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Dynamic *N*-occupancy models: estimating demographic rates and local abundance from detection-nondetection data

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Abstract. Occupancy modeling is a widely used analytical technique for assessing species distributions and range dynamics. However, occupancy analyses frequently ignore variation in abundance of occupied sites, even though site abundances affect many of the parameters being estimated (e.g., extinction, colonization, detection probability). We introduce a new model (“dynamic *N*-occupancy”) capable of providing accurate estimates of local abundance, population gains (reproduction/immigration), and apparent survival probabilities while accounting for imperfect detection using only detection/nondetection data. Our model utilizes heterogeneity in detection based on variations in site abundances to estimate latent demographic rates via a dynamic *N*-mixture modeling framework. We validate our model using simulations across a wide range of values and examine the data requirements, including the number of years and survey sites needed, for unbiased and precise estimation of parameters. We apply our model to estimate spatiotemporal heterogeneity in abundances of barred owls (*Strix varia*) within a recently invaded region in Oregon (USA). Estimates of apparent survival and population gains are consistent with those from a nearby radio-tracking study and elucidate how barred owl abundances have increased dramatically over time. The dynamic *N*-occupancy model greatly improves inferences on individual-level population processes from occupancy data by explicitly modeling the latent population structure.

Key words: barred owl; demographic rates; dynamic; heterogeneity; latent; *N*-mixture model; occupancy; species distribution models.

INTRODUCTION

Occupancy monitoring (i.e., presence/absence at a set of sites) can be a cost-effective approach to document changes in the status of species over broad spatial scales. Occupancy is arguably the most widely used measure to document range shifts (e.g., Tingley and Beissinger 2009), species invasions (e.g., Murray et al. 2015), and declines in rare species (e.g., global amphibian declines; Adams et al. 2013). However, presence/absence monitoring is hindered by imperfect detection (failure to observe a species that is present), which can confound estimates of occupancy. A class of models termed “occupancy models” addresses this challenge by including an explicit detection

model within the analytical framework (MacKenzie et al. 2002, Tyre et al. 2003). Occupancy models have been widely adopted in wildlife analyses and applied to a diverse set of objectives, including habitat modeling (e.g., Ball et al. 2005), metapopulation studies (e.g., Hines et al. 2010), and large-scale monitoring efforts (e.g., Pellet and Schmidt 2005). Occupancy models have also been extended to explicitly model colonization and extinction processes that can change the status of sites (occupied vs. unoccupied) over time using multi-season (i.e., dynamic) occupancy models (MacKenzie et al. 2005).

Variation in detection probability in many occupancy studies is the result of variation in animal abundance among sites; this relationship facilitates estimation of abundance from detection/nondetection data using single season models (Royle and Nichols 2003). Similarly, the extinction probability of a site is likely related to its local

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abundance. For example, all else being equal, a site with many individuals is more likely to remain occupied in the next time step compared to one with few individuals. This suggests a clear link between models that estimate occupancy and those that focus on estimating abundance. Site-level abundance is generally estimated with spatially and temporally replicated count data using the “*N*-mixture model” in which detection probability is specified at the level of the individual, rather than the species (Royle 2004). Dynamic extensions of the *N*-mixture model estimate the underlying processes responsible for changes in local abundances and colonization/extinction dynamics (i.e., births, immigration, apparent survival) using count data collected over multiple seasons or years (Dail and Madsen 2011, Zipkin et al. 2014b).

Estimating demographic rates using only count data allows for inferences on greater spatial scales and provides a detailed understanding of fine-scale population processes without the added difficulties of marking and tracking individuals. The ability to estimate demographic parameters and local abundance using only detection/nondetection data would enable important advances in: (1) the capacity to investigate underlying mechanisms of population fluctuations using a widely collected data type; (2) conservation-focused projects, which often infer range-wide population trends from occupancy analyses without knowledge of demographic rates; and (3) research across large spatial scales where individuals are impossible to identify or track (thus excluding mark-recapture designs).

