

# The roles of competition and habitat in the dynamics of populations and species distributions

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**Abstract.** The role of competition in structuring biotic communities at fine spatial scales is well known from detailed process-based studies. Our understanding of competition's importance at broader scales is less resolved and mainly based on static species distribution maps. Here, we bridge this gap by examining the joint occupancy dynamics of an invading species (Barred Owl, *Strix varia*) and a resident species (Northern Spotted Owl, *Strix occidentalis caurina*) in a 1000-km<sup>2</sup> study area over a 22-year period. Past studies of these competitors have focused on the dynamics of one species at a time, hindering efforts to parse out the roles of habitat and competition and to forecast the future of the resident species. In addition, while these studies accounted for the imperfect detection of the focal species, no multi-season analysis of these species has accounted for the imperfect detection of the secondary species, potentially biasing inference. We analyzed survey data using models that combine the general multistate–multi-season occupancy modeling framework with autologistic modeling, allowing us to account for important aspects of our study system.

We found that local extinction probability increases for each species when the other is present; however, the effect of the invader on the resident is greater. Although the species prefer different habitats, these habitats are highly correlated at the patch scale, and the impacts of invader on the resident are greatest in patches that would otherwise be optimal. As a consequence, competition leads to a weaker relationship between habitat and Northern Spotted Owl occupancy. Colonization and extinction rates of the invader are closely related to neighborhood occupancy, and over the first half of the study the availability of colonists limited the rate of population growth. Competition is likely to exclude the resident species, both through its immediate effects on local extinction and by indirectly lowering colonization rates as Northern Spotted Owl occupancy declines. Our analysis suggests that dispersal limitation affects both the invasion dynamics and the scale at which the effects of competition are observed. We also provide predictions regarding the potential costs and benefits of managing Barred Owl populations at different target levels.

**Key words:** competitive exclusion; extirpation; metapopulation; scale; species range dynamics; *Strix*.

## INTRODUCTION

Competition among species has a prominent role in ecological theory (Lotka 1925, Volterra 1926, MacArthur 1970) to the point where it is viewed as a primary force in the structuring of ecological communities (MacArthur and Wilson 1967, May 1973, McGill 2010). Strong empirical support for the potential importance of interspecific competition came first from classical laboratory experiments (e.g., Gause 1934, Park 1948) and, more recently, from observational and experimental studies over limited spatial scales (e.g., study areas of single investigators, see Schoener 1983,

Gurevitch et al. 1992). At larger (e.g., macroecological) spatial scales, most investigations claiming to provide empirical support for the role of competition in structuring ecological communities have been based on observational data, especially observations on spatial distribution patterns of species (e.g., Diamond 1975, but see Okubo et al. 1989). However, analyses based on static species distribution patterns are often ambiguous, in the sense that results could have been generated by a large number of possible processes, some of which do not include competition (e.g., Connor and Simberloff 1979, Connell 1980, Kareiva et al. 1990). Recent studies of migratory birds suggested that competition affects species distributions at far broader spatial scales than previously predicted (Gotelli et al. 2010, McGill 2010). However, we know of no studies showing how local

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competitive effects scale up to determine species distribution patterns.

In the present investigation, we assess competition using an approach that allows us to understand how local occupancy dynamics scale up to determine species distribution patterns. Specifically, we studied the invasion of an area by one species, the Barred Owl (*Strix varia*), that is a purported competitor of an established species of conservation concern, the Northern Spotted Owl (*Strix occidentalis caurina*; see Plate 1). Our focus on a dynamic system, as opposed to static range distribution maps, provides a unique opportunity to understand the impacts of competition over time in a heterogeneous landscape, as the invading competitor goes from being virtually absent to widespread. Since the two species we studied have overlapping, but distinct, habitat preferences (Wiens 2012), our study also allows us to investigate how competition affects the relationship between occupancy and habitat covariates. This work is thus expected to inform general theory about competition and coexistence in multispecies metapopulation systems in fragmented habitat (Holt 1997, Nee et al. 1997, Taneyhill 2000, Leibold et al. 2004). It will also allow us to evaluate the effects of competition on species distributions, as well as conservation efforts directed at persistence of Northern Spotted Owls in the face of increasing Barred Owl populations (Kelly et al. 2003, Gutiérrez et al. 2007).

Competition between Barred Owls and Northern Spotted Owls is receiving considerable attention because of the recent invasion of the Pacific Northwest by the Barred Owl, the threatened status of the Northern Spotted Owl, and associated management implications (Kelly et al. 2003, Olson et al. 2005, Gutiérrez et al. 2007, Forsman et al. 2011). The two owl species have overlapping habitats and diets, and Barred Owls are believed to be the superior competitor based on their larger size, more aggressive behavior, higher fecundity, and broader use of habitats and prey items (Hamer et al. 2007, Singleton et al. 2010, Wiens 2012). Dynamic single-species occupancy modeling has been used in two previous analyses to study how Barred Owls affected occupancy dynamics of Northern Spotted Owls (Olson et al. 2005, Dugger et al. 2011). While useful, these studies failed to incorporate the population dynamics of Barred Owls, including the effects of dispersal limitation on colonization and extinction rates (Hanski 1999, Yackulic et al. 2012), as well as the reciprocal competitive effects of Spotted Owls on Barred Owls, making it impossible to project future dynamics of the two-species system. In addition, these studies used Barred Owl detections and did not account for the high probability that Barred Owls were present in many patches in which they were not detected. Moreover, Barred Owl detection may be lower when Spotted Owls are present (Bailey et al. 2009), so failure to model the detection process has the potential to bias estimates of the competitive effect of Barred Owls on Spotted Owls.

We used a modeling framework that combined multistate–multi-season occupancy modeling (MacKenzie et al. 2009) and autologistic modeling (Yackulic et al. 2012), while accounting for the detection process to study the dynamics of these two species over a 22-year period in an area of  $\sim 1000$  km<sup>2</sup>. Using this framework, we developed specific models based on different hypotheses about effects of competition, neighborhood occupancy, and habitat on the dynamics of the two-species system. We used a sequential approach to identify the best model for the system using model selection based on Akaike's information criterion (AIC) and used the best model identified through this process to predict future dynamics of the system with and without competitive effects. We also considered the costs, in terms of Barred Owls removed and corresponding searching effort, and the benefits, in terms of equilibrium Northern Spotted Owl occupancy, of managing Barred Owl occupancy at various levels.

## MATERIALS AND METHODS

### *Study area and field methods*

Our analysis is based on 22 years of detection data from 158 contiguous survey polygons (i.e., "patches") that covered an area of  $\sim 1000$  km<sup>2</sup> on the Roseburg District of the Bureau of Land Management in western Oregon, USA (hereafter "Tyee Study Area"). Survey polygon boundaries were delineated based on topography and location of Spotted Owl home ranges. Most, and often all, survey polygons were surveyed every year from 1990 to 2011, and surveyed polygons were visited multiple times between 1 March and 31 August to locate and band the owls and document numbers of young produced (Anthony et al. 2006, Forsman et al. 2011). Surveyors targeted Spotted Owls by imitating their calls (Forsman 1983, Reid et al. 1999). Barred owls were often detected during surveys because they responded aggressively to Spotted Owl calls (Kelly et al. 2003, Crozier et al. 2006). The primary emphasis of these surveys was to identify Spotted Owl breeding pairs, so occupancy of this species was defined in terms of pairs. In a few instances, surveyors were unable to find a mate after exhaustive searches, and these detections of Northern Spotted Owl singlets were treated as a nondetection (of a pair). For Barred Owls, we defined occupancy to include both paired and unpaired individuals, because a more exact assessment through follow-up surveys was usually not made.

Our survey polygons encompassed a mosaic of forest stands of various ages, ranging from recent clearcuts to old-growth forest over 200 years old. Because differences in habitat can be important to coexistence of potential competitors (Leibold et al. 2004), we used habitat covariates in our modeling. We focused on two habitat covariates that performed well in a previous study of Barred Owl dynamics and that were similar to covariates used in many previous analyses of Spotted Owl occupancy. The first covariate was based on the total

amount of older forest within each survey polygon. We calculated the amount of older forest based on a 1988 stand age map (Cohen et al. 2001) in which all map pixels with forest ages  $\geq 80$  years old were considered “old forest.” We updated the map for all years from 1989 to 2008 using LandTrendr data (Kennedy et al. 2010) to remove forest that was harvested or burned. The second covariate was a proxy for riparian forest and was calculated based on the amount of older forest within 120 meters of second-order or greater streams (Strahler 1957). While there was substantial overlap in these two covariates ( $R^2 = 0.76$ ), we hypothesized that 22 years of data for 158 large survey polygons would give us sufficient power to distinguish the effects of different forest types. To avoid potentially spurious results, we did not fit models where the colonization and extinction rates of a species are based on both covariates. Both covariates were standardized to have a mean of 0 and a standard deviation of 0.5.

