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Modeling co-occurrence of northern spotted and barred owls: Accounting for detection probability differences

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ABSTRACT

Barred owls *(Strix* valia) have recently expanded their range and now encompass the entire range of the northern spotted owl (Strix *ocddentalis caulina).* This expansion has led to two important issues of concern for management of northern spotted owls: (1) possible competitive interactions between the two species that could contribute to population declines of northern spotted owls. and (2) possible changes in vocalization behavior and detection probabilities of northern spotted owls induced by presence of barred owls. We used a two-species occupancy model to investigate whether there was evidence of competitive exclusion between the two species at study locations in Oregon, USA.We simultaneously estimated detection probabilities for both species and determined if the presence of one species influenced the detection of the other species. Model selection results and associated parameter estimates provided no evidence that barred owls excluded spotted owls from territories. We found strong evidence that detection probabilities differed for the two species. with higher probabilities for northern spotted owls that are the object of current surveys. Non-detection of barred owls is very common in surveys for northern spotted owls, and detection of both owl species was negatively influenced by the presence of the congeneric species. Our results suggest that analyses directed at hypotheses of barred owl effects on demographic or occupancy vital rates of northern spotted owls need to deal adequately with imperfect and variable detection probabilities for both species.

1. Introduction

The conservation of northern spotted owl *(Strix occidentalis caurina)* populations has been one of the most controversial issues in US conservation history (Thomas et al., 1990; Buchanan et al., 2007). The controversy canbe attributed largely to the association of northern spotted owls with old forests in the Pacific Northwest (e.g., Forsman et al., 1984; Thomas et al., 1990). These forests have substantial value to the timber industry, leading to conflicting views of how they should be managed.

In recent years, conservation of the northern spotted owl has been complicated by the expansion of barred owls *(Strix varia)* into the entire range of the northern spotted owl (Dark et al., 1998; Kelly et al., 2003; Pearson and Livezey, 2003; Gutierrez et al., 2007). This expansion of barred owls has led to two important issues of concern for management of northern spotted owls: (1) possible competitive interactions between the two species that could contribute to population declines of northern spotted owls, and (2) possible changes in vocalization behavior and detection probabilities of northern spotted owls induced by presence of barred owls.

Studies of territory occupancy have led to indirect inferences about competitive interactions between the two species. Kelly et al. (2003) found evidence that occupancy of territories by northern spotted owls in western Oregon declined to a greater extent when barred owls were located nearby than when no barred owls were detected. Similarly, Olson et al. (2005) provided evidence that presence of barred owls was associated with increased probabilities of local extinction and decreased probabilities of colonization of northern spotted owl territories at three study areas in Oregon. Productivity (young per pair) of northern spotted owls in an Oregon study area was reduced in territories in which barred owls were also detected nearby (Olson etl., 2004). Based on these studies and other anecdotal evidence, the 2008 Recovery Plan for the northern spotted owl concluded that available evidence suggests that "competition from the barred owl poses a significant and complex threat to the spotted owl" and included various considerations for management of this emerging threat (US Fish and Wildlife Service. 2008, VII).

The second issue of conservation concern involves possible changes in vocalization behavior and detection probabilities of northern spotted owls in the presence of barred owls and the

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implications of such changes for northern spotted owl monitoring programs. Northern spotted owls may be less likely to vocalize when barred owls are present, a possibility noted by Kelly et al, (2003) and Courtney et al. (2004). Experimental evidence supporting such changes in vocalization behavior was provided by Crozier et aI. (2006). Changes in detection probabilities resulting from decreased probabilities of vocalizing could result in misleading inferences about population change based on auditory surveys of northern spotted owls.

A shortcoming of all but the. experimental inferences about barred owl effects on northern spotted owl populations or detections is the reliance on raw barred owl detection data (Courtney et al., 2004). For example, even occupancy studies that have incorporated detection probabilities of northern spotted owls have used raw detection/non-detection data on barred owls for covariate analyses (e.g., Olson et al., 2005). Detection probabilities of barred owls are not only less than 1, but they are also likely influenced by the presence and reproductive status of northern spotted owls at sample locations (Livezey and Fleming, 2007). This concern led us to consider approaches to the study of co-occurrence of northern spotted owls and barred owls that provide stronger inferences knowing that detection probabilities of both species are <1 and may vary based on co-occurrence patterns.

In this paper we use a two-species occupancy model to investigate patterns of co-occurrence between northern spotted owl and barred owl in western Oregon. Specifically, we investigated whether the two species occur independently or if they co-occur more or less likely than expected under an independence hypothesis. Our prediction, based on a competition hypothesis, was that the two species should co-occur less frequently than expected under a hypothesis of no interactions. We also investigated several hypotheses about detection probabilities. First. because detection data for both species were gathered using survey protocols that targeted northern spotted owls (see below), we expected detection probabilities to be higher for this species than for barred owls. In addition, we investigated whether the presence of one species influenced the detection of the other species. We expected reduced detection probabilities for each species in the presence of the other, although the mechanisms underlying this prediction differ for the two species. We expected detection probabilities for northern spotted owls to be lower in the presence of barred owls because of purported behavioral dominance of the latter species (see Olson et al., 2005; Crozier et al., 2006). We expected reduced detection probabilities of barred owls in the presence of northern spotted owls because of logistical features of the survey protocol (see below). Finally, given co-occurrence, we investigated whether detections of the two species were independent or whether the probability of detecting one species in a given survey was influenced by the detection of the other species. Logistical aspects of the survey procedures lead us to predict that detection of northern spotted owls might lead to decreased detection probabilities for barred owls. Possible behavioral dominance leads to the prediction of reduced northern spotted owl detection probability when barred owls were also heard.

