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6 **Integrating count and detection-nondetection data**  
7 **to model population dynamics**

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27 Running Head: Integrated model for unmarked data

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29 **Abstract**

30 As the spatial and temporal scale of ecological research expands, there is increasing need for  
31 methods that integrate multiple data types into a single analytical framework. Current work on  
32 this topic primarily focuses on combining capture-recapture data from marked individuals with  
33 other data types into integrated population models. Yet, studies of species distributions and  
34 trends often rely on data from unmarked individuals across broad scales where local abundance  
35 and environmental variables may vary. We present a modeling framework for integrating  
36 detection-nondetection and count data into a single analysis to estimate population dynamics,  
37 abundance, and individual detection probabilities during sampling. Our dynamic population  
38 model assumes that site-specific abundance can change over time according to survival of  
39 individuals and gains through reproduction and immigration. The observation process for each  
40 data type is modeled by assuming that every individual present at a site has an equal probability  
41 of being detected during sampling processes. We examine our modeling approach through a  
42 series of simulations illustrating the relative value of count versus detection-nondetection data  
43 under a variety of parameter values and survey configurations. We also provide an empirical  
44 example of the model by combining long-term detection-nondetection data (1995-2014) with  
45 newly collected count data (2015-2016) from a growing population of barred owls (*Strix varia*)  
46 in the Pacific Northwest to examine the factors influencing population abundance over time. Our  
47 model provides a foundation for incorporating unmarked data within a single framework, even in  
48 cases where sampling processes yield different detection probabilities. This approach will be  
49 useful for survey design and to researchers interested in incorporating historical or citizen  
50 science data into analyses focused on understanding how demographic rates drive population  
51 abundance.

52 **Keywords:** Dail-Madsen model, Detection probability, Integrated population model, N-mixture  
53 model, Occupancy, Unmarked data

54  
55 **Introduction**

56 As the focus in ecology and conservation biology shifts towards broader spatial extents  
57 (Allen and Hoekstra 2015), making use of data from multiple sources is increasingly necessary  
58 as no one dataset can adequately characterize a species across its complete geographic range  
59 (Marra et al. 2015). This is particularly true when interest lies in assessing population-level

60 consequences of changing demography relative to climate and/or landscape covariates (Robinson  
61 et al. 2014). One method for combining data sources is through the use of integrated population  
62 models, which estimate population abundance and demographic rates through the joint analysis  
63 of two or more datasets within a single framework (Brooks et al. 2004). Compared to separate  
64 analyses of each data type, integrated population models provide inference on a greater number  
65 of parameters, increased precision, and more accurate accounting of uncertainty (Schaub and  
66 Abadi 2011). To date, integrated population models have focused on combining capture-  
67 recapture data with indices of abundance and other data types (e.g., telemetry, dead-recovery,  
68 reproduction surveys; Abadi et al. 2012, Wilson et al. 2016, Zipkin and Saunders In review).  
69 Capture-recapture data are collected by following marked (naturally or with tags) individuals  
70 through time, which allows for explicit estimation of population vital rates, and is arguably the  
71 most informative approach for tracking populations (Lebreton et al. 1992). Yet capture-recapture  
72 data are expensive and time-intensive to collect and necessarily limited in spatial extent because  
73 of practical difficulties. Furthermore, some species/taxa (e.g., invertebrates) do not readily allow  
74 for capture-recapture sampling techniques.

75         Recently developed approaches allow for the estimation of population abundance and  
76 demographic rates from “unmarked” data types in which individuals are not identified (Chandler  
77 and King 2011, Dail and Madsen 2011, Rossman et al. 2016, Zipkin et al. 2014b). These models,  
78 collectively referred to as dynamic N-mixture models, require repeated surveys (over a short  
79 time frame when the population is assumed to be closed) across spatial locations to account for  
80 detection errors during sampling. This set of surveys is then conducted over successive time  
81 periods to estimate annual or seasonal population abundance (e.g., robust design; Dail and  
82 Madsen 2011). Abundance changes through time by birth/death and immigration/emigration,  
83 which is described through processes of local survival and population gains (recruitment and  
84 immigration) within the N-mixture modeling framework. While unmarked data do not provide  
85 the same level of detail on demography as capture-recapture data (Zipkin et al. 2014a), they are  
86 cheaper and easier to obtain. Count data, along with other less intensive data types such as  
87 detection-nondetection data, are thus particularly valuable in projects with large spatial or  
88 temporal extents and in cases where it is difficult or impossible to track individuals.

