Barred Owls and Northern Spotted Owls
in the Eastern Cascade Range, Washington

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Abstract

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Competitive interactions with barred owls (*Strix varia*) are an important factor contributing to the observed decline in the northern spotted owl (*Strix occidentallis caurina*) population in Washington. My goal was to develop an understanding of barred owl habitat associations at spatial scales corresponding to home ranges and larger landscapes, and to apply that understanding to evaluate potential patterns of population interaction between spotted owls and barred owls in the eastern Cascade Range, Washington. I found that during the breeding season, barred owls used portions of their home ranges characterized as complex-structure mixed grand fir (*Abies grandis*) forest more than open ponderosa pine (*Pinus ponderosa*) or simple-structure Douglas-fir (*Pseudotsuga menziesii*). At a landscape scale, barred owls were associated with a broader range of forest structure and species composition conditions than spotted owls, but barred owls were more strongly associated with gentle slopes in lower topographic positions. Seventy-two percent of the areas used by spotted owls were located on slopes >16 degrees, and 72% of the areas used by barred owls were located on slopes <16 degrees. Overlap between barred owl and spotted owl habitat had a substantial effect on spotted owl pair site occupancy dynamics from 1989 to 2011. Site occupancy probability declined for all of the spotted owl pair sites, but it declined much less for sites with more good spotted owl habitat that overlapped with poor barred owl habitat within 500 ha of the spotted owl activity centers. Despite differences in space use and landscape associations displayed by the two species, displacement by barred owls had substantial detrimental impacts on spotted owl population performance in individual-based population modeling scenarios. The most plausible estimates of barred owl vital rates produced spotted owl population declines of approximately 60% to 80% relative to the spotted owl population estimate without barred owl displacement. Population simulations suggested that this landscape was capable of supporting at least twice as many barred owls as spotted owls, without considering the effects of interspecific competition. When territorial displacement effects were incorporated, this landscape supported more than seven times as many barred owls as spotted owls.

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CHAPTER 1: INTRODUCTION

Interaction with barred owls (*Strix varia*) is an important factor contributing to northern spotted owl (*Strix occidentallis caurina*) population declines (Courtney et al. 2004, Gutierrez et al. 2007, Forsman et al. 2011, USFWS 2011). Spotted owl populations in Washington and northern Oregon declined by approximately 40-60% from 1989 to 2008 (Forsman et al. 2011). Detections of barred owls in spotted owl demography study areas increased substantially during that time (Forsman et al. 2011). Potential impacts of expanding barred owl populations on spotted owls include displacement (Dugger et al. 2011, Kelly et al. 2003, Kroll et al. 2010, Olson et al. 2005), direct mortality (Leskiw and Gutierrez 1998, Van Lanen et al. 2011), competition for prey (Hamer et al. 2001, Wiens 2012), and hybridization (Haig et al. 2004, Kelly and Forsman 2004). Interference competition between the two species may be particularly important for contributing to spotted owl displacement from portions of the landscape occupied by territorial barred owls (Gutierrez et al. 2007, Singleton et al. 2010, Van Lanen et al. 2011, Wiens 2012). However, patterns of displacement of spotted owls and population-level implications of that displacement for spotted owls are not well understood. In 1976, Taylor and Forsman wrote “It seems doubtful that two species so similar in general food and habitat requirements could coexist in the same areas for long, but this relationship remains to be investigated.” Thirty-six years later we are still trying to sort it out.

The work presented in this dissertation was conducted in and around the portion of the Okanogan-Wenatchee National Forest (OWNF: Figure 1.1) within the range of the northern spotted owl. This 1.6 million ha area is characterized by complex, mountainous topography. Elevation ranges from approximately 240 to 2750 m (800 to 9000 ft). Vegetation communities in this area are substantially influenced by the strong moisture gradient associated with the rain-shadow effect of the Cascade Mountains. Annual precipitation ranges from 150 cm in the wettest portions along the Cascade Crest, to 15 cm in the driest eastern edge of the area. Forest types are a mix of moist-mesic conifer forest found in the western portion of the study area (characterized by silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) at higher elevations, and Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and western hemlock (*Tsuga heterophyla*) at lower elevations). Xeric-mesic mixed conifer forest is found at middle elevations through the central portion of the study area (characterized by a mix of Douglas-fir, grand fir, and ponderosa pine (*Pinus ponderosa*)). Dry ponderosa pine woodlands, shrublands, and grasslands are found along the eastern edge of the study area (Johnson and O'Neil 2001, Lillybridge et al. 1995).

Dominant fire regimes in the area range from low frequency – high severity regimes in the moist forest types closer to the Cascade Crest, to high frequency – low severity regimes in the dry forest types in the east (Agee 1993). Much of the mid-elevation mixed conifer zone is within a mixed severity fire regime (Perry et al. 2011). Aggressive fire suppression combined with timber harvest over the last 125 years has contributed to a shift from a mosaic of conditions with substantial areas of open, large tree forest to more uniform distribution of closed canopy, smaller tree stands (Hessburg and Agee 2003). These changes have contributed to conditions conducive to uncharacteristically large, high intensity wildfires, and wildfire has become the primary cause of spotted owl habitat loss in this area (Davis et al. 2011).

Eighty-two percent of the area addressed in this dissertation is within federal land ownership (mostly OWNF, but also a small portion of North Cascades National Park; Figure 1.1). The rest of the area is within state or private land ownership. Within the federal land ownership, 50% was in wilderness or roadless areas, 37% was designated with a special old forest habitat conservation status under the Northwest Forest Plan (Late Successional Reserve, Managed Late Successional Reserve, or Adaptive Management Area), and 19% was designated as matrix lands under the Northwest Forest Plan (Davis et al. 2011).

From 2004 to 2006, I investigated habitat selection by radio-tagged barred owls in the Chumstick and Chiwawa subwatersheds within the OWNF (Singleton et al. 2010). During that study, I conducted call surveys for barred owls across 309 km^2. I confirmed the presence of barred owl pairs at 21 sites, and I collected radiotelemetry movement data on 14 barred owls. I found that barred owl home ranges were located more often than expected in areas with low topographic position, gentle slopes, overstory tree canopy closure >72%, large overstory tree crown diameter, high normalized difference vegetation index (NDVI), and a moderate amount of solar radiation. Much of the work presented in this dissertation builds from that experience.

The focus of this dissertation was to develop an understanding of barred owl habitat associations at spatial scales corresponding to home ranges and larger landscapes, and to apply that understanding to evaluate potential patterns of population interaction between spotted owls and barred owls in drier mixed-conifer forests of the eastern Cascade Range, Washington. In the subsequent chapters of this dissertation, I addressed four research questions focused on barred owl ecology and interactions between barred owl and spotted owl populations. First, I related forest structure characteristics to barred owl intensity of use within home ranges. Second, I mapped and compared landscape-scale habitat associations and habitat overlap for the two species. Third, I evaluated whether habitat overlap patterns influenced spotted owl pair site occupancy dynamics in the Cle Elum spotted owl demographic study area from 1989 to 2011. Fourth, I used individual-based modeling to investigate potential spotted owl population outcomes under a variety of demographic and habitat overlap assumptions. Understanding differences between the two species’ habitat associations at multiple scales, and evaluating the population-level implications of those differences, will contribute to spotted owl conservation planning (USFWS 2011).

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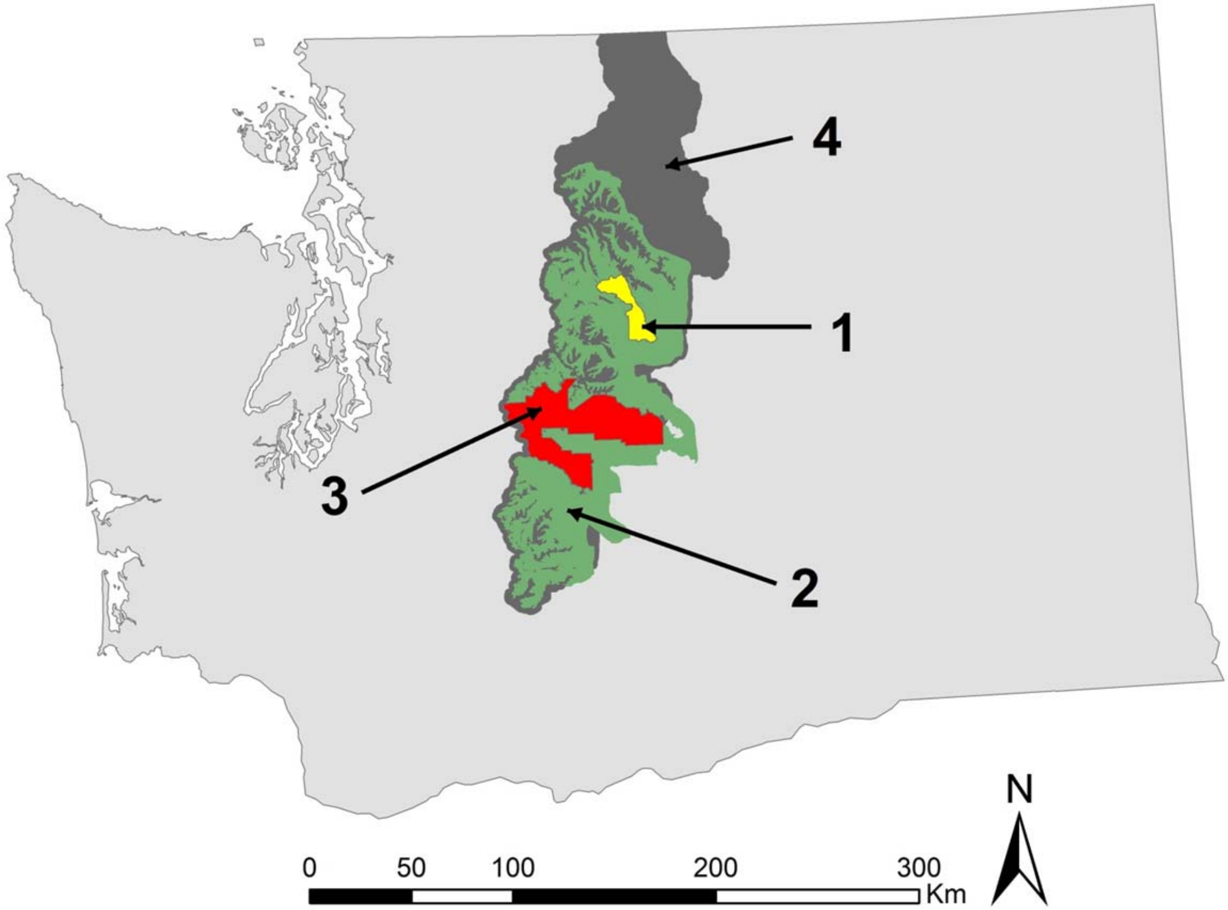
Figure 1.1. Study areas for work presented in each chapter of this dissertation. The overlapping study areas are identified by chapter number: Chapter 1) Forest structure within barred owl home ranges in the eastern Cascade Range, Washington. Chapter 2) Landscape-scale habitat associations for barred owls and spotted owls in the eastern Cascade Range, Washington. Chapter 3) Does overlap of barred owl and spotted owl habitat influence spotted owl pair site occupancy dynamics? Chapter 4) Simulated population-level impacts of territorial interactions with barred owls on spotted owls in the eastern Cascade Range, Washington.



CHAPTER 2: FOREST STRUCTURE WITHIN BARRED OWL HOME RANGES IN THE EASTERN CASCADE RANGE, WASHINGTON.

ABSTRACT

Competitive interactions with barred owls (*Strix varia*) are believed to be an important factor associated with the observed decline of the northern spotted owl (*Strix occidentallis caurina*) population in Washington. Identifying differences between the two species fine-scale habitat associations may help forest managers understand how silvicultural treatments could influence competitive interactions between spotted owls and barred owls. From March 2004 to September 2006 I tracked 14 radio-tagged barred owls (including at least one individual from 12 pairs) in the Okanogan-Wenatchee National Forest in the eastern Cascade Range, Washington. I analyzed forest structure characteristics from 170 plots sampled within areas used by the 12 barred owl pairs where at least one individual was radio-tagged. I identified three forest types present within the barred owl home ranges, including: 1) open ponderosa pine (*Pinus ponderosa*), 2) simple-structure Douglas-fir (*Pseudotsuga menziesii*), and 3) complex-structure grand fir (*Abies grandis*). I compared individual forest structure characteristics and the three forest types to the intensity of barred owl use based on repeated measures of seasonal utilization distribution values at each plot using hierarchical mixed-effects models. Intensity of barred owl use during the breeding season was positively associated with greater abundance of grand fir trees, taller and more diverse tree heights, more total trees per ha, more trees 12.7-

22.9 cm dbh, more tree canopy >4.9 m, and less ground-cover vegetation <0.6 m. During the non-breeding season, intensity of barred owl use was positively associated with more trees 12.7-22.9 cm dbh, more total trees per ha, gentler slopes, and increased tree species diversity. Barred owls used the structurally diverse grand fir forest type more intensively than the other two types during the breeding season. Intensity of use did not differ across the types during the non-breeding season. Comparison of the results from this study to the literature on spotted owl habitat associations suggests that spotted owls in the eastern Cascade Range in Washington may be more likely than barred owls to use Douglas-fir dominated stands, with closed canopies, on steeper slopes, particularly where dwarf mistletoe provides appropriate nesting structures and prey for spotted owls. However, this cannot be tested with the data at hand and remains to be confirmed through more systematic and consistent sampling to compare forest structure attributes in areas used by each species.

INTRODUCTION

Interaction with barred owls (*Strix varia*) is an important factor associated with northern spotted owl (*Strix occidentallis caurina*) population declines (Olson et al. 2005, Forsman et al. 2011, USFWS 2011). Spotted owl populations in Washington and northern Oregon declined by approximately 40-60% from 1989 to 2008 (Forsman et al. 2011). Barred owls were detected at less than 10% of spotted owl sites in demographic study areas in 1989 (Forsman et al. 2011). In 2008 barred owls were detected at up to 60% of spotted owl sites in the demographic study areas in Washington and Oregon (Forsman et al. 2011). Interference competition between the two species may be particularly important for contributing to spotted owl displacement from portions of the landscape occupied by territorial barred owls (Van Lanen et al. 2011, Wiens 2012). Identifying differences between the two species' fine-scale habitat associations, and understanding how those differences may influence competitive interactions between the species, could contribute to the development of landscape management approaches that enhance spotted owl conservation in the face of competition from barred owls (USFWS 2011).

Spotted owl habitat has been characterized as multispecies conifer forest with large (>50 cm dbh) trees, moderate to high (60 to 80%) canopy closure, substantial structural diversity (including snags, down logs, mistletoe clumps, cavities, and broken tops), and canopy layering open enough to allow owls to fly within and beneath it (Thomas et al. 1990:164, Courtney et al. 2004, USFWS 2011). Spotted owls in the eastern Cascades have been found to use a somewhat wider variety of structural conditions than in the western portion of their range, particularly in areas where nest opportunities and canopy structural complexity are enhanced by dwarf mistletoe (*Arceuthobium spp.*) brooms (King 1993, Buchanan et al. 1993 and 1995, Everett et al. 1997, Sovern et al. 2011).

Like spotted owls, barred owls are associated with structurally diverse forest habitats for nesting, foraging, and predator avoidance (Hamer et al. 2007, Livezey 2007, Wiens 2012). As "sit-and-wait" foragers, barred owls use forest stands that provide suitable roosting locations, have tree spacing and canopy structure characteristics that facilitate flight within the stand, and have understory characteristics that facilitate prey detection and capture (Livezey 2007, Mazur and James 2000). Elsewhere, I reported that barred owls tended to locate their home ranges on gentle slopes in relatively low topographic settings, in areas with more green vegetation (as measured by normalized-difference vegetation index: NDVI), more overstory tree canopy cover, and larger trees than the surrounding landscape (Singleton et al. 2010). However, I did not detect substantial within-home range habitat selection patterns based on vegetation maps derived from remotely sensed imagery. Understory structural characteristics are generally difficult to detect based on canopy reflectance values. Vegetation maps derived from remote sensing products in forested environments tend to have moderate to poor accuracy for such characteristics and are generally not well suited for fine-scale habitat selection analysis (for example, Ohmann and Gregory 2002). My inability to detect substantial within-home range habitat selection patterns may have been constrained by the limitations of my vegetation maps derived from remotely sensed data.

My goal for this study was to relate intensity of within-home range space use by barred owls to stand-level forest structure characteristics sampled in the field. I had two objectives in this study: 1) to identify forest structure characteristics that are associated with barred owl use, and 2) to quantify the suite of forest structure characteristics found within barred owl home ranges and evaluate how typical combinations of those characteristics relate to intensity of barred owl use. I expected that closed-canopy forest stands with more complex stand structure, including large trees, logs, and snags, would be used more intensively by resident barred owls than open stands or stands without those structural elements. This information will be useful for forest managers seeking to evaluate the relative effects of silvicultural treatments on barred owl and spotted owl habitat quality.

STUDY AREA

The study area encompassed 309 km^2 in the interior mixed-conifer vegetation zone near Leavenworth and Lake Wenatchee in Chelan County, Washington (120°35’W, 47°48’N, Figure 2.1). This area is within the Wenatchee River Ranger District of the Okanogan-Wenatchee National Forest. Vegetation conditions within the study area are influenced by the strong moisture gradients associated with the rain-shadow effect of the Cascade Mountains and local topography. Average annual precipitation across the study area ranged from 150 cm at the northwest edge to 50 cm at the southeast edge. Forests in the northwestern portion of the study area (closest to the Cascade Crest) were predominantly in moist grand fir (*Abies grandis*) series plant associations, with Douglas-fir (*Pseudotsuga menziesii*) and grand fir as common overstory species (Lillybridge et al. 1995). The southeastern portion of the study area (farthest from the Cascade Crest) supported dry grand fir and Douglas-fir series plant associations, with northern exposures often having an overstory of Douglas-fir, and southern exposures characterized by open ponderosa pine (*Pinus ponderosa*) or non-forest (Lillybridge et al. 1995).

METHODS

I compared intensity of barred owl use to forest structure characteristics at sample plots within barred owl home ranges. I quantified intensity of barred owl use based on seasonal utilization distributions, as described below. Then I used a three-step analysis approach to relate forest structure characteristics to intensity of use. First, I screened individual forest structure characteristics using single-variable models to compare each forest structure characteristic to barred owl intensity of use at the sampling plots. Second, I evaluated the relative importance of forest structure characteristics using a model selection and model averaging approach to evaluate multiple-variable models incorporating all of the forest structure characteristics indicated as potentially associated with owl use in the first step. Third, I used hierarchical cluster analysis to identify a few forest types based on the suite of forest structure conditions found within the barred owl home ranges, and then evaluated the intensity of owl use at sample plots representing each type. I had two objectives for this analysis: 1) to identify forest structure characteristics that were associated with barred owl use (through the single- and multiple-variable modeling), and 2) to provide a more ecologically complete description of the suite of forest structure characteristics found within barred owl home ranges and evaluate how typical combinations of those characteristics relate to barred owl use.

Quantifying Barred Owl Habitat Use

From March 2004 to September 2006 I tracked 14 radio-tagged barred owls, including at least one individual from 12 different resident pairs (Singleton et al. 2010). Locations of tagged owls were documented at least twice a week, with a minimum of 24 hours between locations. Locations documented during the breeding season (1 March to 31 September) were distributed between midday (0800-1600 hr; 37% of locations), morning and evening (0400-0800 hr and 1500-2000 hr: 35%), and night (2000-0400 hr; 29%). During the non-breeding season (1 October to 28 February), locations were generally collected during mid-day because of safety considerations associated with over-snow travel required to access the sites. I calculated utilization distributions for each year and season during which an owl had ≥30 radiotelemetry locations (Singleton et al. 2010). A utilization distribution is a probability density function that estimates the probability of finding the tagged animal at any given point within the home range based on the observed spatial distribution of recorded locations (Marzluff et al. 2004, Millspaugh et al. 2006; Figure 2.2). Lower utilization distribution values indicate more intense use. For example, areas within the 50% utilization distribution isopleth had more intense use than areas within the 100% isopleth (Figure 2.2).

I derived the utilization distributions from fixed-kernel seasonal home ranges mapped at 5% increments using the Animal Movement extension for ArcView (Hooge and Eichenlaub 1997). I used a fixed kernel density smoothing factor (*h*) of 150 m for all kernel home ranges based on the approximate mean of least-squares cross validation calculations for each seasonal home range. Using a single value for *h* ensured that the level of kernel smoothing was consistent across all of the seasonal utilization distributions. I determined the outer boundary (the 100% isopleth) of the utilization distribution for each seasonal home range based on a 150 m buffer of the minimum convex polygon derived from the radiotelemetry locations for that season. These utilization distributions provided repeated measures of the intensity of use for each season and year an individual barred owl was radio-tagged and had adequate location data (Singleton et al. 2010).

Sampling Forest Structure Characteristics

I sampled forest structure characteristics at plots that were randomly located in randomly selected stands within a barred owl home range. The objective of the forest structure sampling was to quantify forest structure at each sample plot, not to map forest structure characteristics across home ranges or characterize entire stands. Plot selection was stratified by stands to provide a representative sample of the variety of forest conditions within the home range. Sample plots were located ≥30m from any stand edge and only one plot was located within a selected stand. Stands were delineated based on the Wenatchee River Ranger District GIS vegetation map updated using orthophoto and remote sensing information (Okanogan-Wenatchee National Forest, Wenatchee WA, corporate GIS data). The goal was to sample approximately 15 plots at each pair site and 10 plots within each utilization distribution. Preliminary analysis of the sample plot data collected during 2006 highlighted that areas with higher levels of barred owl use were inadequately represented in the random sample. In 2008, I sampled 15 additional plots in randomly selected stands that had been heavily used by barred owls.

At each sample plot, I measured live and dead trees, logs, forest canopy characteristics, and other stand structure information (Table 2.1). I recorded data on all trees >12.7 cm dbh within a 7.3 m radius (0.02 ha) plot, and all trees >23 cm dbh within an 18 m radius (0.10 ha) plot. Both plots were centered on the same point. I recorded species, status (live or dead), dbh, total height, height to the lowest live tree crown foliage (unconsolidated live crown), and presence of mistletoe for all trees. I also recorded diameter at mid-point (dmp) and length for all logs >12.7

cm dmp encountered along a 22 m transect following a random azimuth and centered on the plot center. In addition, I calculated percent cover for four vegetation layers (<0.6 m, 0.6-1.8 m, 1.8-4.9 m, and > 4.9 m) using a moosehorn densitometer to determine presence or absence of foliage within each layer at 1 m intervals along the 22 m transect. I calculated the proportion of those points with foliage present to derive percent cover for each layer. Stand structure measurement procedures followed USDA Forest Service Forest Inventory and Analysis (FIA) protocols (USFS 2005). All height measurements were recorded with laser hypsometers (Opti-Logic Corp., Tullahoma TN, model 100LH). These data were collected from August to October 2006 and in August 2008. All covariates were measured in the field except solar radiation, which was estimated using the ArcGIS solar analyst tool (version 9.3, Environmental Sciences Research Institute, Redlands CA).

Statistical Analysis

I assessed the relationship between forest structure characteristics and intensity of barred owl use at each sample plot using three analysis steps. The response variable for all three analyses was the intensity of barred owl use as represented by repeated measures of seasonal utilization distribution probability values at the sample plot centroids. First, I evaluated the importance of each individual structural characteristic using single-variable hierarchical mixed-effects models. Second, I analyzed multiple-variable mixed-effects models including all combinations of the forest structure characteristics that were significant at the $p \leq 0.15$ level in the first step. Third, I used hierarchical clustering to identify a limited number of forest types based on typical combinations of all of the forest structure attributes, and tested the level of owl use across the types using a no-intercept hierarchical mixed-effects model. I analyzed breeding season (March 1 to Sept. 30) and non-breeding season (Oct. 1 to Feb. 28) use separately.

Hierarchical mixed-effects models provide a framework for analyzing non-independent repeated measures data with different sampling intensity across hierarchically correlated study units, like the seasonal barred owl utilization distributions analyzed in this study (Zuur et al. 2009). For example, some of the barred owls were radio-tagged for more than one year, resulting in more than one breeding or non-breeding season utilization distribution for that individual. Some barred owls were also paired, resulting in overlapping and correlated utilization distributions for members of the pair. Combining the forest structure data from the sampling plots with the use intensity estimates from the utilization distributions provided a repeated measure of use at the sample plot for each utilization distribution that encompassed the location of that plot. However, different numbers of forest structure sampling plots fell within different utilization distributions, and use was correlated within each bird for utilization distributions in different years or for paired birds. I specified three random effects levels for the mixed-effects models to address these hierarchical correlation patterns. The hierarchical mixed-effects levels were: 1) the owl pair, to address correlation between overlapping utilization distributions for paired birds, 2) the individual bird, to address correlation when more than one breeding or non-breeding season utilization distribution was recorded for an individual, and 3) a unique code for each seasonal utilization distribution to correctly address the unbalanced sampling across utilization distributions and the repeated measures of use at sample plots that fell within more than one seasonal utilization distribution (Zuur et al. 2009). I calculated separate models for breeding and non-breeding seasons. I conducted the hierarchical mixed-effects modeling analysis using the *lmr* function in the *nlme* package in R (version 15.0, R Development Core Team, Vienna Austria).

I evaluated the importance of 22 forest structure characteristics with single-variable models using this hierarchical mixed-effects model structure. I then used the same hierarchical mixed-effects modeling approach to analyze models that included all combinations of forest structure characteristics with coefficients that were significantly different from zero in the single-variable modeling ($p \leq 0.15$). I screened the covariates for correlation, and eliminated covariates that were highly correlated or were ecologically redundant measures. I evaluated the resulting models using sample size corrected Akaike's information criterion (AICc), and calculated model averaged parameter estimates and variable importance for each covariate (Anderson 2008).