2. Methods

2.1. Study area

The Tyee Density Study Area (DSA; 1025 km") is located northwest of Roseburg, Oregon and includes a mixture of federal lands administered by the Bureau of Land Management (BLM) and intervening sections of private land (Reid et al., 1996). The area is characterized by mountainous terrain with mesic areas consisting of Douglas-fir *(Psudotsuga* menziesii) and western hemlock *(Tsuga heterophylla)* and xeric areas that included mixed coniferous species. These forests represent a mosaic of old and younger forests that have been clear-cut, thinned, or burned (Olson et al., 2005).

2.2. Field methods

Northern spotted owl populations have been monitored throughout the Tyee DSA since 1990 (Reid et al., 1996; Olson et al., 2005). All areas within the DSA are surveyed, including territories that have historically supported spotted owl activity as well as polygons between historic locations. The size of each territory or polygon varies depending on topography and land ownership, but corresponds roughly to the size of a spotted owl territory. We use the term 'territories' to denote all study locations regardless of their previous history of spotted owl activity (e.g., Olson et al., 2005). The number of surveyed 'territories' has remained relatively constant among years (~150-160 territories). Surveys target spotted owls by imitating their calls, and biologists follow established guidelines for locating spotted owls and estimating their productivity (Franklin et al., 1996). For our analysis, we used data from 2002 and 2003 only: this time corresponds to a heightened awareness of the potential threat posed by barred owls (Courtney et al., 2004) and there were enough barred owl detections to facilitate model convergence. Surveys were conducted duringthe breeding season between March 1 and August 31. Both day and night surveys were used to locate owls using a vocal lure (vocal imitation or playback of spotted owl calls) to elicit a response (Forsman, 1983). Daytime only surveys were conducted throughout the season but were more frequent early in the season atterritories that historically supported nesting pairs. These surveys generally involved walking into a territory and visually searching and/or hooting quietly in a localized area near the previous nest location; a survey was terminated if spotted owls were located. Detections of barred owls were noted at any time during this process, while observers were walking through the territory or during the vocal imitation period. Surveys that incorporated a night visit involved calling for ~ 10 min, often at multiple stations within the territory or until spotted owls responded (Franklin et al., 1996). Although barred owls were not the target of vocal lure surveys they do respond to spotted owl calls (Kelly et al., 2003; Crozier et al., 2006).

Note that under the above protocol, the time spent calling and listening at any territory was a function of the detection of northern spotted owls. Once a spotted owl was detected in a given daytime survey, the survey was often stopped. This logistical feature of the surveys led to our predictions that barred owl detection probabilities would be lower at territories where northern spotted owls were present and lower for survey occasions in which northern spotted owls were detected.

2.3. Two-species occupancy model

We used a single season, two-species model (MacKenzie et al., 2004, 2006) to estimate occupancy and detection probabilities for both owl species and to evaluate whether the presence of barred owls influenced the occurrence or detection of northern spotted owls. The original model parameterization implemented in program PRESENCE (Hines, 2006) consists of five types of parameters: ψ_{jIm} is the probability a site (territory) is occupied by species m, regardless of occupancy status of the other species, $P'j'$ is the probability of detecting species m during the jth survey, given only species m is present at the site. $\Gamma J'$ is the probability of detecting species m during the jth survey. given both species are present. φ is the ratio of how likely the species are to co-occur at a territory compared to what would be expected under a hypothesis of independence (Mackenzie et al., 2004 termed this quantity

a species interaction factor), and 3 is a similar interaction factor for detection probabilities given co-occurrence. It is important to note that we use the term 'interaction' in the statistical sense only (e.g., the species are not occurring independently at territories). Behavioral interactions may indeed underlie these statistical interactions, but pattern-based analyses do not permit strong inferences about underlying processes.