89         Here we present an integrated modeling approach to combine unmarked data types. We  
90 analyze count and detection-nondetection time series data within a single model, assuming

91 abundance changes according to biological processes describing survival and gains under the  
92 open-population dynamic N-mixture model (Dail and Madsen 2011; Dorazio 2014). Our  
93 approach thus allows for estimation of demographic rates (i.e., survival and recruitment) while  
94 explicitly accounting for detection errors during data collection. We show the utility of our  
95 modeling approach through a series of simulations illustrating the relative contributions of count  
96 versus detection-nondetection data under a variety of parameter values and survey  
97 configurations. We also demonstrate how the model can be used with empirical data through an  
98 analysis of a barred owl (*Strix varia*) population in the Oregon Coast Ranges, USA. Including  
99 count and detection-nondetection data in a single model allows for more accurate and precise  
100 estimates of population abundance over time, even in cases where detection probabilities differ  
101 by survey type or data are collected at non-overlapping spatial locations or time periods. Our  
102 model provides a framework for combining many types of unmarked data into a single analysis  
103 and will be useful in investigating the optimal design of future surveys as well as providing  
104 capabilities to incorporate historical or citizen science data with more rigorously collected  
105 scientific data.

106

## 107 **Model description**

### 108 *Biological state process*

109 We incorporate count and detection-nondetection data into a single model by combining  
110 dynamic N-mixture (Dail and Madsen 2011, Royle 2004) and occupancy (MacKenzie et al.  
111 2003) modeling frameworks. To do this, we model the latent demographic rates (i.e., the state  
112 process) by assuming that population abundance  $N_{j,t}$  (which is observed imperfectly) at a site  $j$  at  
113 time step  $t$  is conditional on abundance at  $j$  in the previous time step (Dail and Madsen 2011).  
114 We consider an annual cycle but the time step can be modified based on a species' dynamics.  
115 The change in  $N_{j,t}$  between  $t - 1$  and  $t$  is modeled by estimating the number of individuals that  
116 survive and remain at a site ( $S_{j,t}$ ) and those that are gained to a site  $j$  either by recruitment or  
117 immigration ( $G_{j,t}$ ). These quantities are expressed as follows:

$$S_{j,t} \sim Bin(N_{j,t-1}, \omega)$$

$$G_{j,t} \sim Pois(\gamma)$$

118 where  $\omega$  is the apparent annual survival probability of individuals and  $\gamma$  is the expected number  
119 of individuals that are gained to  $j$  between  $t - 1$  and  $t$ . Dail and Madsen (2011) present a density

120 independent process of population gains; yet this assumption can be modified to include density  
121 dependent recruitment when data are available (Bellier et al. 2016; Zipkin et al. 2014a). The  
122 total population abundance at  $j$  in time  $t > 1$  is:

$$123 \quad N_{j,t} = S_{j,t} + G_{j,t}.$$

124 The state process is initialized during the first year of sampling ( $t = 1$ ) by modeling abundance  
125 at each site,  $N_{j,1}$ , according to a Poisson distribution with an expected count of  $\lambda$ :

$$126 \quad N_{j,1} \sim \text{Pois}(\lambda).$$

127 Initial abundance can also be modeled with more flexible distributions (e.g., negative binomial)  
128 if site-specific count data do not fit the Poisson assumption of equal mean and variance  
129 (Hostetler and Chandler 2015). Covariates and/or spatially correlated random effects can be  
130 added to any of the parameters ( $\omega, \gamma, \lambda$ ) using appropriate link functions to incorporate relevant  
131 factors that influence population dynamics across spatial locations or through time.

132 Many population analyses focus on evaluating the extinction risk and resiliency of local  
133 sites. The survival and gains parameters can be used to derive the colonization probability of  
134 unoccupied sites and the extinction probability of occupied sites, quantities that are frequently  
135 estimated using dynamic occupancy models. The colonization probability of an unoccupied site,  
136  $\varphi_{j,t}$ , is the probability that at least one individual is gained to  $j$  in year  $t$ , i.e.,  $1 - P[G_{j,t} = 0]$ ,  
137 which can be derived from the probability mass function of the Poisson distribution for the gains  
138 equation:

$$139 \quad \varphi_{j,t} = 1 - e^{-\gamma}.$$

140 The extinction probability,  $\epsilon_{j,t}$ , of an occupied site is the probability that all individuals die  
141 between  $t - 1$  and  $t$  and that no new individuals immigrate to the site, i.e.,  $P[S_{j,t} = 0] \cap$   
142  $P[G_{j,t} = 0]$ :

$$143 \quad \epsilon_{j,t} = (1 - \omega)^{N_{j,t}} \cdot e^{-\gamma}.$$

144 As a result, extinction rates differ among sites dependent upon local abundance and any  
145 covariates on  $\omega$  or  $\gamma$ . More generally, metapopulation and colonization/extinction dynamics arise  
146 from local demography at the individual level (Ovaskainen and Hanski 2004), processes that  
147 cannot readily be accommodated in typical abundance or occupancy models that do not  
148 incorporate mechanism (e.g., survival and recruitment) explicitly.