I used hierarchical clustering to identify a limited number of forest types that represented common combinations of forest structure attributes, and evaluated the intensity of barred owl use at plots representing the different forest types. To conduct the cluster analysis, I standardized the covariate values by subtracting the mean and dividing by the standard deviation (using the *scale* function in R). I generated a distance matrix using Euclidean distance (with the *vegdist* function in the *vegan* package in R). I used hierarchical cluster analysis to classify plots with similar forest structure characteristics into forest type groups (using the *hclust* function with the Ward method, in the *stats* package in R). Finally, I used a classification tree to identify the covariates that best distinguished between the forest structure type groups identified in the hierarchical cluster analysis (with the *mvpart* function in the *mvpart* package in R). I then used the hierarchical mixed-effects modeling approach described above to test whether the intensity of use based on the seasonal utilization distributions was related to different forest types identified in the cluster analysis. The forest type model included a single categorical predictor variable representing the forest types identified in the hierarchical cluster analysis. This model was evaluated using a no intercept form to calculate coefficient estimates for each forest type (Faraway 2005).

RESULTS

I compared forest structure characteristics at 170 sample plots to repeated measures of barred owl use based on a total of 21 breeding season and 12 non-breeding season utilization distributions. Use intensity from more than one seasonal utilization distribution was assessed for most of the sample plots, resulting in 247 total measures of use intensity during the breeding season and 181 measures of use during the non-breeding season. Three barred owls had adequate radio-telemetry location data (≥ 30 locations per season) to calculate a utilization distribution for all three breeding seasons during the radio-telemetry study, five individuals had adequate location data for two breeding seasons, and five individuals had adequate data to calculate one breeding season utilization distribution (Table 2.2). Two barred owls had adequate location data to calculate utilization distributions for both non-breeding seasons during the study, and seven individuals had adequate data for only one non-breeding season. The number of forest structure plots sampled within each seasonal utilization distribution ranged from one to 44 (mean 13.0, Table 2.2). Seasonal radio-telemetry results and home range sizes for these barred owls were reported in Singleton et al. (2010).

The single-variable mixed-effects models indicated that barred owl intensity of use during the breeding season increased with abundance of grand fir, variation in tree height, trees per ha of any size, canopy closure >4.9 m, trees 12.7-22.9 cm dbh, tall trees, and open ground cover <0.6 m (coefficient estimate $p < 0.05$, Table 2.3). During the non-breeding season, barred owl intensity of use increased with abundance of trees 12.7-22.9 cm dbh, gentle slopes, tree species diversity, and trees per ha of any size (coefficient estimate $p < 0.05$, Table 2.3).

I evaluated 2048 models including all combinations of 11 forest structure characteristics for the breeding season multiple-variable mixed-effects modeling. Thirteen forest structure attributes were identified as potentially influencing intensity of barred owl use in the single-variable mixed-effects modeling ($p \leq 0.15$, Table 2.3). I excluded trees per ha in the 12.7-22.9 cm dbh and 23.0-50.8 cm dbh size classes from the breeding season multiple-variable mixed-effects modeling because they were ecologically redundant with the total trees per ha measure. None of the remaining covariate pairs were highly correlated (Pearsons correlation < 0.5). The best breeding season multiple-variable model included vegetation cover <1.8 m height, percent of dominant and subdominant trees that were grand fir, total trees per hectare, and tree height standard deviation (Table 2.4). However, 10 other models had AICc values within two units of the best model, and 121 models had AICc values within five units of the best model. Percent of dominant and subdominant trees that were grand fir, total trees per hectare, and low vegetation cover (0.6-1.8 m height) were the most important forest structure covariates identified in the breeding season multiple-variable mixed-effects modeling (Table 2.4).

For the non-breeding season multiple-variable mixed effects modeling, I evaluated 32 models including all combinations of five forest structure characteristics (Table 2.3). I excluded trees per ha in the 12.7-22.9 cm dbh size class from the non-breeding season multiple-variable mixed-effects modeling because it was ecologically redundant with the total trees per ha measure. None of the remaining covariate pairs were highly correlated (Pearsons correlation < 0.5). The best non-breeding season model included vegetation cover <0.6 m height, slope angle at the sample plot, and tree species diversity (Table 2.6). However, two other models had AICc values within two units of the best model, and seven models had AICc values within five units of the best model. Slope angle at the sample plot and vegetation cover <0.6 m height were the most important covariates and 95% confidence intervals for model-averaged coefficient estimates for those covariates did not overlap zero (Table 2.7).

The hierarchical cluster analysis identified three forest structure types that captured most of the variation across the sampling plots (Figure 2.3). Type 1 stands were predominantly recently disturbed or open ponderosa pine stands that had fewer large trees, more cover of low vegetation (<0.6 m), less upper-layer canopy cover >4.9 m, and fewer logs and snags than the other types (Table 2.8). Type 2 stands were Douglas-fir dominated stands that had intermediate amounts of upper-layer canopy cover >4.9 m, ground cover <0.6 m, and overall structural diversity, (including snags, logs, and trees >50 cm dbh) relative to the other two types (Table 2.8). Type 3 stands had a mix of grand fir and Douglas-fir trees, had less ground cover <0.6 m, had more upper-level canopy cover (>4.9 m), and much greater overall structural diversity, including more snags, logs, and large trees >50 cm dbh than the other types (Table 2.8). Classification tree analysis indicated that 76% of the sample plots could be correctly classified based on the proportion of basal area in each type that was composed of Douglas-fir or grand fir trees (Figure 2.4). I refer to these types as open ponderosa pine (Type 1), simple-structure Douglas-fir (Type 2), or complex-structure mixed grand fir (Type 3) based on the forest structure characteristics and tree species composition within each type.

The hierarchical mixed-effects model test for difference in breeding season use intensity across the three types showed that barred owls used the complex-structure mixed grand fir forest type more intensively than the open ponderosa pine or simple-structure Douglas-fir types (Table 2.9). Intensity of use did not differ across the forest types during the non-breeding season.

DISCUSSION

The different analysis approaches employed in this study provided different insights into the suite of forest structure characteristics influencing within-home range habitat use by barred owls in the eastern Cascade Range, Washington. The single- and multiple-variable mixed-effects modeling highlighted a few forest structure characteristics that were associated with higher intensity of barred owl use, and the comparison of use across forest types provided additional insight into the combinations of forest structure characteristics associated with differing levels of use. For example, the single- and multiple-variable mixed-effects modeling highlighted that more trees per hectare and more basal area of grand fir trees were associated with more intense barred owl use during the breeding season. In addition, the cluster analysis showed that the areas with grand fir also tended to have more structural diversity in the form of large trees, snags, and logs. Although increased abundance of grand fir and higher numbers of trees per hectare were the most obvious features associated with increased levels of barred owl use, the suite of characteristics within the mixed grand fir stands, including snags, logs, and scattered large trees, are likely to be ecologically important for barred owls, as they are for spotted owls (reviewed by Courtney et al. 2004).

The higher intensity of barred owl use during the breeding season within the complex-structure mixed grand fir forest type relative to the other forest types is consistent with the expectation that closed-canopy stands with larger trees and more complex forest structure characteristics would be used more intensively by resident barred owls than open stands or stands with less structural diversity. Similar to spotted owls, this habitat selection pattern may be associated with characteristics that facilitate barred owl nesting, roosting, and foraging within these stands. For example, Wiens (2012) and Hamer et al. (2007) both found that barred owls used structurally diverse old forest cover types more than available within their study areas in the Oregon Coast Range and North Cascades, respectively. Buchanan et al. (2004) reported that barred owls in the eastern Cascades nested in areas with greater diversity of tree species compared to surrounding areas, similar to the diversity of tree species in the complex-structure mixed grand fir type identified in this study. Analysis of prey remains from barred owl pellets collected during my radiotelemetry study indicated that barred owls captured prey commonly found on the ground (Graham 2012). The reduced ground cover within the complex-structure mixed grand fir stands may increase prey vulnerability and facilitate foraging on ground-dwelling prey species. The dense ground cover and open overstory canopy conditions in the open ponderosa pine type may be less suitable for barred owl use because of reduced thermal cover, fewer foraging opportunities, and greater vulnerability to predation by great horned owls (*Bubo virginianus*) relative to the complex-structure mixed grand fir type. The simple-structure Douglas-fir stands notably lacked important forest structure characteristics (i.e. large trees, a structurally diverse canopy, snags, and logs) that could be important for nesting, roosting, and foraging by barred owls.

I did not detect a difference in intensity of use across the three forest types in the non-breeding season. There are two possible explanations for this. First, energetic requirements and behavioral patterns may be different between the breeding and non-breeding seasons. Barred owls may be more selective of habitat conditions during the breeding season when they are provisioning young and the young are highly vulnerable to predation. Barred owls may function more as habitat generalists within their home ranges during the non-breeding season. The second possible explanation is that the non-breeding utilization distributions could reflect some radiotelemetry sampling bias. Due to safety considerations, the winter locations were generally collected in the daytime, and during periods of relatively good weather. Access to most of the barred owl sites required substantial over-snow travel by snowmobile and or skis. Most of the locations used to calculate the non-breeding season utilization distributions were daytime roosting locations. These non-breeding season findings should be interpreted with caution, but I have included them here because many studies, particularly those addressing spotted owl habitat in the eastern Cascades (for example Buchanan et al. 1993 and 1995, Everett et al. 1997), have focused exclusively on breeding season habitat associations and have not considered habitat associations during the rest of the year. I hope that by including these non-breeding season findings here, and highlighting the potential limitations of that information, I can encourage other researchers to better quantify non-breeding season habitat associations for both spotted owls and barred owls.

Rigorous comparison of forest structure associations for spotted owls and barred owls based on the information from this study and the literature on spotted owl habitat associations in the eastern Cascades is compromised by differences in study methods, but still provides important insights. Forest structure characteristics associated with greater use by barred owls in this analysis were broadly similar to those reported to be used by spotted owls in the eastern Cascades (Buchanan et al. 1993 and 1995, Everett et al. 1997, Sovern et al. 2011). Both species appear to be associated with similar tree species composition and stand structure characteristics. For example, Everett et al. (1997) found that spotted owl nest stands occurred predominantly (92%) in grand fir or Douglas-fir forest series. King (1993) reported that spotted owl radiotelemetry locations were recorded most often in areas where a majority of trees were grand fir or Douglas-fir during her study on the Yakama Indian Reservation. Tree height diversity has also been reported as important in relation to spotted owl habitat use in the eastern Cascades (Buchanan et al. 1995, Everett et al. 1997). Buchanan et al. (1995) reported that tree height of dominant and co-dominant trees at spotted owl nest sites was 31.9 m (SD = 4.7) and canopy height of dominant trees was 15.4 m (SD = 4.3), similar to my measurements of mean tree height of 27.4 m and live crown height of 10.1 m at the complex-structure mixed grand fir plots. Ground cover and understory cover characteristics also appear to be similar for spotted owls and barred owls in this area. King (1993) reported that spotted owls preferred sites with understories characterized by litter or ferns and avoided those where small trees were abundant.

Despite the broad similarities in forest structure associations for spotted owls and barred owls, my findings suggest that there could also be some subtle differences. Relative to barred owls, spotted owls may be more closely associated with Douglas-fir dominated sites that have dense overstory canopy closure. For example, Buchanan et al. (1993 and 1995) found that 92% of the spotted owl nests he investigated in the eastern Cascades were in Douglas-fir trees, and canopy closure at the nest sites was mean 75% (range 57-95%). Everett et al. (1997) reported that overstory canopy cover ranged from 83 to 94% at spotted owl nest sites. King (1993) found that spotted owls were located more often in areas with high canopy closure (93.4%) compared to other areas within their home ranges (85.6% at random sites). These are all more densely closed canopy conditions than those found in the complex-structure mixed grand fir forest type associated with high levels of barred owl use in this study.

There also may be a stronger association with mistletoe for spotted owls than for barred owls. Several studies have reported that Douglas-fir trees infected with dwarf mistletoe are an important habitat component associated with spotted owl nesting in the eastern Cascades (Buchanan et al. 1995, Everett et al. 1997, Sovern et al. 2011). Sovern et al. (2011) reported that 90% of 276 spotted owl nests recorded at 73 territories documented within the Cle Elum Demography Study Area were on platforms, mostly in clumps of deformed limbs caused by dwarf mistletoe. In contrast to spotted owl habitat associations in the area, increased abundance of mistletoe was not associated with increased intensity of barred owl use. In this study, mistletoe was most abundant in the simple-structure Douglas-fir forest type.

At a home range scale, spotted owls have been reported to use areas with steeper slopes than those used by barred owls, and this pattern may be important at a fine scale as well (Wiens 2012, Herter and Hicks 2000, Pearson and Livezey 2003). For example, Buchanan et al. (1993) reported that mean slope at spotted owl nests was 41% (23 degrees), and King (1993) found that spotted owls were located in sites that were slightly steeper than random locations within their home range. In this study, plots with gentle slopes had higher levels of barred owl use than plots in steeper areas during the non-breeding season, but not during the breeding season. In addition, the complex-structure mixed grand fir plots were located on slightly more gentle ground than plots of the other two types, but the difference was not substantial because steep sites were uncommon within the barred owl home ranges.

Given these reported differences, I hypothesize that spotted owls in the eastern Cascades of Washington may be more likely than barred owls to use Douglas-fir dominated stands, with closed canopies, on steeper slopes, particularly where dwarf mistletoe provides appropriate nesting structures and prey for spotted owls. However, this cannot be tested with the data at hand and remains to be confirmed through more systematic and consistent sampling to compare forest structure attributes in areas used by spotted owls to those in areas used by barred owls.

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Table 2.1. Forest structure attribute codes, descriptions, units of measurement, mean values, and standard deviations for attributes measured at 170 plots within barred owl home ranges in the eastern Cascade Range, Washington.

Code	Description	Units	Mean	SD
COVER1	Layer 1 vegetation cover, <0.6 m height	Percent	54.74	25.66
COVER2	Layer 2 vegetation cover, 0.6-1.8 m height	Percent	40.89	23.87
COVER3	Layer 3 vegetation cover, 1.8-4.9 m height	Percent	35.77	20.40
COVER4	Layer 4 vegetation cover, >4.9 m height	Percent	47.26	22.22
LOG_CNT2	Count of logs >22.9 cm diameter at mid-point encountered along a 22 m transect	Count	0.54	0.99
MTOE_PCT	Percent of trees infected with mistletoe	Index	0.08	0.16
PCT_ABGR	Percent of dom. and subdom. trees that are grand fir	Percent	0.16	0.23
PCT_PIPO	Percent of dom. and subdom. trees that are ponderosa pine	Percent	0.22	0.29
PCT_PSME	Percent of dom. and subdom. trees that are Douglas-fir	Percent	0.49	0.35
SLOPE	Slope	Degrees	15.21	10.87
SN_HA	Snags >22.9 cm dbh per hectare	Count	14.45	21.24
SOLR	Solar energy (annual daily mean hundreds of watt hours/m^2)	Watt Hr/m^2	20.88	4.24
SW_DIV	Shannon – Weiner tree diversity	Index	0.67	0.42
TH_S2	Trees per ha., size class 2 (12.7-22.9 cm dbh)	Count	27.22	28.51
TH_S3	Trees per ha., size class 3 (23.0-50.8 cm dbh)	Count	66.68	44.58
TH_S4	Trees per ha., size class 4 (50.9-101.6 cm dbh)	Count	38.37	37.33
TH_S5	Trees per ha., size class 5 (>101.6 cm dbh)	Count	1.50	7.25
TH_TOT	Total Trees per ha. >12.7 cm dbh	Count	133.77	65.81
TR_HT_MN	Mean tree height	Meters	23.42	7.98
TR_HT_SD	Standard deviation of tree height	Meters	6.46	3.54
TR_ULC_MN	Mean height to unconsolidated live tree crown	Meters	10.20	4.42
TR_ULC_SD	Standard deviation of height to unconsolidated live tree crown	Meters	4.46	4.63

Table 2.2. Number of forest structure sampling plots within each seasonal utilization distribution for barred owls monitored during three breeding seasons and two non-breeding seasons in the eastern Cascade Range, Washington. Cells with dashes (-) indicate that inadequate radio-telemetry location data were recorded to calculate a utilization distribution for that individual during that season.

	Breeding Season			Non-breeding Season	
Owl	2004	2005	2006	2004	2005
ACF	-	9	9	-	13
BMF	-	39	12	-	44
CBF	9	-	-	9	-
CBM	5	12	11	13	20
CRF	-	-	-	11	-
CRM	12	17	16	19	19
DCF	-	9	-	-	8
ECM	-	27	-	-	-
EEM	-	12	-	-	-
FLF	-	-	-	-	-
FLM	10	9	-	12	-
GAF	-	10	-	-	-
GCM	-	4	1	-	5
MCM	-	4	10	-	8

Table 2.3. Single-variable mixed-effects model results relating individual forest structure attributes to intensity of barred owl use during the breeding season (df = 225) and non-breeding season (df = 168) in the eastern Cascade Range, Washington. Estimates of fixed-effects shown are the intercept, coefficient (*β*), standard error of the coefficient (*SE*), and probability that the coefficient is equal to zero (*P*). The response variable is the utilization distribution probability, for which low values indicate high utilization; so negative *β* coefficients indicate more intensive use as covariate values increase.

	Breeding Season				Non-Breeding Season			
Covariate	Intercept	*β*	*SE*	*P*	Intercept	*β*	*SE*	*P*
COVER1	**73.27**	**0.15**	**0.07**	**0.03**	**80.11**	**0.12**	**0.06**	**0.06**
COVER2	**86.31**	**-0.12**	**0.07**	**0.10**	89.19	-0.06	0.07	0.37
COVER3	**86.91**	**-0.15**	**0.09**	**0.07**	90.63	-0.11	0.08	0.16
COVER4	**91.30**	**-0.21**	**0.08**	**0.01**	90.27	-0.07	0.07	0.34
LOG_CNT2	82.44	-1.83	1.54	0.23	86.38	0.36	1.26	0.77
MTOE_PCT	80.60	9.18	10.90	0.40	85.54	10.18	9.84	0.30
PCT_ABGR	**86.70**	**-34.17**	**7.50**	**0.00**	88.63	-10.75	7.54	0.16
PCT_PIPO	**78.26**	**12.26**	**6.89**	**0.08**	84.99	1.05	6.23	0.87
PCT_PSME	79.00	6.33	5.44	0.25	86.51	3.64	5.10	0.48
TH_S2	**85.52**	**-0.15**	**0.06**	**0.02**[1]	**92.33**	**-0.21**	**0.05**	**0.00**
TH_S3	**86.28**	**-0.07**	**0.04**	**0.08**[1]	89.30	-0.04	0.04	0.36
TH_S4	83.19	-0.05	0.05	0.30	85.91	0.02	0.04	0.68
TH_S5	81.01	0.19	0.22	0.39	87.10	-0.22	0.23	0.34
SLOPE	80.48	0.07	0.16	0.69	**81.23**	**0.44**	**0.15**	**0.00**
SN_HA	**83.70**	**-0.16**	**0.09**	**0.06**	**89.00**	**-0.14**	**0.08**	**0.07**
SOLR	82.64	-0.06	0.46	0.90	97.59	-0.50	0.48	0.30
SW_DIV	**85.95**	**-6.98**	**4.45**	**0.12**	**94.90**	**-11.08**	**3.90**	**0.01**
TOT	**92.92**	**-0.09**	**0.03**	**0.00**	**94.64**	**-0.05**	**0.03**	**0.03**
TR_HT_MN	**94.72**	**-0.58**	**0.24**	**0.02**	85.32	0.06	0.21	0.79
TR_HT_SD	**93.43**	**-1.89**	**0.53**	**0.00**	87.60	-0.15	0.51	0.77
TR_ULC_MN	83.00	-0.16	0.41	0.71	89.68	-0.28	0.36	0.45
TR_ULC_SD	82.47	-0.24	0.29	0.42	85.72	0.21	0.28	0.46

[1] TH_S2 and TH_S3 were not included in the breeding season multiple-variable mixed-effects modeling because they were ecologically redundant with the TOT (total trees / ha) measure.

Table 2.4. Model selection results for the top (ΔAICc ≤ 2) breeding season multiple-variable mixed-effect models relating forest structure attributes to intensity of barred owl use during the breeding season in the eastern Cascade Range, Washington. All combinations of 11 forest structure characteristics identified as potentially related to barred owl intensity of use in the single-variable mixed-effects modeling were included in this model selection analysis (n = 2048 models).

Formula	K	AICc	ΔAICc	AICcWt	LL	Cum.Wt.
COVER1+COVER2+PCT_ABGR+TOT+TR_HT_SD	10	2328.79	0.00	0.03	-1153.9	0.03
COVER2+PCT_ABGR+TOT+TR_HT_SD	9	2329.46	0.67	0.02	-1155.4	0.04
COVER3+PCT_ABGR+TOT+TR_HT_SD	9	2329.73	0.94	0.02	-1155.5	0.06
COVER1+COVER2+PCT_ABGR+TOT	9	2330.09	1.30	0.01	-1155.7	0.07
COVER1+COVER2+PCT_ABGR+SW_DIV+ TOT+TR_HT_SD	11	2330.21	1.42	0.01	-1153.5	0.09
COVER2+COVER3+PCT_ABGR+TOT+TR_HT_SD	10	2330.39	1.60	0.01	-1154.7	0.10
COVER1+COVER2+COVER4+PCT_ABGR+ TOT+TR_HT_SD	11	2330.43	1.64	0.01	-1153.7	0.11
COVER1+COVER2+COVER3+PCT_ABGR+ TOT+TR_HT_SD	11	2330.46	1.67	0.01	-1153.7	0.12
COVER2+COVER4+PCT_ABGR+TOT+TR_HT_SD	10	2330.53	1.74	0.01	-1154.8	0.13
COVER1+COVER2+PCT_ABGR+SW_DIV+TOT	10	2330.58	1.79	0.01	-1154.8	0.14
COVER1+COVER2+PCT_ABGR+TOT+TR_HT_MN	10	2330.77	1.97	0.01	-1154.9	0.15

Table 2.5. Covariate importance, and model-averaged parameter estimates (Avg. β), standard errors, and 95% lower (LCI) and upper (UCI) confidence intervals of the parameter estimates, for multiple-variable mixed-effects models relating forest structure attributes to breeding season intensity of barred owl use in the eastern Cascade Range, Washington. Variable importance was calculated for models including all combinations of the covariates (n = 2048 models).

Covariate	Importance	Avg. β	SE	LCI	UCI
PCT_ABGR	0.99	-30.22	7.67	-45.26	-15.17
TOT	0.78	-0.08	0.03	-0.14	-0.02
COVER2	0.70	-0.19	0.09	-0.37	-0.02
TR_HT_SD	0.63	-1.04	0.56	-2.14	0.05
COVER1	0.55	0.12	0.08	-0.02	0.27
COVER3	0.46	-0.14	0.11	-0.36	0.07
COVER4	0.42	-0.12	0.11	-0.33	0.09
TR_HT_MN	0.34	-0.21	0.29	-0.79	0.36
SW_DIV	0.31	-3.89	4.78	-13.27	5.49
PCT_PIPO	0.28	3.05	6.60	-9.89	15.99
SN_HA	0.25	0.01	0.09	-0.17	0.19

Table 2.6. Model selection results for the top (ΔAICc ≤ 2) multiple-variable mixed-effect models relating forest structure attributes to intensity of barred owl use during the non-breeding season in the eastern Cascade Range, Washington. All combinations of five forest structure characteristics identified as potentially related to barred owl intensity of use in the single-variable mixed-effects modeling were included in this model selection analysis (n = 32 models).

Formula	K	AICc	ΔAICc	AICcWt	LL	Cum.Wt.
COVER1+SLOPE+SW_DIV	8	1632.26	0.00	0.26	-807.7	0.26
COVER1+SLOPE	7	1632.63	0.36	0.22	-809.0	0.48
COVER1+SLOPE+SN_HA	8	1634.07	1.81	0.11	-808.6	0.59

Table 2.7. Covariate importance, and model-averaged parameter estimates (Avg. β), standard errors, and 95% lower (LCI) and upper (UCI) confidence intervals of the parameter estimates, for multiple-variable mixed-effects models relating forest structure attributes to non-breeding season intensity of barred owl use in the eastern Cascade Range, Washington. Variable importance was calculated for models including all combinations of five covariates (n = 32 models).

Covariate	Importance	Avg. β	SE	LCI	UCI
SLOPE	0.976	0.554	0.174	0.212	0.895
COVER1	0.922	0.196	0.071	0.057	0.336
SW_DIV	0.535	-6.578	4.137	-14.687	1.53
SN_HA	0.299	-0.052	0.08	-0.208	0.104
TOT	0.283	-0.014	0.03	-0.071	0.044

Table 2.8. Mean and standard error of forest structure attributes measured at sampling plots located in three forest types identified within barred owl home ranges in the eastern Cascade Range, Washington, using hierarchical cluster analysis. Column sample sizes indicate the number of plots assigned to each type.

	Open Ponderosa Pine, Type 1 (n = 45)		Simple-structure Douglas-fir, Type 2 (n = 77)		Complex-structure Grand Fir, Type 3 (n = 48)	
	Mean	*se*	*Mean*	*se*	*Mean*	*se*
COVER1	65.53	3.63	58.57	2.76	38.48	3.07
COVER2	46.71	3.47	39.88	2.87	37.04	3.13
COVER3	35.96	2.80	35.05	2.65	36.75	2.47
COVER4	33.96	3.57	47.43	2.11	59.48	2.75
LOG_CNT2	0.09	0.04	0.35	0.08	1.25	0.19
MTOE_PCT	0.03	0.01	0.13	0.02	0.06	0.02
PCT_ABGR	0.05	0.02	0.08	0.01	0.38	0.04
PCT_PIPO	0.50	0.06	0.13	0.02	0.10	0.02
PCT_PSME	0.28	0.05	0.72	0.03	0.31	0.04
SLOPE	15.24	1.64	16.77	1.21	12.67	1.57
SN_HA	3.93	1.18	9.19	1.66	32.74	3.89
SOLR	21.40	0.64	19.40	0.49	22.77	0.42
SW_DIV	0.46	0.05	0.67	0.05	0.87	0.05
TH_S2	34.05	6.32	20.67	2.32	31.31	3.02
TH_S3	39.29	6.15	78.20	5.01	73.88	5.47
TH_S4	12.01	3.26	41.97	3.80	57.30	5.97
TH_S5	0.00	0.00	0.26	0.18	4.91	1.87
TH_TOT	85.35	10.26	141.10	6.46	167.40	7.14
TR_HT_MN	15.76	1.09	25.41	0.62	27.40	1.05
TR_HT_SD	4.02	0.50	6.13	0.31	9.28	0.43
TR_ULC_MN	6.53	0.61	12.41	0.41	10.09	0.51
TR_ULC_SD	2.26	0.26	4.57	0.22	6.33	1.12

Table 2.9. Mixed-effect, no-intercept model estimated utilization distribution value and 95% confidence intervals of that estimate for three forest types within barred owl home ranges in the eastern Cascade Range, Washington. Lower utilization distribution values indicate more intensively used areas.

