Transient dynamics of invasive competition: Barred Owls, Spotted Owls, habitat, and the demons of competition present

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Abstract. The recent range expansion of Barred Owls (*Strix varia*) into the Pacific Northwest, where the species now co-occurs with the endemic Northern Spotted Owl (*Strix occidentalis caurina*), resulted in a unique opportunity to investigate potential competition between two congeneric, previously allopatric species. The primary criticism of early competition research was the use of current species' distribution patterns to infer past processes; however, the recent expansion of the Barred Owl and the ability to model the processes that result in site occupancy (i.e., colonization and extinction) allowed us to address the competitive process directly rather than inferring past processes through current patterns. The purpose of our study was to determine whether Barred Owls had any negative effects on occupancy dynamics of nesting territories by Northern Spotted Owls and how these effects were influenced by habitat characteristics of Spotted Owl territories. We used single-species, multi-season occupancy models and covariates quantifying Barred Owl detections and habitat characteristics to model extinction and colonization rates of Spotted Owl pairs in southern Oregon, USA. We observed a strong, negative association between Barred Owl detections and colonization rates and a strong positive effect of Barred Owl detections on extinction rates of Spotted Owls. We observed increased extinction rates in response to decreased amounts of old forest at the territory core and higher colonization rates when old-forest habitat was less fragmented. Annual site occupancy for pairs reflected the strong effects of Barred Owls on occupancy dynamics with much lower occupancy rates predicted for territories where Barred Owls were detected. The strong Barred Owl and habitat effects on occupancy dynamics of Spotted Owls provided evidence of interference competition between the species. These effects increase the importance of conserving large amounts of contiguous, old-forest habitat to maintain Northern Spotted Owls in the landscape.

Key words: Barred Owl; colonization; competition; extinction; habitat characteristics; Northern Spotted Owl; occupancy modeling; old forest; Southern Cascades, Oregon, USA; Strix occidentalis caurina; Strix varia.

Introduction

The Northern Spotted Owl (*Strix occidentalis caurina*) was listed federally as threatened by the U.S. Fish and Wildlife Service in 1990, and that status was upheld again during a status review in 2004 (USFWS 2004). The original listing of this species was based on the owl's strong association with old conifer forest and declining trends in both old-forest habitat and owl populations (USDOI 1990). More recently, the Barred Owl (*Strix varia*), another medium-sized owl species, has expanded its range in the Pacific Northwest and has come in contact with the endemic Northern Spotted Owl (Kelly et al. 2003, Livezey 2009). The encroachment of the Barred Owl into what was historically Spotted Owl habitat is expected to pose an additional and compet-

itive threat to Spotted Owl persistence. Compared to the Spotted Owl, the Barred Owl is a larger (Hamer et al. 1994), more aggressive species (Gutiérrez et al. 2007) that uses a broad range of forested habitats, including those used by Spotted Owls (Hamer et al. 2007, Singleton et al. 2010). The Barred Owl also has a more generalist diet (review in Gutiérrez et al. 2007) and smaller home ranges, so it occurs in the landscape at higher densities than Spotted Owls in some areas (3–8 Barred Owl territories per Spotted Owl; Hamer et al. 2007, Singleton et al. 2010).

Historical studies of interspecific competition have, by necessity, been based on patterns of species distributions and abundance (Diamond 1975), with these patterns presented as evidence for the competition process because the process itself could not be tested directly without experimental removal of one species. Unfortunately, pattern does not necessarily reflect process, so quantifying the effect of competition on species distributions has been difficult and historical attempts have been strongly criticized (e.g., Connor and

Simberloff 1979). Currently, little data exists regarding the direct impact of Barred Owls on demography of Spotted Owls, but the use of recently developed occupancy models for Spotted Owls suggest Barred Owls have a negative impact on detection probabilities and colonization rates and increase extinction probabilities on Northern Spotted Owl territories (Olson et al. 2005). By investigating the effects of Barred Owl detections on Spotted Owl colonization and extinction rates on Spotted Owl territories over several years where Barred Owls increased in abundance, we had the rare opportunity to investigate the potential processes associated with interspecific competition rather than inferring a past competitive process from current patterns (i.e., the "ghost of competition past"; Connell 1980). Because Spotted Owls are habitat specialists associated with old conifer forests (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005), we also wanted to investigate the combined effects of Barred Owls and vegetative characteristics around nesting territories on occupancy dynamics of territories.

Because of habitat declines, relationships between demographic parameters of Northern Spotted Owls and forest habitat characteristics have been the primary focus of recent modeling efforts (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). These published studies suggested some unifying relationships between territory quality and owl demographics, particularly the importance of old forests for higher reproduction and survival (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005), but there is a lot of variation in the magnitude of the effects of habitat on demography, and these relationships have not been observed for some areas (K. M. Dugger and R. G. Anthony, *unpublished data*). Implicit in the interpretation of these studies is the assumption that Spotted Owls chose high-quality habitat to improve fitness (Fretwell and Lucas 1970), but that may not always be the case, particularly in the face of deleterious or novel habitat alterations that may not be recognized by the birds (Lloyd and Martin 2005, Shochat et al. 2005). In other words, if external factors, such as competition with Barred Owls, are affecting the quality of Spotted Owl habitat, then relationships between habitat structure and fitness may be decoupled. When habitat selection becomes decoupled from habitat quality, then negative effects on fitness and population dynamics can result in ecological traps (Dwernychuk and Boag 1972, Schlaepfer et al. 2002, Kristan 2003). This may explain why populations of Northern Spotted Owls continue to decline in some areas (Anthony et al. 2006, Forsman et al. 2011), even though large amounts of old forest have been protected throughout the subspecies' range (FEMAT 1993).