In our case involving two owl species, the occupancy interaction factor is expressed as:

$$\varphi = \frac{\psi^{BaSp}}{\psi^{Ba}\psi^{Sp}}$$

where ψ^{BaSp} is the probability that the site is occupied by both barred and spotted owls. If the species occupied sites independently, the numerator and denominator would be equal (i.e., $\psi^{BaSp} = \psi^{Ba} \times \psi^{Sp}$ and $\varphi \approx 1$). If the species tended to co-occur more often than expected if they were distributed independently (i.e., $\psi^{BaSp} > \psi^{Ba} \times \psi^{Sp}$) then values of φ would exceed 1. Values of φ less than 1 would suggest that the two species co-occur less often than expected, suggesting possible avoidance or competitive exclusion. Likewise, the detection interaction factor, δ, is expressed as $\delta = \frac{r^{BaSp}}{r^{Ba} \cdot r^{Sp}}$, where r^{BaSp} is the probability of detecting both barred and spotted owls during a survey at a territory occupied by both species. Here, δ values less than 1 would suggest that observers were less likely to detect (hear) one species if the other species was heard during the same survey. Notice that the two species may exhibit independence in the detection process (i.e., $\delta \approx 1$) at co-occupied sites, but the probability of detection could still be influenced by the presence of the other owl species (e.g., $r_j^m < p_j^m$).

All of the parameters defined above can be modeled as a function of relevant covariates using an appropriate link function (MacKenzie et al., 2004, 2006). In general the logit link function is used for all parameters except the interaction factors (α and δ) where the log link function is a more natural choice because these parameters are not bounded between 0 and 1.

2.4. Model set

The objective of this study was to explore five fundamental hypotheses regarding the co-occurrence and detection of barred and spotted owls. Specifically, we addressed whether the species co-occurred independently or if there was evidence of competitive exclusion of spotted owls from territories occupied by barred owls (i.e., $\varphi < 1$). We also addressed four hypotheses about detection probability. Because the surveys were designed for detection of northern spotted owls, we expected this species to have the higher detection probabilities (e.g., $p_j^{Sp} > p_j^{Ba}$) or sites occupied by both species, we explored whether the detection process was independent (i.e., $\delta \approx 1$) or whether detection of one species influenced the probability of detecting the congeneric species during a given survey (i.e., $\delta \neq 1$). We explored whether the presence of barred owl influenced the detection of spotted owls (e.g., $r_j^{BaSp} < p_j^{Sp}$) and vice versa (e.g., $r_j^{BaSp} < p_j^{Ba}$). Previous work has suggested that spotted owl detection is reduced at territories where barred owls are known to be present (Olson et al., 2005; Crozier et al.,2006), but no study has explored whether, under the current survey protocol, barred owl detection may be influenced by the presence of spotted owls. Previous analysis of owl detection data from the Tyee DSA found no evidence that the species' detection probability varied during the breeding season (Olson et al., 2005); however, we did investigate the influence of survey time by differentiating daytime only surveys from surveys that included sampling at night. We included this covariate on all parameters associated with detection probabilities.

We addressed the above biological hypotheses by imposing various constraints on the parameters. For example, we fit models with and without the occupancy interaction factor to address our competitive exclusion hypothesis. To evaluate our four detection probability hypotheses, we included models where p and r were constrained to be equal ($p_j^m = r_j^m$) but varied between species (denoted $p(S)$) or species and survey time, $p(S \times ND)$, and models where p and r were different ($p_j^m \neq r_i^m$) and varied with these same factors (e.g., $p(S \times ND) r(S \times ND)$). We considered model structures with and without the detection interaction factor and models where 3 varied between night and daytime only surveys (denoted $\delta(ND)$). combinations ofthese parameter structures were combined into 36 models, using a consistent species-specific occupancy structure, $\psi(S)$ Appendix A). We fit five additional models, combining the occupancy and detection interaction structures with detection probabilities that were equal among species but varied between night and daytime surveys, $p(ND)\ r(ND)$. All 41 models were fit to the two years of data and maximum likelihood estimates were obtained using program PRESENCE (Hines, 2006). Models were ranked using Akaike's Information Criterion (AIC), where models with small Arc values ($\Delta AIC \leqslant 2.0$) are considered good descriptors of the data. Model weights, w, reflecting the relative weight of evidence for model i were computed for each model, and model-averaged estimates were calculated using all models in the candidate set (e.g., Burnham and Anderson, 2002).

3. Results

One hundred and fifty-nine territories were sampled in both years and there was little difference in the average number of surveys per site between years: $\bar{x}_{2002} = 5.3$ (range: 2-17 surveys) and $\bar{x}_{2003} = 4.9$ (range: 1-14 surveys). Spotted owls were detected at 92 and 106 territories in 2002 and 2003, respectively, while barred owls were detected at 37 and 41 sites.

Model selection results and. associated parameter estimates provide no evidence that barred owls excluded spotted owls from territories in 2002 and 2003 (Tables 1-4). The occupancy interaction estimates provided no evidence that the two species co-occurred less often than expected under an independence

Table 1
Model selection statistics for the top 10 multi-species occupancy models fit to northern spotted owl and barred owl detection data from 159 territories in the western Oregon Coast Ranges in 2002. The terms in parentheses represent the sources of variation in the model parameter; "S" denotes species-specific differences, "ND" indicates models where detection probability parameters differ between Night and Daytime surveys, and "." indicates a parameter set equal across species and survey times. Absence of φ and δ implies no interaction in occupancy or detection probability, respectively (e.g., $\varphi = 1$ and/or $\delta = 1$). The best models without time covariates, $\psi(S)$, $\varphi(.)$, $p(S)$, $r(S)$, and without species-specific detection probabilities, $\psi(S)$, $\varphi(.)$, $p(ND)$, $r(ND)$, are included for comparison.