#### Model descriptions

In order to understand the dynamics of a two-species system in which habitat, competition, and autologistic effects are all important, we combined two recently developed modeling frameworks: multi-season, multi-state models (MacKenzie et al. 2009, Miller et al. 2012) and multi-season, autologistic models (Bled et al. 2011, Yackulic et al. 2012). Each survey polygon within the study area was necessarily in one of four mutually exclusive states during a breeding season: both species present (state 3), only Northern Spotted Owls present (state 2), only Barred Owls present (state 1), and neither species present (state 0). Owl surveys are characterized by imperfect detection (Reid et al. 1999, Bailey et al. 2009); thus states were not observed perfectly. Observation state 0 (no detections of either species) admits the possibility that the sample unit may be in any of the four possible true states. Observation state 1 (Barred Owl detected only) admits the possibility of true states 1 (Barred Owl only present) and 3 (both species present). Similarly, observation state 2 admits the possibilities of true states 2 and 3, whereas observation state 3 is known to be in true state 3. The imperfect detection process was modeled using parameters,  $p_i^{l,m}$ , indicating the probability that a patch in true state  $m$  at time  $t$  was observed to be in observation state  $l$ . These detection parameters were modeled as linear-logistic functions of survey-specific covariates (see next section) and the true state.

Occupancy state dynamics are characterized generally using state transition parameters,  $\phi_i^{l,m}$ , reflecting the probability that a patch in true state  $l$  at time  $t$  is in true state  $m$  at time  $t + 1$  (MacKenzie et al. 2009). For this two-species system, the transition probabilities are written as functions of species-specific probabilities of local colonization and extinction (see Miller et al. 2012). For example, let  $\varepsilon_t^S$  denote the probability that Northern Spotted Owls (S) are absent from a patch at time  $t + 1$  (local extinction), given presence in the patch at time  $t$ .

Similarly, let  $\gamma_t^B$  denote the probability that Barred Owls (B) are present in a patch at time  $t + 1$  (colonization), given that they are absent from the patch at time  $t$ . Thus, we can write the probability of a patch moving from state 2 to state 3 as:  $\phi_i^{2,3} = (1 - \varepsilon_t^S)\gamma_t^B$ . That is, Spotted Owls do not go locally extinct, but remain present in the patch, and Barred Owls colonize the patch. These species-specific probabilities of colonization and extinction are themselves modeled as dependent on survey polygon characteristics (habitat covariates) and on the presence of the other species in the survey polygon at time  $t$ . This multistate framework thus allows for the incorporation of competitive effects in which the local extinction probability for Northern Spotted Owls, for example, may be increased by the presence of Barred Owls. Thus,  $\varepsilon_t^S$  may differ depending on whether the patch is in state 2 (Northern Spotted Owls only) or state 3 (both owl species present) at time  $t$ , with competitive effects indicated by a greater  $\varepsilon_t^S$  when the patch is in state 3. Finally, note that presence or absence of a potential competitor species is not a standard covariate in these models, as true occupancy state of the competitor species is characterized by the same uncertainty that characterizes occupancy state of the focal species.

The incorporation of autologistic modeling acknowledges the potential importance of “neighbor effects” in metapopulation ecology and the dynamics of species invasions (e.g., Hanski 1999, Williamson 1999). Specifically, including an autologistic covariate permits the modeling of local colonization of a survey polygon by a focal species as a function of the occupancy of neighboring survey polygons by the species, with greater neighborhood occupancy perhaps leading to a larger probability of colonization (Bled et al. 2011, Yackulic et al. 2012). Similarly, local extinction may be expected to decrease for patches whose neighborhoods include high patch occupancy of conspecifics (e.g., Brown and Kodric-Brown 1977). Ideas about what area constitutes a neighborhood obviously vary according to species and their associated dispersal abilities. In the case of Northern Spotted Owls and Barred Owls, characterized by potentially long dispersal distances, it is reasonable to include our entire study area as the relevant neighborhood (Yackulic et al. 2012). Our models thus incorporated these neighbor effects, such that species-specific probabilities of colonization and extinction were modeled as linear-logistic functions of average conspecific neighborhood occupancy, as well as of focal patch occupancy of competitor species and habitat covariates.

As an example of our modeling of patch-specific vital rates, consider the following model for local extinction probability of Northern Spotted Owls in survey polygon  $i$ , year  $t$ :

$$\text{logit}(\varepsilon_{i,t}^S) = \beta_0 + \beta_1 \bar{\Psi}_t^S + \beta_2 \Psi_{i,t}^B + \beta_3 H_{i,t} \quad (1)$$

where  $\varepsilon_{i,t}^S$  is the extinction probability for Northern Spotted Owls in patch  $i$  between years  $t$  and  $t + 1$ ,  $\bar{\Psi}_t^S$  is the average patch occupancy for Northern Spotted Owls

over the entire study area in year  $t$  (i.e., an autologistic effect),  $\psi_{i,t}^B$  is the probability that patch  $i$  is occupied by Barred Owls in year  $t$ ,  $H_{i,t}$  is a habitat covariate for patch  $i$  in year  $t$ , and  $\beta_x$  is a set of parameters defining the nature of the relationships between these covariates and Northern Spotted Owl extinction.

In summary, our modeling represented an attempt to incorporate both intraspecific and interspecific effects on system dynamics, while dealing adequately with the substantial uncertainty that characterized our survey-based observation process. Model parameters were estimated using maximum likelihood in PRESENCE version 4.4, a user-friendly software package (free download *available online*).<sup>6</sup>

#### *Model selection*

Rather than fitting an extremely large model set incorporating all plausible combinations of covariates on all model parameters (6272 models given the contrasts we considered), we adopted a sequential approach to identify the best model. We first identified the best model for detection probability. Secondly, we identified the best model of Northern Spotted Owl baseline (i.e., without habitat effects) colonization and extinction rates, retaining in all models potential effects of Barred Owls on Northern Spotted Owl colonization and extinction based on previous studies. Thirdly, we compared models with additional habitat effects. Finally, we identified the best model with full interspecific interactions (i.e., including reciprocal effects of Northern Spotted Owls on Barred Owls) added to habitat effects. A sequential approach could identify a model component in the early stage as important, even though it is not necessary in a later, more complex model. Therefore, we fit sub-models based on removing single factors from the best model identified in model set 4 to determine if all factors were in fact necessary.

#### *Model set 1: detection probability*

Although sources of variation in detection probabilities for the two species were not of primary ecological interest, the ability to model species-specific detection probabilities reasonably was critical to our modeling effort. Based on Bailey et al. (2009), we predicted lower detection probabilities for Spotted Owls in the presence of Barred Owls. We also predicted that Spotted Owl detection would vary between night, day, and dusk, and specifically that Spotted Owls would be most likely to be detected in daytime surveys (Bailey et al. 2009). Finally, we predicted that Spotted Owl detection probabilities would differ between surveys involving stopping to call at particular stations and surveys entailing continuous walks with calling (Yackulic et al. 2012).

Based on Yackulic et al. (2012), we included survey method, time of day (classified as night, day, and dusk,

depending on hour relative to sunset), and whether the survey occurred in the first or second half of the time series as covariates in the Barred Owl detection function. This last covariate was included to account for increasing Barred Owl densities in the second half of the study as compared to the first half, which led to increased detection probability within occupied survey polygons (because occupied survey polygons often included multiple pairs of Barred Owls). Bailey et al. (2009) analyzed two-species static models and found that Barred Owl detection was affected by Spotted Owl presence. As there is no known biological mechanism for this effect, we hypothesized that it may have been an artifact of the survey methodology. Specifically, surveys were stopped after Spotted Owl detections, leading to a shorter time period in which to detect Barred Owls.