Hypotheses regarding the effect of Barred Owls on the habitat selection of Northern Spotted Owls can also be framed in a classic meta-population context where local populations have a substantial probability of extinction and the long-term persistence of a meta-population can only occur at a regional scale by the balance of local extinction and colonization rates (Levins 1969). This classic meta-population model was extended and generalized by Lande (1987) for application to territorial species like the Northern Spotted Owl. By identifying a unit of suitable habitat for individual territories, Lande (1987) established a correspondence between local extinction and the death of individuals inhabiting a territory, and colonization by recruitment and dispersal of individuals into a territory. Most recently, this model has been applied to territorial occupancy of two potentially competing raptor species in relation to habitat availability (Carrete et al. 2005). Their results and the models of Levins and Culver (1971) and Horn and MacArthur (1972) imply that conservation measures for two competing species should require an increase in the amount of suitable habitat in the landscape.

Herein, we describe the relationship between the occupancy dynamics of Spotted Owls in relation to a potential competitor, the Barred Owl, and forest habitat characteristics for a population in the Southern Cascades of Oregon, USA. A natural experiment in the form of dramatic increases in Barred Owl density within the range of the Northern Spotted Owl during the last 10–15 years (see Forsman et al. 2011) has allowed us to investigate the effects of Barred Owl presence on Northern Spotted Owl territory occupancy. The purpose of our study was to investigate (1) the potential competitive effects of Barred Owls on Northern Spotted Owls by determining whether there was a negative relationship between Barred Owl detections and occupancy of breeding territories by Spotted Owls, and (2) the possibility of a synergistic relationship between Barred Owls and the amount of suitable habitat on occupancy dynamics of Northern Spotted Owls. We predicted that, independent of habitat characteristics, Barred Owl detections would increase extinction rates and decrease colonization rates of Spotted Owl territories, thereby decreasing rates of site occupancy. We also predicted an additive effect between Barred Owl detections and habitat characteristics, with higher extinction rates and lower colonization rates expected even when Barred Owls were detected depending on the proportion of older forest and/or fragmentation of older forest surrounding Spotted Owl territories.

Study Area

The Southern Cascades Study Area is one of eight study areas throughout the Northern Spotted Owls' range where data is collected annually on marked individuals to determine survival and productivity as part of the Effectiveness Monitoring Program (Lint et al. 1999) associated with the Northwest Forest Plan (for recent demographic reviews see Anthony et al. 2006, Forsman et al. 2011). This study area was chosen for this analysis because we also had a reliable and accurate map of vegetation characteristics associated with owl territo-

ries on this area, so we were able to investigate associations between occupancy dynamics and both Barred Owl detections and habitat characteristics. The study area is geographically situated on federal lands within the southern terminus of the Oregon Cascades in parts of Douglas, Jackson, and Klamath counties. The climate was characterized by warm summers and cool winters (Baldwin 1973). Annual precipitation occurred mainly during the winter and spring, with summers being characteristically hot and dry. Much of the precipitation at mid to high elevations was in the form of snowfall and a persistent snow cover often extended into late spring. Owl territories were located at elevations ranging from 900 m to 2000 m.

Vegetation primarily reflects five vegetation zones including *Pinus ponderosa*, mixed conifer, *Abies concolor*, *Abies magnifica* var *shastensis*, and *Tsuga mertensiana* from lowest to highest elevation, respectively (Franklin and Dyrness 1973). The study areas was ~2230 km² in size, and >60% of the landscape was covered by mature (80–200 years) or old-growth (>200 years) forest (Anthony et al. 2006).

METHODS

We collected and quantified data to test our predictions with models of occupancy, extinction, and colonization following MacKenzie et al. (2003) and Olson et al. (2005). This included Barred Owl occurrence and habitat characteristics as model covariates. The sampling units for occupancy modeling were individual Spotted Owl territories as delineated by areas with known nesting and roosting activity at any time during the study.

Survey data

Data were collected annually from 1991 to 2006 on marked owls within the Southern Cascades Study Area following a standard protocol used by researchers across the owl's range to estimate survival and productivity (Franklin et al. 1996, Lint et al. 1999). The general field methods for locating and banding of owls, determining sex and age, re-sighting previously marked owls, and determining productivity were described by Franklin et al. (1996), and adaptation of this data for occupancy analysis was described by Olson et al. (2005). Although these survey methods were designed to document survival and productivity, they also were well suited for determining occupancy rates (Olson et al. 2005, Kroll et al. 2010).