149

150 *Observation process*

151 The demographic parameters and the true underlying abundance  $N_{j,t}$  cannot typically be  
152 observed directly. Instead, data are collected on  $N_{j,t}$  at each location  $j$  in each year  $t$  according to  
153 one of two sampling processes: 1) counts of individuals (Royle 2004) or 2) detection-  
154 nondetection of at least one individual of the species (Royle and Nichols 2003). In both cases,  
155 sites are visited within each year on  $K > 1$  occasions over a timeframe during which the  
156 population is assumed to be closed (i.e., abundance is constant). We note that if detection  
157 probabilities are the same across all sites, then only a subset of sites need to be sampled  
158 repeatedly ( $K_j \geq 1$ ). Count data are collected by enumerating all individuals encountered during  
159 a fixed survey time interval while detection-nondetection (occupancy) data are collected by  
160 recording simply whether or not (at least one individual of) the species was detected. Count and  
161 detection-nondetection data can be collected through point counts, transect walks, or other  
162 techniques (MacKenzie et al. 2006, Royle and Dorazio 2008). The key feature of both data types  
163 is that the number of individuals counted,  $n_{j,t,k}$ , at a site  $j$  in year  $t$  during sampling replicate  $k$  or  
164 the observed occupancy status of a site,  $y_{j,t,k}$ , is subject to incomplete detection. That is, not  
165 every individual is detected when collecting count data, such that  $n_{j,t,k} \leq N_{j,t}$ . Similarly, a  
166 species that is present at a site  $j$  could incorrectly be recorded as absent if none of the  $N_{j,t}$   
167 individuals are detected during sampling replicate  $k$ . It is therefore necessary to model the  
168 relationship of the data to the true (unobservable) abundance or occupancy status. In the case of  
169 the count data,  $n_{j,k,t} = 0, 1, 2, \dots$ , we model the observation process as:

$$n_{j,k,t} \sim \text{Bin}(N_{j,t}, p)$$

170 where  $p$  is the detection probability of each individual at each survey event  $k = 1, 2, \dots, K$  (Royle  
171 2004). In the case of the detection-nondetection data, we assume that the probability of recording  
172 a detection ( $y_{j,t,k} = 1$ ) is the probability that at least one individual is observed. Thus the  
173 detection process for the detection-nondetection data can be expressed as (Royle and Nichols  
174 2003, Rossman et al. 2016):

$$y_{j,t,k} \sim \text{Bern}(1 - (1 - p)^{N_{j,t}}).$$

175  
176 In this basic model, the detection probability of individuals ( $p$ ) is assumed to be equal across the  
177 count and detection-nondetection data (although we relax this assumption during simulations  
178 below). When detection is equal across survey types, repeated sampling of sites with detection-

179 nondetection data is not necessary because  $p$  can be inferred from the count data alone. Thus, our  
180 modeling framework could be particularly useful for utilizing historical detection-nondetection  
181 data or data collected in remote locations where repeated sampling is challenging or nonexistent  
182 (assuming that data are collected under a randomized sampling design, absence data is recorded,  
183 and detection probabilities are the same for both survey types; Dorazio 2014). As with the  
184 demographic parameters, detection probability can be indexed by site or year to include relevant  
185 covariates that account for variation in the sampling process across time or space. An implicit  
186 assumption of our modeling framework, and integrated analyses generally, is that the spatial unit  
187 of sites is similar across survey types (but we demonstrate an example of how to reconcile data  
188 from different spatial units in the application section). Additionally, both detection probability  
189 and the demographic parameters are assumed to be equal for all individuals during each survey  
190 event (i.e., no individual heterogeneity) and detection of every individual is independent (Royle  
191 and Nichols 2003, Royle 2004). This assumption could be modified to account for differences in  
192 parameter values across life stages (or other subgroups of the population) if data are available  
193 (Zipkin et al. 2014b).

194

### 195 **Simulation study design**

196 We developed a series of simulations to assess the utility of our combined count and  
197 occupancy model to estimate demographic rates and population abundance and to determine  
198 optimal sampling schemes in cases where parameter values vary across sampling locations (e.g.,  
199 according to covariates) and/or sampling methodology (e.g., differences in detection). We  
200 examined the accuracy and precision of our model over a range of parameter values and  
201 sampling protocols using at least 1000 simulated datasets for all scenarios and number of  
202 surveyed sites. For each analysis and parameter combination, we generated ten years of latent  
203 population abundances at individual sites (using parameter values specific to each scenario),  
204 during which we assumed abundance changed according to the process described in the model  
205 description section. Each of the sites was then “surveyed” three times annually, assuming  
206 independence and closure within intra-annual sampling events, according to either a count- or  
207 occupancy-based protocol (number of sites with a particular sampling protocol varied among  
208 simulation scenarios). We then analyzed the simulated data with the joint model using a  
209 Bayesian analysis with Markov chain Monte Carlo in the programs R and JAGS (Plummer

210 2003). We specified vague priors for all parameters ( $\omega$ ,  $\gamma$ ,  $\lambda$ ,  $p$  as well as any additional  
211 parameters specified below). Model code and implementation details for the simulation studies  
212 are provided in Data S1.