	Breeding Season			Non-Breeding Season		
Forest Type	Estimate	Lower 95% CI	Upper 95% CI	Estimate	Lower 95% CI	Upper 95% CI
Open Ponderosa Pine	89.9	81.8	97.9	85.1	77.4	92.9
Simple-structure Douglas-fir	85.0	78.6	91.5	88.0	81.9	94.2
Complex-structure Grand Fir	69.0	62.2	75.8	85.6	79.1	92.1

Figure 2.1. Location of the barred owl radiotelemetry study area in the eastern Cascade Range, Washington.

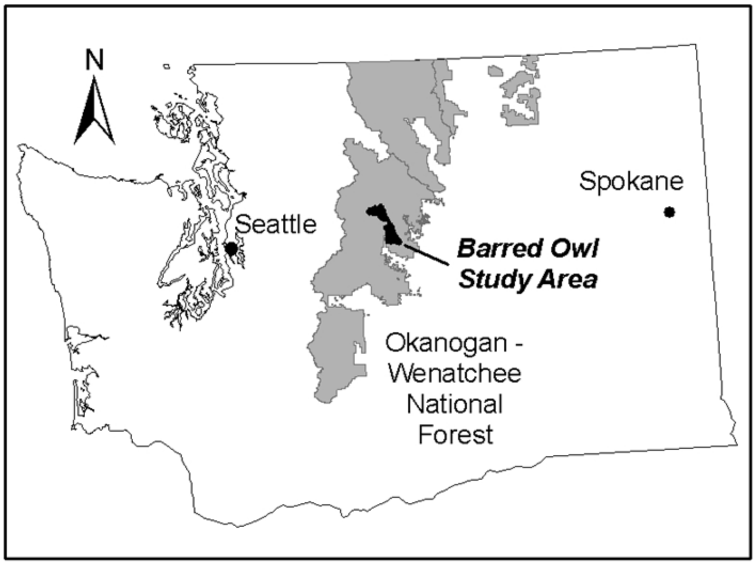


Figure 2.2. An example utilization distribution map for a male barred owl in the eastern Cascade Range, Washington, during the 2006 breeding season showing utilization distribution probability isopleths (i.e., intensity of within-home range use) and forest structure sample plot locations.

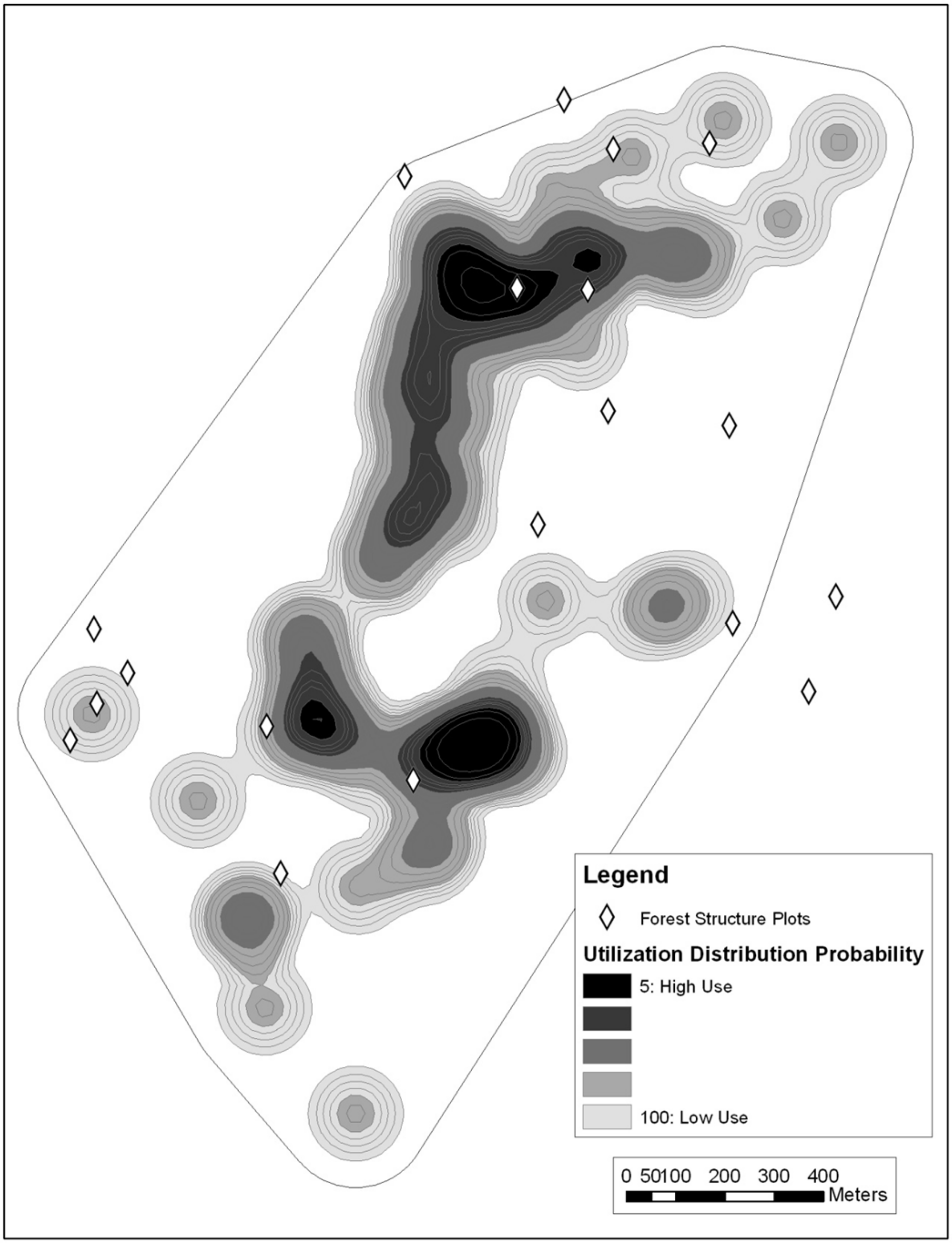


Figure 2.3. Hierarchical cluster analysis dendrogram showing three groups representing forest types found at plots within barred owl home ranges in the eastern Cascade Range, Washington.

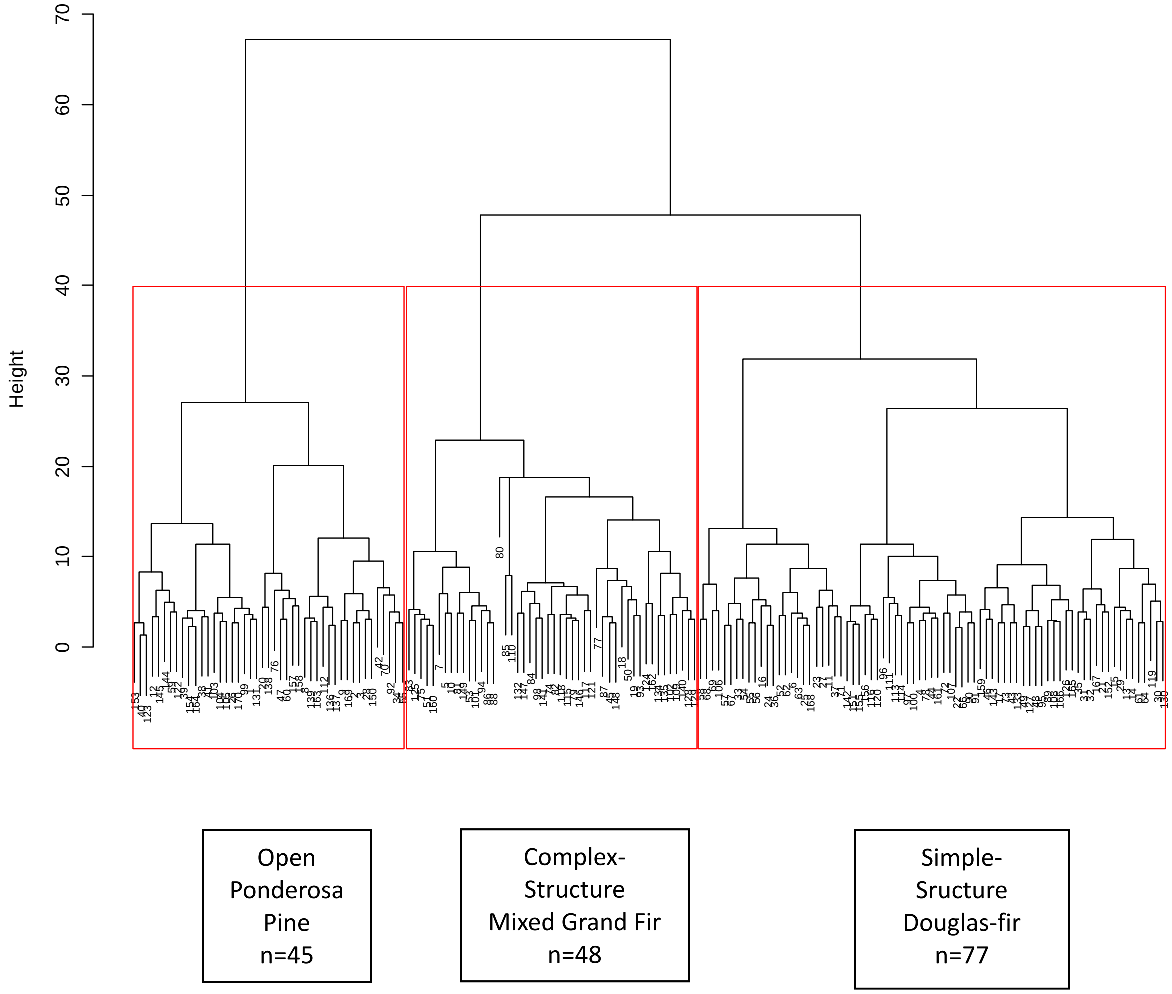
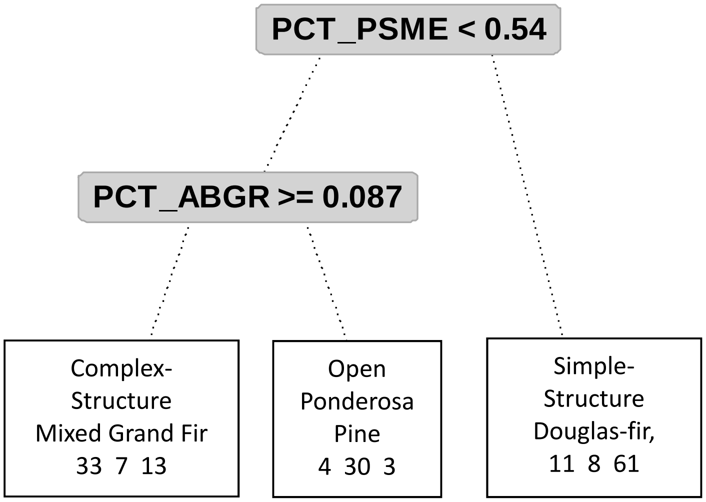


Figure 2.4. A classification tree indicating the variables that best distinguish between the forest types identified by hierarchical cluster analysis of forest structure attributes for plots sampled within barred owl home ranges in the eastern Cascade Range, Washington. Text in the boxes for the leaves of the tree indicate the expected forest type at the leaf and the count of plots assigned to each type that meet the criteria for that leaf (from left to right: complex-structure grand fir, open ponderosa pine, and simple-structure Douglas-fir).



CHAPTER 3: LANDSCAPE-SCALE HABITAT ASSOCIATIONS FOR BARRED OWLS AND SPOTTED OWLS IN THE EASTERN CASCADE RANGE, WASHINGTON.

ABSTRACT

Interaction with barred owls (*Strix varia*) has been identified as an important factor contributing to the continued decline of the northern spotted owl (*Strix occidentallis caurina*) population in Washington. Understanding the current distribution and habitat associations of spotted owls and barred owls is important for understanding potential displacement pressures and population-level consequences of displacement for spotted owls. I used generalized linear mixed models (GLMM) to compare forest structure and topographic characteristics around activity centers for both owl species (n = 214 for spotted owls, and n = 41 for barred owls) to conditions in the surrounding landscape within the Okanogan-Wenatchee National Forest, Washington. Models including linear and quadratic effects for canopy closure, tree size, slope, solar radiation, and topographic position effectively distinguished between used and random points for both species (AUC = 0.79 for spotted owls and AUC = 0.89 for barred owls). Estimates of habitat selection overlapped substantially for the two species (Schoeners *D* = 0.63), but overlap was less than expected at random (Schoeners *D* randomized 95% quantile range 0.83-0.92). The primary differences in habitat associations between the two species were that barred owl sites tended to be located on gentler slopes in lower topographic positions than spotted owl sites, and barred owls used a broader range of forest structure and tree species

composition settings than spotted owls. Slope was the habitat characteristic that best distinguished between areas used by spotted owls or barred owls. Seventy-two percent of the areas used by spotted owls were located on slopes >16 degrees, and 72% of the areas used by barred owls were located on slopes <16 degrees. Out of 199,862 ha of good spotted owl habitat identified in this analysis, only 46,273 ha were identified as poor for barred owls. Even with the observed differences in habitat associations, high-quality habitat available to spotted owls is likely to be substantially reduced if spotted owls are displaced from areas occupied by territorial barred owl pairs.

INTRODUCTION

Northern spotted owl (*Strix occidentallis caurina*) populations in Washington and northern Oregon declined by approximately 40-60% from 1989 to 2008 (Forsman et al. 2011). These declines occurred despite the implementation of the Northwest Forest Plan (NWFP) and other conservation measures that mitigated the rate of habitat loss for spotted owls (Davis et al. 2011, USFWS 2011). Interaction with barred owls (*Strix varia*) has been identified as an important factor contributing to the continued decline of the spotted owl population (USFWS 2011). Barred owls were first detected in the eastern Cascade Range of Washington when spotted owl surveys were initiated in the early 1980s (Okanogan-Wenatchee National Forest, unpublished records). They are now broadly distributed and abundant in some portions of the area (Singleton et al. 2010). Impacts of barred owls on spotted owls may include displacement, direct mortality, and competition for prey (Gutierrez et al. 2004, 2007). Apparent survival of spotted owls in demographic study areas is lower at sites where barred owls have been detected (Kroll et al. 2010, Dugger et al. 2011, Forsman et al. 2011).

Interspecific competition has been a long-standing fundamental theory for explaining the dynamics of ecological communities (Gause 1934, Sommer and Worm 2002). Competition theory indicates that two species with identical resource requirements and utilization strategies will not be able to coexist over time, and eventually the presence of a more effective competitor will cause the extinction of the less effective competitor (Chase and Leibold 2003). Some level of exclusive access to resources is a prerequisite for species coexistence (Sommer and Worm 2002). The partitioning of space by competitors is a common strategy for maintaining exclusive access to resources in bird communities (Cody 1974, Dhondt 2012). For example, Craighead and Craighead (1956) found that home ranges of similar sized hawks did not overlap in their study of the raptor community in central Michigan, and McArthur (1958) found that several warbler species coexisted by foraging on different portions of trees during his classic study in conifer forests of Maine and Vermont.

Competitive ecological interactions can be particularly dynamic in communities that have recently been colonized by a new species. Effects of interactions between species can change rapidly as an invader adapts to a new environment and the residents adjust to the presence of the new competitor (Cox 2004). For example, introduction of the house finch (*Carpodacus mexicanus*) from western North America into cities in the eastern United States caused declines in the house sparrow (*Passer domesticus*) population, another previously introduced species (Bennett 1990). These changes in community dynamics can have substantial impacts on the distribution and abundance of native species (Blackburn et al. 2009). Interaction with alien species is a primary cause of extinction for birds in island landscapes, and such interactions can have important consequences for biodiversity conservation in continental settings too (Wilcove et al. 1998).

Competitive interactions between species can be broadly categorized into two types: resource competition and interference competition (Wiens 1989). In resource competition, individuals that use the same resources do so without directly interfering with each other, but their consumption of the resource limits availability for the competitor. With interference competition, there is usually a direct interaction (for example a territorial encounter) that prevents a competitor from accessing the resource in the first place (Dhondt 2012). Differences in behavior and space use patterns between spotted owls and barred owls suggest that interference competition may be a particularly important factor contributing to spatial partitioning between barred owls and spotted owls (Singleton et al. 2010, Wiens 2012). Barred owls are slightly larger, more aggressive, and use relatively small home ranges that do not overlap with neighboring conspecifics (Singleton et al. 2010, Wiens 2012). Spotted owls use much larger areas that overlap substantially with neighboring conspecific home ranges (Hamer et al. 2007, Wiens 2012).

Identifying and understanding possible patterns of spatial partitioning between spotted owls and barred owls may provide important insights for spotted owl conservation planning. Several studies have independently reported on habitat associations of spotted owls (for example Buchannan et al. 1995, Everett et al. 1997, Herter et al. 2002, and others reviewed by Courtney et al. 2004 and USFWS 2011), and barred owls (Singleton et al. 2010). However, most studies that have described and compared habitat associations for both owl species have reported results from detections of barred owls recorded incidental to spotted owl research or monitoring (Herter and Hicks 2000, Pearson and Livezey 2003, Buchanan et al. 2004). Important exceptions are the work of Hamer et al. (2007) and Wiens (2012). There are two important biases associated with barred owl detections documented during spotted owl call surveys. First, detection rates of barred owls during spotted owl surveys are reduced, resulting in barred owl density estimates that are biased low (Bailey et al. 2009, Wiens et al. 2011). Second, survey effort is often focused on spotted owl habitat, potentially contributing to the perception that habitat associations for the two species are identical (Livezey and Fleming 2007). Analyzing locations recorded during species-specific surveys for both owl species is particularly important for assessing and comparing habitat associations for barred owls and spotted owls.

A potential confounding factor for evaluating spatial partitioning patterns between spotted owls and barred owls is the possibility that spotted owls could have been displaced from the highest quality habitat prior to their locations being documented. Owing to displacement by barred owls, areas where spotted owls have been observed to be most abundant may not be areas that provide optimum resource values for spotted owl survival and reproduction (Van

Horne 1983). Communicating patterns of relative habitat suitability can be particularly challenging in the context of such displacement effects. Distinguishing between habitat use (the consumption of a collection of resources), habitat quality (the ability of the environment to provide conditions appropriate for individual and population persistence), and habitat selection (the hierarchical process involving a series of decisions about what resources an animal chooses to use from the suite of resources available to it) becomes particularly important in this context (definitions from Hall et al. 1997). Despite this complication, understanding the current distribution and habitat associations of spotted owls and barred owls is important for understanding potential displacement pressures and population-level consequences of displacement for spotted owls.

The focus of this analysis was to describe landscape-scale habitat associations for spotted owls and barred owls, and evaluate differences between them. My specific objectives were: 1) to conduct habitat selection analysis using generalized linear mixed models (GLMM) to characterize and compare habitat at barred owl and spotted owl activity centers recorded during species-specific surveys, and 2) to quantify overlap of habitat selection between the two species.

STUDY AREA

This analysis focused on the Okanogan-Wenatchee National Forest south of Lake Chelan, on the east side of the Cascade Range, Washington (Figure 3.1). This area is characterized by complex, mountainous topography. Elevation ranges from approximately 240 to 2750 m (800 to 9000 ft). Vegetation communities in this area are substantially influenced by the strong moisture gradients associated with the rain-shadow effect of the Cascade Range and local topography. Forest cover is a mix of moist-mesic conifer forest at high elevations in the western portion of the study area, xeric-mesic mixed conifer forest at mid elevations, and dry ponderosa pine (*Pinus ponderosa)* woodlands, shrublands, and grasslands along the lower, eastern edge of the study area (Johnson and O'Neil 2001, Lillybridge et al. 1995). The moist-mesic forest is characterized by silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) at higher elevations, and Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and western hemlock (*Tsuga heterophyla*) at lower elevations. The xeric-mesic mixed conifer forest was characterized by a mix of Douglas-fir, grand fir, and ponderosa pine). Large water bodies and areas above 1500 m elevation were excluded from the analysis. Total area included in the analysis was 984,688 ha.

METHODS

I compared conditions in the vicinity of spotted owl and barred owl pair locations to the surrounding landscape using GLMM (Zuur et al. 2009). The spotted owl pair activity center locations that I analyzed were recorded during demographic monitoring and management surveys from 1990 to 2004, including data from the Cle Elum and portions of the Wenatchee Northern Spotted Owl Demography Study Areas (Anthony et al. 2006, and Okanogan-Wenatchee National Forest, Wenatchee WA, unpublished data). The spotted owl call survey protocol used to identify these sites was described by Lint et al. (1999). I excluded spotted owl activity centers that experienced disturbance (primarily habitat loss to fire or harvest) prior to 2006 to match the vegetation map I used for analysis (see below). I used *LandTrendr* disturbance maps (Kennedy et al. 2010) to identify and exclude sites that had moderate or high disturbance effects in more than 10% of the area within five ha of the activity center, resulting in 214 spotted owl activity centers included in the final analysis. I evaluated barred owl habitat use based on detection locations of barred owl pairs and activity centers from species-specific barred owl surveys on the OWNF (n = 41, Singleton et al. 2010 and P. Singleton, U.S. Forest Service, PNW Research Station, Wenatchee WA, unpublished data). These locations were documented during two efforts: 1) sites documented in 2004 to 2006 during surveys in conjunction with a radio-telemetry study in the Chumstick and Chiwawa watersheds (Singleton et al. 2010), and 2) randomized surveys conducted in 2009, stratified based on extrapolation of the Singleton et al. (2010) resource selection function. The barred owl survey protocol used to identify these sites was described by Singleton et al. (2010).

I compiled digital maps of vegetation and topographic characteristics to quantify habitat conditions in the vicinity of owl sites and at random points drawn from the analysis landscape (Table 3.1). All GIS analysis was conducted with ArcGIS (version 10.0, Environmental Science Research Institute, Redlands CA) using a 30 m raster pixel size. Vegetation covariates were derived from generalized nearest neighbor (GNN), maps based on year 2006 Landsat imagery (Ohmann and Gregory 2002, Ohmann et al. 2010). Vegetation covariates were chosen to reflect characteristics that have been identified as important for spotted owls (reviewed by Courtney et al. 2004 and USFWS 2011) and barred owls (Singleton et al. 2010), and included canopy closure, tree size, and tree species composition. I did not include covariates for finer-scale forest stand structure characteristics (e.g., snags, logs, etc.) because these were highly correlated with tree size and canopy closure in the GNN data, and accuracy estimates were low (Ohmann et al. 2010).

I derived topographic covariates (slope, solar radiation, and topographic position) from a United States Geological Survey 10-m digital elevation model (DEM, Table 3.1). I calculated the topographic position of each 30 m pixel relative to the surrounding one km radius area by calculating the minimum elevation within one km radius of the focal pixel, subtracting that minimum from the elevation at the pixel, and dividing that value by the elevation range within the one km radius (Singleton et al. 2010). This produced a topographic position index ranging from 0 to 1, for which values approaching 0 represent valley bottoms and lower slopes, and values approaching 1 represent upper slopes and ridge-tops. I screened all of the covariates for correlation (retaining covariate pairs with Pearson's correlation <0.5).

I used GLMM (Zuur et al. 2009) to compare habitat characteristics around owl activity centers to the study area landscape. To characterize areas used by each species, I sampled the covariate values for 50 pixels within a five ha (126 m radius) circle surrounding each owl activity center. I compared these used points to twice as many available points randomly selected from across the analysis area, corresponding to a Type II sample design (Manly et al. 2002).

I conducted the GLMM analysis separately for barred owls and spotted owls. I used the owl activity center ID as a random intercept effect to address the correlation of pixels sampled around each site (Zuur et al. 2009). I standardized all covariate values to address convergence issues with the GLMM models (Faraway 2005). To standardize the covariate values, I took the mean and standard deviation of each covariate across the analysis area, then subtracted that mean and divided by that standard deviation for the covariate values in the barred owl and spotted owl data sets (Table 3.1). Thus, the standardization was identical between the data sets for the two species, and the coefficient units equal the population standard deviation for the covariate across the entire analysis area.

I evaluated 12 *a priori* candidate models and used AICc for model selection (Table 3.2, Burnham and Anderson 2002). The candidate models were designed to evaluate effects of topography and vegetation independently and in combination, and to evaluate linear and quadratic forms for those covariates. I also evaluated an interaction term for canopy closure and tree size as in the Singleton et al. (2010) barred owl resource selection function. The generalized linear mixed models were run using the *lme4* package in R (version 15.0, R Development Core Team, Vienna Austria).

I was concerned about the potential for model selection bias and over-fitting resulting from drawing a large sample of pixels from the vicinity of each activity center, so I conducted a leave-one-out bootstrap procedure to evaluate model selection and test for over-fitting with the best GLMM model (Manly 1997). To do this, I randomly selected 10 or 25 sampled pixels from each activity center. I compared AICc model selection results across the data sets with 10, 25, or 50 pixels sampled at each site by re-running the candidate models with the three data sets and determining if there was an effect of sample size on model selection. I conducted leave-one-out bootstrap tests for over-fitting with each data set by iteratively removing all of the sampled and random points associated with each owl site, fitting the model without the site, then calculating area under the receiver operating characteristic curve (AUC) and root mean square error (RMSE) for the excluded data.