Each year, we used multiple vocal lure surveys (maximum = 7–9 per year) with Spotted Owl calls to systematically search sites for territorial owls in areas where Spotted Owl use was documented at any time during the study. Boundaries with calling points for surveys associated with each site were established a priori each year and conformed in general to the median home range size of Spotted Owls in southern Oregon. From these multiple surveys within a year we developed detection histories for each visit to each site, and from this detection/nondetection data across multiple seasons we could estimate occupancy dynamics (MacKenzie et al. 2006). The variation in number of yearly visits corresponded to occupancy rates (i.e., fewer visits were made to sites where owls were detected), variation in nesting phenology, and nest success. However, unequal sampling effort across sites within seasons and the rare occasion when a site was not surveyed at all in a particular year (i.e., primarily due to access), can be accommodated with these open occupancy models as long as we assume occupancy dynamics are the same at sites that are and are not surveyed each year (MacKenzie et al. 2006).

We investigated pair occupancy because breeding pairs are the true ecological unit of interest and the basis for viable, breeding populations. Thus, the data set we analyzed here represents the detection of confirmed owl pairs only (Olson et al. 2005). There were 103 territories surveyed for owls and included in this occupancy analysis for the Southern Cascades Study Area between 1991 and 2006.

A Barred Owl covariate was developed to model the effect of Barred Owl presence on site occupancy dynamics. Following Olson et al. (2005), a year-specific binary covariate was coded as "1" if a Barred Owl was detected on the site during any of the surveys and "0" if not detected. This Barred Owl covariate was both year- and site-specific (Olson et al. 2005), which is an improvement over previous measures of Barred Owl occurrence used in demographic modeling (Anthony et al. 2006). Both extinction (epsilon, ε) and colonization probabilities (gamma, γ) (MacKenzie et al. 2003) are interval estimates encompassing the interval from time i to time $i + 1$, so there are two potential time periods at which Barred Owls might be detected (time i and time $i + 1$), which could affect extinction and colonization rates. In order to address this issue we investigated the relationship between Barred Owl presence at time i (BO) and at time $i + 1$ (BO1) in relation to extinction and colonization probabilities (Olson et al. 2005).

Data on vegetative characteristics were collected from the specific sites occupied by territorial Northern Spotted Owls within the study area, following the general approach used by Franklin et al. (2000), Olson et al. (2004), and Dugger et al. (2005) to link habitat characteristics to Spotted Owl demography. We used 730 m and 2230 m radius circles (167 ha and 1565 ha, respectively) centered on nest sites or primary roost areas (site centers) to represent the core use area and home range of owls, respectively. These areas represent the mean 50% and 95% adaptive kernel utilization distributions, respectively, for estimating home range size (Whorton 1989) as determined from analysis of movement data from a nearby area (Wagner and Anthony 1999). If a different nest tree was used in subsequent years, a new site center was established. If the owls were confirmed to be non-nesting, the site

center for that year was assigned to the previous historic nest location. Habitat attributes for sites with multiple centers were calculated as a weighted mean based on the number of years that a specific center was used. We also characterized vegetation in the 1388 ha area within the home range that was not included within the core area (home range − core = ring).

We identified three general vegetation types of interest: older forest, intermediate-aged forest and non-habitat (Appendix A). Older and intermediate-aged forest represented suitable owl habitat and were broadly classified, corresponding to stages of general forest stand development within the study area. Cover types that received essentially no use by radio-marked owls in a previous study (Wagner and Anthony 1999) and included non-forest, early seres, sapling, and moderate and heavy partial cuts, were combined into a single category called "non-habitat" (Appendix A).

Vegetation within the circles was classified by interpretation of stereo pairs of 1996 color aerial photography (1:12 000) and ground reconnaissance. Classified habitats were mapped onto USGS orthophotoquads, which were subsequently digitized and converted to ArcInfo (ESRI 1991) format. Digitized maps were used to tabulate habitat composition as a proportion of the 167-ha and 1565-ha circular areas. Digitized maps were buffered and converted from vector to grid coverage. Landscape pattern (i.e., fragmentation) indices were estimated from the 1565-ha circular areas with program FRAGSTATS (Appendix A; McGarigal and Marks 1995). General classes of habitat used in generating landscape indices were limited to older forest, and we investigated the five pattern variables that most closely reflected the amount of edge and fragmentation within an owl territory (Appendix A).