Here, we develop a model that uses only detection/nondetection data to estimate abundance and demographic rates by assuming that the latent biological process follows that of the dynamic *N*-mixture model (Dail and Madsen 2011). We do this by explicitly modeling the detection probability of individuals at sampling locations (i.e., Royle and Nichols 2003), rather than simply detection of the species as in ordinary occupancy models (MacKenzie et al. 2002). We use simulations to show how our dynamic *N*-occupancy model provides accurate estimates of local abundances, apparent survival probabilities, and gains to the population (via recruitment and immigration) from only detection/nondetection data. We then apply our model to barred owl (*Strix varia*) detection/nondetection data collected in Coastal Oregon over a 26-yr time period. Barred owls are of conservation concern because of their role in the continued decline of northern spotted owls (*Strix occidentalis caurina*; Dugger et al. 2016). Yet basic understanding of barred owl demographic rates and spatio-temporal abundances is limited (but see Wiens et al. 2014). Our analysis reveals (1) strong synchrony between landscape abundances and regional-level recruitment, (2) consistently high apparent survival rates, and (3) dramatically increasing barred owl abundances within the study area over the 26-yr period.

MODEL DESCRIPTION

In most ecological studies, true abundance at a particular location *i* at time *t*, $N_{i,t}$, cannot be observed

directly. We can infer $N_{i,t}$ from detection/nondetection (i.e., occupancy) surveys in which sites are visited within a closed time period on $k > 1$ occasions (MacKenzie et al. 2002). Occupancy data are collected by recording if a species was detected during independent sampling events via site surveys, transect walks, or other techniques (MacKenzie et al. 2005). The salient feature of these data is that the occupancy status of a site *i* in time *t* during sampling replicate *k*, $y_{i,t,k}$, can be mis-specified if a species is present and none of the $N_{i,t}$ individuals are detected during sampling replicate *k*. In classical occupancy analyses, detection data are modeled by assuming that $y_{i,t,k} \sim \text{Bernoulli}(p)$ where *p* is the detection probability of the species. Following Royle and Nichols (2003), we break down the detection model by assuming that a species is recorded if at least one individual is observed. Thus, *p* can be re-written as:

$$p = 1 - (1 - \theta)^{N_{i,t}}$$

where θ is the independent detection probability of all $N_{i,t}$ individuals of the target species. The per individual detection probability, θ , can be indexed by site *i*, sampling replicate *k*, or time *t* such that relevant covariates are included to account for variation in the sampling process across time or space.

We then specify a model for the latent population abundance $N_{i,t}$ and the biological processes that result in changes to abundance over time. The state process is initialized during the first year of sampling ($t = 1$) by modeling abundance at each site, $N_{i,1}$, according to a discrete distribution (e.g., Poisson, negative binomial) with an expected value of λ , $N_{i,1} \sim \text{Poisson}(\lambda)$. We assume that subsequent population abundance at a site *i* is conditional only on abundance at *i* in the previous time step (Dail and Madsen 2011). The change in N_i between $t - 1$ and *t* is modeled by estimating the number of individuals that survive at a site ($S_{i,t}$) and the number of individuals that are gained to the population by recruitment and immigration combined ($G_{i,t}$). These quantities are expressed as follows:

$$S_{i,t} \sim \text{Binomial}(N_{i,t-1}, \omega)$$

$$G_{i,t} \sim \text{Poisson}(\gamma)$$

where ω is the annual apparent survival probability of individuals, and γ is the expected number of individuals that are gained to location *i* between $t - 1$ and *t*. The total population abundance at site *i* in time $t > 1$ is the sum of individuals that survive and are gained: $N_{i,t} = S_{i,t-1} + G_{i,t-1}$. Covariates can be added to any of the parameters (ω , γ , λ , θ) using appropriate link functions to incorporate relevant biotic and/or abiotic factors (e.g., weather, habitat, density dependence) that may influence population dynamics and/or detection across spatial locations. Both detection probability and the demographic parameters are assumed to be equal across all individuals (i.e., no individual heterogeneity).

SIMULATION STUDY

We performed a simulation study to test the ability of the dynamic N -occupancy model to recover demographic parameters and estimates of population abundance. We used the previously described model, which assumes that initial abundance, gains, survival, and detection are independent of time, as well as environmental and sampling covariates. For each simulation, a single value for each parameter was drawn from the following distributions: $\lambda \sim \text{uniform}(0.5, 3)$; $\gamma \sim \text{uniform}(0, 2)$; $\omega \sim \text{uniform}(0, 1)$; and $\theta \sim \text{uniform}(0, 1)$. The data generation process followed the assumptions of the model: site abundance in year 1 was simulated for all i sites using a Poisson distribution with mean λ . Individuals survived and remained at site i according to a Bernoulli distribution with parameter ω . Gains at each site were randomly drawn from a Poisson distribution with mean γ . Data were simulated in this fashion for 10 yr and the total number of survey sites was set to either 25, 75, or 150. For each year, all sites were sampled three times over a period in which the population was closed, with an individual detection probability of θ . If any individuals were observed at a sampling event, the site was considered to have a “detection” for that particular sampling replicate and a one was recorded in the dataset. We estimated model parameters with Bayesian inference and used Markov chain Monte Carlo (MCMC) to sample from posterior distributions for each parameter with the programs R version 3.2.3 and JAGS (Plummer 2003). Complete

model details along with the R and JAGS code can be found in Metadata S1.