Based on this reasoning, and because their analysis only accounted for Barred Owls, Yackulic et al. (2012) used survey duration as a covariate. Here, we directly compared the hypothesis that Spotted Owls directly affect Barred Owl detection, with an alternative hypothesis that Barred Owl detection is a function of survey length through model comparison. We assessed these hypotheses through comparison of eight models, which differed in the covariates included in their detection functions, but shared the same general structure describing colonization and extinction rates. Specifically, all models used a structure where Barred Owl colonization and extinction rates were described by autologistic functions (Yackulic et al. 2012), Northern Spotted Owl colonization differed between empty survey polygons and survey polygons already occupied by Barred Owls, Northern Spotted Owl extinction rates differed when survey polygons were also occupied by Barred Owls, and Northern Spotted Owl colonization and extinction rates were assumed to differ among years. This structure was based on results from previous analyses of single-species dynamics of both Northern Spotted Owls and Barred Owls (Olson et al. 2005, Dugger et al. 2011, Yackulic et al. 2012).

#### *Model set 2: baseline model of Northern Spotted Owl occupancy dynamics*

A recent study of Barred Owl dynamics at our study site found a strong autologistic effect on Barred Owl colonization and extinction (Yackulic et al. 2012), so we assumed this model for Barred Owl dynamics and used the detection covariates identified in the previous modeling step. Past studies of Northern Spotted Owl occupancy dynamics at the Tye Study Area and elsewhere have either assumed a temporal trend or assumed that colonization and extinction rates varied only in response to Barred Owl detections (Olson et al. 2005, Dugger et al. 2011). We hypothesized that colonization rates might vary substantially among years (even without the effects of habitat and interspecific competition) because studies of Northern Spotted Owl life history suggest that there is substantial yearly

<sup>6</sup> <http://www.mbr-pwrc.usgs.gov/software/presence.shtml>

variation in fecundity (Forsman et al. 2011). We included this effect in our models by having different intercepts for different years. We predicted that yearly variation in colonization might be more substantial than yearly variation in extinction rates because colonization is more directly linked to successful reproduction. We also thought it possible that Spotted Owl colonization and extinction rates might vary as a function of mean occupancy in the landscape since occupancy rates fluctuated around a relatively constant value for the first half of the study period. At the same time, we recognized that it can be difficult to estimate autologistic effects, even when they exist, unless there has been substantial variation in occupancy over the course of a study, for example, during a species invasion or decline (Yackulic et al. 2012). One consequence of this fact is that invasions or declines may substantially accelerate or decelerate as occupancy changes, and this effect may not be predictable from studies when a species is near equilibrium.

We compared seven models that all included a Barred Owl effect on both colonization and extinction of Northern Spotted Owls (i.e., a parameter equivalent to  $\beta_2$  in Eq. 1 was estimated for both colonization and extinction of Northern Spotted Owls in all seven models). In one model, Northern Spotted Owl colonization and extinction also included an autologistic effect (i.e., a parameter equivalent to  $\beta_1$  in Eq. 1 was estimated for both colonization and extinction, in addition to parameters equivalent to  $\beta_0$  and  $\beta_2$ ), while in two other models, only colonization or extinction were represented by autologistic effects, while the other rate was estimated only in terms of an intercept and an effect of Barred Owls. Similarly, we considered a model with year-specific intercepts for colonization and extinction rates for Northern Spotted Owl (i.e., a different  $\beta_{0,t}$  for each period  $t$  and a constant effect of Barred Owls,  $\beta_2$ ), as well as a model in which only the colonization intercept or only the extinction intercept was assumed to vary by year and the other intercept was assumed constant (i.e., a single  $\beta_0$  and  $\beta_2$  were estimated). Lastly, we fit a final model in which both Northern Spotted Owl colonization and extinction included a constant intercept (i.e., a single  $\beta_0$  and  $\beta_2$  were estimated for each of the two rates).

*Model set 3: habitat effects on Northern Spotted Owl colonization and extinction rates*

Previous natural history work (summarized in Gutiérrez et al. 2007), and our own modeling (Yackulic et al. 2012), have shown that Barred Owl extinction is lower and colonization higher in survey polygons that contain larger quantities of older riparian forest. We were interested in whether Spotted Owls responded to the same habitat covariates or if their occupancy dynamics were more closely tied to the amount of older forest in a survey polygon as would be predicted by previous studies (Gutiérrez et al. 2007). Therefore, we

compared seven models that shared in common the best structure identified from model set 2 with the addition of the older riparian forest covariate to colonization and extinction equations for Barred Owls. The seven models differed in whether the older riparian forest covariate, the older forest covariate, or no habitat covariate was used in the equation for Northern Spotted Owl colonization and extinction probabilities, and we did not consider models that included both habitat covariates at the same time. That is, we fit a pair of models in which both Northern Spotted Owl colonization and extinction were a function of either older forest or riparian forest. We fit four sub-models in which only one rate was a function of one of the two habitat covariate. Lastly, we fit a model in which neither rate was affected by the habitat covariates (this model differed from the best model in model set 2 only in that older riparian forest had been added to the equations describing colonization and extinction in Barred Owls).

*Model set 4: interspecific interactions between the two species*

Based on natural history information and studies of Northern Spotted Owl occupancy dynamics (Olson et al. 2005, Dugger et al. 2011), we predicted that presence of Barred Owls in a survey polygon unoccupied by Northern Spotted Owls would decrease the probability that the survey polygon would be colonized by Spotted Owls. Likewise, we predicted that local extinction probability of Spotted Owls would be larger for survey polygons co-occupied by Barred Owls than for survey polygons not occupied by Barred Owls (Olson et al. 2005, Dugger et al. 2011).

Although previous work has focused on Barred Owl influences on Spotted Owls, it is possible that Spotted Owls may influence Barred Owl dynamics as well. In areas where the two owl species are sympatric, there is evidence of substantial diet overlap (Hamer et al. 2001, Wiens 2012). Thus, use of common food resources may lead to reductions in food that might produce lower colonization probabilities and higher extinction probabilities of Barred Owls in patches inhabited by Spotted Owls. We included 16 models in the final set, all of which used the habitat and detection covariates from the best-performing model in the habitat model set. The 16 models varied only in which of the four potential interspecific interactions were modeled.

*Simulating future dynamics*

We used the best model identified through the process described in the *Model Selection* section to project the dynamics of this two-species system into the future. We simulated 1000 trajectories of the 158 survey polygons in our two-species system over the 22 years in which data were collected (initial occupancy was simulated, followed by 21 intervals in which colonization and/or extinction were possible) and through the subsequent 21

years. For each simulation, parameter values were drawn from the multivariate normal distribution based on the maximum likelihood estimates and variance–covariance matrix associated with the best model identified through model selection, with one exception: The year-specific values of the intercept in the Spotted Owl colonization equation were set to their maximum likelihood estimates in those years where colonization was near zero and standard errors were not estimable. Year-specific values of the intercept in the Spotted Owl colonization equation for future years (years 22–42 in the simulation) were drawn randomly from estimates in the second half of the observed record. We assumed that habitat covariates did not change over the second half of the simulation period and used the final observed habitat values for the observed portion of the simulation. We kept track of Spotted Owl occupancy values for each year of each simulation and used these values to estimate expected values and 95% confidence intervals. After examining a few simulations, it became clear to us that Northern Spotted Owls were recovering from declines in many simulations and that such recovery might be unlikely to occur in the real world. Therefore, we kept track of how frequently simulations fell to low population sizes. In particular, we kept track of whether each simulated occupancy trajectory dropped below an occupancy level equivalent to 25, 10, or 5 pairs within the study area. To determine the impacts of interspecific interactions on equilibrium occupancy levels, we ran a second set of simulations using the same basic procedure, but with the interspecific effects set to zero.