Model development

We modeled site occupancy using models developed by MacKenzie et al. (2003) for open populations. We estimated site occupancy for the first primary sampling period (ψ_1), extinction probability (ε), and colonization probability (γ) for primary sampling periods, and detection probability (ρ_{tj}) given presence in survey j (secondary samples within seasons) within primary sampling period t (MacKenzie et al. 2003). All models were generated and occupancy parameters estimated using Program MARK (White and Burnham 1999). Extinction and colonization probabilities were developed for intervals between year i and year $i+1$, and they are conditional on status at year i (time prior to each time interval) (MacKenzie et al. 2003). Because we had a large number of habitat covariates to consider on extinction and colonization parameters, we chose to use a multi-stage approach to build models, which was similar to the approach of Olson et al. (2005). We used an information theoretic approach (Burnham and Anderson 2002) to select the best and competing models at each stage. We also calculated year-specific site

occupancy probabilities using the equation from MacKenzie et al. (2003):

$$\hat{\psi}_t = \hat{\psi}_{t-1}(1 - \hat{\varepsilon}_{t-1}) + (1 - \hat{\psi}_{t-1})\hat{\gamma}_{t-1}.$$

First, we modeled detection probabilities by investigating time trends including linear (T), pseudo-threshold ($\ln T$), and quadratic (TT) trends, as well as general time-specific effects (t) on between and within year detection probabilities, and the annual presence of Barred Owls (BO, BO1). The best detection probability model was retained and used for the rest of the modeling. During the second stage of modeling we investigated time-specific (t) and time trend (T, $\ln T$, TT) models on extinction and colonization probabilities. Finally, Barred Owl covariates were then added to the best time-specific models, and the best model structure for time and Barred Owl effects were used to model the effects of habitat on extinction and colonization rates. A candidate model set for the habitat covariates that described predicted relationships between the habitat variables and occupancy parameters were developed from a set of a priori predictions regarding the direction of effects (Appendix A).

Other studies found relationships between owl demographic parameters and habitat variables that were not linear (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). However, we could not envision a quadratic relationship between extinction and colonization probabilities and habitat characteristics, so our models included only two structural forms (linear and pseudo-threshold) of the habitat covariates.

Model selection

We used information theoretic approaches as detailed by Burnham and Anderson (2002) to select the best models at each step. We used the corrected version of Akaike's information criterion (AIC_c) for small sample sizes and Akaike weights to rank models (Burnham and Anderson 2002:66, 75–79). The degree to which 95% confidence intervals for slope coefficients (β_i) overlapped zero was also used to evaluate the strength of evidence for the importance of variables in competing models (<2 AIC_c values). During modeling we generally selected the model with the lowest AIC_c value as our "best" model unless confidence intervals on slope coefficients suggested there was more support for a closely competing model (within one AIC_c unit of the best model). For habitat modeling, we reduced the total model list by ranking all the models by AIC_c, and then retained only the "best" scale and structure for each variable. We did this to reduce the number of competitive models and redundancy that often resulted when scales and structures for individual covariates were correlated.

RESULTS

Pair occupancy data from the visit histories included a total of 125 secondary sampling periods across all years

and sites during 1991–2006 (16 primary sampling periods). Barred Owls were detected on <5% of the Spotted Owl territories until 1999, when the proportion of territories affected by Barred Owls doubled. Since that time, the proportion of Spotted Owl territories where Barred Owls were detected increased steadily and reached a high of 30% in 2006 (Fig. 1). This increase in Barred Owls provided for a natural experiment by which we were able to investigate the effects on Spotted Owls.

Detection probabilities

We found a time trend on detection probabilities within years for Spotted Owl pairs (Appendix B). The trend within years exhibited a pseudo-threshold structure (lnT), but the direction of the trend on detection probabilities varied between years (Appendix B: Fig. B1). During most of the study, detection probabilities of Spotted Owls decreased and then stabilized throughout the season, but during the later part of this study detection probabilities exhibited a positive pseudo-threshold pattern, with owl detectability increasing, and then stabilizing as the season progressed (Appendix B: Fig. B1).

Detection probabilities between years were modeled to investigate time effects in addition to the effects of Barred Owls. The best model describing detection probabilities included an interaction between the effect of Barred Owls and time ($t \times$ BO; Appendix B: Fig. B1). Excluding the earliest years of this study, detection probabilities <0.20 for pairs were typical when Barred Owls were detected, compared to substantially higher rates (>0.50) when Barred Owls were not detected. This structure including an interaction between time and a Barred Owl effect between years was retained for further modeling along with the pseudo-threshold affect on within season detection probabilities ($p(t \times$ BO, lnT)).

Occupancy parameters

Barred Owl and time effects.—We found strong support for an association between the detection of Barred Owls and extinction and colonization rates of Spotted Owl pairs (Table 1). The detection of Barred Owls in year i was associated with increased extinction rates ($\hat{\beta} = 1.39 \pm 0.34$ [mean $\pm$ SE], 95% CI = 0.67 to 2.11) and decreased colonization rates ($\hat{\beta} = -2.55 \pm 0.72$, 95% CI = -3.95 to -1.14) in year $i + 1$ as predicted. Our best model had strong support as it accounted for most of the AIC weight ($w_i = 0.99$); it also included general time variation (t) on extinction probabilities (Table 1).