### 213 214 *Accuracy and precision of the basic model*

215 We determined the accuracy and precision of the basic model under a wide range of  
216 parameter values and across a realistic range of possible count/occupancy site combinations. To  
217 that end, we generated datasets by randomly selecting parameter values from the following  
218 distributions:  $\lambda \sim U(0.5,3)$ ,  $\omega \sim U(0,1)$ ,  $\gamma \sim U(0,2.5)$ ,  $p \sim U(0,1)$ . These distributions cover  
219 the complete parameter space for survival and detection probabilities and represent conditions  
220 for which site abundance and occupancy is likely to vary among sites. For example, we set an  
221 upper bound of 2.5 individuals for  $\gamma$  (expected number of recruits/immigrants gained annually  
222 per site) because site-specific population abundance becomes very high – leading to no  
223 unoccupied sites – when the expected number of individuals gained to sites is large. In such  
224 situations, collection of detection-nondetection data would be uninformative. Parameters were  
225 drawn independently to guarantee ample coverage across the specified parameter space. We  
226 examined the benefits of combining either 0, 25, 75, or 150 sites with detection-nondetection  
227 data to either 5, 15, or 30 sites with count data. For each count/occupancy site combination, we  
228 generated 5000 datasets to ensure that a sufficiently wide range of possible parameter  
229 combinations was included in the results.

### 230 231 *Determining optimal sampling schemes*

232 Combining count and detection-nondetection data will be particularly useful in cases  
233 where it is difficult to obtain sufficient data across a covariate space using a single sampling  
234 protocol. For this simulation, we assume that a covariate influences the survival probability of  
235 individuals across spatial locations as follows:

$$236 \quad \text{logit}(\omega_j) = \beta_0 + \beta_1 \cdot \text{covariate}_j.$$

237 For simplicity, we assume that  $\beta_1$  is positive and thus survival increases as the value of the  
238 covariate increases. We envision a scenario where either detection-nondetection or count data  
239 could be added to existing data to improve precision in parameter estimates and examined four  
240 such cases: 1) both count and detection-nondetection data are available over the complete range



241 of the covariate ( $-3 < covariate_j < 3$ ); 2) count data are collected at sampling locations over a  
242 range where survival, and thus abundance, is high ( $1 < covariate_j < 3$ ) and detection-  
243 nondetection data are collected at locations where survival, and thus abundance, is low ( $-3 <$   
244  $covariate_j < 1$ ); 3) count data are collected at locations with average survival probabilities  
245 ( $-1 < covariate_j < 1$ ) and detection-nondetection data are collected at locations where  
246 survival is either high ( $covariate_j > 1$ ) or low ( $covariate_j < -1$ ); and 4) both count and  
247 detection-nondetection data are available over a subset of the range of the covariate, where  
248 survival is high ( $1 < covariate_j < 3$ ). We generated 1000 datasets for each of these scenarios  
249 using the following parameter values:  $\lambda = 4$ ,  $\beta_0 = 0.5$ ,  $\beta_1 = 0.7$ ,  $\gamma = 2$ ,  $p = 0.5$  and assumed  
250 a fixed number of 40 sites with count data and 100 with detection-nondetection data.

251

### 252 *Combining data sources when detection probabilities differ*

253 We have so far considered scenarios where detection probabilities are equal for  
254 individuals across both count- and occupancy-based sampling schemes. The degree to which this  
255 assumption is reasonable depends on individual survey protocols. For example, the detection  
256 probability of individuals may differ by surveys because of the duration of the collection process,  
257 the area surveyed, or the manner in which individuals are detected (e.g., audial versus visual  
258 surveys). The best approach for dealing with differences in detection is to include relevant  
259 covariates (MacKenzie et al. 2006; Royle and Dorazio 2008). However, in some situations the  
260 baseline detection for individuals may be different enough that each survey type requires  
261 independent estimation of the detection probability. We explored both scenarios where this could  
262 be true: 1) detection probability of individuals is higher in the count data ( $p_{count} = 0.5$ ) than in  
263 the detection-nondetection data ( $p_{occ} = 0.3$ ); and 2) detection probability is lower in the count  
264 data ( $p_{count} = 0.3$ ) than in the detection-nondetection data ( $p_{occ} = 0.5$ ). We also examined the  
265 situation in which detection probability differs between sampling protocols but is incorrectly  
266 modeled assuming that they are equivalent (i.e.,  $p_{count} = p_{occ}$ ). We generated 1000 datasets for  
267 each of these scenarios across a range of count (5, 15, 30) and occupancy (25, 75, 150) site  
268 combinations using the following demographic parameter values:  $\lambda = 1$ ,  $\omega = 0.7$ ,  $\gamma = 1.5$ .

269

### 270 **Simulation study results**

271 Simulation results indicate that our model combining unmarked data types can provide  
272 accurate estimates of demographic rates, population abundance, and individual detection  
273 probabilities across the comprehensive range of parameter values that we examined (Figures 1-  
274 3). Precision in parameter estimates varied by the amount of data included in analyses and not  
275 surprisingly, increased with additional data (Figure 1; Appendix S1, which shows results from  
276 the basic simulation with only five years of data). Count data undoubtedly inform parameter  
277 values more efficiently than detection-nondetection data (i.e., Figure 1, comparison across panel  
278 colors). However, the addition of a small number of occupancy sites (e.g., 25) to existing count  
279 data improved precision of parameters and abundance estimates in all scenarios, especially when  
280 the amount of available count data was relatively low (Figure 1, grey and blue panels; Appendix  
281 S1).