#### Management implications

Removal of Barred Owls to benefit Northern Spotted Owls is currently being considered in an experimental framework by the United States Fish and Wildlife Service. We are not involved in these efforts, nor are we advocating for or against this approach. However, we felt our modeling could provide some context for these policy and management decisions. Unlike in island settings, complete removal is unlikely to be an attainable goal, so we instead considered the implications of maintaining Barred Owl occupancy at different levels. Specifically, we estimated the equilibrium Northern Spotted Owl occupancies if Barred Owl occupancy is maintained at levels between 0.05 and 0.95. We also computed the annual removals of Barred Owls that would be necessary to achieve these occupancy levels, and the expected number of hours required to undertake these removals. In calculating these values, we ignored many important issues (e.g., we ignored habitat and the possibility that Northern Spotted Owls may go extinct; we assumed that detection probabilities we estimated also apply to removal efforts and that detection of a single Barred Owl will lead to removal of all other Barred Owls in the survey polygon; and we assumed that removal efforts are done over a sufficiently large spatial

scale to lower regional Barred Owl occupancy), which we address in the *Discussion*. We emphasize that the reported results capture general contours of the problem as opposed to exact values. Caveats aside, we calculated the expected Northern Spotted Owl equilibrium occupancy ( $\psi_{S,Eq}$ ) based on the mean colonization rate over all years of the study ( $\overline{\gamma_S}$ ), the extinction rates for patches that were co-occupied ( $\varepsilon_{S|B}$ ) or singly occupied ( $\varepsilon_{S|-B}$ ), and the target Barred Owl occupancy ( $\psi_B$ ) using the following equation:

$$\psi_{S,Eq}(\psi_B) = \frac{\psi_B \overline{\gamma_S}}{\overline{\gamma_S} + \varepsilon_{S|B}} + \frac{(1 - \psi_B) \overline{\gamma_S}}{\overline{\gamma_S} + \varepsilon_{S|-B}}. \quad (2)$$

We then calculated the annual change in Barred Owl occupancy ( $\Delta\psi_B$ ) associated with the target Barred Owl occupancy and resulting Northern Spotted Owl occupancy in order to determine how many Barred Owls would have to be removed on an annual basis to maintain a given target Barred Owl occupancy. This value was calculated as:

$$\Delta\psi_B = (1 - \psi_B)\gamma_B - \varepsilon_B\psi_B \quad (3)$$

where  $\gamma_B$  and  $\varepsilon_B$  are both functions of  $\psi_B$  and  $\psi_S$ , and were calculated using a logit link and values estimated from the best model.

Lastly, we calculated the expected cost per survey polygon, in terms of hours spent searching,  $\bar{h}$ , for maintaining a target Barred Owl occupancy by first determining the stopping time,  $h^*$ , that satisfies the following equation:

$$\Delta\psi_B = (\psi_B + \Delta\psi_B)p_B(h^*) \quad (4)$$

where  $p_B$  is calculated on a logit scale assuming a mixture of methods and day surveys conducted under conditions better represented by the first half of the study period. We estimated  $h^*$  as the quantity that minimized the following expression:

$$\left| \frac{\Delta\psi_B}{\psi_B + \Delta\psi_B} - p_B(h^*) \right| \quad (5)$$

which was accomplished using the optimize function in R (version 3.15.0). Having obtained the stopping rule,  $h^*$ , we determined  $\bar{h}$  using the following equation:

$$\begin{aligned} \bar{h} = & h^*(1 - \psi_B + \Delta\psi_B) + h^*(\psi_B + \Delta\psi_B) \left(1 - p_B(h^*)\right) \\ & + (\psi_B + \Delta\psi_B)p_B(h^*)E(h|h < h^*) \end{aligned} \quad (6)$$

where the first part of the equation refers to patches that are empty, the second part refers to occupied patches that are not detected before the stopping rule is reached (under these two situations, the patch is searched for  $h^*$  hours), and the third part of the equation refers to the expected amount of time spent searching before detection,  $E(h|h) < h^*$ , for those patches in which

Barred Owls are present and detected. The expected time to detection is defined as:

$$E(h | h < h^*) = \int_0^{h^*} h \frac{dp_B(h)/p_B(h^*)}{dh} \quad (7)$$

Complete R code for all calculations in this section is available in Appendix C.

## RESULTS

### *Model set 1: detection probability*

In agreement with Bailey et al. (2009), we found that Northern Spotted Owl detection probabilities were lower in survey polygons occupied by Barred Owls (Table 1). Survey method also affected detection probability for Northern Spotted Owl (Table 1 and Appendix B). The best model of detection probability for Barred Owls included survey length instead of Spotted Owl occupancy, in agreement with our hypothesis that Spotted Owls affect Barred Owl detection because of an artifact of the sampling procedure (i.e., surveys end if a Northern Spotted Owl is detected, decreasing the amount of time in which Barred Owls can be detected at a site).

### *Model set 2: baseline model of Northern Spotted Owl occupancy dynamics*

All models considered in this set used the best detection probability model from model set 1, included autologistic effects in the Barred Owl colonization and extinction models, did not include habitat effects on any rates, and included an effect of Barred Owl presence on Northern Spotted Owl extinction and colonization. The models in this set differed in whether the intercepts in the colonization and extinction equations for Northern Spotted Owls were constant or varied among years, and if they were constant, whether they were accompanied by an autologistic covariate or not. The best model used year-specific intercepts (i.e., different  $\beta_0$ 's for each year) to describe Northern Spotted Owl colonization and a constant intercept to describe extinction. This agreed with our a priori hypotheses that yearly variation in colonization would be substantial, while the extinction process was less variable and might be adequately modeled by a constant rate. Models that incorporated an autologistic effect for either Northern Spotted Owl colonization or extinction were not favored, which was expected because simulations have shown that autologistic effects are difficult to detect except when species decline or increase substantially during a study period (Yackulic et al. 2012).

### *Model set 3: habitat effects on Northern Spotted Owl colonization and extinction rates*

As hypothesized, Northern Spotted Owl colonization rates were higher in survey polygons that contained a greater amount of older forest. The second best model

also contained older forest in the extinction equation, and suggested that Northern Spotted Owl extinction rates were lower in survey polygons with a greater amount of older forest. Despite the relatively high correlation between riparian and older forest covariates, there was an AIC difference of 13 between the best model including older forest and the best model including riparian forest (Table 1). From 1990 to 2008, the mean amount of older forest per survey polygon declined slightly (from 210 ha to 181 ha), and absolute losses were greater in survey polygons that began with more older forest (e.g., a decline from 291 ha to 248 ha for survey polygons that began above the median value, as opposed to a decline from 130 ha to 114 ha for survey polygons that began below the median value in 1990). These declines were relatively small in comparison to existing spatial variation in the amount of older growth forest among survey polygons (e.g., the variance among survey polygons was 25–32 times the mean variance over time within survey polygons).

### *Model set 4: interspecific interactions*

Building on previous model sets, we considered 16 models that differed in whether one or both species had different extinction rates in co-occupied patches vs. singly occupied patches, and whether one or both species had different colonization rates when the other species was already present in a patch. The four models identified through model selection (Table 1) all supported the inference that extinction probability increases for each species when the other is present, suggesting a strong role of competition in structuring occupancy dynamics. Evidence for the effects of competition on local colonization rates was more equivocal. Two of the top four models suggested that Spotted Owls were less likely to colonize survey polygons that were already occupied by Barred Owls. Interestingly, two of the top four models, including the top two models (with a combined Akaike weight of 0.91), suggested that Barred Owls were more likely to colonize survey polygons already occupied by Spotted Owls. The AICs of models where we removed single factors from the best model (e.g., removing the effect of survey length on detection of Barred Owls) were always worse, suggesting that our sequential approach was adequate in identifying the best model possible given the alternatives considered.

Northern Spotted Owl colonization was highly variable over the 22-year study, reflecting variation in the colonization intercept (i.e., the base rate), as well as the detrimental effect of increased numbers of Barred Owls over time. In contrast, Barred Owl colonization rates steadily increased over the study period (Fig. 1a), which is consistent with increased Barred Owl occupancy over the study duration and the positive autologistic relationship between occupancy and colonization (Appendix A; also see Yackulic et al. 2012). In addition, Barred Owl extinction rates declined over time, while Northern Spotted Owl extinction rates increased (Fig.

TABLE 1. Model selection results.