Model	K[a]	ΔAIC[b]	w[c]	$-2l$[d]
$\psi(S)$, $p(S \times ND)$, $r(S \times ND)$	10	0.00	0.31	1287.77
$\psi(S)$, $\phi(.)$, $p(S \times ND)$, $r(S \times ND)$	11	0.01	0.31	1285.78
$\psi(S)$, $\phi(.)$, $p(S \times ND)$, $r(S \times ND)$, $\delta(.)$	12	1.69	0.14	1285.46
$\psi(S)$, $p(S \times ND)$, $r(S \times ND)$, $\delta(.)$	11	1.77	0.13	1287.54
$\psi(S)$, $\varphi(.)$, $p(S \times ND)$, $r(S \times ND)$, $\delta(ND)$	13	3.63	0.05	1285.40
$\psi(S)$, $p(S \times ND)$, $r(S \times ND)$, $\delta(ND)$	12	3.68	0.05	1287.45
$\psi(S)$, $\varphi(.)$, $p(S)$, $r(S \times ND)$	9	9.19	0.00	1298.96
$\psi(S)$, $\varphi(.)$, $p(S)$, $r(S \times ND)$, $\delta(.)$	10	10.6	0.00	1298.37
$\psi(S)$, $\varphi(.)$, $p(S)$, $r(S \times ND)$, $\delta(ND)$	11	12.59	0.00	1298.36
$\psi(S)$, $p(S)$, $r(S \times ND)$	8	13.18	0.00	1304.95
$\psi(S)$, $\varphi(.)$, $p(S)$, $r(S)$	7	21.21	0.00	1314.98
$\psi(S)$, $\phi(.)$, $p(ND)$, $r(ND)$	7	34.23	0.00	1328.00

[a] The number of estimated parameters in the model.
[b] The relative difference in AIC values.
[c] AIC model weight.
[d] Twice the negative log-likelihood.

Table 2
Model selection statistics for the top 10 multi-species occupancy models fit to northern spotted owl and barred owl detection data from 159 territories in the western Oregon Coast Ranges in 2003. The terms in parentheses represent the sources of variation in the model parameter; with "S" denoting species-specific differences, "ND" indicates models where detection probability parameters differed between Night and Daytime surveys, and "·" indicates a parameter set equal across species and survey times. Absence of φ and δ implies no interaction in occupancy or detection probability, respectively (e.g., $\varphi = 1$ and/or $\delta = 1$). The best models without time covariates, $\psi(S)$, $p(S)$, $r(S)$, and without species-specific detection probabilities, $\psi(S)$, $\varphi(.)$, $p(ND)$, $r(ND)$, $\delta(ND)$, are included for comparison.

Model	K[a]	ΔAIC[b]	w[c]	−2l[d]
$\psi(S)$, $\varphi(.)$, $p(S)$, $r(S \times ND)$, $\delta(ND)$	11	0.00	0.23	1289.44
$\psi(S)$, $\varphi(.)$, $p(S)$, $r(S \times ND)$;	9	0.99	0.14	1294.43
$\psi(S)$, $p(S)$, $r(S \times ND)$, $\delta(ND)$	10	1.28	0.12	1292.72
$\psi(S)$, $\varphi(.)$, $p(S)$, $r(S \times ND)$, $\delta(.)$	10	1.59	0.10	1293.03
$\psi(S)$, $p(S)$, $r(S \times ND)$	8	2.07	0.08	1297.51
$\psi(S)$, $\varphi(.)$, $p(S \times ND)$, $r(S \times ND)$, $\delta(ND)$;	13	2.81	0.06	1288.25
$\psi(S)$, $p(S)$, $r(S \times ND)$, $\delta(.)$;	9	3.38	0.04	1296.82
$\psi(S)$, $\varphi(.)$, $p(S \times ND)$, $r(S \times ND)$	11	4.07	0.03	1293.51
$\psi(S)$, $p(S \times ND)$, $r(S \times ND)$, $\delta(ND)$	12	4.18	0.03	1291.62
$\psi(S)$, $\varphi(.)$, $p(S \times ND)$, $r(S \times ND)$, $\delta(.)$	12	4.66	0.02	1292.10
$\psi(S)$, $p(S)$, $r(S)$	6	5.23	0.02	1304.67
$\psi(S)$, $\varphi(.)$, $p(ND)$, $r(ND)$, $\delta(ND)$	0	23.32	0.0	1316.76

[a] The number of estimated parameters in the model.
[b] The relative difference in AIC values.
[c] AIC model weight.
[d] Twice the negative log-likelihood.

assumption within our study area (model-averaged estimates: $\hat{\varphi}_{2002} = 1.09$ (SE = 0.12), $\hat{\varphi}_{2003} = 1.06$ (SE = 0.04), Tables 3 and 4).