We ran 5,000 simulations each for the three scenarios (25, 75, 150 sites). We retained mean parameter estimates, as well as the “true” parameter values. We assessed the bias and precision of our dynamic N -occupancy model by subtracting the “true” value from the estimate. Results from our simulation study demonstrate that population-level estimates of initial abundances, population gains, survival probability, and detection are all unbiased (median estimates are near zero; Fig. 1). Additionally, we queried results across the range of true parameter values (e.g., examined precision and accuracy of survival as a function of true detection probability) and found no evidence of bias when at least 75 sites are surveyed; we found slight bias when only 25 sites are surveyed (Appendix S1). Model precision was highest when the gains and initial abundance parameter values were low (Appendix S1: Figs. S1, S2). For all parameters, precision increased with the number of survey sites (boxplot widths decrease across x -axes; Fig. 1). In general, estimates generated from 150 occupancy sites were similar in precision to a standard dynamic N -mixture model using 25 count sites.

APPLICATION: ESTIMATING BARRED OWL INVASION CHARACTERISTICS USING OCCUPANCY DATA

The barred owl's historic distribution spanned the south-central and southeastern portions of Canada, as well as the eastern United States. However, over the last

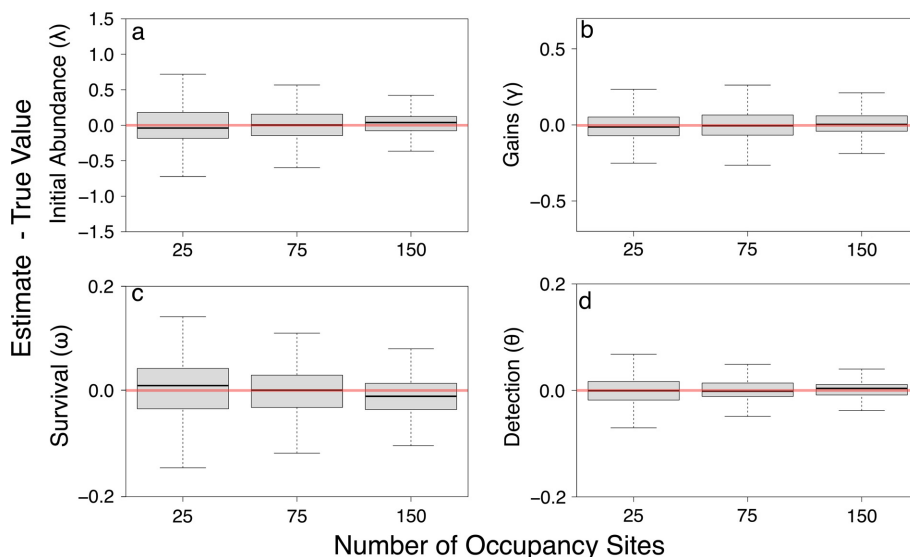


FIG. 1. Simulation results showing estimated minus true parameter values for the following: (a) initial abundance, (b) expected local population gains, (c) survival, and (d) detection. Red lines indicate where estimates and true values are equal (i.e., estimated – true = 0). Negative values on the y -axes indicate underestimation by the model whereas positive values indicate overestimation. Dark lines within boxes represent median values (of 5000 median estimates from simulated datasets) for three levels of occupancy (25, 75, 150 sites; x -axes). Bottom and top of boxes represent the first and third quartiles, respectively. Whiskers show the highest/lowest values within ± 1.5 times the interquartile range. Estimates generated from 150 occupancy sites (last boxplot in all panels) are similar in precision to a standard dynamic N -mixture model using 25 count sites.