Spotted Owl			Barred Owl			$\Delta AIC^\dagger$	$w^\dagger$	$K$	AIC
$\hat{\gamma}_S$	$\hat{\varepsilon}_S$	$\hat{\rho}_S$	$\hat{\gamma}_B$	$\hat{\varepsilon}_B$	$\hat{\rho}_B$				
First model set: detection probability									
B, $\beta_{0,t}$	B, $\beta_{0,t}$	MT, B, TD	$\psi_B$	$\psi_B$	SL, $\beta_{2H}$ , TD, MT	0	1	63	16062
B, $\beta_{0,t}$	B, $\beta_{0,t}$	MT, TD	$\psi_B$	$\psi_B$	SL, $\beta_{2H}$ , TD, MT	16	0	62	16077
B, $\beta_{0,t}$	B, $\beta_{0,t}$	MT, B, TD	$\psi_B$	$\psi_B$	S, $\beta_{2H}$ , TD, MT	31	0	63	16093
B, $\beta_{0,t}$	B, $\beta_{0,t}$	MT, TD	$\psi_B$	$\psi_B$	S, $\beta_{2H}$ , TD, MT	40	0	62	16102
B, $\beta_{0,t}$	B, $\beta_{0,t}$	B, TD	$\psi_B$	$\psi_B$	SL, $\beta_{2H}$ , TD, MT	328	0	61	16390
B, $\beta_{0,t}$	B, $\beta_{0,t}$	TD	$\psi_B$	$\psi_B$	SL, $\beta_{2H}$ , TD, MT	358	0	60	16419
B, $\beta_{0,t}$	B, $\beta_{0,t}$	B, TD	$\psi_B$	$\psi_B$	S, $\beta_{2H}$ , TD, MT	361	0	61	16423
B, $\beta_{0,t}$	B, $\beta_{0,t}$	TD	$\psi_B$	$\psi_B$	S, $\beta_{2H}$ , TD, MT	383	0	60	16444
Second model set: baseline models for Spotted Owl vital rates									
B, $\beta_{0,t}$	B, ‡	§	$\psi_B$	$\psi_B$	§	0	0.95	43	16058
B, $\beta_{0,t}$	B, $\beta_{0,t}$	§	$\psi_B$	$\psi_B$	§	3.5	0.03	63	16062
B, ‡	B, $\psi_{S,t}$	§	$\psi_{B,t}$	$\psi_{B,t}$	§	4.0	0.02	24	16062
B, $\psi_{S,t}$	B, $\psi_{S,t}$	§	$\psi_{B,t}$	$\psi_{B,t}$	§	5.9	0	25	16064
B, ‡	B, ‡	§	$\psi_{B,t}$	$\psi_{B,t}$	§	12	0	23	16070
B, $\psi_{S,t}$	B, ‡	§	$\psi_{B,t}$	$\psi_{B,t}$	§	12	0	24	16070
B, ‡	B, $\beta_{0,t}$	§	$\psi_{B,t}$	$\psi_{B,t}$	§	12	0	43	16071
Third model set: habitat effects									
F, B, $\beta_{0,t}$	B, ‡	§	R, $\psi_{B,t}$	R, $\psi_{B,t}$	§	0	0.88	46	15993
F, B, $\beta_{0,t}$	F, B, ‡	§	R, $\psi_{B,t}$	R, $\psi_{B,t}$	§	2	0.12	47	15995
R, B, $\beta_{0,t}$	B, ‡	§	R, $\psi_{B,t}$	R, $\psi_{B,t}$	§	13	0	46	16006
R, B, $\beta_{0,t}$	R, B, ‡	§	R, $\psi_{B,t}$	R, $\psi_{B,t}$	§	14	0	47	16008
B, $\beta_{0,t}$	F, B, ‡	§	R, $\psi_{B,t}$	R, $\psi_{B,t}$	§	46	0	46	16039
B, $\beta_{0,t}$	R, B, ‡	§	R, $\psi_{B,t}$	R, $\psi_{B,t}$	§	49	0	46	16042
B, $\beta_{0,t}$	B, ‡	§	R, $\psi_{B,t}$	R, $\psi_{B,t}$	§	53	0	45	16046
Fourth model set: interspecific interactions									
F, $\beta_{0,t}$	B, ‡	§	S, R, $\psi_{B,t}$	S, R, $\psi_{B,t}$	§	0.0	0.59	47	15986
B, F, $\beta_{0,t}$	B, ‡	§	S, R, $\psi_{B,t}$	S, R, $\psi_{B,t}$	§	0.6	0.32	48	15987
F, $\beta_{0,t}$	B, ‡	§	R, $\psi_{B,t}$	S, R, $\psi_{B,t}$	§	2.3	0.06	46	15988
B, F, $\beta_{0,t}$	B, ‡	§	R, $\psi_{B,t}$	S, R, $\psi_{B,t}$	§	3.1	0.03	47	15989
F, $\beta_{0,t}$	B, ‡	§	R, $\psi_{B,t}$	R, $\psi_{B,t}$	§	6.3	0	45	15992
B, F, $\beta_{0,t}$	B, ‡	§	R, $\psi_{B,t}$	R, $\psi_{B,t}$	§	7.1	0	46	15993
F, $\beta_{0,t}$	B, ‡	§	S, R, $\psi_{B,t}$	R, $\psi_{B,t}$	§	8.0	0	46	15994
B, F, $\beta_{0,t}$	B, ‡	§	S, R, $\psi_{B,t}$	R, $\psi_{B,t}$	§	8.8	0	47	15995
B, F, $\beta_{0,t}$	‡	§	S, R, $\psi_{B,t}$	S, R, $\psi_{B,t}$	§	10	0	47	15996
B, F, $\beta_{0,t}$	‡	§	R, $\psi_{B,t}$	S, R, $\psi_{B,t}$	§	13	0	46	15999
B, F, $\beta_{0,t}$	‡	§	R, $\psi_{B,t}$	R, $\psi_{B,t}$	§	14	0	45	16000
B, F, $\beta_{0,t}$	‡	§	S, R, $\psi_{B,t}$	R, $\psi_{B,t}$	§	16	0	46	16002
F, $\beta_{0,t}$	‡	§	S, R, $\psi_{B,t}$	S, R, $\psi_{B,t}$	§	16	0	46	16002
F, $\beta_{0,t}$	‡	§	R, $\psi_{B,t}$	S, R, $\psi_{B,t}$	§	20	0	45	16006
F, $\beta_{0,t}$	‡	§	R, $\psi_{B,t}$	R, $\psi_{B,t}$	§	23	0	44	16009
F, $\beta_{0,t}$	‡	§	S, R, $\psi_{B,t}$	R, $\psi_{B,t}$	§	24	0	45	16010

Notes: Models were compared in each of four sequential model sets. Model notation abbreviations are:  $\hat{\gamma}_B$ ,  $\hat{\gamma}_S$ , colonization by Barred Owls (subscript B) or Spotted Owls (subscript S);  $\hat{\varepsilon}_B$ ,  $\hat{\varepsilon}_S$  extinction for Barred Owls or Spotted Owls;  $\hat{\rho}_B$ ,  $\hat{\rho}_S$ , detection covariates for Barred Owls or Spotted Owls;  $\beta_{2H}$ , change in Barred Owl detectability in second half of study; SL, survey length; TD, time of day (day, dusk, night); MT, survey method (continuous walk, irregular spot call, mixture);  $\beta_{0,t}$ , year-specific intercepts;  $\psi_{B,t}$ ,  $\psi_{S,t}$  occupancy of Barred Owls or Spotted Owls in the study area at the beginning of interval (autologistic effect). Other abbreviations are: B, detection, colonization, or extinction of Northern Spotted Owls being different when Barred Owl are present in a survey polygon; S, detection, colonization, or extinction of Barred Owls being different when Northern Spotted Owls occupy a survey polygon; F, amount of older forest; and R, amount of older riparian forest.

†  $\Delta AIC$  and Akaike weight ( $w$ ) were based only on models within each set, whereas AIC values are comparable across sets.

‡ Time-independent intercept.

§ Detection functions in model sets 2–4 were based on the best model in the first model set.

1b). At the local (patch) scale, Spotted Owls had an extinction probability of 0.09 per year when Barred Owls were not present, as opposed to 0.29 when they were present, while at 2011 occupancy levels, Barred Owl extinction increased from 0.01 to 0.06 when Spotted Owls were present. These results suggest that the increasing population-wide extinction rate for Spotted Owls was at least partly, if not mainly, due to increasing Barred Owl numbers.