Detection probabilities for the two species were substantially different. Consistent with our predictions, detection probabilities of northern spotted owls were higher than those for barred owls for both survey types (day, night) and for territories occupied by one or both species (Tables 3 and 4: models with equal detection probabilities between species had $w_i = 0$). Detection probabilities of both species were strongly influenced by the presence of the opposite species. Models that constrained $p_i^m = p_j^m$ were not supported by the data ($w_i = 0$); instead each species was often twice as likely to be detected if the other species did not also occupy the territory (Tables 3 and 4). Survey time also influenced detection probability for both species with barred owls being extremely difficult to detect during daytime only surveys (Tables 3 and 4).

We found no strong or consistent interaction in the detection process at territories occupied by both species. The top two models using the 2002 data (combined $w = 0.62$) suggested that detection probabilities were independent, and model-averaged estimates of δ were near 1 with relatively high unconditional standard errors (Table 3). Models fit to the 2003 data also suggested that the detection of owls of both species was independent, at least among surveys conducted at night (model averaged $\hat{\delta}_{2003} = 1.03$, SE = 0.22). There was some indication from daytime surveys only that detection of both species occurred less often than expected if owls called

Table 3
Parameter estimates under top three multi-species occupancy models fit to 2002 northern spotted owl and barred owl detection data from 159 potential northern spotted owl territories in the western Oregon Coast Ranges. Model-averaged estimates using the entire candidate set are also presented.

Parameter	Model: $\psi(S)$, $p(S \times ND)$, $r(S \times ND)$		Model: $\psi(S)$, $\phi(.)$, $p(S \times ND)$, $r(S \times ND)$		Model: $\psi(S)$, $\phi(.)$, $p(S \times ND)$, $r(S \times ND)$, $\delta(.)$		Model averaged	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
$\hat{\psi}^{Sp}$	0.60	0.04	0.60	0.04	0.61	0.04	0.60	0.04
$\hat{\psi}^{Ba}$	0.33	0.05	0.35	0.05	0.35	0.05	0.34	0.05
$\hat{\varphi}$	1.00	–	1.18	0.12	1.18	0.11	1.09	0.12
$\hat{p}^{Sp}_{day}$	0.84	0.03	0.86	0.04	0.86	0.03	0.85	0.03
$\hat{p}^{Sp}_{night}$	0.60	0.07	0.63	0.09	0.64	0.09	0.62	0.08
$\hat{p}^{Ba}_{day}$	0.09	0.06	0.10	0.07	0.10	0.07	0.09	0.06
$\hat{p}^{Ba}_{night}$	0.41	0.09	0.45	0.09	0.46	0.09	0.43	0.09
$\hat{r}^{Sp}_{day}$	0.37	0.05	0.37	0.05	0.37	0.05	0.37	0.05
$\hat{r}^{Sp}_{night}$	0.48	0.06	0.46	0.05	0.46	0.06	0.47	0.06
$\hat{r}^{Ba}_{day}$	0.04	0.03	0.08	0.03	0.07	0.03	0.08	0.03
$\hat{r}^{Ba}_{night}$	0.31	0.05	0.28	0.05	0.28	0.05	0.29	0.06
$\hat{\delta}_{day}$	1.0	–	1.0	–	1.08	0.15	1.04	0.11
$\hat{\delta}_{night}$	1.0	–	1.0	–	1.08	0.15	1.02	0.07

Table 4
Parameter estimates under top three multi-species occupancy models fit to 2003 northern spotted owl and barred owl detection data from 159 potential northern spotted owl territories in the western Oregon Coast Ranges. Model-averaged estimates using the entire candidate set are also presented.

Parameter	Model: $\psi(S)$, $\varphi(.)$, $p(S)$, $r(S \times ND)$, $\delta(ND)$		Model: $\psi(S)$, $\varphi(.)p(S)$, $r(S \times ND)$		Model: $\psi(S)$, $p(S)$, $r(S \times ND)$, $\delta(ND)$		Model averaged	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
$\hat{\psi}^{Sp}$	0.74	0.05	0.74	0.05	0.74	0.05	0.74	0.06
$\hat{\psi}^{Ba}$	0.60	0.06	0.59	0.06	0.59	0.06	0.59	0.07
$\hat{\varphi}$	1.11	0.06	1.10	0.06	1.0	–	1.06	0.04
$\hat{p}^{Sp}_{day}$	0.86	0.04	0.86	0.04	0.84	0.04	0.86	0.05
$\hat{p}^{Sp}_{night}$	0.86	0.04	0.86	0.04	0.84	0.04	0.86	0.05
$\hat{p}^{Ba}_{day}$	0.44	0.08	0.44	0.08	0.37	0.07	0.40	0.10
$\hat{p}^{Ba}_{night}$	0.44	0.08	0.44	0.08	0.37	0.07	0.42	0.09
$\hat{r}^{Sp}_{day}$	0.53	0.05	0.51	0.05	0.51	0.05	0.50	0.06
$\hat{r}^{Sp}_{night}$	0.36	0.05	0.35	0.05	0.39	0.05	0.36	0.05
$\hat{r}^{Ba}_{day}$	0.06	0.02	0.05	0.02	0.06	0.02	0.06	0.02
$\hat{r}^{Ba}_{night}$	0.11	0.02	0.11	0.02	0.10	0.02	0.10	0.02
$\hat{\delta}_{day}$	0.37	0.22	1.0	–	0.38	0.20	0.64	0.33
$\hat{\delta}_{night}$	1.09	0.29	1.0	–	1.21	0.30	1.03	0.22