century, their range has expanded westward and barred owls are now found throughout the Pacific Northwest (Gutiérrez et al. 2007, Livezey 2009). Barred owl expansion is of intense conservation interest because barred owls often force threatened northern spotted owls from their territories, contributing to their continued decline (Wiens et al. 2014, Yackulic et al. 2014, Diller et al. 2016, Dugger et al. 2016). We applied our dynamic *N*-occupancy model to estimate demographic rates and spatiotemporal variation in abundances for a population of barred owls in the Pacific Northwest. Our model is especially appropriate for this system because (1) barred owl abundances are not well known and local sites are large enough to potentially include many barred owls (Wiens et al. 2014), (2) vital rates have only been studied in one barred owl population in the Pacific Northwest and only in the later stages of invasion, and (3) wildlife officials are currently removing barred owls from selected experimental removal areas in the Pacific Northwest, but these efforts will be most effective if they are informed by detailed knowledge of barred owl demographic rates and variations in local abundances.

Our analysis incorporated 26 yrs of detection/non-detection data collected at 158 independent sites within contiguous polygons created for the survey within Douglas County, Oregon, USA (delineated based on topography and northern spotted owl territories; see Fig. 2f). A total of 19,228 surveys were conducted according to a standardized protocol designed for northern spotted owls and sites were visited between 1 March and 31 August annually during 1990–2015. Most, but not all, sites were sampled on up to eight occasions in every year during the study period. We assumed population closure during the sampling events that occurred within years but that population abundance could change between years (see Yackulic et al. 2012 for more information on the data collection process). Although barred owls were not the target of the vocal lures, they were often detected incidentally during surveys because they respond aggressively to spotted owl calls (Crozier et al. 2006, Wiens et al. 2014).

We modified the basic structure of our dynamic *N*-occupancy model to include several covariates affecting the abundance and detection processes. Annual barred owl gains at individual sites are likely density-dependent, based on the regional population size in the previous year (Yackulic et al. 2012). As such, we specified the following time-varying model for γ_t :

$$\log(\gamma_t) = \alpha_0 + \alpha_1 \bar{N}_{t-1}$$

where $\bar{N}_{t-1}$ is the regional average (site-specific) population size in the previous year. The barred owl's dispersal capability ($\mu = 41.3$ km, median = 22.6 km) is roughly equivalent to the size of the study area (50 km $\times$ 20 km; Livezey 2009, Yackulic et al. 2012) which suggests that densities within the study area are a good proxy for densities within the region. We incorporated a habitat covariate on the apparent survival probability (ω) that

has been consistently important in predicting barred owl occupancy using a log link function (Hamer et al. 2007, Yackulic et al. 2012, 2014): the total amount of older (approx. ≥ 80 yr) riparian forest (hectares) within each survey polygon. We calculated the amount of older riparian forest based on maps used for monitoring of woodlands that have achieved structures commonly associated with mature, late-successional, and old-growth forests (Davis et al. 2015). Thus, site-specific older forest cover was variable by site and year, either remaining stationary due to lack of disturbances (e.g., timber harvest) or declining in response to disturbance, but never increasing since recruitment takes several decades (i.e., beyond the time scale of this study). We also included a covariate for time of day (classified as day [46.5% of surveys], crepuscular [10.5% of surveys], and night [43.0% of surveys] depending on hour relative to sunrise/sunset) on detection probability (θ) using a logit link function. We expected highest detection probabilities during crepuscular and nighttime because barred owls are known to hunt animals that are active nocturnally (Hamer et al. 2007, Bailey et al. 2009). Additional factors may be influencing model parameters; however, for the purposes of this application, we chose to present a simplified model structure using only the most influential covariates as demonstrated in previous analyses of barred owls (Hamer et al. 2007, Yackulic et al. 2012, 2014).

We estimated model parameters using a Bayesian approach with vague priors (see details in the simulation study and Metadata S1). Complete model details and JAGS code for this application is provided in Metadata S2. For each year, we also calculated the proportion of empty sites that barred owls colonized and the proportion of occupied sites where they went extinct as derived quantities using the latent abundance estimates for individual sites. Finally, we examined the ability of our model to recover parameter values by simulating 5000 datasets generated with the mean parameter values estimated from the case study. We then ran the barred owl model with each of the simulated datasets and evaluated the precision and bias of all parameters.