282 Combining count and detection-nondetection data was especially useful in simulations  
283 with a covariate on survival, particularly if a single data type was not available throughout the  
284 complete range of the covariate (Figure 2; Appendix S2). Accurate and precise estimation of a  
285 covariate effect depends on whether the available data span the complete range of the covariate  
286 value and not on the data type, whether generated from count or occupancy protocols (Figure 2,  
287 blue boxes compared to red boxes). These results demonstrate that the inclusion of detection-  
288 nondetection data in addition to count data (or count data in addition to detection-nondetection  
289 data) allows for estimates of demographic rates and abundance in locations with only detection-  
290 nondetection data while simultaneously improving precision on estimates of the covariate effect  
291 in areas with count data.

292 Our model produces accurate estimates of demographic rates and abundance even in  
293 cases where detection varies by the data collection method (Figure 3, blue boxes in light grey  
294 panels; Appendix S3). This is true regardless of whether individual detection probability is  
295 higher with either count- or occupancy-based protocols. The precision of parameter estimates,  
296 however, depends on the amount of available data; increasing the number of parameters requires  
297 more data for comparable precision (Appendix S3 compared to Figure 1). For this parameter  
298 combination, population gains are underestimated while survival probabilities are overestimated  
299 when we incorrectly assume that detection is equal across sampling methods when in fact it is  
300 different (Figure 3, red boxes in dark grey panels; Appendix S3). Our simulation results indicate  
301 that abundance is overestimated (Figure 3, dark red boxes) when detection in the detection-

302 nondetection data is higher than that in the count data and underestimated in the reverse situation  
303 (Figure 3, light red boxes), likely due to the inclusion of more occupancy than count sites. Thus,  
304 when detection is underestimated at the majority of sites, abundance is naturally overestimated  
305 (with the reverse also being true; Royle and Nichols 2003). The degree to which parameter  
306 biases, caused by mis-specifying the detection process, are significant will depend on the  
307 magnitude of the differences in detection probabilities among sampling protocols and the relative  
308 amount of sites surveyed for each data type. Additional simulations across a wider parameter  
309 space would allow for a more nuanced understanding of the consequences of mis-specifying the  
310 detection process.

311

### 312 **Application to empirical data**

313 We applied our modeling framework to survey data collected on an expanding population  
314 of barred owls in a 1,692 km<sup>2</sup> region in the central Oregon Coast Ranges, over a period of two  
315 decades. Barred owls were historically limited to eastern North American forests, but their range  
316 has expanded into the Pacific Northwest over the last century with local densities increasing  
317 dramatically over the last decade (Dugger et al. 2016; Yackulic et al. 2012). There is  
318 considerable interest in understanding the population dynamics of barred owls because of their  
319 potential negative impact on threatened northern spotted owls (*Strix occidentalis caurina*) and  
320 other native wildlife (Holm et al. 2016, Wiens et al. 2014, Yackulic et al. 2014). Detection-  
321 nondetection data on barred owls were collected incidentally within spotted owl surveys from  
322 1995-2014 (Lint et al. 1999). Spotted owl surveys followed a standardized protocol (Lint et al.  
323 1999) and were focused on 106 historical breeding territories (e.g., sites), which averaged 9.9  
324 km<sup>2</sup> in size (Fig. 4a). During annual surveys of spotted owls, observers visited each site up to  
325 eight times during the breeding season (March – August) and additionally recorded whether  
326 territorial barred owls (individuals or pairs) were detected.

327 A new count-based survey protocol, targeting barred owls, was initiated in 2015 as part  
328 of a broader study to improve estimation of barred owl abundances and examine the effects of  
329 experimental removals on the population demography of northern spotted owls (Wiens et al.  
330 2011, Diller et al. 2016). The experiment included locations where barred owls were either  
331 removed (treatments, about a third of the study area) or not (controls), but for the purposes of  
332 this study we restricted estimates to pre-treatment (2015) survey data collected on both areas,

333 and post-treatment survey data on the control area only (i.e., to avoid confounding effects in our  
334 analysis of barred owl removals in treatment areas). The barred owl surveys employed a standard  
335 design in which a grid of 5 km<sup>2</sup> hexagons were overlaid to include historical breeding territories  
336 of spotted owls (Figure 4a). Each of these hexagonal sites were surveyed up to three times during  
337 the breeding season. During each survey, observers used an amplified megaphone (Wildlife  
338 Technologies, Manchester, N.H.) to broadcast digitally recorded barred owl calls at established  
339 call points that provided complete coverage of the site. All territorial pairs and single owls were  
340 recorded. Barred owl individuals were assumed to be part of a territorial pair when: (1) both  
341 sexes were observed within 400 m of each other on the same visits; or (2) at least one adult was  
342 observed with young (Wiens et al. 2011).