I used the Schoeners *D* niche overlap index to assess the degree of overlap in habitat selection maps predicted by the GLMM analysis for spotted owls and barred owls (Rodder and Engler 2011). Rodder and Engler (2011) demonstrated that Schoeners *D* performed well for evaluating overlap in probabilistic species distribution maps relative to other commonly used niche overlap indices. Schoeners *D* was calculated as:

$$D(p_x,\ p_y) = 1 - \tfrac{1}{2}\sum_i \left|p_{xi} - p_{yi}\right|,$$

where p_x and p_y denote the habitat selection estimates for species *x* and species *y* at pixel *i*, after the habitat selection scores have been transformed so that they sum to 1 across all of the pixels being evaluated (Rodder and Engler 2011). This produces an overlap index ranging from 0 to 1, where 0 indicates no overlap and 1 indicates complete overlap. I used randomization tests to determine if observed values for *D* were substantially different from those derived when the habitat selection models were re-calculated with sites randomly assigned as being spotted owl or barred owl, while maintaining the observed proportion of sites occupied by each species, for 100 replicates (Warren et al. 2008).

I evaluated spatial patterns of habitat overlap between the two species using the following steps. For both species, I investigated the degree of use relative to availability of the predicted habitat selection values using Type II selection ratios (Manly et al. 2002). I examined the observed distribution of predicted habitat selection values at the used and random points for each species, then categorized the predicted habitat selection maps into three classes representing: 1) “good habitat” - areas used in proportions greater than their availability, 2) “moderate habitat” – areas used approximately equal to availability, and 3) “poor habitat” - areas used less than available. It is important to note that these labels reflect habitat selection, which is distinct from the concept of habitat quality. As pointed out in the introduction, use-availability analysis of habitat selection can be confounded by issues related to displacement resulting from inter-specific competition, and areas observed to be “good” may or may not correspond to areas of high habitat quality (e.g., Van Horne 1983). Nevertheless, these selection patterns provide important information on observed animal distribution in relation to habitat characteristics. I combined the habitat class maps for the two species to identify spatial patterns of habitat overlap, resulting in nine habitat overlap classes (e.g., areas with poor habitat for both species, areas with good habitat for both species, areas with good habitat for one species and poor for the other, etc.).

To further distinguish the characteristics of the areas selected by the two owl species, I conducted two classification tree analyses (using the *rpart* package in R). First, to distinguish between areas used by each species, I compared the used sample points from spotted owl activity centers to those around barred owl activity centers. I used the *weight* function in *rpart* to equalize the sample weight for the two species. Second, to distinguish between areas of least overlap (i.e., good for one species and poor for the other), or greatest overlap (i.e., good for both species), I compared 3500 random points from each of three habitat overlap classes; 1) areas with good habitat for spotted owls and poor habitat for barred owls, 2) areas with good habitat for barred owls and poor habitat for spotted owls, and 3) areas with good habitat for both species. I used a classification tree to identify the covariates and values that best distinguished between those classes.

RESULTS

Vegetation and topographic characteristics were important for predicting resource selection for both barred owls and spotted owls. The full model with quadratic effects had 100% of the AICc model weight for both species (Table 3.3), and these models effectively distinguished between used and random locations (Figure 3.2). Model selection results were not influenced by the number of pixels sampled at each site. The full model with quadratic effects had 100% of the AICc model weight for both species when 10, 25, or 50 pixels were sampled at each site, and bootstrapped estimates of AUC and RMSE were stable across the range of sampling intensity (bootstrapped AUC = 0.78 for the spotted owl model and 0.86 for the barred owl model, bootstrapped RMSE = 0.42 for the spotted owl model and 0.37 for the barred owl model). Subsequent results are all from the analysis of 50 pixels within five ha of each activity center. No covariates were excluded due to correlation with other covariates. Maximum correlation between a pair of covariates was 0.47 for canopy closure and tree size.

Randomization tests of the Schoeners *D* niche overlap metric indicated that while there was substantial overlap between the two species, the degree of that overlap was much less than expected at random. Observed Schoeners *D* based on predicted values from the full quadratic models for both species was 0.63, well outside the randomized 95% quantile range of 0.83 to 0.92.

For both species, areas with predicted habitat selection values <0.2 were used less than available (classified as “poor habitat”), areas with predicted habitat selection values from 0.2 to 0.45 were used in proportion to availability (“moderate habitat”), and areas with predicted habitat selection values >0.45 were used more than available (“good habitat”, Figures 2.4 and 2.5). The models identified more spotted owl habitat on the landscape than barred owl habitat (Table 3.5). Fifty-three percent of the analysis area was predicted to be moderate or good spotted owl habitat and 32% of the landscape was predicted to be moderate or good barred owl habitat. Within the analysis area, 46,651 ha were classified as good for spotted owls and poor for barred owls, 17,345 ha were classified as good for barred owls and poor for spotted owls, and 87,428 ha were identified as good for both.

For spotted owls, habitat selection increased with increasing canopy closure, increasing tree size, more Douglas-fir, moderate amounts of grand fir, lower topographic position, moderate amounts of solar radiation, and moderately steep slopes (Table 3.4 and Figure 3.3). Habitat selection increased for barred owls in areas with moderate canopy closure, moderate tree size, more Douglas-fir, moderate amounts of grand fir, lower topographic position, moderate amounts of solar radiation, and gentle slopes (Table 3.7 and Figure 3.3). Coefficient estimates for tree size were relatively small for both species. The models including only topographic covariates ranked better than the vegetation only models for both species, highlighting the importance of topographic setting in this landscape (Tables 2.3 and 2.4).

The greatest differences in habitat covariate effects between the species were in topographic characteristics. Slope and topographic position had more influence (i.e., larger absolute value of coefficient estimates) in the barred owl model than in the spotted owl model. Good barred owl habitat was located on gentler slopes in lower topographic positions than good spotted owl habitat (Table 3.4, Figure 3.3). Canopy closure and tree size had larger coefficient estimates in the spotted owl model than in the barred owl model. Good spotted owl habitat had more canopy closure and larger trees than good barred owl habitat (Table 3.4, Figure 3.3).

Slope was the habitat characteristic that best distinguished between areas used by each species. Classification tree analysis comparing points surrounding spotted owl activity centers to those around barred owl activity centers highlighted that 72% of the barred owl used points fell on slopes < 16 degrees, whereas 72% of the spotted owl used points were on slopes >16 degrees (Figure 3.6). Classification tree analysis to distinguish between areas of greatest or least habitat overlap showed that two splits based on slope correctly classified 78% of 10,500 random points drawn from areas with good habitat for spotted owls and poor habitat for barred owls, good habitat for barred owls and poor habitat for spotted owls, or good habitat for both (Figure 3.7). Areas with slope <8.5 degrees were predominantly good habitat for barred owls and poor habitat for spotted owls, areas with slope > 21.5 degrees were predominantly good habitat for spotted owls and poor habitat for barred owls, and areas with intermediate slope (8.5 to 21.5 degrees) had substantial overlap.

DISCUSSION

The primary differences in habitat associations between the two species highlighted in this analysis were that barred owls used a broader range of forest structure and species composition conditions than spotted owls, and that barred owl sites tended to be located on flatter slopes in lower topographic positions than spotted owl sites. My classification tree analysis indicated that the degree of slope steepness was the best predictor for distinguishing areas used by each species and for distinguishing between areas with good habitat for spotted owls and poor habitat for barred owls (Figures 2.6 and 2.7). Other assessments of barred owl habitat have noted similar patterns. For example, Buchanan et al. (2004) found that, compared to spotted owl nest sites in the eastern Cascades, barred owl nest sites were in areas with gentler terrain, closer to water, and with greater tree species diversity (including deciduous trees). Herter and Hicks (2000) reported that spotted owl sites had more old forest nearby (<0.8 km radius) than barred owl sites. They also noted that barred owls were commonly located in moist forest situations along major river or stream drainages. Similar patterns have been noted in comparisons of spotted owl and barred owl habitat associations in other parts of the Pacific Northwest (Pearson and Livezey 2003, 2007, Hamer et al. 2007, Wiens 2012, Gremmel 2005). For example, Wiens (2012) found that spotted owls and barred owls overlapped substantially in their selection of forest cover types in the Oregon Coast Range, but barred owls tended to avoid steep slopes. The landscape-scale habitat associations found for spotted owls and barred owls in this study were similar to results reported from other studies in the eastern Cascades and around the Pacific Northwest. However, the important contribution from this work is the consistent analysis of barred owl and spotted owl habitat associations at a landscape scale, so that the degree of habitat overlap could be mapped and quantified.

In this study, good spotted owl habitat was characterized as forests with mean tree dbh >25 cm, canopy closure >50%, and a substantial component of Douglas-fir and grand fir, located on moderate to steep slopes (6-33 degrees), in lower- to mid-topographic positions (5-55%, Table 3.6). This is consistent with northern spotted owl habitat characteristics reported for the eastern Cascades and other parts of its range (reviewed by Courtney et al. 2004 and USFWS 2011). For example, Buchanan et al. (1995) reported that spotted owl nest sites within my analysis area in the eastern Cascades had more 35-60 cm dbh Douglas-fir trees than random sites within the same stand, and mean slope at nest sites was approximately 20 degrees. Everett et al. (1997) reported that spotted owls used stands that had a more complex, multi-layered canopy and more large (>41 cm dbh) trees than unused stands. Herter et al. (2002) reported that spotted owl roost sites in the moist conifer forest closer to the crest of the Cascade Range had mean canopy closure of 84% (SD = 14%), mean tree dbh of 37 cm (SD = 11 cm), and were located at lower elevations than random points within their study area.

My analysis showed that barred owls selected forests with a wide range of forest structure conditions (mean tree dbh >19 cm and canopy closure >34%), located on gentle slopes (<25 degrees) in low topographic positions (<25%, Table 3.9). These findings are consistent with habitat associations reported for barred owls across their range (reviewed by Livezey 2007), but reflect a broader range of forest structure conditions than reported by some studies in the

Pacific Northwest. For example, Singleton et al. (2010) found that barred owl home ranges were located more frequently than expected in areas with low topographic position, gentle slopes, large overstory tree-crown diameter, high normalized difference vegetation index (NDVI), overstory tree canopy closure >72%, and a moderate amount of solar radiation. Hamer et al. (2007) reported that an “old forest” cover type (trees >25 cm dbh) was used by barred owls more than other forest cover types within their study in the North Cascades. Wiens (2012) reported that barred owls used old conifer forest and hardwood forest more than expected based on availability. Buchannan et al. (2004) reported that 10 barred owl nests in the eastern Cascades of Washington were situated on gentle slopes or flat areas (mean slope 6 degrees), closer to water, in areas with a diversity of tree species. It is worth noting that most of these studies were conducted in areas where barred owls were sympatric with spotted owls (Hamer et al. 2007, Singleton et al. 2010, Wiens 2012), and may not have captured the range of forest conditions used by barred owls across broader landscapes.

Despite the notable differences in habitat associations between the two species, overlap in resource selection was still very substantial (Schoeners *D* = 0.63). Nearly half of the good habitat area for spotted owls was predicted also to be good for barred owls, and only about a quarter of the spotted owl good habitat area was predicted to be poor for barred owls (Table 3.8). Out of 199,862 ha of good spotted owl habitat, only 46,273 ha were identified as poor for barred owls.

Several differences in life history strategies between spotted owls and barred owls are likely to contribute to the observed differences in habitat associations. Barred owls are prey generalists that forage on the ground, while arboreal mammals are the primary prey for spotted owls (Hamer et al. 2001, Forsman et al. 2001, 2004, Livezey 2007, Wiens 2012). Forests with flat or gentle slopes may be more productive, contributing to greater abundance and vulnerability of ground dwelling prey for barred owls (Wiens 2012). Spotted owls also use home ranges that are substantially larger than barred owls (Hamer et al. 2007, Singleton et al. 2010, Wiens 2012). For example, Singleton et al. (2010) found that mean annual 95% fixed-kernel home-range size for barred owls in a portion of my analysis area was 194 ha (n = 4, SD = 70) for females and 288 ha (n = 5, SD = 114) for males, compared to annual spotted owl pair 95% adaptive kernel home-range sizes of 1,467 ha to 2,891 ha in the Cle Elum Demography Study Area (mean = 2,327 ha, n = 4 pairs; E. Forsman, U.S. Forest Service, PNW Research Station, unpublished data). Overlap of home ranges between adjacent pairs of barred owls is very limited and barred owls aggressively defend their small home ranges (Singleton et al. 2010, Wiens 2012). These differences in foraging strategies, space use, and territorial behavior suggest that spotted owls may be forced to “work around” areas occupied by territorial barred owls (Singleton et al. 2010, Wiens 2012).

These fundamental differences in natural history are likely contribute to spatial partitioning between spotted owls and barred owls, but with the data at hand it is impossible to distinguish between niche partitioning (i.e., the degree of differential resource use by coexisting species, Chase and Leibold 2003) and displacement effects from interference competition (i.e., displacement of spotted owls into lower quality habitat, Gutierrez et al. 2007). It is important to consider whether spotted owls have been displaced into lower quality habitats due to interference competition with barred owls. It may be the case that areas identified as “good” habitat based on the distribution of historic spotted owl sites may not be “high quality” habitat in terms of providing adequate resources for survival and reproduction (*sensu* Hall et al. 1997). This could be a situation where density of spotted owl sites is a misleading indicator of spotted owl habitat quality (Van Horne 1983).

My analysis identified 199,862 ha of good spotted owl habitat and 153,588 ha of good barred owl habitat (Table 3.5). However, it is important to note that there was more uncertainty regarding the estimate of habitat selection for spotted owls than for the barred owls. This could be a consequence of spotted owls being displaced into areas that are in the margins of their niche space, so spotted owls are using a broader range of conditions that were more difficult to capture in the GLMM models. The model uncertainty may also reflect map uncertainty for the covariates and their relative importance in the models for the two species. Topographic characteristics are generally easy to map reliably from digital elevation models, but forest structure characteristics, particularly tree size and species composition, are much more difficult to map (Ohmann et al. 2010). The strong association of barred owls with gentle slopes in valley bottoms, and their use of a broad range of forest structure conditions, may make habitat easier to map for barred owls than for spotted owls.

The greater area predicted to be good spotted owl habitat should not be interpreted to suggest that there is habitat to support more spotted owls than barred owls in this landscape due to differences in space-use between the two species (Singleton et al. 2010, Wiens 2012). It is also important to note that using binomial models with use–availability data presents some challenges because predicted values are not scaled between 0 and 1 and generally do not reflect true probabilities of resource selection (Manly et al. 2002, Keating and Cherry 2004). However, this approach does provide an informative and unbiased method for ranking habitat use and for comparing relative probability of use (Keating and Cherry 2004, Johnson et al. 2006). These maps should not be interpreted to suggest that barred owls are absent from portions of the landscape with moderate or poor habitat conditions, only that territorial spotted owl or barred owl pairs are expected to be more abundant in portions of the landscape with good habitat conditions.

Several notes of caution are appropriate here in interpreting habitat association differences between the two species. First, these differences may be transient, as barred owl populations grow and expand the range of habitats that they occupy. Empirical information on barred owl population trends is lacking. At this time we do not know whether barred owl populations are continuing to grow and expand the range of conditions that they occupy in the eastern Cascades Range of Washington. Second, the observed differences in habitat associations may be the result of displacement that took place prior to the documentation of the spotted owl activity centers. Barred owls were first detected in this area in the early 1980s when local spotted owl surveys were initiated. Most of the spotted owl activity centers were documented in the early- and mid-1990s. Substantial displacement by barred owls may already have taken place when these spotted owl sites were documented. Finally, continuing population declines in the Cle Elum Demography Study Area do not provide any indication that the spotted owl population has stabilized after adjusting to the presence of barred owls (Forsman et al. 2011). Despite these cautions, understanding spatial partitioning patterns between spotted owls and barred owls provides useful insights for understanding the population-level implications of displacement of spotted owls by barred owls and identifying areas where spotted owl pairs are most likely to persist and reproduce in the face of interference competition from barred owls. Even with the observed differences in habitat associations, high-quality habitat available to spotted owls is likely to be greatly limited if spotted owls are displaced from areas occupied by territorial barred owl pairs.

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Table 3.1. Vegetation and topography covariates used to characterize habitat associations for spotted owls and barred owls in the eastern Cascade Range, Washington, including the covariate means and standard deviations used for standardizing covariate values for GLMM analysis.

Covariate	Description	Source	Mean	SD
CANOPY	Canopy cover of all live trees	GNN[1] CANCOV	52.8	32.1
MNDBHBA	Basal-area weighted mean diameter of all live trees	GNN MNDBHBA_ALL	34.3	20.8
PCT_ABGR	Percent of the basal area of all live trees >= 2.5 cm dbh composed of grand fir	GNN (ABGR_BA / BAA_GE_3)	9.0	16.8
PCT_PSME	Percent of the basal area of all live trees >= 2.5 cm dbh composed of Douglas-fir	GNN (PSME_BA / BAA_GE_3)	31.8	31.6
SLOPE	Slope in degrees	DEM	19.7	11.1
SOLRAD	Annual daily mean direct solar energy in watt-hours per square meter	DEM	3107.3	533.9
TPOS1K	Percentile in the elevation range within 1 km radius (see text).	DEM	42.9	20.7

[1] GNN refers to generalized nearest neighbor GIS data described by Ohmann et al. (2010). CANCOV, MNDBHBA_ALL, ABGR_BA, PSME_BA, and BAA_GE_3 are attributes in the original GNN data.

Table 3.2. *A priori* generalized linear mixed models evaluated to characterize habitat associations for spotted owls and barred owls in the eastern Cascade Range, Washington. Covariate forms are indicated as linear (L), quadratic (Q), and a CANOPY x MNDBHBA interaction term (I). The owl site was used as a random intercept effect in all models.

Model	Covariates						
Name	CANOPY	MNDBHBA	PCT_ABGR	PCT_PSME	SLOPE	SOLRAD	TPOS1K
Null							
Full_L	L	L	L	L	L	L	L
Full_LI	I	I	L	L	L	L	L
Full_Q	Q	Q	Q	Q	Q	Q	Q
M2_L	L	L	L	L	L		L
M2_LI	I	I	L	L	L		L
M2_Q	Q	Q	Q	Q	Q		Q
Veg_L	L	L	L	L			
Veg_Q	L	L	Q	Q			
Topo_L					L	L	L
Topo_Q					Q	Q	Q
Full_IQ	I	I	Q	Q	Q	Q	Q

Table 3.3. AICc model selection results for generalized linear mixed models to characterize habitat associations for spotted owls and barred owls in the eastern Cascade Range, Washington, including the model name (see Table 2 for formulas), number of parameters (K), AICc, difference in AICc from the lowest AICc model (ΔAICc), AICc model weight (AICc Wt), and log-liklihood (LL).

<u>Spotted Owls:</u>

Model	K	AICc	ΔAICc	AICcWt	LL
Full_Q	16	33107.56	0.00	1	-16537.77
Full_IQ	15	33148.99	41.43	0	-16559.49
M2_Q	14	33410.62	303.06	0	-16691.30
Full_L	9	34499.96	1392.40	0	-17240.98
Full_LI	10	34501.82	1394.26	0	-17240.91
Topo_Q	8	37235.30	4127.74	0	-18609.65
Topo_L	5	38824.31	5716.75	0	-19407.15
Veg_Q	8	35117.12	2009.56	0	-17550.56
Veg_L	6	35728.52	2620.96	0	-17858.26
M2_LI	9	34647.79	1540.23	0	-17314.89
M2_L	8	34645.80	1538.24	0	-17314.90
Null	2	40868.21	7760.65	0	-20432.10

<u>Barred Owls:</u>

Model	K	AICc	ΔAICc	AICcWt	LL
Full_Q	16	4858.13	0.00	1	-2413.02
Full_IQ	15	4873.06	14.94	0	-2421.49
M2_Q	14	4949.61	91.49	0	-2460.77
Full_LI	10	5125.16	267.04	0	-2552.56
M2_LI	9	5170.13	312.01	0	-2576.05
Full_L	9	5191.82	333.69	0	-2586.90
M2_L	8	5239.63	381.50	0	-2611.80
Topo_Q	8	5646.46	788.34	0	-2815.22
Topo_L	5	5861.23	1003.10	0	-2925.61
Veg_Q	8	6622.91	1764.78	0	-3303.44
Veg_L	6	6912.92	2054.79	0	-3450.45
Null	2	7833.13	2975.00	0	-3914.56

Table 3.4. Fixed effect estimates and standard errors for the best generalized linear mixed model characterizing habitat associations for spotted owls and barred owls in the eastern Cascade Range, Washington.

	Spotted Owl		Barred Owl	
	Estimate	SE	Estimate	SE
(Intercept)	-0.526	0.037	-0.909	0.117
CANOPY	0.479	0.022	0.020	0.058
CANOPY^2	-0.117	0.025	-0.330	0.071
MNDBHBA	0.294	0.026	0.053	0.067
MNDBHBA^2	-0.034	0.012	-0.143	0.042
PCT_ABGR	0.524	0.031	0.957	0.078
PCT_ABGR^2	-0.100	0.011	-0.243	0.030
PCT_PSME	0.559	0.023	0.669	0.063
PCT_PSME^2	-0.248	0.019	-0.202	0.055
SLOPE	0.233	0.021	-0.987	0.073
SLOPE^2	-0.389	0.017	-0.143	0.054
SOLRAD	-0.321	0.019	-0.600	0.068
SOLRAD^2	-0.130	0.014	-0.366	0.058
TPOS1K	-0.503	0.017	-1.417	0.079
TPOS1K^2	0.0450	0.014	-0.326	0.055

Table 3.5. Proportion of the 984,541 ha analysis area within each combination of thee predicted habitat selection classes for spotted owl (columns) and barred owl (rows) activity centers in the eastern Cascade Range, Washington.

	Spotted Owl			
Barred Owl	Poor	Moderate	Good	Total
Poor	0.409	0.222	0.047	0.679
Moderate	0.039	0.059	0.067	0.165
Good	0.018	0.050	0.089	0.156
Total	0.466	0.331	0.203	1.000

Table 3.6. Covariate means (and 90% quantile ranges) within three predicted habitat selection classes for spotted owls and barred owls in the eastern Cascade Range, Washington.

	Spotted Owl Habitat Selection Class		
	Poor	Moderate	Good
CANOPY	33(0-90)	68(29-92)	75(49-92)
MNDBHBA	25(0-63)	41(19-68)	45(25-77)
PCT_PSME	17(1-92)	41(1-95)	49(10-91)
PCT_ABGR	3(1-12)	10(1-58)	22(1-64)
TPOS1K	50(12-83)	41(8-71)	29(5-56)
SOLRAD	3245(2078-3885)	3047(2058-3772)	2885(2134-3581)
SLOPE	19(1-40)	21(4-36)	21(6-33)

	Barred Owl Habitat Selection Class		
	Poor	Moderate	Good
CANOPY	48(0-92)	61(0-91)	67(34-91)
MNDBHBA	33(0-69)	36(0-64)	39(19-65)
PCT_PSME	28(1-94)	37(1-94)	44(3-83)
PCT_ABGR	6(1-38)	12(1-60)	21(1-62)
TPOS1K	51(22-81)	30(6-54)	20(2-43)
SOLRAD	3133(1993-3869)	3056(2282-3627)	3051(2467-3499)
SLOPE	23(4-39)	16(1-30)	11(1-25)

Figure 3.1. Location of the area analyzed to characterize habitat associations for spotted owl and barred owl activity centers in the eastern Cascade Range (in black) within the state of Washington (in grey).

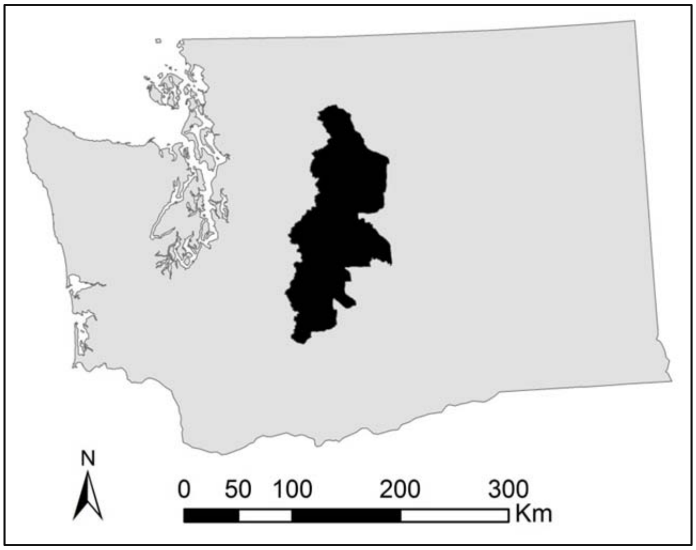
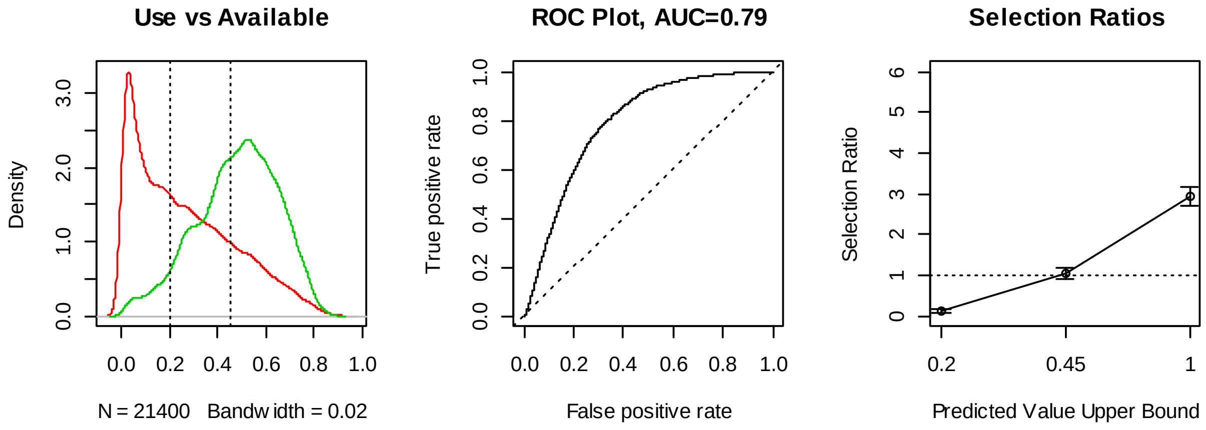


Figure 3.2. GLMM model performance for spotted owls (top row) and barred owls (bottom row), including density plots for comparing the distribution of predicted resource selection values at used points (green line) and available random points (red line), receiver observation characteristics (ROC) plots, and selection ratio plots for three habitat classes (selection ratio error bars indicate 95% Bonferroni confidence intervals). The vertical dotted lines in the density plots indicate the habitat class thresholds.