Application results

Application of our dynamic *N*-occupancy model to the barred owl dataset led to precise estimates of apparent survival (hereafter referred to as survival), annual per capita rates of population gains, local and regional abundances, and detection probabilities (Fig. 2). Individual detection probability was significantly higher during night (median = 0.17, 95% credible interval [95% CI] = 0.15–0.19) and crepuscular (median = 0.12, 95% CI = 0.10–0.15) periods than during daytime (median = 0.03, 95% CI = 0.02–0.04; Fig. 2a). As predicted a priori, annual survival probabilities were positively related to the total amount of older riparian forest cover (Fig. 2b). Annual barred owl survival ranged from 0.82 (95%

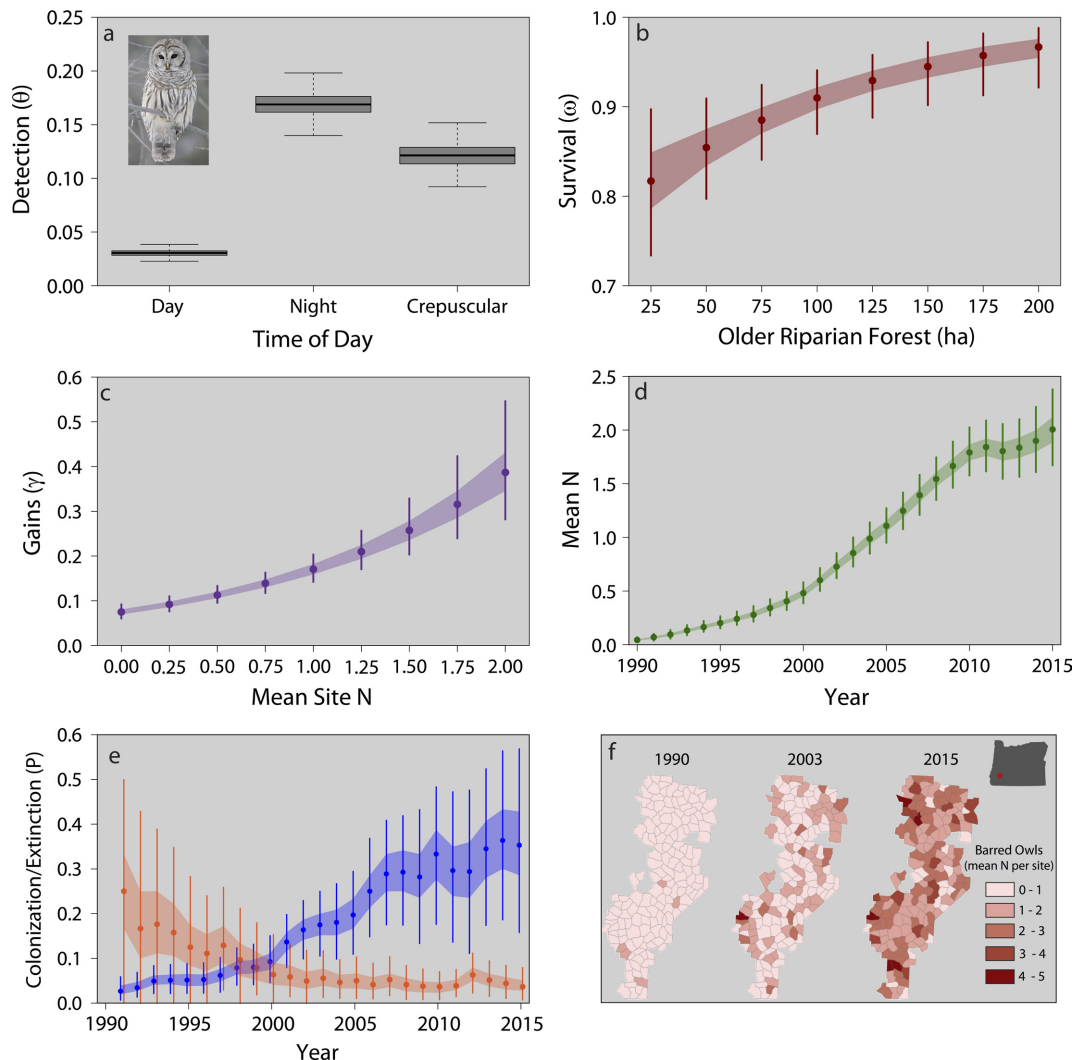


Fig. 2. Parameter estimates of: (a) individual-level detection probabilities, θ , according to time of day with medians (black lines in boxes), interquartile ranges (box), and ± 1.5 times the interquartile ranges shown (whiskers); (b) apparent survival, ω , relative to the amount of old riparian forest (hectares) within survey polygons; (c) gains, γ , relative to mean regional abundance across the study region in the previous year; (d) mean local abundance during 1990–2015; and (e) annual colonization (blue) and extinction (orange) probabilities over the study period. In b–e, vertical lines represent 95% credible intervals; shaded regions represent 50% credible intervals. Panel (f) shows the estimated mean abundance per site of barred owls within the Tyee study area (red star in inset; Douglas County, Oregon, USA) for three different time periods (1990, 2003, and 2015). Means were calculated from the estimated latent abundance distributions.

CI = 0.77–0.90) in areas with 25 ha of old riparian forest cover up to 0.97 (95% CI = 0.92–0.99) in areas with 200 ha. Our average estimate of barred owl survival ($\mu = 0.88$, 95% CI = 0.78–0.95) was comparable to estimates derived from radio-tracking barred owls over a 36-month period at a nearby site ($\mu = 0.92 \pm 0.04$ [SE]; Wiens et al. 2014).

Gains (recruitment/immigration) to the barred owl population were significantly and positively influenced by the previous year's regional abundance (Fig. 2c), suggesting that rapid population growth over the last

15 years has primarily been a result of increasing recruitment and/or immigration (Fig. 2d) coupled with high apparent survival. Rapid gains in barred owl numbers are consistent with studies suggesting high fecundity of barred owl pairs in the Pacific Northwest (Wiens et al. 2014). Increasing barred owl abundance over the study period has consequently led to declines in their extinction rates at local sites (Fig. 2e). Although our study area was relatively large, this focal population is likely not demographically closed because barred owl dispersal distances are also large. Thus, the effects of