Habitat characteristics.—The amount of old forest at the core of home ranges (cOF) most strongly influenced extinction rates for Spotted Owl pairs (Table 2). This was a strong effect, as all the top 10 models contained this effect on extinction probabilities (Table 2). As predicted, extinction rates increased with decreased amounts of old forest at the core ($\hat{\beta} = -0.01 \pm 0.003$, 95% CI = -0.02 to -0.01), and this effect was 2–3 times greater when Barred Owls were detected (Fig. 2).
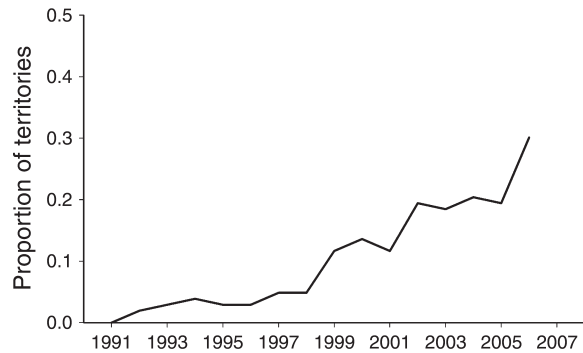

FIG. 1. Annual proportion of Northern Spotted Owl (*Strix occidentalis caurina*) territories with Barred Owl (*Strix varia*) detections (BO covariate) in this study in southern Oregon, USA, 1991–2006.

The strongest effect on colonization rate for pairs was Barred Owls and the $\log_e$ structure of the mean nearest-neighbor distances of old-forest patches (BO + ln_MNNof; Table 2). The 95% confidence intervals for the habitat effect overlapped zero only slightly ($\hat{\beta} = -0.24 \pm 0.12$, 95% CI = -0.48 to 0.01), and the direction of the relationship was negative as predicted (Fig. 3). In addition, the detection of Barred Owls decreased (additive effect) the probability of colonization of vacated nesting territories as the nearest-neighbor distance between old-forest patches increased (Fig. 3). This model had an AIC weight of 0.63 and was ~2.5 times more likely than the second model. The second competitive model (<2 AIC_c) included an interaction between the Barred Owl effect and the distance between old-forest patches, with a stronger effect of habitat on colonization rates when Barred Owls are not present (Table 2).

Mean annual site occupancy was generally high and more variable when Barred Owls were not detected near breeding territories (Fig. 4). In contrast, we observed greatly decreased annual site occupancy rates when Barred Owls were detected, and occupancy rates were consistently low in the latter years of the study when Barred Owls were frequently detected (Fig. 4).

DISCUSSION

The strong effect of Barred Owls on the site occupancy dynamics of Northern Spotted Owls we observed in this study support the hypothesis that these two species are competitors and that the Barred Owl is currently displacing Spotted Owls from historical breeding territories. This was a retrospective study that did not include an experimental control, but rather took advantage of a natural experiment that is ongoing as Barred Owl densities increased over time within the range of the Spotted Owl. Our results indicated a negative effect of Barred Owls on the Northern Spotted Owl and evidence that competition is currently occurring between these two species.

TABLE 1. Model selection results for the 10 best models relating time and Barred Owl (*Strix varia*) covariates to extinction (ε) and colonization (γ) probabilities of Northern Spotted Owl (*Strix occidentalis caurina*) pairs on territories in southern Oregon, USA (1991–2006).

Model	ΔAIC$_c$†	K	w	Deviance
ε(*t* + BO) γ(BO)	0.00	67	0.99	7811.91
ε(*t*) γ(BO)	9.98	66	0.01	7824.07
ε(*t*) γ(lnT + BO)	12.08	67	0.00	7823.99
ε(*t*) γ(*T* + BO)	12.15	67	0.00	7824.06
ε(*t* + BO) γ(.)	22.31	66	0.00	7836.40
ε(*t* + BO) γ(lnT)	23.53	67	0.00	7835.44
ε(*t* + BO) γ(*T*)	24.17	67	0.00	7836.08
ε(*t*) γ(BO1)	26.72	66	0.00	7840.82
ε(*t*) γ(lnT + BO1)	28.47	67	0.00	7840.38
ε(*t*) γ(*T* + BO1)	28.81	67	0.00	7840.72
ε(*t*) γ(*t*)	56.91	79	0.00	7842.41

Notes: Models were ranked according to Akaike's information criterion adjusted for small sample size (AIC$_c$). The model deviance, number of parameters (K), ΔAIC$_c$, and AIC$_c$ weights (w) are given for all models. General time effects (*t*), a linear time trend (*T*), a pseudo-threshold time trend (lnT), a quadratic time trend (TT), and a Barred Owl effect (Barred Owl presence at time *i* [BO] and at time *i* + 1 [BO1]) were added to a base model that included no effect on ψ(.) and the best detection probability structure [*p*(*t* × BO, lnT)]. Plus signs denote additive effects, and ×'s denote interactions. The base model with time dependence on ε and γ is also included for comparison.

† Lowest AIC$_c$ = 7961.93.

Our findings are consistent with, but even stronger than, those reported for Spotted Owl pairs by Olson et al. (2005), who found colonization rates affected by Barred Owl presence for one study area and extinction rates affected on the remaining two. This previous research reported on the effects of time and Barred Owl detections (Olson et al. 2005) on site occupancy dynamics in Oregon. In California, researchers investigated Spotted Owl occupancy in relation to changes in habitat (Seamans and Gutiérrez 2007); however, our study represents the first attempt to describe the synergistic effects of Barred Owls and habitat characteristics of territories on extinction and colonization rates of Northern Spotted Owls.