Spotted Owls:



Barred Owls:

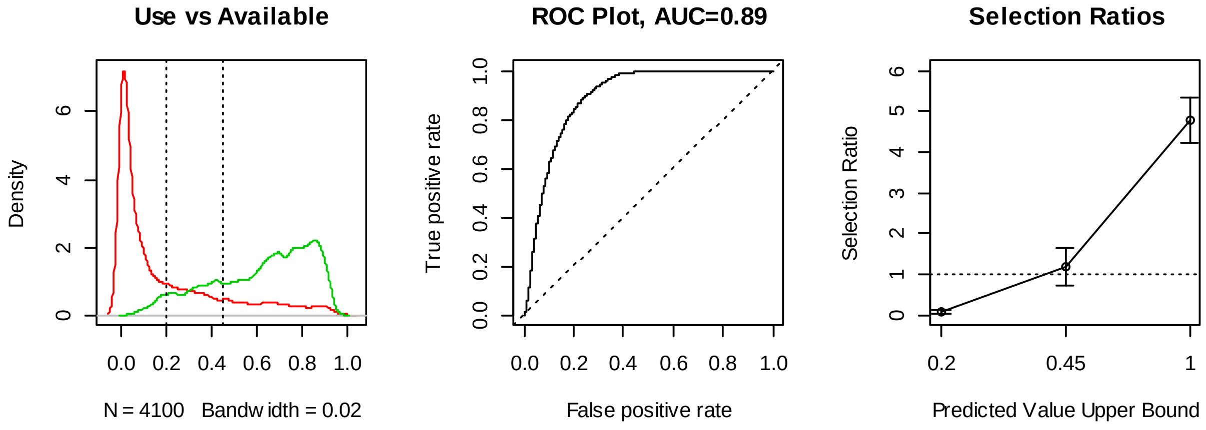
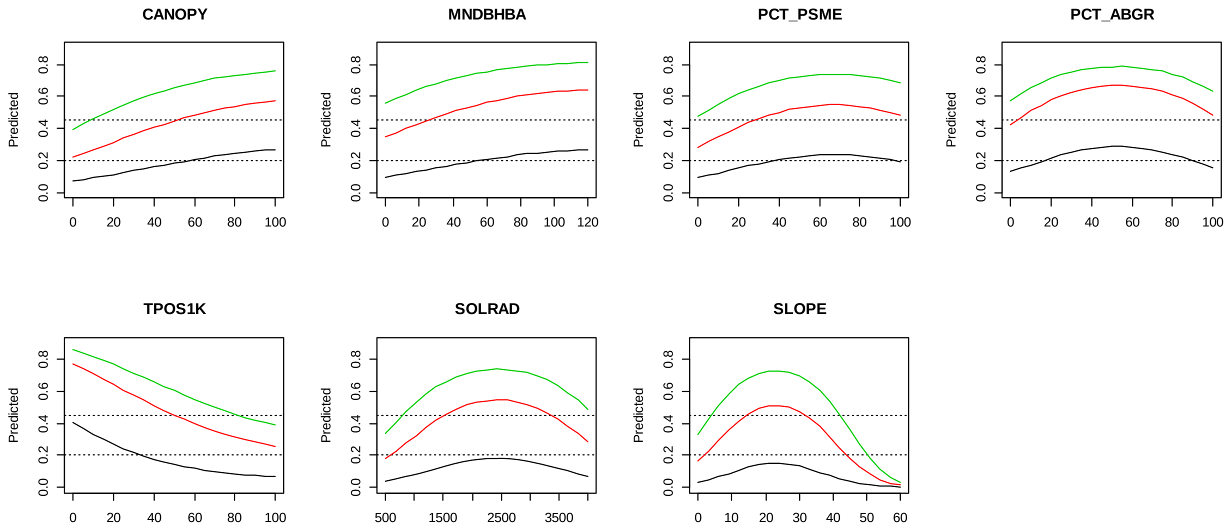
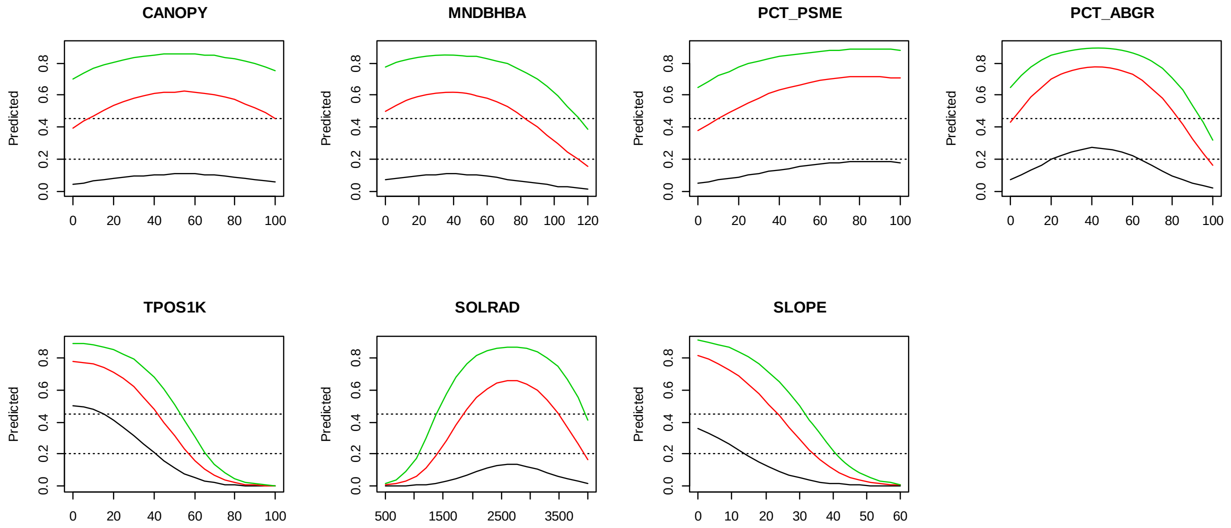


Figure 3.3. Covariate response curves calculated using the best GLMM model for habitat associations of spotted owls and barred owls in the eastern Cascade Range, Washington. The curves were calculated with simulated data representing the range of values for each covariate, with all other covariates fixed at their means for poor (black), moderate (red), or good (green) resource selection classes.

Spotted Owls:



Barred Owls:



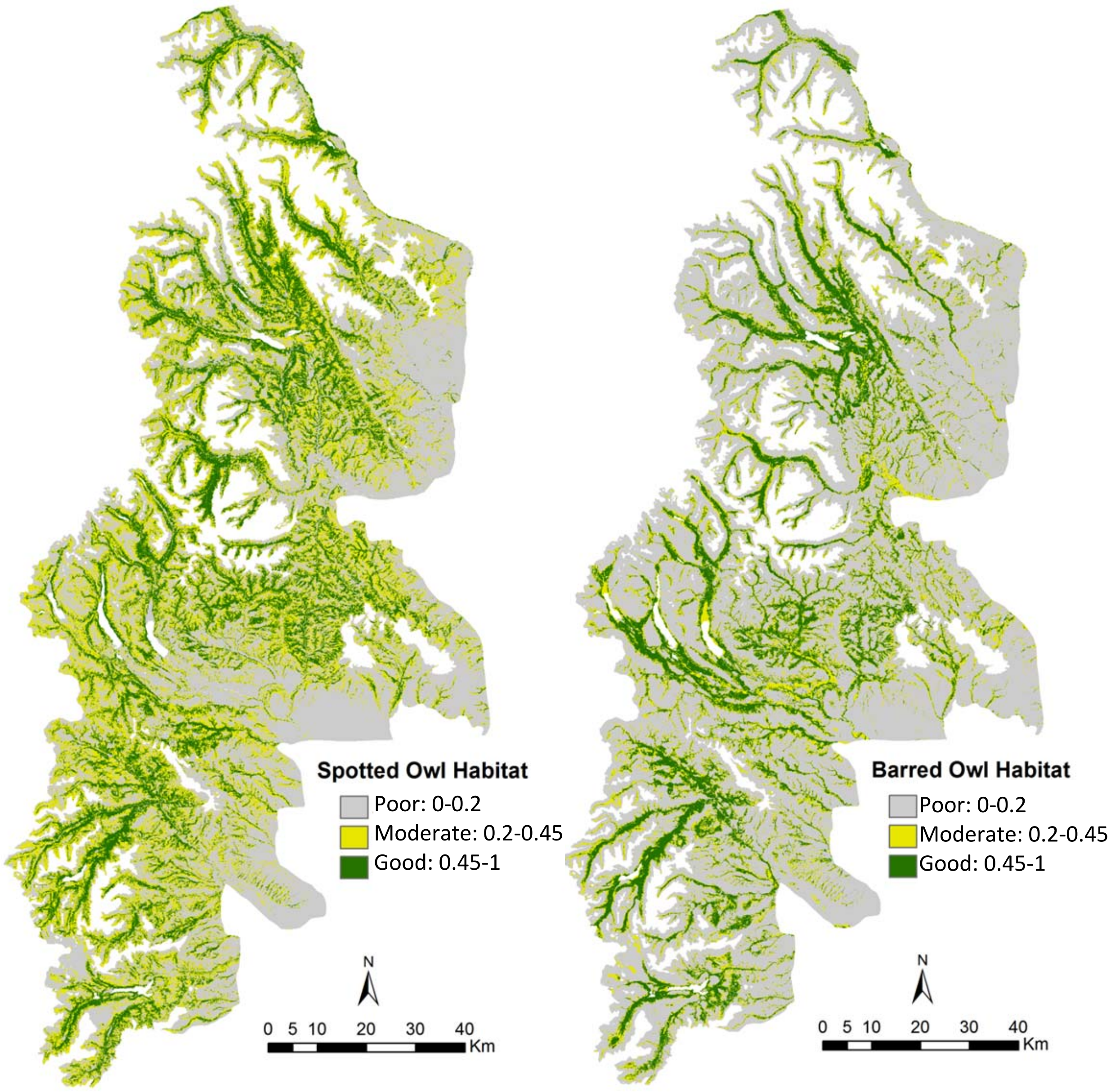


Figure 3.4. Maps of predicted habitat classes for spotted owls and barred owls in the eastern Cascade Range, Washington.

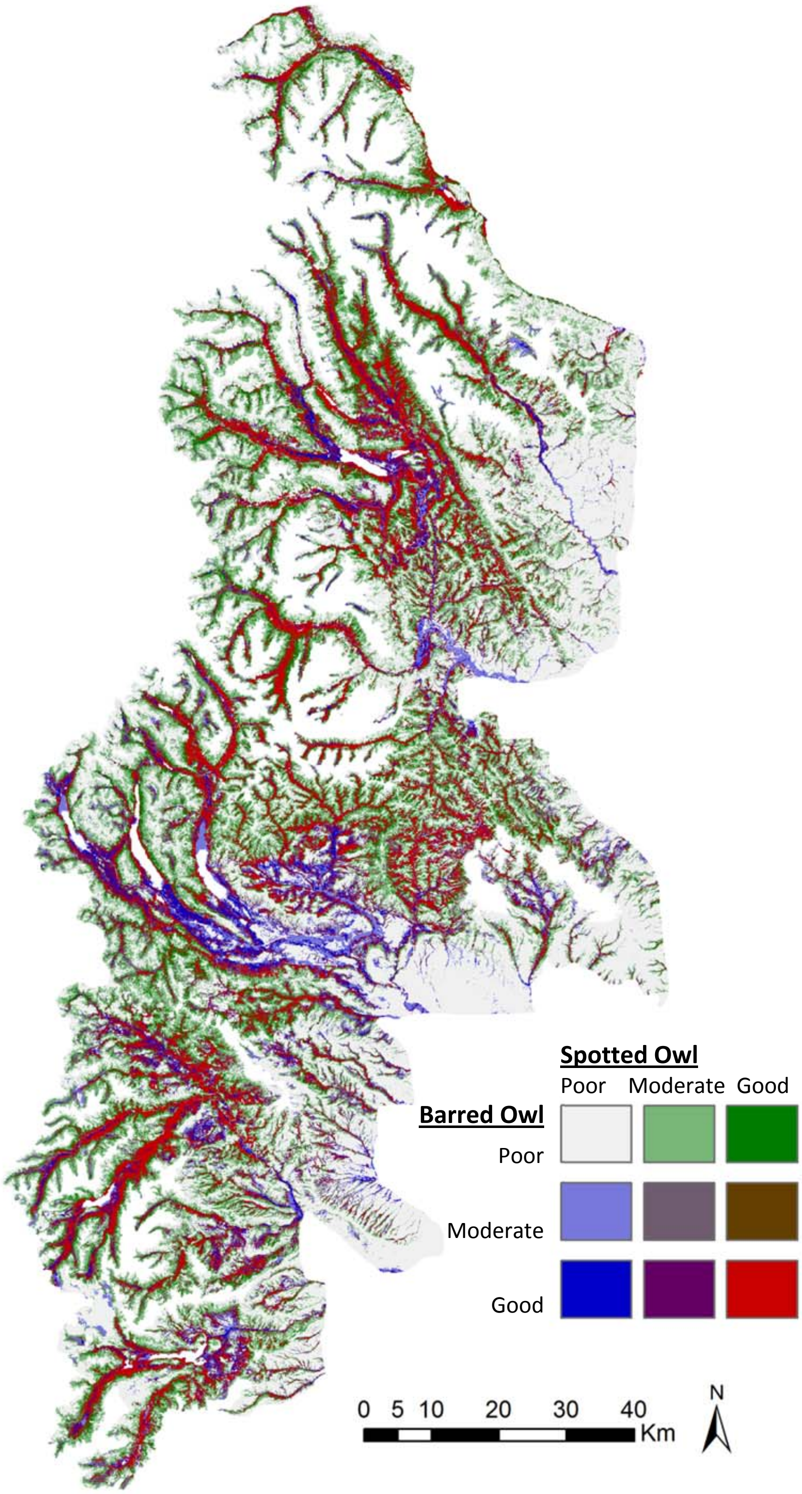


Figure 3.5. Overlap of predicted habitat classes for barred owls and spotted owls in the eastern Cascade Range, Washington.

Figure 3.6. Classification tree contrasting areas within five ha of spotted owl activity centers from areas within five ha of barred owl activity centers in the eastern Cascade Range, Washington. Branches to the left indicate cases where the criterion in the shaded box was met, branches to the right indicate cases where the criterion was not met. Text in the boxes for the leaves at the bottom show the expected class at the leaf (spotted owl: SPOW, or barred owl: BDOW), and the proportion of all barred owl (left) and spotted owl (right) sample points that meet the criteria for that leaf. This tree correctly classifies 71% of the barred owl sample points and 79% of the spotted owl sample points.

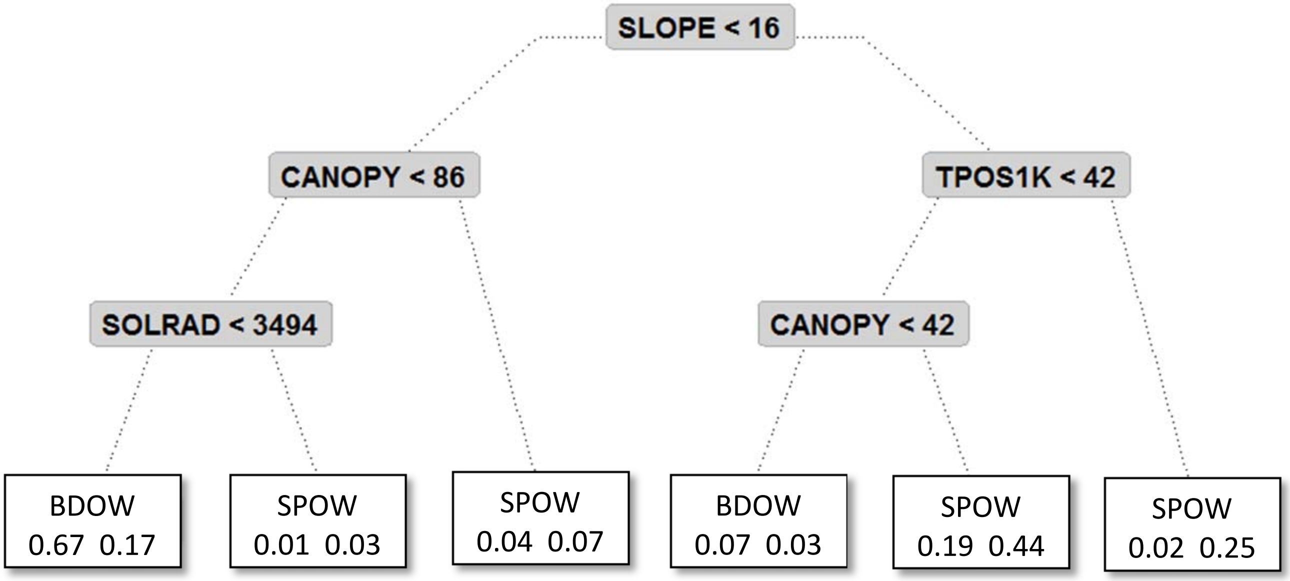
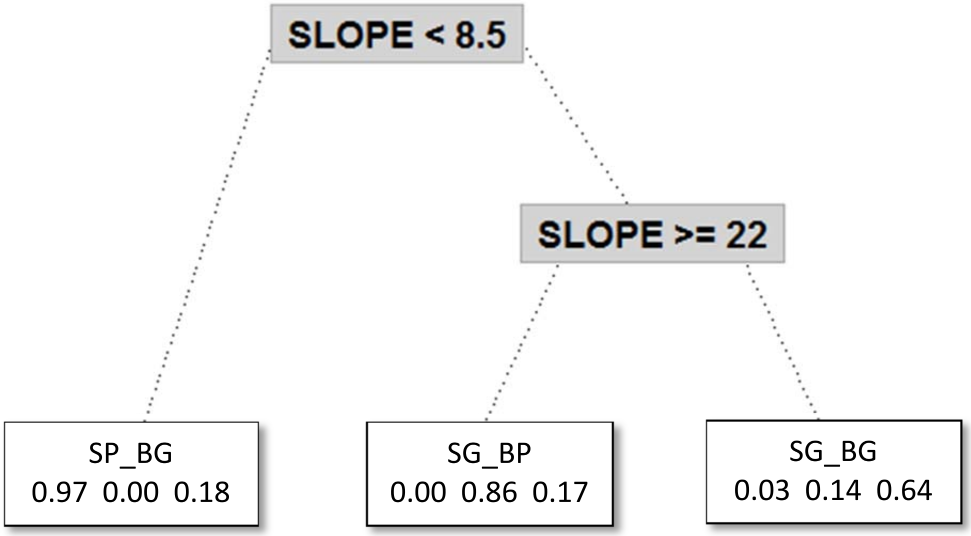


Figure 3.7. Classification tree to distinguish between areas predicted to be good spotted owl and poor barred owl habitat (SG_BP), poor spotted owl and good barred owl habitat (SP_BG), and areas that are good habitat for both (SG_BG) based on GLMM model estimates at 10,500 random points (3500 in each class) in the eastern Cascade Range, Washington. Counts indicated at each node show the proportion of points within each class that meet the criteria for that node (SP_BG / SG_BP / SG_BG). This tree correctly classified 83% of the sampled points.



CHAPTER 4: DOES OVERLAP OF BARRED OWL AND SPOTTED OWL HABITAT INFLUENCE SPOTTED OWL PAIR SITE OCCUPANCY DYNAMICS?

ABSTRACT

Competitive interactions with barred owls (*Strix varia*) are recognized as an important factor contributing to northern spotted owl (*Strix occidentallis caurina*) population declines in Washington. Most studies addressing impacts of barred owl interactions on spotted owl site occupancy dynamics and demographic rates have used incidental detections of barred owls recorded during spotted owl surveys for an index of barred owl interaction effects.

This approach has important limitations, including potential barred owl detection bias associated with spotted owl survey protocols and inability to detect cumulative effects of multiple neighboring barred owls. As an alternative, I evaluated whether habitat overlap for spotted owls and barred owls influenced spotted owl pair site occupancy rates using multi-year dynamic occupancy models. I analyzed site occupancy histories for 60 spotted owl pair sites over 23 years (1989 to 2011) in the eastern Cascade Range, Washington. I mapped good, moderate, or poor habitat for each species based on resource selection probability maps, then combined that information into a map of nine habitat overlap classes. I measured the area of each habitat overlap class within circles centered on yearly spotted owl pair activity center locations at scales corresponding to the nesting core area (100 ha), breeding season home range (500 ha), and annual home range (2000 ha). The breeding season home range scale (500

ha) models performed best based on AICc scores. Overlap between barred owl and spotted owl habitat had a substantial effect on spotted owl pair site occupancy dynamics during this study. Spotted owl pair site occupancy probability declined through the study for all of the spotted owl pair sites, but it declined much less for sites with more good spotted owl habitat that overlapped with poor barred owl habitat. This analysis demonstrated that a habitat overlap approach was informative for quantifying expected effects of competitive interactions with barred owls on spotted owl pair site occupancy dynamics. The portions of my study area identified as good spotted owl habitat overlapping with poor barred owl habitat were important for spotted owl pair site persistence over the duration of this study.

INTRODUCTION

Northern spotted owls (*Strix occidentallis caurina*) were listed as a federally threatened species in 1990 (USFWS 2011). That listing was largely due to the species association with old forests and impacts from commercial timber harvest (Thomas et al. 2006). Since the time of the listing, barred owls (*Strix varia*) have become abundant in some areas and spotted owl numbers have declined in the eastern Cascade Range, Washington, as well as in other parts of the spotted owl's range (Forsman et al. 2011, Gutierrez et al. 2007, Livezey 2009). Relative to spotted owls, barred owls are slightly larger, more aggressive, and use smaller home ranges (Hamer et al. 2007, Livezey 2007, Singleton et al. 2010, Wiens 2012). Recent assessments have highlighted the importance of interactions with barred owls as a factor contributing to spotted owl population declines (Gutierrez et al. 2007, USFWS 2011). Understanding how interactions with barred owls influence the distribution and abundance of spotted owls will be important for developing effective spotted owl conservation strategies.

Several studies have addressed effects of competitive interactions with barred owls on spotted owl distribution and demography through occupancy modeling (Olson et al. 2005, Bailey et al. 2009, Kroll et al. 2010, Dugger et al. 2011), mark-recapture studies (Anthony et al. 2006, Forsman et al. 2011), and other approaches (Kelly et al. 2003, Crozier et al. 2006, Van Lanen et al. 2011). For example, Kelly et al. (2003) found that raw estimates of occupancy (not corrected for detection probability) declined more at spotted owl sites where barred owls were detected than where they were not detected in western Oregon. Forsman et al. (2011) found evidence of negative relationships between demographic rates of spotted owls and the presence of barred owls on most of the 11 study areas included in their meta-analysis of spotted owl demographic rates. Presence of barred owls was associated with decreased probability of spotted owl pair site colonization and increased probability of extinction in several study areas in western Oregon and eastern Washington (Dugger et al. 2011, Kroll et al. 2010, Olson et al. 2005).

These studies have contributed substantially to understanding effects of interactions with barred owls on spotted owl distribution and abundance; however there are important limitations in the ways these studies have quantified barred owl interactions. Most studies have used a binary attribute indicating whether barred owl detections were recorded incidental to spotted owl survey activities (Kelly et al. 2003, Olson et al. 2005, Anthony et al. 2006, Bailey et al. 2009, Kroll et al. 2010, Dugger et al. 2011, Forsman et al. 2011). There are several important limitations associated with this approach. First, barred owl detection probability is potentially biased by survey methods focused on documenting spotted owl presence and reproductive status (Bailey et al. 2009, Wiens et al. 2011). For example, barred owls are less likely to be detected during daytime site searches at historical spotted owl nest locations than they are during nighttime call surveys (Bailey et al. 2009), and barred owls respond less frequently to spotted owl calls than they do to conspecific calls (Wiens et al. 2011). Second, a binary attribute indicating whether or not a barred owl has been detected near a site will be insensitive to potential cumulative effects of displacement when more than one territorial pair of barred owls is present in the surrounding landscape. Finally, effects of interactions with barred owls on resident spotted owls are likely to differ depending on the territorial or transient (floater) status of the barred owls. Territorial barred owls may exclude neighboring spotted owls from specific habitat patches, while non-territorial floaters may have intermittent agonistic interactions with resident spotted owls as the barred owl seeks an area in which to establish a territory (Wiens 2012). Failing to distinguish between floater and territorial pair responses may over-estimate the number of spotted owl sites “occupied” by barred owls, and under-estimate the cumulative impacts of nearby territorial barred owl pairs on resident spotted owls.

