 – 0.23), declining to 0.15 (CI: 0.11 – 0.19) by 2018 (Franklin et al., 2021). Across all combinations of site characteristics (barred owl removal and historical territory) our estimates were substantially lower than estimates from long-term demographic studies of spotted owls and California spotted owls (Tempel et al., 2016; Wood et al., 2020; Reid et al., 2021). For example, the territorial occupancy estimates for pairs reported by Franklin et al. (2021) for 2018 were 2.54-fold higher than our mean pair occupancy estimate on historical territories (non-removal sites only), and 2.73-fold higher than our Coast Range scale estimates of pair occupancy. We expected some differences because our survey hexagons were randomly sampled across the Coast Range study area and our change of support procedures recast the territory data into 500-ha hexagons, which is less than the average size of spotted owl territory polygons used in our analysis (mean 872 ha) but within the range of territory sizes (357–1,567 ha). However, the large differences in occupancy estimates derived from bioacoustic data compared to historical territory-based studies suggests that territorial occupancy estimates likely do not generalize well to the unsampled landscape.

Barred owls are competitively dominant to spotted owls and interactions between these congeneric owls resulting in joint competition for resources or territorial displacement have been associated with reductions in spotted owl vital rates (Wiens et al., 2014), increases in territory extinction (Yackulic et al., 2014, 2019; Diller et al., 2016;

Franklin et al., 2021) and changes to dispersal dynamics (Jenkins et al., 2019). Furthermore, competitive interactions between barred owls and spotted owls are associated with considerable reductions in territorial occupancy of spotted owls in Oregon and Washington (Olson et al., 2005; Dugger et al., 2016; Mangan et al., 2019; Yackulic et al., 2019). General positive effects on spotted owl survival and population trends were observed after competitive release from barred owl through lethal removal experiments (Wiens et al., 2021). We hypothesized that the positive demographic effects of barred owl removal would result in increases to spotted owl occupancy (Diller et al., 2016). We found a consistent positive effect of barred owl removal across all parameters in both the integrated and singular models. Importantly the effects were more pronounced for parameters related to occupancy by spotted owl pairs relative to use by non-paired owls. Lesmeister et al. (2021) conducted simulations to establish a passive acoustic monitoring design that was capable of estimating trends in spotted owl use over many scenarios. The data used in our study were sampled under a similar protocol to that suggested by Lesmeister et al. (2021) and we found the design sufficient to detect a consistent positive effect of barred owl removal on occupancy of paired spotted owls. This finding indicates that the bioacoustics monitoring framework may serve as an important component of quantifying effectiveness of future recovery actions for spotted owls.

Integrated analyses have consistently observed increased precision in parameter estimates relative to non-integrated models (Abadi et al., 2010; Schaub and Abadi, 2011). Although this observation is typically noted, the importance of reduced uncertainty can be difficult to appreciate when parameter point estimates are similar and the measures of uncertainty typically overlap in singular and integrated analyses. For example, increased precision in our estimates did not change the interpretation or management implications of our results; however, the outcomes of an individual analysis should not be conflated with the broader utility of reducing uncertainty. Here we suggest three motivating reasons for reducing uncertainty. First, increased precision in

estimates results in an increased ability to detect effects when they are present. For example, Fletcher et al. (2016) detected a significant relationship between fox squirrel (*Sciurus niger*) presence and the distance to forest edge using an integrated distribution model, where a singular presence-only distribution model did not detect the effect. Similarly, seemingly modest reductions in estimates of uncertainty lead to more accurate predictions by reducing propagation of error. Second, within a decision-making framework process uncertainty is an important consideration (Conroy and Peterson, 2013). Increasing the precision in parameter estimates improves our understanding of individual pieces in a larger puzzle, which can in turn be linked together within a larger decision-making framework. For example, Duarte et al. (2017) adopted an integrated model structure into a decision-support model to evaluate tradeoffs in potential management actions related to the translocation of animals within an adaptive management framework. Third, wildlife management and conservation necessarily involve human dimensions given decisions are a means to achieve the decision maker(s) objective(s). In light of this, data integration approaches can garner support by valuing legacy datasets that managers and stakeholders invested valuable resources to collect, rather than discarding these data in updated analyses. Instead, previous data can add value by broadening the analytical scope and increasing precision.