We observed additive effects of both Barred Owls and habitat characteristics around nesting centers on extinction and colonization of breeding territories by Spotted Owls. The extinction probability of pairs from territories varied from 0.11 to 0.23 when Barred Owls were not detected, but then nearly tripled to 0.33–0.54 when Barred Owls were detected. Conversely, the probability of colonization of vacant territories by pairs varied from

TABLE 2. Model selection results for the 10 best models relating habitat characteristics to extinction (ε) and colonization (γ) probabilities of Northern Spotted Owl pairs on territories in southern Oregon (1991–2006).

Model	ΔAIC$_c$†	K	w	Deviance
ψ(.) ε(*t* + BO + cOF) γ(BO + ln_MNNof)	0.00	69	0.63	7794.67
ψ(.) ε(*t* + BO + cOF) γ(BO × ln_MNNof)	1.90	70	0.24	7794.40
ψ(.) ε(*t* + BO × cOF) γ(BO × ln_MNNof)	3.50	71	0.11	7793.81
ψ(.) ε(*t* + BO) γ(BO + ln_MNNof)	9.52	68	0.01	7806.39
ψ(.) ε(*t* + cOF) γ(BO + ln_MNNof)	11.11	68	0.00	7807.99
ψ(.) ε(*t* + BO) γ(BO × ln_MNNof)	11.58	69	0.00	7806.26
ψ(.) ε(*t* + cOF) γ(BO + rOF)	12.50	68	0.00	7809.38
ψ(.) ε(*t* + cOF) γ(BO + rNON)	12.55	68	0.00	7809.42
ψ(.) ε(*t* + cOF) γ(BO + rGF)	12.57	68	0.00	7809.45
ψ(.) ε(*t* + BO) γ(BO)	12.85	67	0.00	7811.91
ψ(.) ε(*t* + cOF) γ(BO)	13.07	67	0.00	7812.13

Notes: Models were ranked according to Akaike's information criterion adjusted for small sample size (AIC$_c$). The model deviance, number of parameters (K), ΔAIC$_c$, and AIC$_c$ weights (w) are given for all models. Habitat characteristics were added to a base model (included for comparison) containing a Barred Owl (BO) and general time effect (*t*) on extinction rates, a Barred Owl effect on colonization rates, Barred Owl and general time interaction on between-year detection probabilities and pseudo-threshold trends on within-year detection probabilities [ψ(.) ε(*t* + BO) γ(BO) *p*(*t* × BO, lnT)]. These 10 highest ranking models included the following habitat covariates: the pseudo-threshold structure of mean nearest-neighbor distance between old forest patches (ln_MNNof), the amount of old forest at the ring scale (rOF; ring = home range scale – core), the amount of non-habitat at the ring scale (rNON), and the amount of general forest at the ring scale (rGF). Plus signs denote additive effects, and ×'s denote interactions.
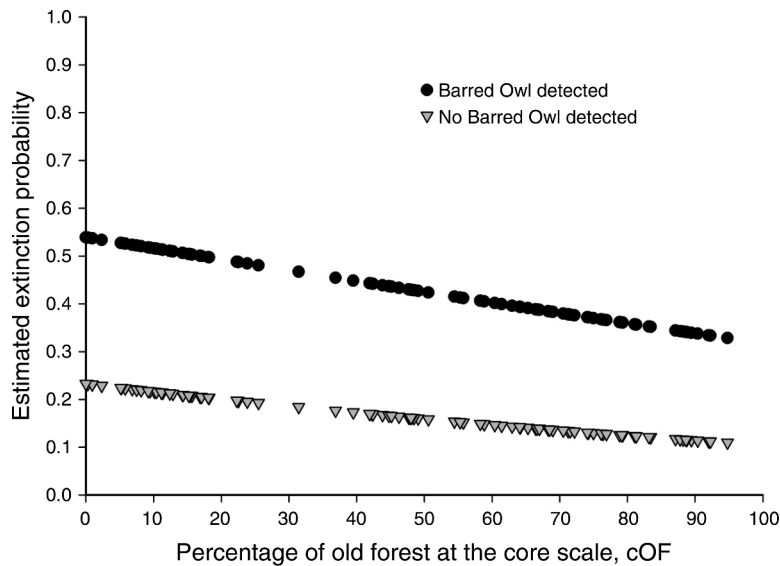
† Lowest AIC$_c$ = 7939.10.