In response to these limitations, several authors have suggested that conducting concurrent surveys for both spotted and barred owls will be important for effectively documenting barred owl interaction effects on spotted owl site occupancy (Livezey and Flemming 2007, Bailey et al. 2009, Wiens et al. 2012, Kroll et al. 2010). However, there are three important challenges associated with conducting widespread concurrent surveys for both species: 1) increased workload and associated costs, 2) potential to reduce spotted owl response rates after barred owl calls have been broadcast in an area and, 3) undue harassment of spotted owls by broadcasting barred owl calls (Kroll et al. 2010).

An alternative to using either incidental detections of barred owls or concurrent surveys for spotted owls and barred owls for estimating impacts of competitive interactions is to use estimates of barred owl resource selection to identify areas where barred owl pairs are most likely to occur. A habitat-based approach would have several important advantages. First, a habitat-based approach would not be sensitive to potential biases associated with local single or concurrent dual species survey efforts. Second, it could specifically represent the probability of occupancy by territorial barred owl pairs, and therefore would be less likely to be confounded by differences between barred owl floaters and territorial pairs. Third, using spatially explicit resource selection maps for evaluating interaction patterns would allow analysis results to be projected to un-surveyed areas within an appropriate scope of inference.

In Chapter 2 of this dissertation I developed landscape-scale resource selection maps for spotted owls and barred owls in the eastern Cascade Range, Washington, based on results of species-specific call surveys. I demonstrated that there are differences in habitat and landscape associations between the two species. I showed that barred owls used a broader range of forest structure conditions than spotted owls, and barred owl pair activity centers were more commonly associated with gentle slopes (<16 degrees) than spotted owl activity centers. Similar patterns have been noted in other work (Herter and Hicks 2000, Gremmel 2004, Hamer et al. 2007, Singleton et al. 2010, Wiens 2012). These maps specifically represented habitat selection (i.e., use relative to availability, *sensu* Hall et al. 1997) for barred owl and spotted owl territorial pairs. However, it is important to note that the distribution of spotted owl activity center locations used in this analysis may have been influenced by competitive interactions with barred owls, and observed spotted owl habitat selection (i.e., use relative to availability) may not be synonymous with spotted owl habitat quality (i.e., the capability of an area to support individual or population persistence, *sensu* Hall et al. 1997).

A fundamental question for evaluating the effectiveness of a resource selection-based approach for assessing potential impacts of competitive interactions with barred owls is whether the degree of overlap in habitat between spotted owls and barred owls relates to spotted owl pair site occupancy dynamics. Occupancy modeling has emerged as an important analysis tool for wildlife conservation over the past 10 years and is well suited for addressing this kind of question (MacKenzie et al. 2006, Royle et al. 2008). These models use a maximum likelihood statistical framework to evaluate multiple processes at the same time. Typical occupancy models evaluate the probability of occupancy (ψ, the probability that the animal is at a site), as well as the probability of detection (p, the probability that an animal is observed at the site given that it is present). This class of models has been broadly applied for wildlife monitoring activities for a variety of species, including spotted owls (MacKenzie et al. 2003, Bailey et al. 2009, Dugger et al. 2011, Olson et al. 2005, and Kroll et al. 2010). This multi-process modeling framework has been expanded to address processes beyond simple occupancy and detection probabilities. In particular, dynamic multi-year occupancy modeling methods have been developed to evaluate the probability that a site transitions from occupied to unoccupied (ε, extinction) and the probability that a site transitions from unoccupied to occupied (γ, colonization, MacKenzie et al. 2006). This approach has recently been used to evaluate the effect of habitat and landscape characteristics on site occupancy processes over time for a variety of species (for example, Martin et al. 2010, Frey et al. 2012, McNew et al. 2012, Pederson et al. 2012).

My objective for this study was to evaluate if the degree of overlap between spotted owl and barred owl habitat was predictive of spotted owl pair site persistence. I used multi-year dynamic occupancy modeling to test if estimates of spotted owl resource selection, barred owl resource selection, and the overlap between them were predictive of spotted owl pair site occupancy over time. I expected that detection rates would be higher, colonization rates would be higher, and extinction rates would be lower at sites where good spotted owl habitat was present in areas that were unlikely to be used by barred owls compared to sites where good spotted owl habitat overlapped with areas likely to be used by barred owls. I also expected that local spotted owl pair site occupancy would decline over time due to decreasing colonization rates and increasing extinction rates, as a consequence of the increasing barred owl abundance over the duration of this study.

STUDY AREA

This analysis is based on spotted owl site occupancy data drawn from the Cle Elum demographic study area in the eastern Cascade Range, Washington (Anthony et al. 2006, Forsman et al. 2011). The Cle Elum study area encompasses 178,978 ha within the Yakima River watershed in the central portion of the Okanogan-Wenatchee National Forest, Washington (approximately 47°11’ S, -120°59’ E, Figure 4.1). Vegetation communities in this area are substantially influenced by the strong moisture gradients associated with the rain-shadow effect of the Cascade Range and local topography. Forest cover is a mix of moist-mesic conifer forest at high elevations in the western portion of the study area, xeric-mesic mixed conifer forest at mid elevations, and dry ponderosa pine (*Pinus ponderosa*) woodlands, shrublands, and grasslands along the lower, eastern edge of the study area (Lillybridge et al. 1995, Johnson and O’Neil 2001). The moist-mesic forest is characterized by silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) at higher elevations, and Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and western hemlock (*Tsuga heterophyla*) at lower elevations. The xeric-mesic mixed conifer forest was characterized by a mix of Douglas-fir, grand fir, and ponderosa pine. The lower portion of the landscape, adjacent to the Yakima River, is predominantly private residential and agricultural land, or riparian forest. A checkerboard pattern of public and private land ownership, combined with past land uses, has resulted in highly fragmented landscape patterns for portions of the Cle Elum study area. Much of the area experienced intensive commercial timber harvest through the 1980s. Timber sale activities within spotted owl habitat on federal lands declined substantially with the listing of the spotted owl in 1990 (Thomas et al. 2006). In 1994, 58,300 ha of the study area were designated as Late Successional Reserves under the Northwest Forest Plan. Harvests on state and private lands have continued.

METHODS

I used multi-year dynamic occupancy models to evaluate the effect of habitat overlap between spotted owls and barred owls on spotted owl pair site occupancy dynamics following methods developed and implemented by MacKenzie et al. (2003), Olson et al. (2005), Kroll et al. (2010), and Dugger et al. (2011). I conducted this analysis at three scales corresponding to nesting core area (100 ha), breeding season home range (500 ha), and annual home range (2000 ha) sizes to evaluate the relative importance of habitat overlap at different scales and identify whether effects were different across scales.

I analyzed 23 years of spotted owl occupancy data collected from 1989 to 2011 to evaluate the effect of overlap between spotted owl and barred owl habitat on spotted owl site colonization and extinction rates (Forsman et al. 2011, and Eric Forsman, USDA Forest Service, Pacific Northwest Research Station, Corvallis OR, unpublished data). My resource selection mapping methods were described in Chapter 2 of this dissertation and are summarized below. The spotted owl occupancy data were collected for a mark-recapture demographic monitoring study to determine spotted owl survival and reproductive rates (Anthony et al. 2006, Foresman et al. 2011), but these data are also well suited for analysis with occupancy modeling methods (MacKenzie et al. 2003, Olson et al. 2005, Kroll et al. 2010, Dugger et al. 2011). Call surveys in the Cle Elum study area followed standard protocols described by Lint et al. (1999). Survey visits included day or night call surveys, as well as follow-up daytime visits to determine reproductive status and band adult or juvenile spotted owls. Using the approach described by Olson et al. (2005:932), I considered a visit to a site to be complete if an owl was found at the site and adequate follow-up visits to document reproductive status were conducted, or if all of the call survey stations in the vicinity of a site were surveyed within a seven-day period without response. Sites received at least three or four complete visits per year, though several sites had more visits in some years. Additional visits often reflected efforts to band adults or juveniles and thus did not reflect standard survey effort (Stan Sovern pers. commun.). I used only the first four complete visits per year because this captured final occupancy status for all of the sites and using additional visits where site status and location were previously known (as in return visits for banding) could bias detection probability estimates (MacKenzie et al. 2006). A few of the owls included in the Cle Elum demography study were radio-tagged from 1989 to 1990 (Stan Sovern pers. commun.). Locations collected from radio-tagged individuals were not included in this analysis.

A pair site was defined as an area of traditional use by a pair of spotted owls, where one or more members of that pair were repeatedly found over the course of more than one breeding season. These traditional territories often encompassed more than one nest structure, so the specific activity center location for most sites shifted over time. Unique activity center coordinates were compiled for each year the site was occupied. Yearly activity center coordinates were determined based on the following hierarchy: 1) the nest site location during that year, 2) the first early-season juvenile roosting location (before August 1), 3) the first daytime adult pair roosting location recorded during that season, or 4) the earliest pair location of any type, including call survey responses. Sites were considered to be unoccupied by a pair if no detection was recorded for that year or if only a single, unpaired spotted owl was detected at the site. Activity center coordinates for unoccupied years were based on the most recent previous pair location for that site. Coordinates for sites that were surveyed in years prior to pairs being detected at the site were taken from the first pair location recorded for the site.

I used the following screening criteria to assure site location accuracy and habitat data consistency. I excluded sites with fewer than six visits over the duration of the study (i.e., at least two years of survey effort meeting the Lint et al. 1999 protocol), or never occupied by a pair. I used *Landtrendr* disturbance maps (Kennedy et al. 2010) to screen out sites where disturbances caused conditions to be substantially different from those represented by my resource selection maps. I screened out sites if >10% of the area surrounding a spotted owl pair site (within 100 ha, 500 ha, or 2000 ha circles) experienced substantial disturbance relative to 2006, the year of the vegetation map on which the resource selection estimates were based. This eliminated sites where the habitat mapping was likely to be in error due to timber harvest or fire impacts.

The resource selection analysis methods used to derive the habitat overlap maps for this study were described in Chapter 2 of this dissertation. Briefly, I derived resource selection maps based on binomial generalized linear mixed model analysis of 50 points from five ha surrounding the activity centers for spotted owls (n=214) and barred owls (n=41), compared to three times as many random points taken from the Okanogan-Wenatchee National Forest analysis area. Activity centers were located during species-specific call surveys for both spotted owls and barred owls to avoid potential bias associated with barred owl detections recorded incidental to spotted owl survey efforts. Model covariates included forest characteristics (canopy cover, tree size, and species composition from GNN classified satellite imagery for 2006; Ohmann and Gregory 2002) and topographic characteristics derived from a 10 m digital elevation model (slope, solar radiation, and topographic position). Areas over 1500 m elevation were considered to be unavailable to both species of owl based on the observed distribution of the owl sites, and were excluded from this analysis. Based on use-availability analysis results, I collapsed the resource selection maps into three categories representing poor (areas used less than expected based on availability), moderate (areas used in proportion to availability), and good habitat (areas used more than expected based on availability). I combined the classified resource selection maps for spotted owls and barred owls, and used a two-digit numeric coding scheme to track the habitat overlap classes (Table 4.1, Figure 4.2).

I calculated the proportion of the area surrounding each yearly spotted owl pair activity center location that was within each of the nine habitat overlap classes (Figure 4.2). Proportions were calculated using circles of 100 ha (564 m radius), 500 ha (1262 m radius), and 2000 ha (2523 m radius) to evaluate effects at scales that approximate sizes of the nesting core area, the breeding season home range, and the annual home range based on local spotted owl radio-telemetry data (Stan Sovern, USDA Forest Service, Pacific Northwest Research Station, Cle Elum WA, unpublished data). It is important to acknowledge that these circular sample areas are not realistic representations of space use by the resident owls, but these circles do provide a simple measure of habitat availability at multiple, ecologically-relevant scales surrounding each site, and this is a common approach for systematically sampling landscape characteristics surrounding spotted owl activity centers (e.g., Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005).

I used the *colext* function in the *unmarked* package for R to compute multi-year dynamic occupancy models for spotted owl pairs in the Cle Elum study area (R version 2.15.1, R Development Core Team, Vienna Austria; unmarked version 0.9-8, Fiske and Chandler 2011). The sample unit for this analysis was the unique spotted owl pair site. The primary sampling occasions were years, and the secondary sampling occasions were individual site visits. I compiled visit histories for each spotted owl pair site (Figure 4.3). I used the dynamic occupancy modeling framework to apply a multinomial likelihood model to these data and estimate covariate effects on detection (p), colonization (γ), and extinction (ε) rates (MacKenzie et al. 2003, 2006). I compared the resulting models using an information theoretic approach based on sample size corrected Akiake's information criterion (AICc) tables compiled with the *AICcmodavg* package for R (version 1.26, Mazerolle 2012). Yearly site covariates included measures of time and habitat overlap for spotted owls and barred owls (Table 4.1). Habitat covariates included the proportion of 100 ha, 500 ha, and 2000 ha circles surrounding the activity center that fell within each of the nine habitat overlap classes described above. I also calculated the total amount of good or moderate spotted owl and barred owl habitat at each scale. I included these summary covariates to investigate whether spotted owl site colonization and extinction rates were simply a function of the amount of spotted owl or barred owl habitat surrounding a site, regardless of overlap between the two species. I centered all of the habitat covariates (taking the observed proportion for each class at each site, each year, minus the mean for all sites, all years) to facilitate the maximum likelihood optimization calculations (Fiske and Chandler 2011).

Barred owl detections increased substantially within the Cle Elum study area over the duration of the study (Forsman et al. 2011). I evaluated two time covariates to address temporal changes in the effect of habitat overlap with barred owls. First, I included a continuous measure of year (year), centered on the year 2000. This covariate allowed me to investigate the linear effect of time on detection probability. Second, I split the duration of the study into three seven- or eight-year time periods representing the early (period 1: 1989 to 1995), middle (period 2: 1996 to 2003), and later (period 3: 2004 to 2011) portions of the study. I used these time periods as a categorical factor for estimating detection, colonization, and extinction rates.

Following the procedures of Olson et al. (2005), Kroll et al. (2010), and Dugger et al. (2011), I used a two-step approach for model selection. First, I evaluated a set of *a priori* detection models (Table 4.2) while holding the occupancy, colonization, and extinction components constant with an intercept-only (null) parameterization. I selected the detection model that had the lowest AICc score (ΔAICc = 0) across the majority of the three scales. I used the same detection model across all three scales of analysis in order to keep subsequent analyses as comparable as possible. In the second analysis step, I evaluated a set of 12 *a priori* colonization and extinction models using the best detection model identified during the first step (Table 4.3). I held the occupancy component for all models constant with an intercept-only parameterization because initial probability of occupancy did not vary in this analysis. All combinations of the *a priori* colonization and extinction models were run for each scale. I analyzed each scale separately and did not combine covariates across scales in order to identify differences in covariate effects across different scales of analysis. I considered models within two AICc units of the best model (ΔAICc < 2) to be well supported and used model averaging to derive parameter estimates from the these models at each scale (Burnham and Anderson 2010). I limited the model averaging analysis to the models with ΔAICc < 2 because this captured the models with the majority of the model weight at each scale and it substantially reduced the number of parameters included in the model averaging, leading to a simpler analysis that focused on the most important parameters. If the optimization calculations for a model failed to converge, I used parameter values from the same model formula successfully run at a different scale as starting values for the optimization calculation (Fiske and Chandler 2011). If the model still failed to converge, it was eliminated from consideration.

MacKenzie et al. (2003, 2006) showed that occupancy probability at time *t* could be estimated from the initial occupancy probability in combination with colonization and extinction rates through time using the equation: $\psi_t = \psi_{t-1}(1 - \varepsilon_{t-1}) + (1 - \psi_{t-1})\gamma_{t-1}$. I used this approach to calculate occupancy probability at the end of the study for sites with differing levels of habitat overlap using model-averaged estimates of extinction (ε) and colonization (γ) from the supported models at each scale.

RESULTS

Sixty spotted owl pair sites met the disturbance and sample criteria for my dynamic occupancy modeling analysis (Figure 4.3). The total number of spotted owl pair sites visited in a year ranged from 22 in 1989 to 59 in 2004 through 2007 (Figure 4.4). The number of sites occupied by spotted owl pairs ranged from 38 sites in 1992 to eight sites in 2009 through 2011. There were 84 colonization events (where a site transitioned from unoccupied in year *t* to occupied in year *t*+1) and 121 extinction events (where a site transitioned from occupied in year *t* to unoccupied in year *t*+1). Occupancy probability declined through the study for all sites, but it declined most for sites with little or no good spotted owl habitat overlapping with poor barred owl habitat (h31), and the effect was most substantial at the broader scales.

Detection rates did not change substantially through time, but did vary with habitat overlap characteristics. Detection rates were slightly higher from 1995-2003 (time period 2) than during other portions of the study, though differences across the time periods were not substantial (Table 4.6, Figure 4.5). Detection rates were lower for sites that had more good spotted owl habitat overlapping with poor barred owl habitat (h31), higher in sites that had more good spotted owl habitat overlapping with moderate barred owl habitat (h32), and the amount of area of good spotted owl habitat that overlapped with good barred owl habitat (h33) did not substantially influence detection rates. The detection model incorporating the overlap between good spotted owl habitat and the three classes of barred owl habitat, in combination with the effect of time period (*p*(h31+h32+h33+period)), was the best model at the 100 ha and 2000 ha scales, and second best at the 500 ha scale (Table 4.4). The model incorporating the amount of good barred owl habitat and an interaction with the time periods (*p*(BDg*period)) was the best at the 500 ha scale and second best at the 100 ha scale. With this model, probability of detection was higher in areas with more good barred owl habitat, and this effect increased over time (not a significant effect in period 1, but increasing effect in periods 2 and 3). I chose to use the *p*(h31+h32+h33+period) detection model for subsequent colonization and extinction modeling because it was the best model for two out of the three scales. The mean detection rate throughout the study based on model-averaged fitted values from the supported models at the 500 ha scale was 0.73 (SD = 0.09).

Time period and the degree of overlap between spotted owl and barred owl resource selection classes had substantial influence on spotted owl pair site colonization rates, but had less influence on extinction rates. The best complete dynamic occupancy model was

$$\psi(.)\ \gamma(\text{h31+h32+h33+period})\ \varepsilon(\text{SPg})\ p(\text{h31+h32+h33+period})$$

at the 500 ha scale (Table 4.5). Only one competitive model did not include the degree of overlap with barred owl habitat in the colonization component across all three scales of analysis (Table 4.5). No competitive models included overlap with barred owl habitat in the extinction component. Models including only time covariates for colonization and extinction components did not receive any model weight in the AICc analysis, indicating that the habitat characteristics surrounding spotted owl pair sites in the Cle Elum study area did influence site occupancy dynamics. Optimization calculations for all of the *a priori* models converged for the 500 ha scale. Three models failed to converge for the 100 ha scale, and two failed to converge for the 2000 ha scale, even after providing starting values (Table 4.5).

Colonization rates declined through time, but sites with more area of good spotted owl habitat that overlapped with poor barred owl habitat (h31) had substantially higher probability of colonization (Table 4.6, Figure 4.6). The amount of area surrounding a site that was good spotted owl habitat overlapping with poor barred owl habitat (h31) was the most influential parameter in the colonization models at all scales. The amount of good spotted owl habitat that overlapped with moderate barred owl habitat (h32) contributed to increased colonization rates at the 100 ha scale, but not at 500 ha or 2000 ha. The area of good spotted owl habitat that overlapped with good barred owl habitat (h33) had a positive parameter estimate, but 95% confidence limits overlapped zero for all scales, indicating little influence on colonization rates. Colonization rates declined through time, with the 2004-2011 period having substantially lower colonization rates than earlier portions of the study (Figure 4.5). The mean observed colonization rate based on model-averaged fitted values from the supported models at the 500 ha scale was 0.32 (SD = 0.13) in time period 1, 0.16 (SD = 0.09) in time period 2, and 0.04 (SD = 0.03) in time period 3.

Extinction rates were relatively constant across the duration of the study and were not substantially influenced by habitat characteristics (Figure 4.5). The mean extinction rate throughout the study based on model-averaged fitted values from the supported models at the 500 ha scale was 0.21 (SD = 0.04). Model-averaged parameter estimates indicated a slight increase in extinction rate during period 2, but these effects were not strongly reflected in the model-averaged fitted values. Covariates representing overlap between spotted owl and barred owl habitat were not included in the supported extinction models at any scale. A parameter representing the total amount of good spotted owl habitat, regardless of overlap with barred owl habitat (SPg) was included in the supported models. Parameter estimates for this covariate were all positive, but 95% confidence limits overlapped zero for the 100 ha and 2000 ha scales, and were close to overlapping zero for the 500 ha scale, indicating that the amount of spotted owl habitat surrounding a site was not a strong predictor of site extinction rates.

Occupancy probability declined through the study for all sites, but it declined most for sites with little or no good spotted owl habitat overlapping with poor barred owl habitat (h31), and the effect was most substantial at the broader scales. The estimate of initial occupancy probability (ψ) for this data set was 0.85. When all other covariates were held at their means, model-averaged estimates of year 2011 occupancy probability were 0.09, 0.07, and 0.06 for sites without h31, and 0.29, 0.39, and 0.48 for sites with 25% h31 (approximately the maximum observed amount) at the 100 ha, 500 ha, and 2000 ha scales, respectively. In other words, the sites that had the most h31 were three to eight times more likely to be occupied in 2011 than sites without any h31, depending on the scale of analysis.

DISCUSSION

Overlap between barred owl and spotted owl habitat had a substantial effect on spotted owl pair site occupancy dynamics during this study. Occupancy probability declined through the study for all sites, but as expected, it declined most for sites with little or no good spotted owl habitat that overlapped with poor barred owl habitat (overlap class h31). This pattern was largely due to the influence of habitat overlap with barred owls on spotted owl pair site colonization rates. Areas with more h31 had higher colonization rates throughout the study. Habitat overlap patterns had less influence on extinction or detection rates. This pattern was consistent with my expectation that sites with more h31 would have higher colonization rates, but it was not consistent with my expectation that such areas would have lower extinction or higher detection rates. As expected, colonization rates declined through time, but extinction rates were relatively constant throughout the study. Observed declines in site occupancy were likely a result of the increasing abundance of barred owls in the study area and a decline in the spotted owl population across the landscape (Forsman et al. 2011). Overall, the dramatic decline in the number of occupied spotted owl pair sites on the Cle Elum study area indicates substantial cause for concern regarding the long-term persistence of the local spotted owl population (Forsman et al. 2011). This analysis suggests that areas identified as good spotted owl habitat overlapping with poor barred owl habitat were disproportionately important for spotted owl pair site persistence over the duration of this study, but the prospects for long-term persistence of the spotted owl population in this area appear to be uncertain.

The decline in occupancy probability that I observed for the Cle Elum study area paralleled declines reported for other spotted owl pair site occupancy studies in Washington and Oregon (Olson et al. 2005, Kroll et al. 2010, Dugger et al. 2011), but site occupancy rates were more strongly influenced by habitat overlap in my analysis than by barred owl presence reported in some studies (Olson et al. 2005, Kroll et al. 2010). In my analysis, the observed model-averaged mean spotted owl pair site occupancy probability declined from 0.49 (SD = 0.05) in 1990 to 0.33 (SD = 0.05) in 2003, and further declined to 0.13 (SD = 0.03) in 2011, but sites with abundant h31 were approximately five times more likely to be occupied in 2011 than sites without any h31. Kroll et al. (2010) showed a similar decline in occupancy probability in their Wenatchee study area (including areas immediately to the north and south of the Cle Elum study area) from approximately 0.75 in 1990 to 0.35 in 2003. However, they found only a weak association between barred owl presence and spotted owl pair site occupancy over time. Olson et al. (2005) estimated that barred owl presence reduced spotted owl pair site occupancy by 7% for the HJ Andrews, 37% for the Tyee, and 23% for the Coast Range study areas in Oregon. Effects of barred owl presence on spotted owl pair site occupancy reported by Dugger et al. (2011) were more consistent with the effects of habitat overlap in my study. Dugger et al. (2011) found that spotted owl pair site occupancy probability at their study area in Oregon was relatively high at sites without barred owl detections (0.85 in 1991 to 0.70 in 2006), but substantially lower at sites with barred owl detections (declining to 0.1 in 2006).

There are three potential reasons for the differences among these studies. First, the barred owl population has been established longer in the eastern Cascades of Washington than in western Oregon, so there may have been more impact from barred owl displacement in my study compared to the Olson et al. (2005) study. Second, I used site occupancy data from 1989 to 2011, while the other studies only had data up to 2002-2006. Barred owls have become more abundant in recent years, so there may have been more barred owl interaction effects during the later years of my analysis compared to the other studies. Finally, Kroll et al. (2010) noted that 75% of the site visits analyzed in their study were daytime visits, which may have contributed to reduced detection of barred owls and under-estimation of barred owl interaction impacts in their study (Bailey et al. 2009). Despite these differences, the greater effect of habitat overlap on spotted owl pair site occupancy indicates that quantifying habitat overlap was a useful alternative to incidental barred owl detections for assessing impacts of barred owl interactions on spotted owl pair site occupancy.

Differences in occupancy over time across spotted owl pair sites were largely driven by the relationship between habitat overlap and colonization rates. The colonization rates that I observed were similar to those reported for the same time periods in other studies (Olson et al. 2005, Kroll et al. 2010, Dugger et al. 2011), but habitat overlap patterns had more influence on colonization rates in my analysis than barred owl presence did in some of these studies. For example, Kroll et al. (2010) found colonization rates declining over time, with annual colonization rates declining from approximately 0.35 in 1990 to 0.10 in 2003. These rates are very similar to my observed means of 0.32 (SD=0.13) for 1989 to 1995 (period 1) and 0.16 (SD=0.09) for 1996 to 2003 (period 2). Also similar to my results, Kroll et al. (2010) found that their observed decline in pair occupancy rates was a consequence of declining colonization rates combined with variable extinction rates through time. Barred owl effects on colonization were significant for their analysis including both singles and pairs, but not when the analysis was constrained to pair sites only. Olson et al. (2005) reported that colonization rates were variable across their three study areas, with annual means ranging from 0.11 to 0.38, also similar to my mean rates from 1989 to 2003 (periods 1 and 2). Presence of barred owls was important for decreasing pair site colonization rates in HJ Andrews, but not in the Tyee or Coast Range study areas (Olson et al. 2005). Effects of habitat overlap on colonization rates were similar to effects of barred owl presence reported by Dugger et al. (2011). Spotted owl pair site colonization probability varied from approximately 0.33-0.73, depending on old forest habitat patterns when barred owls were not detected, but this probability was much lower (0.03-0.20) when barred owls were detected (Dugger et al. 2011). These rates are very similar to rates from 1989 to 1995 (period 1) in my analysis, with sites that had more h31 having rates similar to those reported for sites without barred owls in the Dugger et al. (2011) analysis. Again, different barred owl colonization histories for Washington and Oregon, and different durations of the studies, were probably important contributors to differences between these analyses.