independently (model averaged. $\hat{\delta}_{2003} = 0.64$, SE = 0.33, Table 4). Stated differently, the daytime only data suggested that if one species was detected, observers were less likely to detect the congeneric species, given the territory was occupied by both species.

The relatively low detection probabilities for barred owls lead to large discrepancies between naive and estimated occupancy probabilities for this species. For example, barred owls were detected at 24.5% and 25.7% of the sites in 2002 and 2003, respectively, but detection-adjusted occupancy estimates were substantially higher (model-averaged estimates: $\hat{\psi}^{Ba}_{2002} = 0.34$ (SE = 0.05) and $\hat{\psi}^{Ba}_{2003} = 0.59$ (SE ~ 0.07)). Both species were detected at 21 of the 159 territories in 2003 (13.2%),but model-averaged estimates adjusted for non-detection and species interaction would suggest that $\hat{\psi}^{BaSp} = \hat{\psi}^{Ba} \times \hat{\psi}^{Sp} \times \hat{\varphi} = 0.46$ (SE = 07). Overall, our results suggest that barred owls may be present at approximately twice as many sites as previously detected and that the number of sites occupied by both species may be >3 times larger than indicated by raw detections.

4. Discussion

We have presented results of analyses directed at hypotheses about the spatial distribution pattern of two potential competitor species, northern spotted owls and barred owls. We incorporated detection probabilities into the analyses and also tested hypotheses about sources of variation in species-specific detection probabilities. To our knowledge, this is the first study to simultaneously incorporate detection probabilities for both northern spotted owls and barred owls when assessing the strength of potential interactions. We were also able to provide some of the first estimates of species-specific detection probabilities for the two species on the same study area.

Our analyses provided no evidence of a predicted negative association between occupancy of a territory by the two species. This prediction was based on studies reporting declines in northern spotted owl occupancy at territories where barred owls were detected (Kelly et al., 2003), declines in colonization and increases in local extinction probabilities of northern spotted owls in the presence of barred owls (Olson et al., 2005), and lower reproductive rates of northern spotted owl pairs in territories occupied by barred owls (Olson et al., 2004). The prediction was also supported by anecdotal evidence. The two species have also been thought to compete for the same prey (Dunbar et al., 1991; Herter and Hicks, 2000; Courtney et al., 2004), and barred owls may occasionally kill northern spotted owls (Leskiw and Gutierrez, 1998).

We emphasize two caveats associated with inferences about possible competition based on our analysis of spatial pattern of the two species. First, the two years of study were early in the establishment of barred owls on the study area. Thus, it is possible that sufficient time had not elapsed for the spatial pattern of northern spotted owls to have adjusted because of interactions with barred owls. Second, and most important, inferences about processes (such as competition) based on spatial pattern are usually weaker than inferences based on direct experimentation and on investigations of species dynamics (MacKenzie et al., 2006, pp. 17-20). While our study is the first to deal adequately with detection probabilities of both species, it is based on pattern rather than on direct influences of barred owls on local rates of extinction and colonization or on reproductive rates of northern spotted owls (e.g., Olson et al., 2004, 2005). Spatial patterns of species occurrence are often influenced by factors other than competition, for example habitat selection. Future spatial analyses can incorporate species-specific habitat covariates if they are available (e.g., Seamans and Gutierrez, 2007). Still, the strongest inferences will come from additional experimental work and from multi season studies of two-species occupancy dynamics that account for detection probabilities of both species (see "Recommendations").

We found strong evidence that detection probabilities differed between the two species. As predicted, detection probabilities of barred owls were lower than those of northern spotted owls. However, we were somewhat surprised by the magnitudes of these differences and by how small the estimated barred owl detection probabilities actually were. Non-detection of barred owls was very common in surveys for northern spotted owls, arguing for the use of occupancy-type modeling whenever existing data are analysed to provide inference about barred owl occurrence or assess relationships between the two species.

We also provided strong evidence of effects of the presence of each species on the detection probability of the other. If a territory was co-occupied by both species, then each species showed lower detection probabilities than for territories occupied by just a single species. The estimated magnitudes of the differences in detection probabilities were substantial, and these results were consistent across day and night surveys and for both years of the study. The occupancy studies of Olson et al. (2005) led them to infer that detection probabilities of northern spotted owls were lower at sites where barred owls were detected. Moreover, the experiments of Crozier et al. (2006) provided evidence that northern spotted owls responded less frequently to conspecific vocalizations in the simulated presence of barred owls. Our results are thus consistent with these two studies and also lead to the new inference that barred owl detection probabilities were lower at territories occupied by northern spotted owls. Our data do not permit inferences about the underlying mechanism associated with decreased detection of barred owls, and we noted one possibility dealing with the cessation of survey effort at a territory once northern spotted owls are detected.