regional abundance on dynamics may represent processes operating at a greater spatial scale than the study area (see Yackulic et al. 2012 for further discussion). Interestingly, our results suggest that barred owl population growth and colonization has slowed over the last 5 (Fig. 2d–e), potentially indicating that sites within this region are approaching saturation. A population will be at equilibrium when the number of individuals dying or emigrating out of the study area, $\sum_i N_i(1 - S_i)$, equals the number of individuals gained, $\sum_i G_i$. In the case of our model, we can consider that a population is near this point when $N_i(1 - \omega_{i,t}) = \gamma_i$. Although annual expected gains in the population are consistently higher than deaths/emigration, the proportion of sites with at least one detection has declined slightly since 2011, suggesting that the population may be stabilizing. Future analyses of the barred owl data should consider modeling population gains using a negative density component (e.g., a square term on density in γ_i), which will be possible with additional years of data if the population is at, or near, dynamic equilibrium.

Our dynamic N -occupancy model reveals a synchrony between regional densities and gains, as well as estimates of spatial variation in local abundances (Fig. 2f), which can help guide decisions about barred owl removal. Because sites within our study area were designated based on northern spotted owl space needs and because barred owls are known to require smaller home ranges (Hamer et al. 2007), it is not surprising that sites may harbor large numbers of barred owls. This implies that multiple barred owls may need to be removed before spotted owls are able to reclaim a site. The synchrony between regional density and gains suggests that barred owl removals will be most cost-effective in the long-term if conducted at a sufficient intensity and spatial scale to adequately lower regional densities. Future work incorporating additional covariates and interactions with spotted owls can help elucidate recent barred owl invasion characteristics (i.e., within last 5 yr) and potential changes in demographic rates of the two species.

Without a financially and logistically intensive mark-recapture study, our analysis revealed that barred owl population gains dramatically increased over the study period, survival rates were consistently high region-wide, and local abundances increased substantially and have only recently leveled off. Our case study simulation further demonstrated that we were able to recover estimated parameters with high precision and little to no bias (Appendix S2). Only the slope on the covariate for gamma (i.e., mean population in prior year) was slightly underestimated, resulting in less than a 0.1 difference in estimated gains across the full range of covariate values (and no important differences in model interpretation; Appendix S2). Estimating γ_i accurately is difficult because it depends on accurate estimation of site-level abundance, which becomes less precise at high local densities. By utilizing extensive detection/nondetection data instead of more costly and limited count or movement

data, we vastly expanded the spatiotemporal scope of inference that can be reasonably extrapolated across the region. Additionally, our model provides a more mechanistic approach to population monitoring than can be achieved using a standard occupancy framework by revealing patterns of site-level abundance across large spatial and temporal scales (Fig. 2f).