*Simulating future dynamics*

Although both species had increased local extinction rates as a consequence of interspecific competition, simulations suggested that competition will have a much more substantial impact on equilibrium occupancy values of Spotted Owls than of Barred Owls. Comparisons based on the final years of simulations with and without interspecific interactions suggested that Spotted

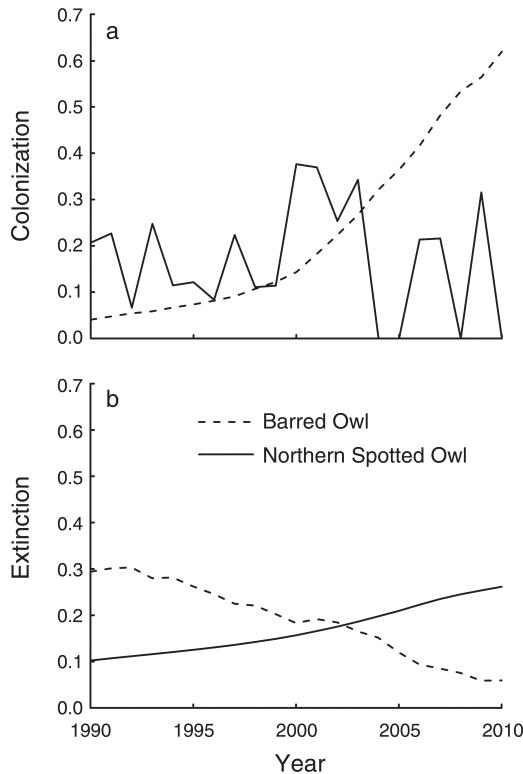


FIG. 1. Mean probabilities of local (a) colonization and (b) extinction for two owl species by year. Values were calculated by averaging over all survey polygons and 1000 simulations.

Owl equilibrium occupancy was lowered from an average of 0.61 to 0.35 (Fig. 2a), while Barred Owl occupancy only declined from 0.98 to 0.96 (Fig. 2b). Uncertainty in future predictions is much higher than our estimates based on historical data because of the uncertainty associated with which years will be good vs. bad years for Northern Spotted Owl colonization rates, a factor that became clear as we examined individual simulations.

We were interested in whether the interspecific relationships that we observed suggested that Barred Owls were likely to competitively exclude Spotted Owls from our study area over the next few decades. On the surface, these simulations suggested that Spotted Owl numbers will be depressed, but that they will not be completely excluded (i.e., go to zero; Fig. 3a). During individual simulations, Northern Spotted Owls would often decline to occupy only a few patches, sometimes even becoming locally extinct over the entire study area, only to quickly recover. For example, in simulation 3 (Fig. 3a), Northern Spotted Owl populations decline to 12 pairs in 2019 and then increase to 57 pairs in 2020 (475% increase in breeding population), while in simulation 1, the breeding population declines to 2 pairs in 2030, followed by an increase to 32 pairs in 2031 (1600% increase in the breeding population). Overall, 54% of our simulations declined below 25 occupied survey polygons

(or pairs, since each occupied survey polygon for Spotted Owls corresponds to a breeding pair) at least once over the 20 year future (Fig. 3b). Likewise, there are 9% and ~2% chances that thresholds of 10 and 5 survey polygons (or pairs) will be crossed over the next 20 years. In contrast, when the Barred Owl effect was set to zero (i.e., without competition), none of the 1000 simulations ever dropped below 25 pairs within 20 years.

We also investigated how the invasion by Barred Owls has affected, and likely will affect, the distribution of Spotted Owls with respect to habitat by comparing the average occupancy for a particular site at the end of our simulations to the expectation based on average colonization rates and assuming no Barred Owl effect (i.e., with Barred Owl occupancy equal to zero for all survey polygons). This analysis indicated that the effect of Barred Owls on Spotted Owls was to flatten the relationship between habitat and occupancy (Fig. 4a). This occurred because many of the highest quality patches for Spotted Owls corresponded to high-quality patches for Barred Owls (Fig. 4b).

*Management implications*

Using values from the best model and code available in Appendix C, we developed rough estimates of the

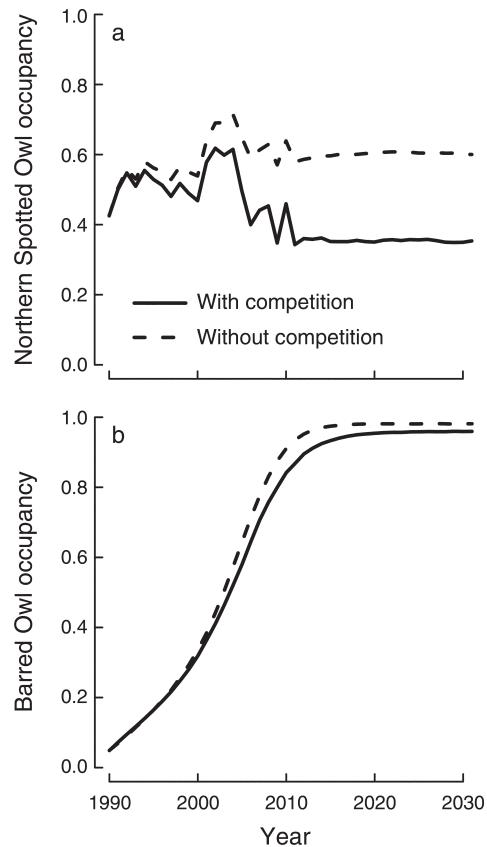


FIG. 2. Effects of competition on (a) mean Northern Spotted Owl occupancy predictions and (b) mean Barred Owl occupancy predictions.

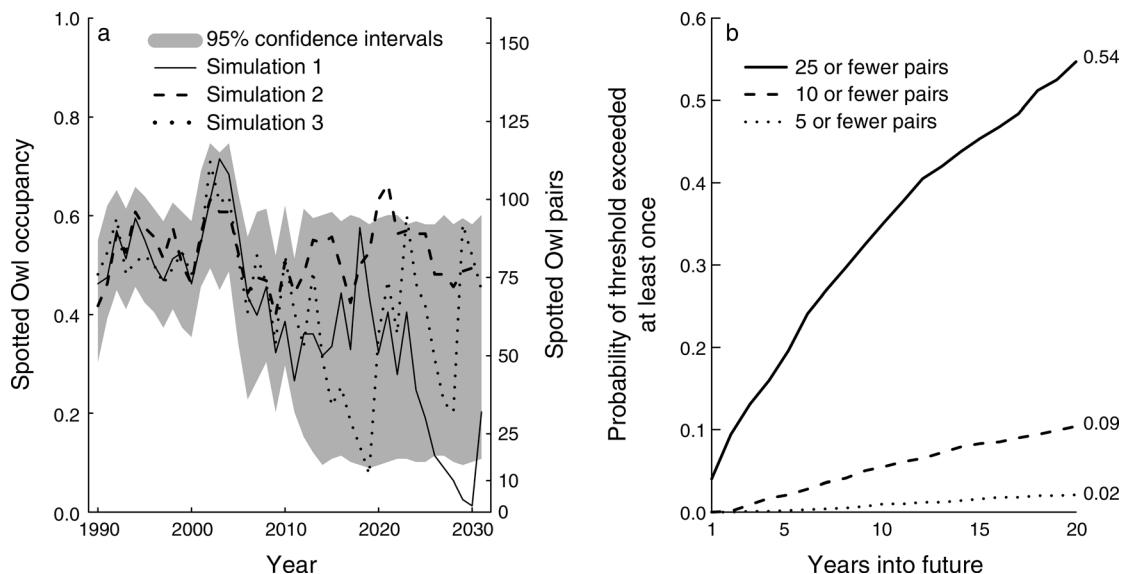


FIG. 3. Northern Spotted Owl occupancy estimated over the course of the 22-year study and simulated over the next 20 years. (a) The fitted model predicts coexistence; however, this prediction assumes that colonization rates are unrelated to conspecific occupancy levels within the study region (i.e., the prediction assumes there is an outside source of colonists). (b) Simulations suggest that there is a high probability that the population will dip below certain thresholds where small-population effects might be important. For example, in 54% of the simulations, the population fell below 25 pairs at least once over 20 years, in 9% of simulations, the population fell below 10 pairs, and in 2.4% of simulations, the population fell below five pairs within 20 years.

expected costs and benefits of managing Barred Owl populations for specific occupancies. These calculations are based on numerous assumptions, and are meant to provide a general guide rather than precise estimates. Nonetheless, the exercise illustrates a number of points relative to proposed management actions. While the benefits of removals (i.e., increases in expected Northern Spotted Owl occupancy) increase linearly as target Barred Owl occupancy is decreased, the costs either in terms of the number of survey polygons that must be cleared of Barred Owls to maintain the target, or in terms of a rough estimate of searching time, show a highly nonlinear response (Fig. 5). The expected searching time here is expressed as the average number of hours that would be spent at a patch and is always lower than the stopping rule (sometimes not by very much), because when Barred Owls are detected, this should almost always occur sometime before the stopping rule is reached. Note that this calculation does not consider the time spent reaching a remote patch or the time spent removing a Barred Owl once it is detected. Whereas the annual change in Barred Owl occupancy peaks at intermediate, but relatively high, target occupancies, the expected search time has a modest peak at intermediate target occupancies, as well as a much more substantial increase at low target occupancies.