For sites occupied by both species, there was equivocal evidence (daytime surveys during one year, 2003) that both species were not always detected during the same survey as frequently as expected under a null hypothesis of no interaction in calling behavior. This result of possible interaction was consistent with the experimental work of Crozier et al. (2006), who found evidence of decreased vocal responsiveness of northern spotted owls in the presence of imitation barred owl calls.

We emphasize that these various inferences about species detection probabilities are not statistical fine points. Our analyses provided evidence that barred owls were present on twice as many surveyed sites as indicated by raw detections. Estimates of territories at which both species occurred were >3 times larger than indicated by detections alone. Thus, the potential for species interactions is far greater than indicated by raw detection data.

4.1. Recommendations

Our inferences about possible competitive interactions between the two owl species are relatively weak for three reasons. The first reason concerns our selection of early years of barred owl establishment and the possibility that northern spotted owl spatial pattern had not yet adjusted to the invading barred owls. The second reason concerns the lack of potentially important habitat covariates in our analyses (Seamans and Gutierrez, 2007). In cases where habitat is a determinant of pattern, it is wise to try to incorporate habitat covariates in analyses investigating other determinants of pattern. Initially, we did not believe that this issue would be important, because the entire study area consisted of relatively good habitat for both species. Still, having territory-specific habitat covariates to incorporate into future analyses would be useful and help alleviate any confounding between habitat preferences and species interaction. The third and most important weakness with our inferences about competition is the reliance on

species distribution patterns rather than on experimental studies or studies of species occupancy dynamics (see MacKenzie et al., 2006; MacKenzie et al., 2009). Studies of demographic parameters (rates of survival and reproduction) and occupancy dynamics (probabilities of local colonization and extinction) of northern spotted owls at territories that are and are not occupied by barred owls are likely to provide stronger inferences about effects of barred owls on northern spotted owl population dynamics. Previous studies have followed this approach with reproductive rates (Olson et al.. 2004) and probabilities of local extinction and colonization (Olson et al., 2005), providing evidence of negative effects of detected barred owl presence on northern spotted owl population processes. We believe that the studies of Olson et al. (2004, 2005) are very important, but we also note that they treated barred owl presence and absence as known covariates based on observed detections. Livezey and Fleming (2007:320) argued that this sort of treatment was not appropriate and went as far as to state: " ..we do not recommend continued collection of barred owl data in the manner that has occurred previously". Our analyses provide the first estimates of barred owl detection probabilities and strong evidence that many of the concerns of Livezey and Fleming (2007) are indeed justified.

However, our recommendation is not that incidental barred owl data cannot be used, but rather that their use requires models that deal adequately with imperfect and variable detection probabilities. For example, analyses directed at hypotheses of possible barred owl influences on demographic rates of northern spotted owls (e.g., survival probabilities) may benefit from the use of multistate capture-recapture models similar to those developed by Kendall et al. (2003) to deal with state uncertainty. Dynamic multistate occupancy modeling is an active area of research and should enable researchers to assess barred owl influence on northern spotted owl reproduction, local extinction and colonization rates (e.g., MacKenzie et al., 2009). We note that most of the recommended analyses can be conducted using currently available models and software, with little or no adaptation; the dynamic multistate occupancy model is currently implemented in program PRESENCE, MacKenzie et al. (2009).

The modeling presented in this paper permits inference using existing incidental barred owl data together with data collected specifically for northern spotted owls in analyses of co-occurrence patterns. However, this flexibility does not mean that future surveys should not be modified to reflect a direct interest in barred owls and their potential effects on spotted owls. We also note that current surveys can be be modified in ways designed to strengthen inferences about the influence of barred owls on northern spotted owl populations. More specifically, modifications can increase detection probabilities of barred owls and decrease sources of variation in these probabilities. Detection probabilities for barred owls could be improved by using vocal lures of both species and randomizing the order of the species calls for each survey. While there are various reasons to retain current spotted owl survey protocols to obtain demographic information, simply continuing to conduct *surveys* at all stations within a territory, or until both species are detected during a survey, could achieve the targeted spotted owl information while improving barred owl detection probabilities. We note that the new modeling approaches that we have advocated in these recommendations would still be needed for surveys redesigned to focus on both barred and spotted owls as researchers would still need to consider non-detection of both species as well as detection dependence. Finally, we believe that such dynamic modeling of occurrence' and demographic data over large areas should be coupled, when possible, with experimental work (e.g., attempts at barred owl reductions in experimental areas, Gutierrez et al., 2007) and investigations focused on specific mechanisms hypothesized to underlie any detected effects. Such an integrated approach should provide the greatest likelihood of understanding interspecific interactions and their consequences.