DISCUSSION

Our dynamic N -occupancy model allows researchers to produce unbiased and precise estimates of demographic rates across space and time using only detection/nondetection data. We demonstrate how site-specific estimates of abundance, population gains (i.e., recruitment/immigration), and apparent survival probability can be obtained by explicitly modeling detection at an individual, rather than species, level. Our model requires only repeated detection/nondetection data across spatial locations, data that are frequently collected when individuals of a target species cannot be easily detected, counted, or tracked. Occupancy data are typically collected at larger spatial scales than more traditionally labor-intensive count or mark-recapture data, which have previously been the only available data sources from which to obtain demographic estimates (Lebreton et al. 1992, Dail and Madsen 2011, Zipkin et al. 2014b). The dynamic N -occupancy model is the first to allow estimation of individual demographic rates from broad-scale detection/nondetection data, one of the most widely collected data types (MacKenzie 2005), allowing for comprehensive inference at unprecedented spatial extents.

As demonstrated by our simulation study, the accuracy and precision of demographic parameter estimates depend on the amount and quality of available data (Fig. 1). Our results illustrate the ability of the N -occupancy model to recover demographic parameters with as few as 25 sites; however, too few sites can lead to bias, particularly when detection is low (Appendix S1: Figs. S1–S4 top rows). Our model utilizes heterogeneity in detection to estimate site-level abundance (N_i), thus when N_i becomes large enough to make the probability of not detecting any individuals very small, the model will have difficulty estimating abundance and subsequently other demographic parameters with precision. For this reason, the dynamic N -occupancy model will perform best when sites harbor fairly low densities (e.g., pond-breeding amphibians, cooperative-breeding birds), particularly in situations where estimating population size is the primary goal or parameters are expressed as density-dependent rates.

As with standard occupancy models, more robust estimates result from a greater number of sampling locations (MacKenzie 2005, McKann et al. 2013); thus, the dynamic N -occupancy model will be most useful when there are ≥ 25 surveyed sites (assuming at least 10 years of data; Fig. 1). In Appendix S1, we demonstrate that with

75 survey sites, all estimated parameters were unbiased across the complete range of parameter space examined. However, precision in parameter estimates still varied across the parameter space (Appendix S1). Our barred owl application consisted of 26 survey years, but this longevity is often difficult to achieve. Simulation results demonstrate that five yr of data are capable of producing accurate estimates of demographic rates (Appendix S3). However, as the length of the time series decreases, additional sites are required to achieve reasonable estimates (minimum recommendation of at least 75 sites for 5 yr of data) and results are likely to be less precise or potentially biased than cases with the same total number of sampling events but more years (e.g., long time series increase precision better than adding more sites within a shorter time series; Zipkin et al. 2014b). We suggest that researchers using the dynamic *N*-occupancy model explore the accuracy and precision of their analyses using the model structure and data availability specific to their study.

Identifiability issues prevented the independent estimation of recruitment and immigration in this study, but incorporating stage- or age-structured data (i.e., multi-state occupancy) into this model could allow for the separation of these two parameters in future analyses (e.g., Zipkin et al. 2014a). Our dynamic *N*-occupancy model offers a much-needed framework for estimating demographic rates and local abundances in situations where only detection/nondetection data are available (e.g., many citizen science programs), facilitating exciting possibilities for quantifying fine-scale population dynamics from occupancy data collected by large-scale monitoring programs.