#### DISCUSSION

In the future, we hope that more studies of species distribution will focus on processes such as colonization and extinction as opposed to occupancy patterns. One

advantage of focusing on occupancy dynamics is that species interactions are more readily detected than is the case for simple co-occurrence data (Hastings 1987). For example, a previous study at the Tye Study Area, based on static analyses of distribution patterns of the two species, found no evidence of competition (Bailey et al. 2009), whereas we found very convincing evidence. Studies of occupancy dynamics are likely to be especially important in making accurate predictions based on ongoing climate and habitat change because they do not make the restrictive assumptions about systems being in equilibrium that are implicit in static analyses. Inclusion of autologistic elements can also help account for the role of neighborhood characteristics in determining local dynamics and rates of spread. In many cases, unbiased estimates of dynamic rates will also rely on modeling the important aspects of the detection process. Here, we have built on previous studies and strived to represent the detection process to the best of our ability by investigating alternative hypotheses concerning detection covariates. Although all models are imperfect, efforts to control for important processes such as the effects of Barred Owls on Northern Spotted Owl detection rates are essential to obtain reasonable estimates of the effect of Barred Owls on Northern Spotted Owl colonization and extinction rates.

Our analysis focused on a single pair of competitors; however, the general mechanisms we observed are likely to operate in many other systems as competitors invade and, in some cases, exclude resident species. We have provided strong evidence, perhaps the strongest evidence possible in the absence of large-scale replicated exper-

iments, that competition at the patch scale leads to increased rates of local extinction. For Northern Spotted Owls, this effect on local extinction rates is unlikely to directly lead to absolute competitive exclusion, although it will result in reduced equilibrium occupancies of Spotted Owls. In addition, local competition will determine regional persistence if Northern Spotted Owl colonization rates decline in response to declining Northern Spotted Owl occupancy. In other words, if colonization rates do not decline and there are sources of colonists outside the study area, then the effects of competition will only be felt at the patch scale, leading to a lower occupancy and abundance of Spotted Owls, but not extirpation and the concomitant change in the geographic range of the Spotted Owls. On the other hand, if patch colonization rates for Spotted Owls decline because of decreasing occupancy, then the effects of local competition will be felt throughout the study area (and beyond) and competitive exclusion will become more likely.

Over the study period (1990–2011), Northern Spotted Owl colonization rates were highly variable and were better described using year-specific colonization rates than using an autologistic model; however, this is not unexpected given the sensitivity of Northern Spotted Owl fecundity to highly variable climatic conditions (Glenn et al. 2010, Glenn et al. 2011) and the difficulty in distinguishing autologistic effects early in a decline or invasion (Yackulic et al. 2012). Common sense suggests that at some level of occupancy, Spotted Owl colonization rates must decline, just as Barred Owl colonization rates were limited during the beginning of their invasion by the lack of sources of colonists. For example, 1600% annual increases in the number of Northern Spotted Owl breeding pairs, such as observed in some simulations (simulation 1; Fig. 3a) are highly unlikely. Moreover, since Barred Owls have also invaded the areas surrounding the study area, and habitat loss for Spotted Owls is probably higher on nonfederal lands outside of the study area, inputs of colonists from surrounding areas in the future are likely to be low. Northern Spotted Owls have already declined dramatically in much of the Northern portion of their range, where Barred Owls first invaded (Forsman et al. 2011), providing further empirical support for the likelihood of future competitive exclusion on the Tye Study Area.

It is also possible that we underestimated the effects of competition from Barred Owl pairs on Northern Spotted Owl pairs because we were unable to define Barred Owl occupancy in terms of pairs (recall that we defined Northern Spotted Owls in terms of pairs, because surveyors visually determined that pairs were present on each survey, while Barred Owl occupancy could include single individuals because surveyors did not confirm the presence of Barred Owl pairs visually). If Barred Owl pairs have a greater negative effect than single Barred Owls on Northern Spotted Owls, the effect we estimated represents the aggregate effect of a mixture

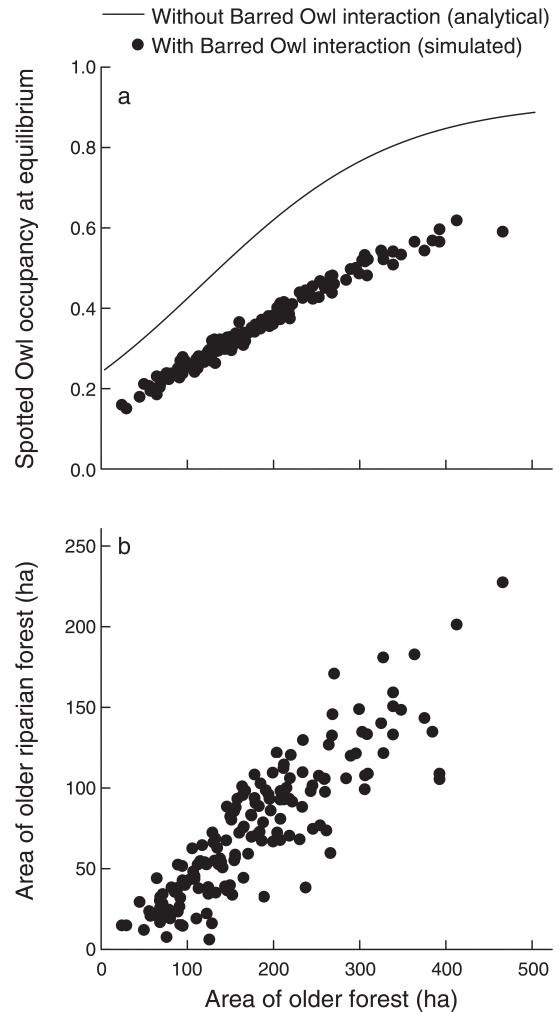


FIG. 4. (a) Presence of Barred Owls leads not only to a drop in average occupancy of Spotted Owls, but also to the weakening of the association between the amount of older forest ( $\geq 80$  years old) in a survey polygon and probability of Spotted Owl occupancy. (b) This occurs because, although Barred Owls and Spotted Owls have different habitat preferences, the amounts of these two habitats are highly correlated ( $R^2 = 0.77$ ) at the survey polygon scale within our study area (plot and  $R^2$  based on the distribution of habitat in 2008).

of single and paired Barred Owls, and if the proportion of survey polygons with pairs of Barred Owls increases over time, then we may underestimate future effects of competition.