343 While our simulation study focused on instances in which detection-nondetection and  
344 count data come from spatially distinct sites, our modeling framework can also be used in cases  
345 where the two data types are collected in the same locations in different time periods. Sites can  
346 be alternatively sampled using either occupancy- or count-based protocols as long as they are  
347 independent and the basic assumptions outlined in the model description section are met. In the  
348 case of this study, we needed to standardize the data from the two survey methods in which sites  
349 overlapped, but where barred owls were sampled at different spatial scales (Figure 4a) in order to  
350 combine the historical barred owl detection-nondetection data with the newer count data. To do  
351 this, we reassigned each of the counts of territorial pairs detected within the 5 km<sup>2</sup> hexagonal  
352 sites (collected during barred owl-specific surveys in 2015 and 2016) to the larger spotted owl  
353 survey sites (i.e., historical territories) using the GPS coordinates of each pair observation. As a  
354 result, the 106 sites used for our analysis were defined according to the historical survey design,  
355 from which most of the data originate, and the finer-resolution count data were reconfigured to  
356 fit within that framework. Within our model, we allowed detection probabilities to differ  
357 between sampling schemes because of the very different spatial scales and protocols used for the  
358 surveys. In the case of the occupancy data, we assumed that detection of individuals ( $p_{occ}$ ) was  
359 constant across sites and years as data were all collected by trained observers in the early  
360 morning. However, we specified the detection process for the count data ( $p_{count}$ ) using the  
361 proportion of the total area of the historical site  $j$  that was surveyed during replicate  $k$  in year  $t$ ,  
362  $area_{j,k,t}$ , as an offset with the *cloglog* link function:

$$363 \quad cloglog(p_{count,j,k,t}) = \alpha_0 + \log(area_{j,k,t}).$$

364 Thus, if a given count-based sampling event only covered half the area of the larger occupancy  
365 site, we recorded 0.5 for the offset on detection. Similarly, if a hexagon count site overlapped  
366 more than one historical occupancy site, only the proportion of that hexagon that overlapped the  
367 focal occupancy site was used. The *cloglog* link function is designed for encounter-  
368 nonencounter data given a Poisson intensity function, which arises in our model due to a Poisson  
369 recruitment process and a Bernoulli survival process. It has the useful property that, given low  
370 area-swept, a doubling of area-swept results in a doubling of encounter probability, and was  
371 consequently a natural choice for our analysis.

372 We assumed that the barred owl population was closed to changes within years but that  
373 local site-level abundance could change annually through survival and gains. We included a  
374 covariate on the annual apparent survival probability of individuals based on area of older  
375 (approx.  $\geq 80$  yr.) coniferous forest patches (Davis et al. 2015) within each site (using the same  
376 approach as in the simulation study). This covariate was calculated annually and, due to low  
377 levels of recent older forest disturbance and the slow rate of forest succession within the study's  
378 time frame, was fairly constant across most sites. Finally, recent evidence suggests that site-level  
379 gains in abundance may be dependent on the total regional population size as barred owls are  
380 exceptionally good at colonizing new sites (Yackulic et al. 2012, 2014). As such, we included a  
381 covariate on the gains parameter,  $\gamma$ , to account for a potential effect of regional population size:

$$\log(\gamma_t) = \delta_0 + \delta_1 \cdot \bar{N}_{t-1} + \delta_2 \cdot \bar{N}_{t-1}^2$$

382 where  $\bar{N}_{t-1}$  is the average abundance of all sites in year  $t - 1$ , which we normalized by  
383 subtracting 1 (a value that was close to the average site-specific abundance over the two decades  
384 of the study). We standardized all of the covariate data (e.g., forest cover) and analyzed the  
385 model using the programs R and JAGS, assuming uninformative prior distributions for each of  
386 the parameters (see Appendix S4 for model code and implementation details).

387 Model results show that the barred owl population grew substantially over the course of  
388 the survey period from a mean site-specific value of 0.13 (95% CI: [0.06, 0.48]) territorial owls  
389 (individuals and pairs) in 1995 to 7.5 (95% CI: [4.26, 11.53]) in 2016 (see Table E1 for a  
390 complete list of parameter estimates). This increase can be largely attributed to a positive density  
391 dependent effect on population gains,  $\gamma$  (Figure 4b). We estimated a significant positive effect of  
392 mean regional abundance on the expected number of territorial owls gained to sites annually  
393 (mean  $\delta_1$ : 0.59; 95% CI: [0.41, 0.78]) that did not decline when abundance was high (mean  $\delta_2$ : -