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LITERATURE CITED

- Adams, M. J., et al. 2013. Trends in amphibian occupancy in the United States. *PLoS ONE* 8:e64347.
- Bailey, L. L., J. A. Reid, E. D. Forsman, and J. D. Nichols. 2009. Modeling co-occurrence of northern spotted and barred owls: accounting for detection probability differences. *Biological Conservation* 142:2983–2989.
- Ball, L. C., P. F. Doherty, and M. W. McDonald. 2005. An occupancy modeling approach to evaluating a Palm Springs ground squirrel habitat model. *Journal of Wildlife Management* 69:894–904.
- Crozier, M. L., M. E. Seamans, R. J. Gutiérrez, P. J. Loschl, R. B. Horn, S. G. Sovern, and E. D. Forsman. 2006. Does the presence of Barred Owls suppress the calling behavior of Spotted Owls? *Condor* 108:760–769.
- Dail, D., and L. Madsen. 2011. Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics* 67:577–587.
- Davis, R. J., J. L. Ohmann, R. E. Kennedy, W. B. Cohen, M. J. Gregory, Z. Yang, H. M. Roberts, A. N. Gray and T. A. Spies. 2015. Northwest forest plan—the first 20 years (1994–2013): status and trends of late-successional and old-growth forests. Gen. Tech. Rep. PNW-GTR-911: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Diller, L. V., K. A. Hamm, D. A. Early, D. W. Lamphear, K. M. Dugger, C. B. Yackulic, C. J. Schwarz, P. C. Carlson, and T. L. McDonald. 2016. Demographic response of northern spotted owls to barred owl removal. *Journal of Wildlife Management* 80:691–707. <http://dx.doi.org/10.1002/jwmg.1046>
- Dugger, K. M., et al. 2016. The effects of habitat, climate, and Barred Owls on long-term demography of Northern Spotted Owls. *Condor* 118:57–116.
- Gutiérrez, R., M. Cody, S. Courtney, and A. B. Franklin. 2007. The invasion of barred owls and its potential effect on the spotted owl: a conservation conundrum. *Biological Invasions* 9:181–196.
- Hamer, T. E., E. D. Forsman, and E. M. Glenn. 2007. Home range attributes and habitat selection of barred owls and spotted owls in an area of sympatry. *Condor* 109:750–768.
- Hines, J., J. Nichols, J. Royle, D. MacKenzie, A. Gopalaswamy, N. S. Kumar, and K. Karanth. 2010. Tigers on trails: occupancy modeling for cluster sampling. *Ecological Applications* 20:1456–1466.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Livezey, K. B. 2009. Range expansion of Barred Owls, part I: chronology and distribution. *American Midland Naturalist* 161:49–56.
- MacKenzie, D. I. 2005. What are the issues with presence-absence data for wildlife managers? *Journal of Wildlife Management* 69:849–860.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2005. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier, San Diego, California, USA.
- McKann, P., B. R. Gray, and W. E. Thogmartin. 2013. Small sample bias in dynamic occupancy models. *Journal of Wildlife Management* 77:172–180.
- Murray, R. G., V. D. Popescu, W. J. Palen, and P. Govindarajulu. 2015. Relative performance of ecological niche and occupancy models for predicting invasions by patchily-distributed species. *Biological Invasions* 17:2691–2706.
- Pellet, J., and B. R. Schmidt. 2005. Monitoring distributions using call surveys: estimating site occupancy, detection probabilities and inferring absence. *Biological Conservation* 123: 27–35.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the Third International Workshop on Distributed Statistical Computing. R Project for Statistical Computing, Vienna, Austria.
- Royle, J. A. 2004. N-Mixture models for estimating population size from spatially replicated counts. *Biometrics* 60: 108–115.

- Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84:777–790.
- Tingley, M. W., and S. R. Beissinger. 2009. Detecting range shifts from historical species occurrences: new perspectives from old data. *Trends in Ecology and Evolution* 24:625–633.
- Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. P. Possingham. 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecological Applications* 13:1790–1801.
- Wiens, J. D., R. G. Anthony, and E. D. Forsman. 2014. Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon. *Wildlife Monographs* 185:1–50.
- Yackulic, C. B., J. Reid, R. Davis, J. E. Hines, J. D. Nichols, and E. Forsman. 2012. Neighborhood and habitat effects on vital rates: expansion of the Barred Owl in the Oregon Coast Ranges. *Ecology* 93:1953–1966.
- Yackulic, C. B., J. Reid, J. D. Nichols, J. E. Hines, R. Davis, and E. Forsman. 2014. The roles of competition and habitat in the dynamics of populations and species distributions. *Ecology* 95:265–279.
- Zipkin, E. F., T. S. Sillett, E. H. C. Grant, R. B. Chandler, and J. A. Royle. 2014a. Inferences about population dynamics from count data using multi-state models: a comparison to capture-recapture approaches. *Ecology and Evolution* 4:417–426.
- Zipkin, E. F., J. T. Thorson, K. See, H. J. Lynch, E. H. C. Grant, Y. Kanno, R. B. Chandler, B. H. Letcher, and J. A. Royle. 2014b. Modeling structured population dynamics using data from unmarked individuals. *Ecology* 95: 22–29.

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