FIG. 2. Mean extinction probability (ε) from 1991 to 2005 for Northern Spotted Owl territories when Barred Owls were detected and not detected plotted against the percentage of old forest at the core scale (cOF). Estimates were generated from the best model [ψ(.) $\varepsilon(t + \text{BO} + \ln\_\text{cOF})$ $\gamma(\text{BO} + \ln\_\text{MNNof})$ $p(t \times \text{BO}, \ln T)$]. The best model included the following: no effects (.) on initial site occupancy (ψ); general time effects (t) plus additive effects of Barred Owls and the pseudo-threshold effect of old forest at the core ($\ln\_\text{cOF}$) on extinction rates (ε); the additive effects of Barred Owls and the pseudo-threshold structure of the mean nearest-neighbor distance between old forest patches ($\ln\_\text{MNNof}$) on colonization rates (γ); a pseudo-threshold trend within seasons ($\ln T$) and an interaction between Barred Owl effects and time (t) across seasons on detection rates (p). The core use area was represented as a 167-ha circle centered on the nest site or primary roost area (site center) of each pair.

approximately 0.33 to 0.73, depending on habitat characteristics when Barred Owls were not detected, but this probability was much lower (0.03–0.20) when Barred Owls were detected. Extinction probabilities for pairs decreased as the amount of old-forest habitat (cOF) near the nest site increased. In addition, colonization probabilities were highest when the nearest-

neighbor distance between old-forest patches ($\ln\_\text{MNNof}$) was the lowest, which corresponds to lower fragmentation of older forest.

Thus, colonization rates for Spotted Owl pairs were higher on territories with old-forest patches that were closer together, indicating owls reoccupied territories at a higher rate when there was less fragmented amounts of
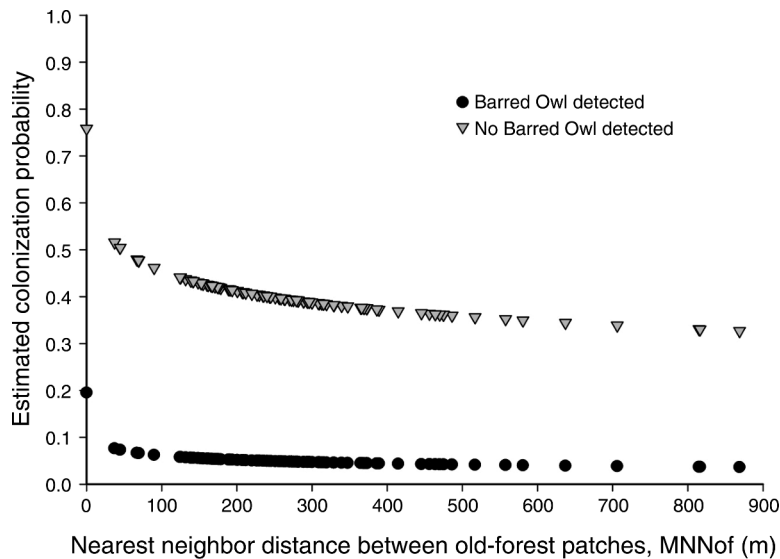

FIG. 3. Estimated colonization probabilities (γ) from 1991 to 2005 for Northern Spotted Owl territories when Barred Owls were detected and not detected plotted against the mean nearest-neighbor distances between old-forest patches (MNNof). Estimates were generated from the best model [ψ(.) $\varepsilon(t + \text{BO} + \ln\_\text{cOF})$ $\gamma(\text{BO} + \ln\_\text{MNNof})$ $p(t \times \text{BO}, \ln T)$]. See Fig. 2 for abbreviations.
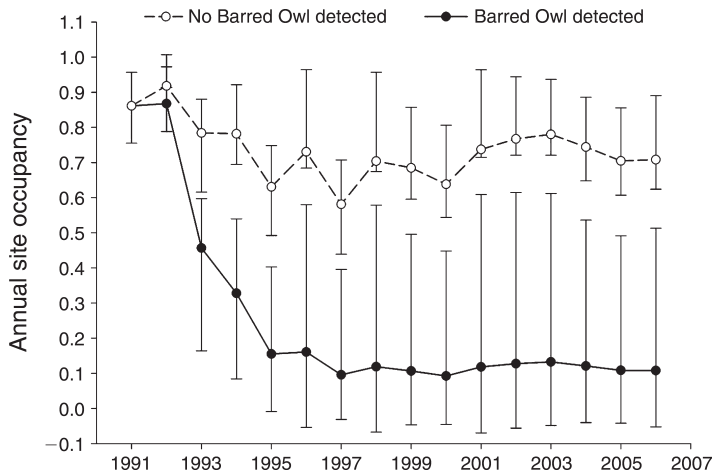
Fig. 4. Estimates of mean annual site occupancy generated across all Northern Spotted Owl territories from 1991 to 2006. Estimates incorporate each combination of territory-specific habitat characteristics and whether Barred Owls were detected or not detected, using initial occupancy, extinction, and colonization parameters from the best model [ψ(.) ε(t + BO + ln_cOF) γ(BO + ln_MNNof) p(t × BO, lnT)]. See Fig. 2 for abbreviations.

old forest at the home range scale. In essence, our results suggest that a balance between extinction and colonization of territories by Spotted Owls (i.e., population stability) will likely be possible only when the amount of old forest in the core (<730 m radius from nest center) is maximized and the amount of fragmentation of this old forest within the home range (<2230 m radius of nest center) is minimized.