394 0.02; 95% CI: [-0.06, 0.02]; Figure 4b), suggesting that the population has not yet saturated the  
395 study region. Annual survival probabilities were quite high (average range: 0.86-0.93) and  
396 increased with the amount of older coniferous forest cover available within a site (Figure 4c).  
397 The intercepts for the  $\gamma$  and  $\omega$  parameters were negatively correlated (-0.55), although this is not  
398 unexpected as survival and gains are the only processes by which abundance can change within  
399 the model structure. Estimates of annual survival, and relationships with forest conditions, were  
400 strikingly similar to those derived from more intensive (and costly) studies of radio-marked  
401 individuals conducted in the region (Wiens et al. 2014). We used the parameter estimates and our  
402 derived equations to calculate annual colonization and extinction probabilities (Figure 4d).  
403 Colonization, or the probability that an unoccupied site becomes occupied, increased steadily  
404 over the time frame of the survey from a low of 0.14 (95% CI: [0.10, 0.17]) in 1996 to a high of  
405 0.90 (95% CI: [0.81, 0.96]) in 2016. Site extinction probabilities were fairly low throughout the  
406 two decade period, averaging 0.07 in 1996 (95% CI: [0.00, 0.14]) and declining to practically  
407 zero by 2016. Not surprisingly, barred owl detection probabilities were much higher during the  
408 count surveys as compared to the detection-nondetection surveys and increased with the area  
409 sampled (Figure 4e).

## 410 **Discussion**

411 Estimating demographic rates, population abundance, and trends is a universal objective  
412 in ecology and is necessary to inform population management. Capture-recapture data of marked  
413 individuals is the gold standard because such data allow for detailed demographic analyses.  
414 However, many pressing questions related to population dynamics are difficult to answer using  
415 capture-recapture data, particularly in the case of invasions that are ongoing or have already  
416 occurred, and because capture-recapture data tend to be spatially limited. Successive surveys of  
417 spatially replicated counts and occurrences can provide similar, although less detailed,  
418 information on population abundance, demographic rates, and/or colonization and extinction  
419 dynamics (MacKenzie et al. 2003, Royle 2004, Dail and Madsen 2011). Combining count and  
420 detection-nondetection data into a single integrated model can lead to a more accurate  
421 understanding of population demography and changes over time than is possible with  
422 independent analyses (Figure 1).

423 Integrated population models have typically focused on approaches to augment capture-  
424 recapture data with other data types (Schaub and Abadi 2011; Zipkin and Saunders In Review).

425 However, we show how combining only unmarked data types can provide increased accuracy  
426 and precision in estimates of population abundance and spatially varying demographic rates,  
427 even in cases where the sampling process leads to different detection probabilities among data  
428 types. As with other integrated analyses, this is because the different data are assumed to derive  
429 from the same underlying biological processes (Dorazio 2014). As a result, combining the data in  
430 a single model leads to a more efficient analysis. In some cases, such as in our barred owl  
431 example, researchers may switch from collecting one unmarked data type to another (e.g., from  
432 detection-nondetection to count) within a specific study area. Our modeling approach provides a  
433 framework to include the entire time series of data in a single analysis, regardless of this type of  
434 change. Zipkin et al. (2014b) found that the length of the time series of data had a greater  
435 contribution to parameter precision than the number of sites surveyed in a stage-structured N-  
436 mixture model. We anticipate a similar result for the combined detection-nondetection-count  
437 model based on estimates from our simulation study (Figure 1, Appendix S1): longer time series  
438 seem to lead to disproportionate parameter precision for a fixed number of total sampling events.  
439 Our results further suggest that a site with count data is approximately equivalent to three sites  
440 with detection-nondetection data in a model with no covariates; yet the exact information  
441 tradeoff is dependent on variation in site-level abundance and detection probabilities and will  
442 naturally be case specific.

443 Studies of species distributions, abundances, and dynamics over broad spatial extents  
444 often rely on either detection-nondetection data or counts of unmarked individuals. The potential  
445 to combine count and detection-nondetection data into a unified analysis lays the foundation for  
446 a number of analysis possibilities, particularly in terms of survey design. For example,  
447 monitoring invasive species typically involves detection-nondetection surveys combined with  
448 detailed count surveys at sites that are known to be occupied. In many such cases, it will not be  
449 feasible to conduct counts at every location where the species is encountered; simulations can  
450 help determine the optimal placement of count sites relative to detection-nondetection surveys.  
451 In general, researchers may want to target count-based protocols at locations with high quality  
452 habitat (i.e., with covariates in which survival and/or gains are expected to be high) and save less  
453 intensive detection-nondetection protocols for locations in marginal habitats. Such survey  
454 methodologies could provide high quality inferences as long as sites span the complete range of  
455 covariate space (Figure 2). We envision that future work could include presence-only data in

456 combination with other unmarked protocols (Dorazio 2014). This may be particularly useful for  
457 monitoring emerging species, where reports of detections (e.g., of the salamander chytrid fungus  
458 *B. salamandrivorans*) could then trigger cluster count samples in nearby areas. Although  
459 presence-only data are often associated with the analysis of historical and archival data sets, they  
460 may also arise in citizen-science data sets or other survey protocols.