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Appendix A

Candidate models were fit to 159 potential northern spotted owl territories in the western Oregon Coast Ranges in 2002 and 2003. Models consist of five types of parameters: ψ is the probability of occupancy for each species, p is the probability of detecting the species during a survey given one species present at the site, r is the probability of detecting a species during a survey of sites where both species are present, φ and δ are species interaction factors for occupancy and detection probabilities, respectively. The terms in parentheses represent the sources of variation considered for the respective parameters; "5" denotes species-specific differences and *"ND"* indicates models where detection probability parameters differed between Daytime only surveys and surveys that include sampling at *Night.* For example, $p(S \times ND)$ indicates a model where detection probability varies independently among the two species and between day and night surveys. The notation (.) indicates a parameter set equal across species and survey times. Absence of r implies r = p while the absence of (φ and δ parameters indicates no interaction in occupancy or detection probability, respectively (i.e., $\varphi = 1$ and/or $\delta = 1$). K is the number of estimated parameters In each model: the global (or most parameterized) model is listed first.

	Model	K
1	$\psi(S)$, $\varphi(.)$, $p(S \times ND)$, $r(S \times ND)$, $\delta(ND)$	13
2	$\psi(S)$, $\phi(.)$, $p(S \times ND)$, $r(S \times ND)$, $\delta(.)$	12
3	$\psi(S)$, $p(S \times ND)$, $r(S \times ND)$, $\delta(ND)$;	12
4	$\psi(S)$, $\varphi(.)$, $p(S)$, $r(S \times ND)$, $\delta(ND)$	11
5	$\psi(S)$, $p(S \times ND)$, $r(S \times ND)$, $\delta(.)$	11
6	$\psi(S)$, $\phi(.)$, $p(S \times ND)$, $r(S \times ND)$	11
7	$\psi(S)$, $\phi(.)$, $p(S \times ND)$, $r(S)$, $\delta(ND)$;	11
8	$\psi(S)$, $p(S)$, $r(S \times ND)$, $\delta(ND)$	10
9	$\psi(S)$, $\phi(.)$, $p(S)$, $r(S \times ND)$, $\delta(.)$	10
10	$\psi(S)$, $p(S \times ND)$, $r(S \times ND)$	10
11	$\psi(S)$, $p(S \times ND)$, $r(S)$, $\delta(ND)$	10
12	$\psi(S)$, $\phi(.)$, $p(S \times ND)$, $r(S)$, $\delta(.)$	10
13	$\psi(S)$, $\phi(.)$, $p(S \times ND)$, $r(S)$	9
14	$\psi(S)$, $\phi(.)$, $p(S)$, $r(S)$, $\delta(ND)$	9
15	$\psi(S)$, $p(S \times ND)$, $r(S)$, $\delta(.)$	9
16	$\psi(S)$, $\phi(.)$, $p(S \times ND)$, $\delta(ND)$	9
17	$\psi(S)$, $\varphi(.)$, $p(S)$, $r(S \times ND)$	9
18	$\psi(S)$, $p(S)$, $r(S \times ND)$, $\delta(.)$	9
19	$\psi(S)$, $\phi(.)$, $p(ND)$, $r(ND)$, $\delta(ND)$	9
20	$\psi(S)$, $p(S)$, $r(S \times ND)$	8
21	$\psi(S)$, $\varphi(.)$, $p(S)$, $r(S)$, $\delta(.)$	8
22	$\psi(S)$, $p(S)$, $r(S)$, $\delta(ND)$	8
23	$\psi(S)$, $p(S \times ND)$, $r(S)$	8
24	$\psi(S)$, $p(S \times ND)$, $\delta(ND)$	8
25	$\psi(S)$, $\phi(.)$, $p(S \times ND)$, $\delta(.)$	8
26	$\psi(S)$, $\phi(.)$, $p(ND)$, $r(ND)$, $\delta(.)$	8
27	$\psi(S)$, $\varphi(.)$, $p(S)$, $r(S)$	7
28	$\psi(S)$, $p(S)$, $r(S)$, $\delta(.)$	7
29	$\psi(S)$, $p(S \times ND)$, $\delta(.)$	7
30	$\psi(S)$, $\phi(.)$, $p(S \times ND)$	7

Appendix A (*continued*)

	Model	*K*
31	$\psi(S)$, $\phi(.)$, $p(S)$, $\delta(ND)$	7
32	$\psi(S)$, $p(ND)$, $r(ND)$, $\delta(.)$	7
33	$\psi(S)$, $\phi(.)$, $p(ND)$, $r(ND)$	7
34	$\psi(S)$, $p(S)$, $r(S)$	6
35	$\psi(S)$, $p(S \times ND)$	6
36	$\psi(S)$, $\phi(.)$, $p(S)$, $\delta(.)$	6
37	$\psi(S)$, $p(S)$, $\delta(ND)$	6
38	$\psi(S)$, $p(ND)$, $r(ND)$	6
39	$\psi(S)$, $\phi(.)$, $p(S)$;	5
40	$\psi(S)$, $p(S)$, $\delta(.)$	5
41	$\psi(S)$, $p(S)$	4

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