Contrary to my expectation, habitat overlap patterns did not have a substantial effect on spotted owl pair site extinction rates. The total amount of good spotted owl habitat regardless of overlap with barred owl habitat (SPg) and time period were the parameters included in the extinction components of the supported models, but effects of these parameters were small (Table 4.6). Model-averaged estimates of overall extinction probability based on the supported 500 ha models ranged from 0.10-0.34 (mean 0.21, SD=0.04) for the Cle Elum study area. These extinction rates are similar to those reported in other studies, but two studies reported greater effects of barred owl presence on spotted owl pair site extinction than I detected (Olson et al. 2005, Dugger et al. 2011), and one study (Kroll et al. 2010) showed little effect of barred owl presence on spotted owl pair site extinction rates. For example, Dugger et al. (2011) reported that pair site extinction probability varied from 0.11 to 0.23 when barred owls were not detected, but nearly tripled to 0.33-0.54 when barred owls were detected, and Olson et al. (2005) reported that barred owl effects were important for increasing pair site extinction in two of the three study areas they analyzed in Oregon. Kroll et al. (2010) reported that extinction rates varied by year, ranging from approximately 0.10 to 0.30, similar to what I found both in terms of extinction rate estimates and lack of a substantial trend over time. Barred owl presence significantly increased extinction rates for their simple model, but not the pair model. One possible explanation for the lack of effect of habitat overlap on extinction rates could be that spotted owls were being displaced into marginal habitat. For example, extinction rates may have been relatively high in the good habitat areas most likely to be occupied by barred owls due to barred owl displacement effects, while extinction rates may also have been relatively high in areas with the least habitat overlap because these areas had marginal habitat conditions for spotted owls pair site persistence.

Also contrary to my expectation, habitat overlap patterns did not influence spotted owl pair detection rates. Other work has shown that spotted owl pair detection probability was lower at sites where barred owls were detected (Olson et al. 2005, Bailey et al. 2009, Kroll et al. 2010, Dugger et al. 2011). Pair detection rates in my analysis were slightly higher than rates reported for similar studies of spotted owl site occupancy dynamics (MacKenzie et al. 2003, Olson et al. 2005, Dugger et al. 2011). None of these studies evaluated the effect of habitat on detection probability. My expectation was that spotted owl detection rates would be higher in areas where barred owl pairs were less likely to be present. As expected, the amount of good spotted owl habitat that overlapped with moderate barred owl habitat (h32) had a positive influence on detection rates, and the effect increased as the scale broadened. In contrast, the amount of good spotted owl habitat that overlapped with poor barred owl habitat (h31) had a negative effect on detection rates. The positive effect of h32 on detection rate for the 500 ha and 2000 ha models was substantially greater than the other parameters, so this model structure captured some of the expected effect of higher spotted owl detection rates in areas less likely to be occupied by barred owl pairs, but the negative effect of the h31 overlap class on detection probability is difficult to explain. As expected, the candidate models that did not include overlap with barred owl habitat indicated that sites surrounded by more good spotted owl habitat (SPg) had higher detection rates. But contrary to expectation, sites with more good barred owl habitat (BDg) also had higher detection rates.

The scales at which habitat characteristics influenced site occupancy dynamics on the Cle Elum study area were similar to scales reported as important in other studies addressing the relationship between habitat and spotted owl pair site occupancy or demography (Dugger et al. 2011, 2005, Franklin et al. 2000, Olson 2004). Overall, the dynamic occupancy models for the Cle Elum study area performed best at the 500 ha scale, approximating the size of a typical breeding season home range. Comparing AICc support for models across the three scales, the supported 500 ha models had 92% of the AICc model weight, the supported 100 ha models had 7% of the model weight, and the supported 2000 ha models had 1% of the model weight (Table 4.5). The 500 ha scale appears to represent a “happy medium” between the nesting core-sized (100 ha) circles that that may have been too small to capture adjacent areas important to resident spotted owls, and the much larger annual home range-scale (2000 ha) circles that may have been so large that they encompassed areas not regularly used by the resident spotted owls. Covariate effects were generally consistent across the three scales of analysis, though the positive association between site colonization and areas of good spotted owl habitat that overlapped with poor barred owl habitat (h31) increased at broader scales. The h31 habitat overlap class may provide opportunities for spotted owls to “work around” barred owl territories for foraging, and thus may be important for spotted owl activities at relatively broad scales. For example, Wiens (2012) found that radio-tagged spotted owls rarely entered neighboring barred owl territories during foraging movements.

The habitat overlap approach for evaluating potential effects of competitive interactions with barred owls on spotted owl pairs was supported in this analysis. To my knowledge, this is the first study to incorporate overlap of barred owl and spotted owl resource selection maps into spotted owl site occupancy dynamics analysis. Spotted owl pair site occupancy probability declined through time for the 60 sites in the Cle Elum study area, but it declined much less for sites surrounded by more good spotted owl habitat that overlapped with poor barred owl habitat (h31). This pattern indicates that such areas were important for spotted owl pair site occupancy over the duration of the study. However, the dramatic decline in the number of occupied spotted owl pair sites on the Cle Elum study area indicates substantial cause for concern regarding the persistence of the local spotted owl population (Forsman et al. 2011). The observed decline in the number of spotted owl sites within the Cle Elum demographic study area suggests that these patterns of exclusive habitat use may not be sufficient to provide for long-term spotted owl population persistence in this area. Barred owls have been present in the Cascade Range of Washington longer than they have in other parts of the northern spotted owl's range (Livezey 2009). Understanding how habitat overlap patterns operate in relation to spotted owl pair occupancy dynamics could prove to be particularly important in other parts of the species' range where population-level impacts from competitive interactions with barred owls are not yet so pronounced. I would encourage researchers in other areas where spotted owl populations have not yet experienced such declines to consider similar courses of research to evaluate how spatial patterns of habitat selection overlap for the two species may influence spotted owl persistence over time in those areas. Persistence of populations of native species in the face of novel competitive interactions with invasive species often depends on the native species’ ability to shift space-use and resource acquisition strategies in response to new competitive pressures (Cox 2004, Dhondt 2012). Understanding the effect of habitat overlap with barred owls on spotted owl pair site persistence will provide important insights for understanding how competitive interactions with barred owls may influence spotted owl distribution and population function.

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Table 4.1. Habitat overlap and time covariates used to evaluate spotted owl pair site detection probability (p), colonization probability (γ), and extinction probability (ε) in the Cle Elum study area, Washington. Covariate codes, descriptions, and mean proportion of the area surrounding spotted owl pair sites in each habitat class at each scale. The means were calculated for all sites (both occupied and unoccupied), across all years. Numeric codes indicate habitat class for spotted owls and barred owls in the first and second digit respectively. Numeric values of 1 indicate poor habitat, 2 indicate moderate habitat, and 3 indicate good habitat.

		Scale		
Code	Description	100ha	500ha	2000ha
year	Continuous linear year effect: numeric variable for year centered on year 2000 (i.e. year 1989 = -11, 2000 = 0, 2011 = 11)	--	--	--
period	Categorical index for 3 time periods: 1 = years 1989 to 1995, 2 = 1996 to 2003, 3 = 2004 to 2011	--	--	--
h11	Proportion in poor spotted owl habitat and poor barred owl habitat	0.10	0.13	0.18
h12	Proportion in poor spotted owl habitat and moderate barred owl habitat	0.01	0.02	0.02
h13	Proportion in poor spotted owl habitat and good barred owl habitat	0.00	0.01	0.01
h21	Proportion in moderate spotted owl habitat and poor barred owl habitat	0.21	0.26	0.27
h22	Proportion in moderate spotted owl habitat and moderate barred owl habitat	0.06	0.07	0.06
h23	Proportion in moderate spotted owl habitat and good barred owl habitat	0.05	0.05	0.05
h31	Proportion in good spotted owl habitat and poor barred owl habitat	0.12	0.11	0.09
h32	Proportion in good spotted owl habitat and moderate barred owl habitat	0.19	0.16	0.13
h33	Proportion in good spotted owl habitat and good barred owl habitat	0.27	0.21	0.17
BDg	Proportion in good barred owl habitat, regardless of overlap with spotted owl habitat	0.32	0.26	0.23
BDm	Proportion in moderate barred owl habitat, regardless of overlap with spotted owl habitat	0.26	0.24	0.21
SPg	Proportion in good spotted owl habitat, regardless of overlap with barred owl habitat	0.59	0.48	0.39
SPm	Proportion in moderate spotted owl habitat, regardless of overlap with barred owl habitat	0.32	0.37	0.38

Table 4.2. *A priori* models relating habitat and time covariates to spotted owl pair detection probability (*p*), including the model formula and the expectation that model was designed to evaluate.

Formula	Expectation
p(.)	Detection rates were similar regardless of time or habitat – the null model
p(year)	Detection rates declined over time (linear effect)
p(factor(year))	Detection rates varied independently by year (including a parameter for each year)
p(period)	Detection rates varied across 3 7-8 year time periods representing the early, middle, and late periods of the study
p(BDg)	Detection rates were lower in areas where territorial barred owl pairs were more likely to be present
p(SPg)	Detection rates were higher in areas with more good spotted owl habitat
p(BDg+period)	Detection rates are lower where barred owl pairs were more likely to be present and declined across the 3 time periods
p(BDg*period)	Detection rates were lower where barred owl pairs were more likely to be present and declined across the 3 time periods as an interaction
p(SPg+period)	Detection rates were higher in areas with more good spotted owl habitat and declined across the 3 time periods
p(SPg*period)	Detection rates were higher in areas with more good spotted owl habitat and declined across the 3 time periods as an interaction
p(h31+h32+h33)	Detection rates were higher in areas where good spotted owl habitat overlapped least with good barred owl habitat
p(h31+h32+h33+period)	Detection rates were higher in areas where good spotted owl habitat overlapped least with good barred owl habitat and declined across the 3 time periods

Table 4.3. *A priori* models relating habitat and time covariates to spotted owl pair colonization probability (γ) and extinction probability (ε), including the model formula and the expectation that model was designed to evaluate.

Formula	Expectation
(.)	Colonization and/or extinction did not change in relation to time period or habitat characteristics – the null model
(period)	Colonization decreased and/or extinction increased by time period, but were not substantially influenced by habitat
(SPg)	Colonization increased and/or extinction decreased with more good spotted owl habitat
(SPg+period)	Colonization increased and/or extinction decreased with more good spotted owl habitat, and effects changed across the time periods
(SPg+SPm)	Colonization increased and/or extinction decreased with more good and moderate spotted owl habitat
(SPg+SPm+period)	Colonization increased and/or extinction decreased with more good and moderate spotted owl habitat, and effects changed across the time periods
(h31+h32+h33)	Colonization increased and/or extinction decreased with more good spotted owl habitat that overlapped least with good barred owl habitat
(h31+h32+h33+period)	Colonization increased and/or extinction decreased with more good spotted owl habitat that overlapped least with good barred owl habitat, and this changed across time periods
(h21+h22+h23+h31+h32+h33)	Colonization increased and/or extinction decreased with more good and moderate spotted owl habitat that overlapped least with good or moderate barred owl habitat
(h21+h22+h23+h31+h32+h33+ period)	Colonization increased and/or extinction decreased with more good and moderate spotted owl habitat that overlapped least with good barred owl habitat, and this changed across time periods
(h12+h13+h21+h22+h23+h31+ h32+h33+period)	Colonization increased and/or extinction decreased in areas that overlapped least with good and moderate barred owl habitat
(h12+h13+h21+h22+h23+h31+ h32+h33+period)	Colonization increased and/or extinction decreased in areas that overlapped least with good and moderate barred owl habitat, and this changed across time periods

Table 4.4. Model selection results for *a priori* models relating habitat and time covariates to spotted owl pair detection probability (p) in the eastern Cascade Range, Washington. Occupancy, colonization, and extinction components of the dynamic occupancy models were fixed using the intercept only parameterization (ψ(.)γ(.)ε(.)).

100 ha

Model	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
p(h31+h32+h33+period)	9	2837.78	0.00	0.71	0.71	-1408.09
p(BDg*period)	9	2839.80	2.02	0.26	0.98	-1409.10
p(SPg*period)	9	2844.73	6.95	0.02	1.00	-1411.56
p(BDg+period)	7	2850.52	12.74	0.00	1.00	-1417.18
p(period)	6	2851.66	13.88	0.00	1.00	-1419.04
p(SPg+period)	7	2852.15	14.37	0.00	1.00	-1418.00
p(h31+h32+h33)	7	2859.36	21.58	0.00	1.00	-1421.60
p(factor(year))	26	2864.24	26.45	0.00	1.00	-1384.84
p(year)	5	2867.06	29.28	0.00	1.00	-1427.98
p(BDg)	5	2870.88	33.10	0.00	1.00	-1429.88
p(.)	4	2872.19	34.41	0.00	1.00	-1431.73
p(SPg)	5	2872.37	34.59	0.00	1.00	-1430.63

500 ha

Model	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
p(BDg*period)	9	2826.02	0.00	0.90	0.90	-1402.21
p(h31+h32+h33+period)	9	2831.57	5.54	0.06	0.95	-1404.98
p(SPg*period)	9	2831.93	5.90	0.05	1.00	-1405.16
p(BDg+period)	7	2842.49	16.47	0.00	1.00	-1413.17
p(SPg+period)	7	2842.97	16.95	0.00	1.00	-1413.41
p(period)	6	2851.66	25.64	0.00	1.00	-1419.04
p(h31+h32+h33)	7	2853.66	27.64	0.00	1.00	-1418.75
p(BDg)	5	2862.10	36.07	0.00	1.00	-1425.49
p(SPg)	5	2863.54	37.52	0.00	1.00	-1426.22
p(factor(year))	26	2864.24	38.21	0.00	1.00	-1384.84
p(year)	5	2867.06	41.04	0.00	1.00	-1427.98
p(.)	4	2872.19	46.16	0.00	1.00	-1431.73

2000 ha

Model	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
p(h31+h32+h33+period)	9	2833.07	0.00	0.81	0.81	-1405.73
p(SPg*period)	9	2836.24	3.18	0.17	0.98	-1407.32
p(SPg+period)	7	2841.22	8.16	0.01	0.99	-1412.53
p(BDg*period)	9	2842.73	9.66	0.01	1.00	-1410.56
p(BDg+period)	7	2849.85	16.78	0.00	1.00	-1416.85
p(h31+h32+h33)	7	2851.48	18.42	0.00	1.00	-1417.66
p(period)	6	2851.66	18.60	0.00	1.00	-1419.04
p(SPg)	5	2858.21	25.14	0.00	1.00	-1423.55
p(factor(year))	26	2864.24	31.17	0.00	1.00	-1384.84
p(year)	5	2867.06	34.00	0.00	1.00	-1427.98
p(BDg)	5	2867.93	34.87	0.00	1.00	-1428.41
p(.)	4	2872.19	39.12	0.00	1.00	-1431.73

Table 4.5. Model selection results for *a priori* models relating habitat and time covariates to spotted owl pair site colonization (γ) and extinction (ε) probability for all models with model weight >0.005, plus the null model. The models include components for initial occupancy (ψ), colonization (γ), extinction (ε), and detection (*p*). The table shows the model formula, number of parameters (K), sample size corrected AIC score (AICc), change in AICc relative to the best model (ΔAICc), model weight (AICcWt), cumulative model weight (CumWt), and the model log-liklihood (LL). Supported models (ΔAICc < 2) are shown in bold font.

a) 100 ha Scale:

Model Formula[1]	K	AICc	ΔAICc	AICcWt	CumWt	LL
ψ(.) γ(h31+h32+h33+period) ε(SPg) *p*(h31+h32+h33+period)	**15**	**2789.60**	**0.00**	**0.31**	**0.31**	**-1374.34**
ψ(.) γ(h31+h32+h33+period) ε(period) *p*(h31+h32+h33+period)	**16**	**2789.91**	**0.32**	**0.27**	**0.58**	**-1372.63**
ψ(.) γ(h31+h32+h33+period) ε(SPg+period) *p*(h31+h32+h33+period)	**17**	**2791.22**	**1.63**	**0.14**	**0.72**	**-1371.33**
ψ(.) γ(h31+h32+h33+period) ε(SPg+SPm) *p*(h31+h32+h33+period)	16	2793.24	3.64	0.05	0.77	-1374.29
ψ(.) γ(SPg+period) ε(SPg) *p*(h31+h32+h33+period)	13	2794.19	4.60	0.03	0.80	-1380.14
ψ(.) γ(SPg+period) ε(period) *p*(h31+h32+h33+period)	14	2794.22	4.62	0.03	0.83	-1378.44
ψ(.) γ(h12+h13+h21+h22+h23+h31+ h32+h33+period) ε(SPg) *p*(h31+h32+h33+period)	20	2795.18	5.59	0.02	0.85	-1366.82
ψ(.) γ(SPg+period) ε(SPg+period) *p*(h31+h32+h33+period)	15	2795.21	5.61	0.02	0.87	-1377.15
ψ(.) γ(H31+h32+h33+period) ε(SPg+SPm) *p*(h31+h32+h33+period)	18	2795.28	5.69	0.02	0.89	-1371.30
ψ(.) γ(h21+h22+h23+h31+h32+h33+ period) ε(SPg) *p*(h31+h32+h33+period)	18	2795.50	5.91	0.02	0.91	-1371.41
ψ(.) γ(h21+h22+h23+h31+h32+h33+ period) ε(period) *p*(h31+h32+h33+period)	19	2795.53	5.94	0.02	0.92	-1369.27
ψ(.) γ(h12+h13+h21+h22+h23+h31+ h32+h33+period) ε(period) *p*(h31+h32+h33+period)	21	2795.72	6.12	0.01	0.94	-1364.70
ψ(.) γ(H31+h32+h33+period) ε(SPgBDg) *p*(h31+h32+h33+period)	17	2796.43	6.83	0.01	0.95	-1373.93
ψ(.) γ(SPg+SPm+period) ε(SPg) *p*(h31+h32+h33+period)	14	2797.24	7.64	0.01	0.96	-1379.95
ψ(.) γ(SPg+period) ε(SPg+SPm) *p*(h31+h32+h33+period)	14	2797.41	7.81	0.01	0.96	-1380.04
ψ(.) γ(SPg+SPm+period) ε(period) *p*(h31+h32+h33+period)	15	2797.42	7.82	0.01	0.97	-1378.26
ψ(.) γ(.) ε(.) *p*(h31+h32+h33+period)	4	2872.19	82.59	0.00	1.00	-1431.73

[1] The following models failed to converge at this scale and were eliminated from consideration:

ψ(.) γ(h12+h13+h21+h22+h23+h31+h32+h33+period) ε(h12+h13+h21+h22+h23+h31+h32+h33+period) *p*(h31+h32+h33+period)
ψ(.) γ(h12+h13+h21+h22+h23+h31+h32+h33+period) ε(h12+h13+h21+h22+h23+h31+h32+h33) *p*(h31+h32+h33+period)
ψ(.) γ(h12+h13+h21+h22+h23+h31+h32+h33) ε(h12+h13+h21+h22+h23+h31+h32+h33+period) *p*(h31+h32+h33+period)

Table 4.5 (cont.). Model selection results for *a priori* models relating habitat and time covariates to spotted owl pair site colonization (γ) and extinction (ε) probability for all models with model weight >0.005, plus the null model. The models include components for initial occupancy (ψ), colonization (γ), extinction (ε), and detection (*p*). The table shows the model formula, number of parameters (K), sample size corrected AIC score (AICc), change in AICc relative to the best model (ΔAICc), model weight (AICcWt), cumulative model weight (CumWt), and the model log-liklihood (LL). Supported models (ΔAICc < 2) are shown in bold font.

b) 500 ha Scale:

Model Formula	K	AICc	ΔAICc	AICcWt	CumWt	LL
ψ(.) γ(h31+h32+h33+period) ε(SPg) *p*(h31+h32+h33+period)	**15**	**2784.13**	**0.00**	**0.29**	**0.29**	**-1371.61**
ψ(.) γ(SPg+period) ε(SPg) *p*(h31+h32+h33+period)	**13**	**2785.24**	**1.12**	**0.16**	**0.45**	**-1375.67**
ψ(.) γ(h31+h32+h33+period) ε(period) *p*(h31+h32+h33+period)	**16**	**2785.50**	**1.38**	**0.14**	**0.60**	**-1370.43**
ψ(.) γ(h31+h32+h33+period) ε(SPg+period) *p*(h31+h32+h33+period)	17	2786.16	2.04	0.10	0.70	-1368.80
ψ(.) γ(SPg+period) ε(SPg+period) *p*(h31+h32+h33+period)	15	2787.06	2.93	0.07	0.77	-1373.07
ψ(.) γ(SPg+period) ε(period) *p*(h31+h32+h33+period)	14	2787.85	3.73	0.04	0.81	-1375.26
ψ(.) γ(h31+h32+h33+period) ε(SPg+SPm) *p*(h31+h32+h33+period)	16	2787.87	3.74	0.04	0.86	-1371.61
ψ(.) γ(SPg+SPm+period) ε(SPg) *p*(h31+h32+h33+period)	14	2788.51	4.39	0.03	0.89	-1375.59
ψ(.) γ(SPg+period) ε(SPg+SPm) *p*(h31+h32+h33+period)	14	2788.66	4.54	0.03	0.92	-1375.67
ψ(.) γ(h31+h32+h33+period) ε(SPg+SPm+period) *p*(h31+h32+h33+period)	18	2790.27	6.15	0.01	0.93	-1368.79
ψ(.) γ(SPg+SPm+period) ε(period) *p*(h31+h32+h33+period)	16	2790.63	6.51	0.01	0.94	-1372.99
ψ(.) γ(h31+h32+h33+period) ε(SPg+BDg) *p*(h31+h32+h33+period)	17	2790.76	6.64	0.01	0.96	-1371.10
ψ(.) γ(SPg+period) ε(SPg+SPm+period) *p*(h31+h32+h33+period)	16	2790.79	6.66	0.01	0.97	-1373.07
ψ(.) γ(SPg+SPm+period) ε(period) *p*(h31+h32+h33+period)	15	2791.29	7.17	0.01	0.97	-1375.19
ψ(.) γ(SPg+SPm+period) ε(SPg+SPm+period) *p*(h31+h32+h33+period)	15	2792.08	7.96	0.01	0.98	-1375.59
ψ(.) γ(SPg+period) ε(SPg+BDg) *p*(h31+h32+h33+period)	15	2792.09	7.97	0.01	0.98	-1375.59
ψ(.) γ(.) ε(.) *p*(.)	4	2872.19	88.06	0.00	1.00	-1431.73

Table 4.5 (cont.). Model selection results for *a priori* models relating habitat and time covariates to spotted owl pair site colonization (γ) and extinction (ε) probability for all models with model weight >0.005, plus the null model. The models include components for initial occupancy (ψ), colonization (γ), extinction (ε), and detection (*p*). The table shows the model formula, number of parameters (K), sample size corrected AIC score (AICc), change in AICc relative to the best model (ΔAICc), model weight (AICcWt), cumulative model weight (CumWt), and the model log-liklihood (LL). Supported models (ΔAICc < 2) are shown in bold font.

c) 2000 ha Scale:

Model Formula[1]	K	AICc	ΔAICc	AICcWt	CumWt	LL
ψ(.) γ(h31+h32+h33+period) ε(period) *p*(h31+h32+h33+period)	**16**	**2792.04**	**0.00**	**0.34**	**0.34**	**-1373.70**
ψ(.) γ(h31+h32+h33+period) ε(SPg) *p*(h31+h32+h33+period)	**15**	**2793.02**	**0.98**	**0.21**	**0.55**	**-1376.05**
ψ(.) γ(h12+h13+h21+h22+h23+h31+ h32+h33+period) ε(period) *p*(h31+h32+h33+period)	21	2794.70	2.66	0.09	0.64	-1364.19
ψ(.) γ(h31+h32+h33+period) ε(SPg+period) *p*(h31+h32+h33+period)	17	2794.89	2.85	0.08	0.73	-1373.16
ψ(.) γ(h12+h13+h21+h22+h23+h31+ h32+h33+period) ε(SPg) *p*(H31+h32+h33+period)	20	2795.51	3.47	0.06	0.79	-1366.99
ψ(.) γ(h31+h32+h33+period) ε(SPg+SPm) *p*(h31+h32+h33+period)	16	2796.64	4.60	0.03	0.82	-1376.00
ψ(.) γ(SPg+period) ε(period) *p*(h31+h32+h33+period)	14	2796.87	4.83	0.03	0.85	-1379.77
ψ(.) γ(SPg+period) ε(SPg) *p*(h31+h32+h33+period)	13	2797.38	5.34	0.02	0.87	-1381.74
ψ(.) γ(period) ε(period) *p*(h31+h32+h33+period)	13	2798.17	6.13	0.02	0.89	-1382.13
ψ(.) γ(h31+h32+h33+period) ε(h31+h32+h33) p(h31+h32+h33+period)	17	2798.59	6.55	0.01	0.90	-1375.01
ψ(.) γ(SPg+period) ε(SPg+period) *p*(h31+h32+h33+period)	15	2798.85	6.81	0.01	0.91	-1378.97
ψ(.) γ(h12+h13+h21+h22+h23+h31+ h32+h33+period) ε(SPg+period) *p*(h31+h32+h33+period)	22	2798.91	6.87	0.01	0.93	-1363.78
ψ(.) γ(h31+h32+h33+period) ε(SPg+SPm+period) *p*(h31+h32+h33+period)	18	2798.92	6.88	0.01	0.94	-1373.12
ψ(.) γ(h21+h22+h23+h31+h32+h33+period) ε(period) *p*(h31+h32+h33+period)	19	2799.03	6.99	0.01	0.95	-1371.02
ψ(.)γ(h21+h22+h23+h31+h32+h33+period) ε(SPg) *p*(h31+h32+h33+period)	18	2799.87	7.82	0.01	0.95	-1373.59
ψ(.) γ(SPg+SPm+period) ε(period) *p*(h31+h32+h33+period)	15	2800.18	8.13	0.01	0.96	-1379.63
ψ(.) γ(h12+h13+h21+h22+h23+h31+ h32+h33+period) ε(SPg+SPm) p(h31+h32+h33+period)	21	2800.26	8.22	0.01	0.96	-1366.97
ψ(.) γ(SPg+SPm+period) ε(SPg) *p*(h31+h32+h33+period)	14	2800.33	8.29	0.01	0.97	-1381.50
ψ(.) γ(.) ε(.) *p*(.)	4	2872.19	80.15	0.00	1.00	-1431.73