These results are consistent with previous demographic models for Spotted Owls in southern Oregon that identified the importance of old forest at the core of their home range on reproduction (Dugger et al. 2005) and survival (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). Old forest at the territory core is necessary for suitable nest sites (Swindle et al. 1999) and to provide prey resources for raising young close to the nest. Our results are also consistent with those reported by Seamans and Gutiérrez (2007) in California, who observed higher colonization and lower extinction rates for female California Spotted Owls on territories with more mature conifer forest.

We did investigate interactions between the best habitat covariates and Barred Owl detections on colonization and extinction rates and found some support for an interaction between Barred Owl detections and the $\log_e$ mean nearest-neighbor distances between old-forest patches (ln_MNNof) on colonization. Thus, the negative effects of forest fragmentation on colonization rates were weaker when Barred Owls were not detected, but less fragmentation did not decrease the effect of Barred Owls, possibly because high-quality, unfragmented Spotted Owl habitat on our study area is also suitable for Barred Owls.

We believe that the interactions between the species is a form of interference competition whereby Spotted Owls are driven from and excluded from their breeding territories by the larger (Hamer et al. 1994) and more aggressive Barred Owl (Gutiérrez et al. 2007). Northern Spotted Owls are food specialists, which prey on medium-sized arboreal mammals (Forsman et al. 2001,

2004), whereas Barred Owls eat a broader range of prey items (Hamer et al. 2001), which is likely the reason Barred Owl home ranges are 3–8 times smaller than those of Spotted Owls (Hamer et al. 2007, Singleton et al. 2010).

The extension by Carrete et al. (2005) of Lande's (1987) territory occupancy model to include two competing species suggests that, in order for both species to persist, there must be exclusively suitable habitat for both species (i.e., areas only used by one of the two species). There is currently little evidence suggesting that suitable Spotted Owl habitat is not also used by Barred Owls (i.e., suitable habitat exclusive to Spotted Owls is very low; Gutiérrez et al. 2007). Conversely, Barred Owls have been documented using a wider range of forest types (younger seral stages with more fragmentation) than Spotted Owls (Kelly et al. 2003, Hamer et al. 2007). Consequently, the loss of late-successional old-growth forest and increased fragmentation of these forests will decrease the amount of suitable habitat for Spotted Owls. The fact that we had no strong support for interactions between Barred Owls and habitat characteristics supports the conclusion that on our study area, exclusive suitable Spotted Owl habitat may not exist, as the degree of fragmentation and amount of old forest at the core did not ameliorate the effects of Barred Owls when they were detected. However, Barred Owls were never detected during the course of this study on 53% of the territories surveyed, so less than half the study area was impacted by Barred Owls. In addition, some Spotted Owl pairs retained their territories and continued to survive and successfully reproduce during our study even on territories where Barred Owls were detected. Thus, there may be refugia where Spotted Owls will be able to coexist with Barred Owls, but much more information is needed on the degree to which these species partition specific resources (exploitive competition) within the habitats used by both species.

In summary, we found that occupancy rates for Northern Spotted Owls were related to the amount and degree of fragmentation of older forest; occupancy increased when the proportion of old forest increased and/or the degree of fragmentation was decreased. In addition, occupancy rates decreased when Barred Owls were detected regardless of the habitat configuration of a territory. Extinction of Spotted Owl territories was lowest in areas where old forests were most abundant, and colonization was highest in less-fragmented forests. The presence of Barred Owls in Spotted Owl territories influenced these relationships, so it's vitally important to consider the effect of Barred Owls when trying to understand the relationship between habitat use/selection and occupancy of Spotted Owls. The number of Spotted Owl territories where Barred Owls are detected each year continues to increase on our study area (Fig. 1), so it's clear the two species have not yet reached equilibrium, and the habitat relationships we observed may change as Barred Owl densities continue to increase.

Finally, our results support those of Carrete et al. (2005), who recommended an increase in suitable habitat for two potentially competing raptors, the Golden Eagle (*Aquila chrysaetos*) and Bonelli's Eagle (*Hieraaetus fasciatus*) in southern Spain. Thus, increased habitat protection for Spotted Owls may be necessary to provide for sustainable populations in the presence of Barred Owls, and it is obvious from our results that these two additive stressors on Spotted Owl populations cannot be decoupled in any conservation efforts. Experimental removal of Barred Owls from Spotted Owl territories will be important to fully understand the effect of Barred Owls on the demography of Northern Spotted Owls (Buchanan et al. 2007) and the potential for interference and/or exploitive competition between the species. The final recovery plan for Spotted Owls (USFWS 2008) recommends these kinds of experiments to understand this relationship more completely, and we support such recommendations.

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APPENDIX A

Acronyms, brief descriptions, and direction of predicted effects of habitat and landscape variables used to model site occupancy dynamics including initial occupancy, extinction, and colonization probabilities of Northern Spotted Owls in southern Oregon, USA, 1991–2006 (*Ecological Archives* A021-108-A1).

APPENDIX B

Model selection results for the 10 best models relating time and Barred Owl covariates to between- and within-year detection probabilities of Northern Spotted Owl pairs on territories in southern Oregon, USA, 1991–2006 (*Ecological Archives* A021-108-A2).