Even without including declining colonization in our simulations (and potentially underestimating future effects of competition), the number of survey polygons with breeding pairs of Spotted Owls frequently fell to low numbers (Fig. 3b). For example, in 54% of our simulations that included competitive effects, the population in our study area fell below 25 pairs of Spotted Owls at some point within the next 20 years. In 9% of the simulations, the population fell to fewer than 10 pairs, and in 2.4% of the simulations, the population fell

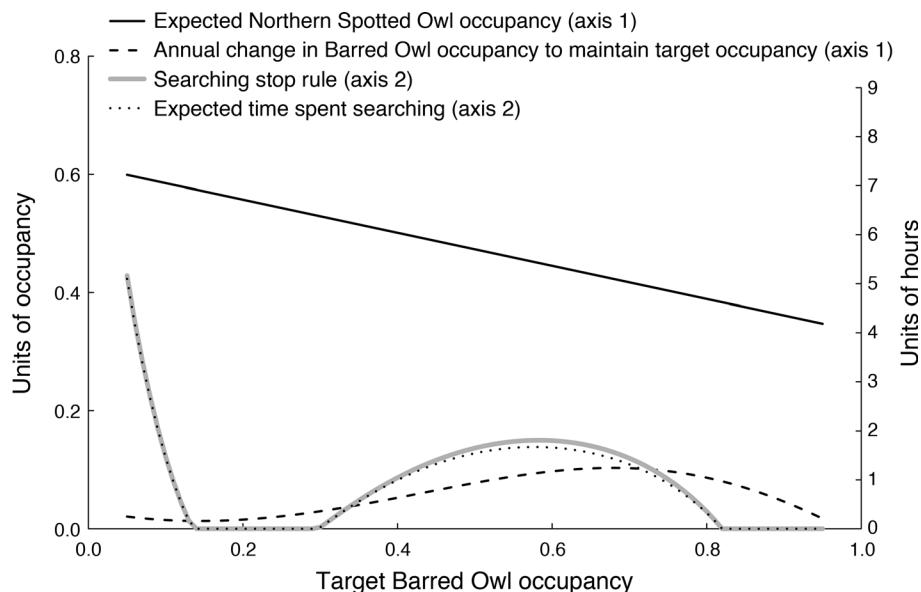


FIG. 5. Comparison of the expected costs and benefits of hypothetical management of Barred Owl occupancy suggests that maintaining Barred Owls at relatively low occupancies ( $\sim 0.2$ ) may minimize long-term costs, while also benefiting Northern Spotted Owls nearly as much as eradication would benefit them. The benefit is expressed as the expected average occupancy of Northern Spotted Owls. Costs can be measured either in terms of the number of Barred Owls that would have to be removed annually to maintain a given level of Barred Owl occupancy or as the expected number of hours surveyors would have to spend searching at each site to ensure the appropriate number of removals.

below 5 pairs at some point (Fig. 2). In contrast, when competitive effects were left out of simulations, the population did not decline below 25 pairs within the next 20 years in any of the 1000 simulations. The potential for extirpation of the population at our site is particularly disturbing because, until recently, this population was one of the most stable Spotted Owl populations of all those under study in this region (Anthony et al. 2006, Forsman et al. 2011), and the amount of habitat loss in recent decades has been modest (e.g., temporal variation in the amount of older forest is substantially smaller than the pre-existing spatial variation among potential survey polygons).

In recent years, there has been considerable attention given to species distribution models based on the distribution of habitat and/or climate. Here, we have shown that the effect of habitat on the distribution of Northern Spotted Owls at the patch scale is modified by species interactions. Since the distribution of Barred Owl and Northern Spotted Owl habitat is highly correlated at the survey polygon scale (Fig. 3b), the effects of competition on Spotted Owls are most apparent in areas that are otherwise the most suitable (Fig. 3a). While Northern Spotted Owls still prefer survey polygons with a greater area of older forest, regardless of Barred Owl prevalence within the landscape, the relationship between amount of older forest and probability of Spotted Owl occupancy becomes less pronounced as Barred Owls become more common. The degree to which this observation generalizes to other study areas within the Northern Spotted Owl range is likely to depend on the

degree of correlation between preferred Barred Owl and Northern Spotted Owl habitat in other areas. Within our area, studies of Northern Spotted Owl habitat associations early in the Barred Owl invasion would have been expected to find stronger habitat relationships than studies conducted more recently. This example illustrates the difficulty in predicting species occupancy patterns based purely on habitat and climatic variables.

The two best models in our analysis included a positive effect of Northern Spotted Owl occupancy on Barred Owl colonization rates. While this result is unexpected based on a hypothesis of competition, it could be a consequence of the imperfect nature of our habitat covariates (another general concern when predicting species occupancy patterns). That is, there may be some habitat cue, not accounted for in our crude habitat proxies, that Barred Owls use to choose survey polygons, and this habitat cue may be correlated with Northern Spotted Owl occupancy. Alternatively, Barred Owls may be using the presence of Spotted Owls as a habitat cue. While the latter explanation seems less likely, there is extensive evidence suggesting that Barred Owls seek out and aggressively confront Northern Spotted Owls that are vocalizing, so there is clear evidence that Barred Owls can easily determine where Northern Spotted Owls are found.

Although Northern Spotted Owls suffer more from competition, we have shown that there are effects of Spotted Owls on Barred Owls. Extinction rates for Barred Owls increased from 0.01 to 0.06 when they co-occupied survey polygons with Spotted Owls. However,



PLATE 1. Male Northern Spotted Owl photographed in the study area (Oregon, USA). Photo credit: J. Reid

equilibrium occupancy of Barred Owls only decreased from 0.98 to 0.96 in the presence of equilibrium Spotted Owl occupancy. Declines in Barred Owl occupancy are minimized because Barred Owls have extremely high colonization rates now that occupancy has increased and there are many sources of colonists (Fig. 1a), and because declining Spotted Owl occupancy means that Barred Owls are less frequently co-occupying survey polygons than they did at earlier times.

Barred Owl removal has been proposed as a management option, and if this management option is pursued, our study provides some insights. To be absolutely clear, in providing interpretation of our results with respect to proposals to remove Barred Owls, we are neither endorsing nor discouraging Barred Owl removal as a management tool. Our simple calculations of costs and benefits related to maintaining Barred Owl occupancy at various levels rest on a

number of assumptions. Firstly, we assumed that the Barred Owl detection function was a reasonable proxy for the amount of time that would be spent searching for Barred Owls if removal efforts were attempted. This is likely to underestimate searching time if the goal is removal of all Barred Owls, as opposed to a single Barred Owl from a survey polygon because the survey polygons could contain multiple pairs of Barred Owls (Wiens et al. 2011). This effect could be limited by searching for Barred Owls at a finer scale (Northern Spotted Owl territories are two to four times larger than Barred Owl territories [Hamer et al. 2007, Wiens et al. 2011]). In addition, it is likely that surveys designed specifically for Barred Owls would be more efficient than the surveys considered here, which were designed primarily for detection of Northern Spotted Owls. Our simple calculations also assumed that removal efforts are conducted over a sufficiently large scale.

Importantly, while these caveats may change the exact values in Fig. 5, they should not change the general pattern, and this exercise outlines many important aspects of the management problem. Firstly, since Barred Owls will constantly disperse into the study area, complete eradication is unlikely. Secondly, at lower Barred Owl target levels (~0.15 or less), there is very little annual change in Barred Owl occupancy; however, the amount of time spent searching to counteract these small changes is large, because so much time is spent searching patches that do not in fact have Barred Owls. At some low, but intermediate level (around 0.2 based on our calculations) costs, both in terms of the number of patches that must be cleared of Barred Owls and in terms of search time per patch, are minimized. At higher target occupancies, search costs are relatively modest, but a large number of Barred Owls must be removed each year because of higher colonization rates. While we did not consider habitat variation among patches in our simple calculations, managers might also explore whether it is more effective to focus removal efforts on patches with higher amounts of older forest. In addition, it will be sensible to focus initial removal efforts on areas where Northern Spotted Owls have typically had high reproductive rates and/or that are currently or have recently been observed to be occupied by Northern Spotted Owls. Importantly, any Barred Owl removal efforts will have to be conducted indefinitely in order to be effective.

Our detailed examination of competitive dynamics between Barred and Northern Spotted Owls during the invasion of Barred Owls over a 22-year period suggests that overlap in preferred habitat and changes in the availability of colonists play a key role in determining whether competitive effects remain at the local scale or are amplified to determine patterns at broader spatial scales. Thus, we provide a link between detailed studies at finer scales and work at large scales that has typically been based on analyses of static patterns. Understanding how interspecific interactions modify habitat relationships and how the distribution of habitat can amplify local interspecific interaction will remain a challenge as ecologists seek to predict changes in species distributions in response to ongoing environmental change.

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#### SUPPLEMENTAL MATERIAL

##### Appendix A

Selected estimated coefficients for the top four models from the fourth model set ([Ecological Archives E095-023-A1](#)).

##### Appendix B

Estimates of detection components of model taken from best model in the fourth set ([Ecological Archives E-095-023-A2](#)).

##### Supplement

R code for calculating costs and benefits of maintaining Barred Owl occupancy at various levels ([Ecological Archives E095-023-S1](#)).