461 Population closure is not a reasonable assumption for some sampling protocols and  
462 integrating such data may involve adding alternative observation models including those that  
463 allow for false positives, double counting, or species misidentification (Chambert et al. 2016,  
464 Miller et al. 2014, Thorson et al. 2014). Our results suggest that these efforts can provide  
465 accurate parameter estimates if the detection process is modeled correctly, but may still provide  
466 useful, if somewhat biased, estimates otherwise (e.g., Figure 3). Parameter identifiability and/or  
467 accuracy can be a problem in analyses that estimate demographic rates from unmarked data  
468 (Bellier et al. 2016, Zipkin et al. 2014a). Although we did not have this issue in our application  
469 of the model (Appendix S4), analyses using comparatively sparser datasets may have difficulties  
470 with convergence or identifiability. The incorporation of auxiliary information can increase the  
471 accuracy and precision of parameter estimates through the use of informative priors (Morris et al.  
472 2015) or by explicitly integrating available demographic data into the modeling framework. This  
473 may be particularly advantageous in cases where model assumptions are not strictly met (Bellier  
474 et al. 2016). We anticipate a growing importance for studies that combine data from multiple  
475 sampling protocols and thus encourage additional research regarding optimal data collection and  
476 analysis methods on integrated model structures.

477

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485

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## 588 **Figure Legends**

589 **Figure 1.** Boxplots summarizing the accuracy and precision of analyses with simulated data  
590 under an array of sites surveyed using count- and occupancy-based protocols. The x-axis  
591 indicates the number of detection-nondetection sites for each simulation and the colored panels  
592 indicate the number of count sites. Each panel shows the median (thick line within boxes), 50%  
593 quantiles (boxes), and  $\pm 1.5$  times the interquartile range (whiskers) for the median estimated  
594 value minus the true value of parameters (top four panels) and abundance (bottom panels) for  
595 5000 simulated datasets with random combinations of the true parameter values. Parameter  
596 estimates equal the true values where the y-axis equals zero (black lines).

597  
598 **Figure 2.** Estimates of a covariate effect on survival under a number of sampling protocols. The  
599 left panel shows the relationship between the covariate and survival. The other two panels show  
600 the estimated intercept ( $\beta_0 = 0.5$ ; middle) and slope ( $\beta_1 = 0.7$ ; right) under six scenarios: count  
601 data only (blue boxes), available across the whole range of the covariate (X1) and only where  
602 survival is high (X2); a combination of count and detection-nondetection data (red boxes)  
603 available across the range of the covariate (X3), from count data where survival is high and  
604 detection-nondetection data where survival is low (X4), from count data where survival is  
605 average and detection-nondetection data where survival is low or high (X5), and where both  
606 count and detection-nondetection data are only available where survival high (X6). Boxplots  
607 show median parameter estimates (thick line within boxes), 50% quantiles (boxes), and  $\pm 1.5$   
608 times the interquartile range (whiskers) for 1000 simulated datasets. True parameter values are  
609 shown with a thick black line.

610

611 **Figure 3.** Accuracy and precision of parameter values under four scenarios for 15 count and 75  
612 detection-nondetection sites. The first two (blue) assume data are modeled according to the data  
613 generating process where: individual detection probability is higher in the count than in the  
614 detection-nondetection data (X1) and detection is higher in the detection-nondetection than in the  
615 count data (X2). Scenarios X3 and X4 (red) model data generated in X1 and X2 using the  
616 standard model, which assumes that detection probability is equal across both sampling  
617 protocols. Black lines show the true values of the data generation process. Boxplots show the  
618 median (dark lines), 50% quantiles (boxes), and  $\pm 1.5$  times the interquartile range (whiskers) for  
619 1000 simulations.

620  
621 **Figure 4.** Study area and results from the barred owl application: (a) Map of the study area in the  
622 central Oregon Coast Ranges, USA. The grey areas with black outlines depict breeding  
623 territories of northern spotted owls (i.e., detection-nondetection sites) where barred owls were  
624 detected incidentally during surveys of spotted owls from 1995 to 2014. Blue hexagons (i.e.,  
625 count sites) indicate where barred owl-specific count surveys were completed in 2015 and 2016.  
626 Blue dots demonstrate the GPS locations of barred owl counts that we used in reconciling  
627 detections of territorial pairs between the different spatial scales of the survey sites; (b) Expected  
628 site-specific gains,  $\gamma$ , relative to average regional abundance in the previous year; (c) Apparent  
629 annual survival,  $\omega$ , relative to the amount of older growth forest cover within sites; (d) Mean  
630 annual colonization ( $\varphi$ , grey circles) and extinction ( $\epsilon$ , black diamonds) probabilities over the  
631 study period shown with 95% CI; (e) Detection probabilities for the count (left panel) and  
632 detection-nondetection (right panel) data. In panels b, c, and e black lines indicate mean values,  
633 plotted with 50% CI (dark grey region) and 95% CI (light grey region). In panel e, the boxplot  
634 for  $P_{occ}$  shows the mean (black lines in box), 50% CI (box), and 95% CI (whiskers).

### 635 **Supporting Information**

636 Additional Supporting Information may be found in the online version of this article:

637 **Appendix S1.** Basic model run with five years of data

638 **Appendix S2.** Complete simulation results for the covariate model

639 **Appendix S3.** Complete simulation results for the model with different detection probabilities  
640 for count and detection-nondetection data

641 **Appendix S4.** Barred owl application implementation details, model code, and parameter  
642 estimates  
643 **Data S1.** R Code for the combined count and detection-nondetection model

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