We found that the relative information content of the bioacoustic and territory datasets differed. Our integrated estimates were most similar—a smaller Bhattacharyya distance between the posterior distributions of the estimates—to the single model estimates for probabilities best represented by the sampling design associated with the different data types (bioacoustic vs territory-based). For example, the territory survey data was not well suited to model general use across the study area, perhaps because these data were collected on known historical spotted owl territories which were not established through random site selection. The bioacoustic data was sampled across a larger extent and hexagons were randomly selected within federal lands. Our posterior estimate for use from the integrated model was nearly identical to the bioacoustic posterior estimate alone, whereas the integrated posterior estimate differed from the territory posterior estimate. This was especially clear in preliminary analyses that did not account for historical territory status of hexagons (Table A1). Another example shows that relative to the bioacoustic data the historical territory survey data were more informative to the integrated posterior estimate for the probability a site was occupied by a pair given that use was previously confirmed. Both structured datasets provided inferential value to different components of the biological processes (Zipkin et al., 2021). However, when datasets are of differing quality, a shared model integration approach should be carefully considered relative to other data fusion procedures (Pacifi et al., 2017). Future spotted owl analyses may explore the relative information content of these datasets data in a model-based approach to balance their relative contributions (Wang, 2001; Wang and Zidek, 2005; Francis 2011; Punt, 2017; Fletcher et al., 2019; Miller et al., 2019).

We hypothesized that both recording time and background noise would influence the detection probability of spotted owls using the bioacoustic data and in both cases our estimates were consistent with previous findings. We found a strong positive relationship between increased recording time and all three bioacoustic detection probabilities. Intuitively we expected the relationship between recording time and detection probability to be linear log-log, which asymptotes at a maximum detection. In other words, the longer we sample the more likely we are to detect a call if the species is present, a pattern consistent with or sampling relationships such as the species-area (Lawton, 1999) and species-time (Preston, 1960) relationships in biodiversity surveys or their correlate in bioacoustic-based biodiversity surveys (de Carmargo et al., 2019; Wood et al., 2021). This is generally what we found; however, detection probabilities only increased gradually until the weekly recording time exceeded ~2,000 min, after which they increased much faster. The relationship between detection probability and

recording time is season- and species-specific (Duchac et al., 2020; La and Nudds, 2016) and identifying objective-specific minimum sampling thresholds could influence precision and accuracy of estimates (Cole et al., 2022). For example, for species that restrict calling behavior to certain times of the day the detection-recording time relationship should saturate faster if recordings are restricted to periods with highest calling activity. We also found a strong negative relationship between background noise and all three bioacoustic detection probabilities. Environmental and anthropogenic noise has been a major obstacle to bioacoustic event detection (Lostanlen et al., 2019; Juodakis and Marsland, 2022). Noise sources such as wind, rain, traffic and rivers reduce the performance of event detection and classification algorithms likely by masking or degrading target sound events (Digby et al., 2013; Salamon et al., 2016; Duchac et al., 2020; Cole et al., 2022).

The need for continued spotted owl population monitoring has increased through time, especially as populations continue to decline and face persistent threats (Franklin et al., 2021; Lesmeister et al., 2018). Furthermore, the realities of population and environmental conditions highlight the need for an adaptive monitoring approach to best inform management and conservation decisions (Lesmeister et al., 2021). One challenge for any monitoring program undergoing transition will be to determine the best approaches to incorporate early inferences as monitoring protocols adapt to new questions and technologies. One approach may include incorporating estimates from previous analyses into ongoing monitoring efforts as informative priors on future models in a Bayesian analytical framework. Another non-exclusive approach could be integrating datasets as presented here to link time series, incorporate auxiliary demographic information, and inform spatially explicit processes. Further research may be best focused on extending our approach to model occupancy dynamics (colonization and extinction) for multiple biological states and to estimate probabilities associated with spotted owl movement among sampling units.

7. Authors' contributions

Matthew J. Weldy, Damon B. Lesmeister, and Charles B. Yackulic conceptualized and designed the analysis; Damon B. Lesmeister, Cara L. Appel, Chris McCafferty, and J. David Wiens collected the data; Matthew J. Weldy and Charles B. Yackulic analyzed the data; Matthew J. Weldy led the writing of the manuscript. All authors contributed to manuscript review and editing and gave final approval for publication.

CRediT authorship contribution statement

Matthew J. Weldy: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft. **Damon B. Lesmeister:** Conceptualization, Methodology, Data curation, Funding acquisition, Project administration, Supervision, Writing – review & editing. **Charles B. Yackulic:** Conceptualization, Methodology, Supervision, Validation, Writing – review & editing. **Cara L. Appel:** Data curation, Writing – review & editing. **Chris McCafferty:** Data curation, Writing – review & editing. **J. David Wiens:** Methodology, Data curation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109815>.

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