[1] The following models failed to converge at this scale and were eliminated from consideration:
ψ(.) γ(h12+h13+h21+h22+h23+h31+h32+h33+period) ε(h12+h13+h21+h22+h23+h31+h32+h33) *p*(H31+h32+h33+period)
ψ(.) γ(h12+h13+h21+h22+h23+h31+h32+h33) ε(h12+h13+h21+h22+h23+h31+h32+h33) *p*(H31+h32+h33+period)

Table 4.5 (cont.). Model selection results for *a priori* models relating habitat and time covariates to spotted owl pair site colonization (γ) and extinction (ε) probability for all models with model weight >0.005, plus the null model. The models include components for initial occupancy (ψ), colonization (γ), extinction (ε), and detection (*p*). The table shows the model formula, number of parameters (K), sample size corrected AIC score (AICc), change in AICc relative to the best model (ΔAICc), model weight (AICcWt), cumulative model weight (CumWt), and the model log-liklihood (LL). Supported models (ΔAICc < 2) are shown in bold font.

d) Comparison of supported models across the three scales of analysis

Scale	Model Formula	K	AICc	ΔAICc	AICcWt	CumWt
500	ψ(.) γ(h31+h32+h33+period) ε(SPg) *p*(h31+h32+h33+period)	15	2784.13	0.00	0.44	0.44
500	ψ(.) γ(SPg+period) ε(SPg) *p*(h31+h32+h33+period)	13	2785.24	1.11	0.25	0.70
500	ψ(.) γ(h31+h32+h33+period) ε(period) *p*(h31+h32+h33+period)	16	2785.50	1.37	0.22	0.92
100	ψ(.) γ(h31+h32+h33+period) ε(SPg) *p*(h31+h32+h33+period)	15	2789.60	5.47	0.03	0.95
100	ψ(.) γ(h31+h32+h33+period) ε(period) *p*(h31+h32+h33+period)	16	2789.91	5.78	0.02	0.97
100	ψ(.) γ(h31+h32+h33+period) ε(SPg+period) *p*(h31+h32+h33+period)	17	2791.22	7.09	0.01	0.99
2000	ψ(.) γ(h31+h32+h33+period) ε(period) *p*(h31+h32+h33+period)	16	2792.04	7.91	0.01	0.99
2000	ψ(.) γ(h31+h32+h33+period) ε(SPg) *p*(h31+h32+h33+period)	15	2793.02	8.89	0.01	1.00

Table 4.6. Model-averaged parameter estimates and confidence limits from supported (ΔAICc <2) spotted owl pair site occupancy dynamics models at three scales, including the model averaged parameter estimate (Est), the 95% upper confidence limit (UCL), the 95% lower confidence limit (LCL), and the number of models included in the model averaging for that scale (No). Period 1 was included in the models as the reference time period.

		100 ha				500 ha				2000 ha			
Component	Parameter	Est	UCL	LCL	No	Est	UCL	LCL	No	Est	UCL	LCL	No
Detection (p)	Intercept	0.78	0.96	0.60	3	0.79	0.97	0.61	3	0.79	0.97	0.61	2
	h31	-2.03	-0.62	-3.43	3	-2.97	-0.32	-5.62	3	-3.80	-0.05	-7.54	2
	h32	2.56	4.07	1.05	3	5.61	8.50	2.73	3	8.34	12.60	4.08	2
	h33	0.13	1.09	-0.83	3	1.16	2.89	-0.57	3	0.46	2.73	-1.81	2
	period 2	0.70	0.99	0.42	3	0.69	0.98	0.40	3	0.67	0.97	0.38	2
	period 3	0.15	0.46	-0.17	3	0.09	0.42	-0.23	3	0.13	0.46	-0.19	2
Colonization	Intercept	-0.86	-0.30	-1.43	3	-0.85	-0.29	-1.40	3	-0.87	-0.28	-1.45	2
	h31	6.73	10.57	2.89	3	10.31	16.49	4.12	2	13.37	22.47	4.26	2
	h32	4.36	7.67	1.06	3	1.90	8.52	-4.72	2	1.05	9.82	-7.71	2
	h33	1.76	3.93	-0.40	3	2.85	6.86	-1.16	2	1.35	7.07	-4.38	2
	SPg					4.51	6.97	2.04	1				
	period 2	-0.94	-0.26	-1.61	3	-0.95	-0.28	-1.62	3	-0.88	-0.19	-1.57	2
	period 3	-2.58	-1.71	-3.46	3	-2.52	-1.66	-3.38	3	-2.39	-1.53	-3.25	2
Extinction	Intercept	-1.50	-1.06	-1.94	3	-1.41	-1.05	-1.77	3	-1.51	-1.07	-1.96	2
	SPg	1.06	2.29	-0.17	2	2.26	4.40	0.11	2	1.96	4.71	-0.79	1
	period 2	0.64	1.15	0.13	2	0.63	1.14	0.13	1	0.64	1.15	0.13	1
	period 3	0.44	1.06	-0.18	2	0.79	0.97	0.61	1	0.54	1.16	-0.07	1

Figure 4.1. Location of the Cle Elum spotted owl demographic study area within Washington State.

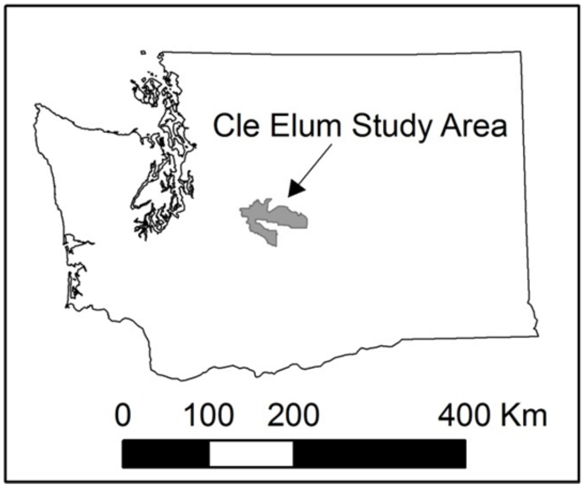


Figure 4.2. Map of habitat overlap classes within the Cle Elum study area. The Cle Elum spotted owl study area is outlined in black. White areas were excluded from the habitat analysis because they were above the elevation range of spotted owls, large bodies of water, or outside the extent of the vegetation base data.

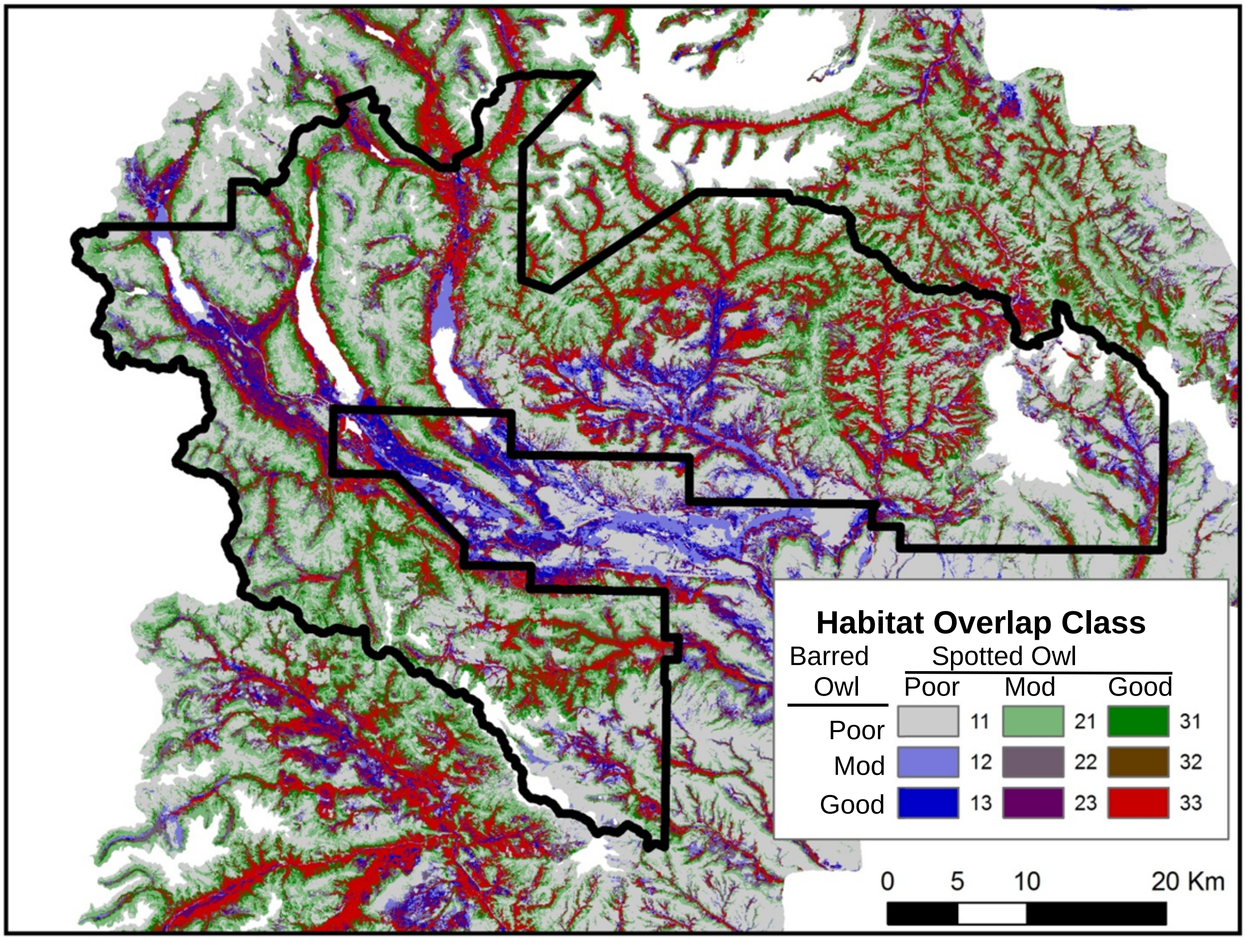


Figure 4.3. Spotted owl pair sites included in dynamic occupancy modeling for the Cle Elum study area, Washington. Individual owl sites are shown in different colors.

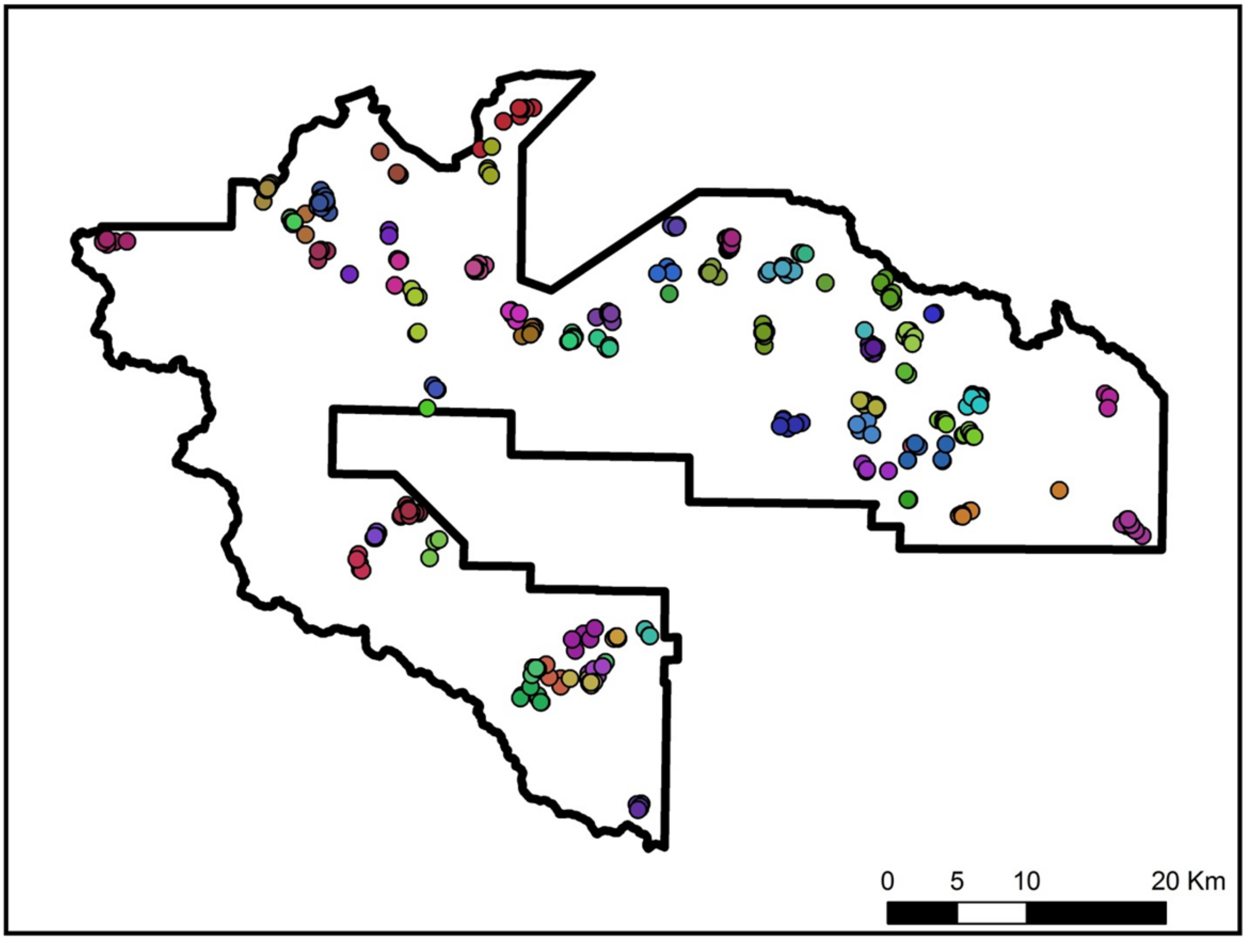


Figure 4.4. Occupancy history from 1989 to 2011 for 60 spotted owl sites included in dynamic occupancy modeling for the Cle Elum study area, Washington. Rows represent individual owl sites. Columns represent observed status by year: black cells indicate years when a pair was detected at that site, grey indicates that the site was surveyed but not occupied by a pair, and white indicates no surveys at that site. The vertical white lines indicate the splits between the three time periods included as a categorical covariate in the occupancy modeling.

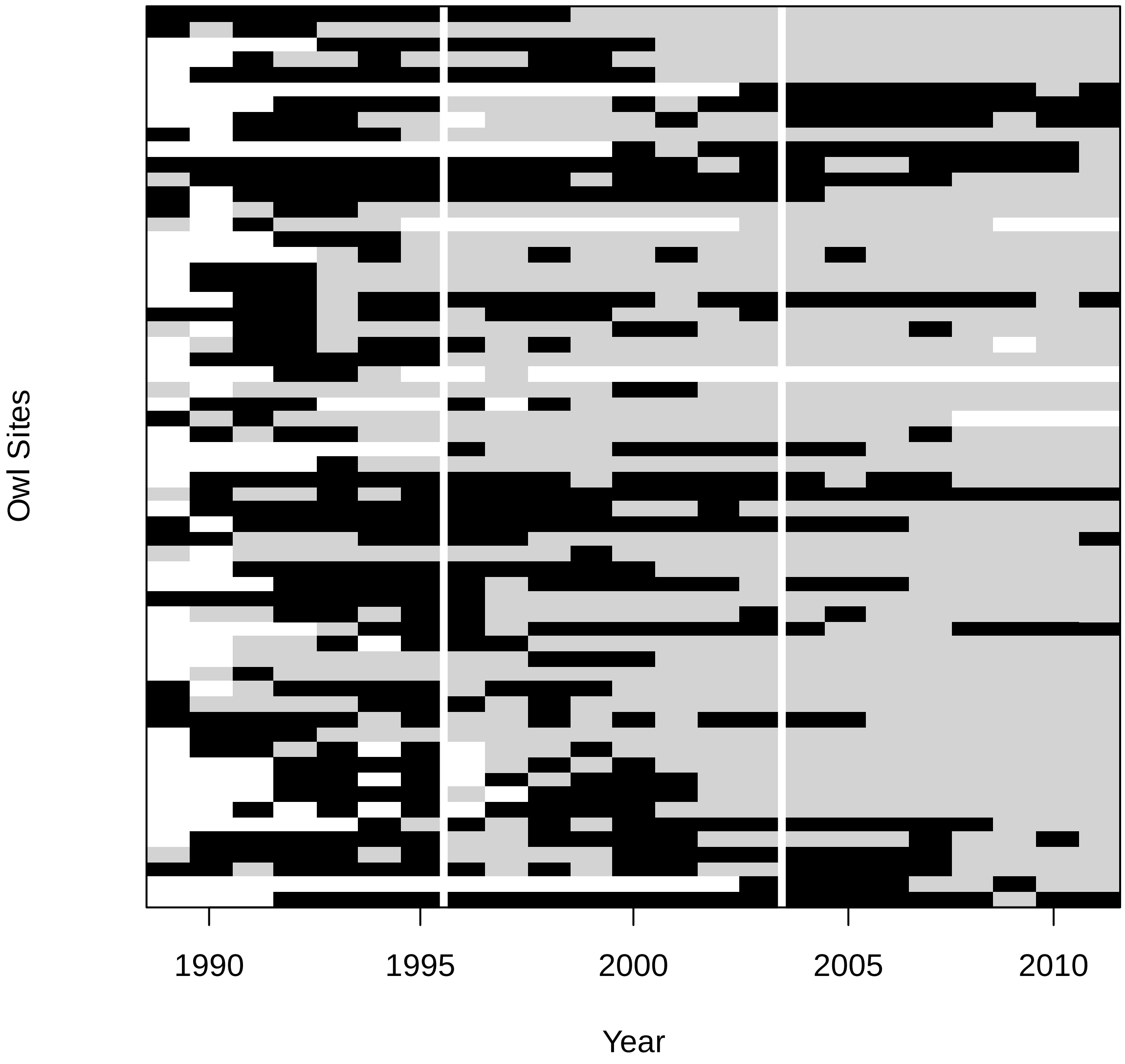


Figure 4.5. Observed colonization, extinction, and detection rates based on fitted values from the model averaged estimate for the supported 500 ha models.

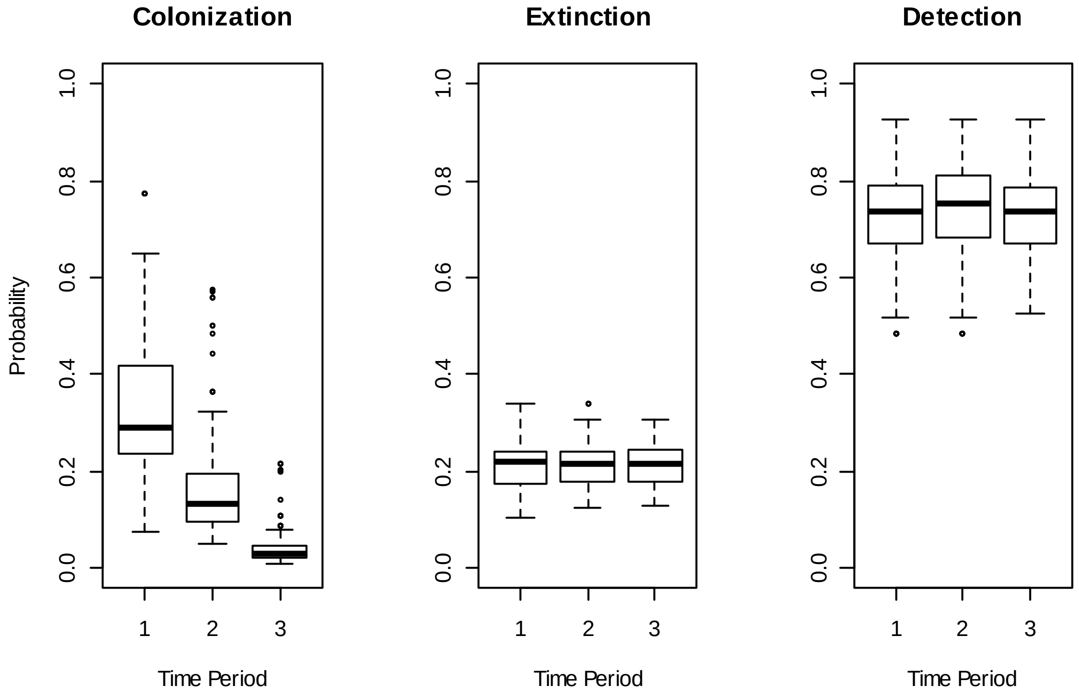
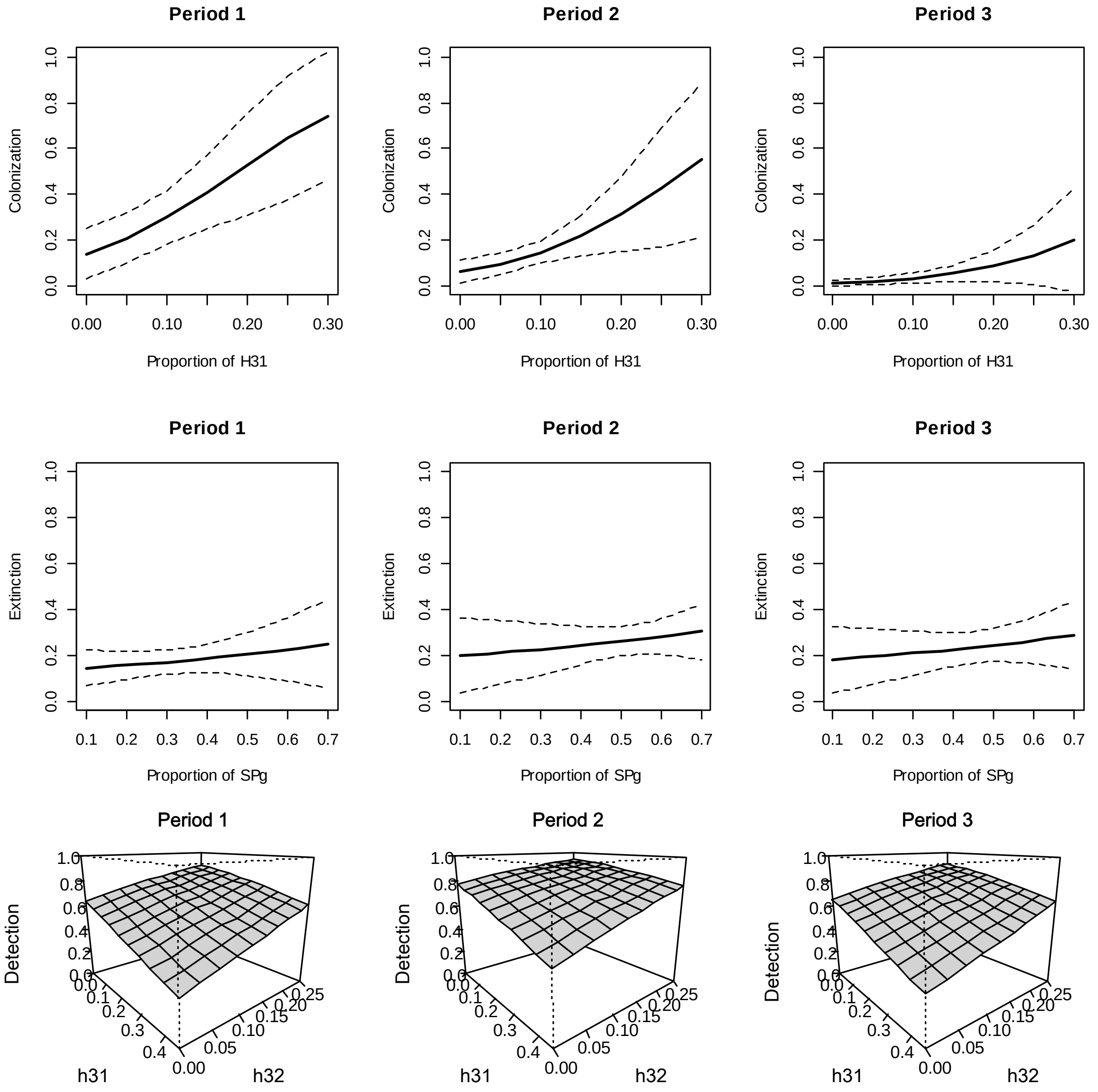


Figure 4.6. Response curves showing the effect of significant covariates on model averaged estimates of spotted owl colonization, extinction, and detection, based on supported 500 ha scale models. Dashed lines show 95% confidence limits around estimates of colonization and extinction. The range of habitat proportions displayed on the x-axis reflects the proportions observed in the sample.



CHAPTER 5: SIMULATED POPULATION-LEVEL IMPACTS OF TERRITORIAL INTERACTIONS WITH BARRED OWLS ON NORTHERN SPOTTED OWLS IN THE EASTERN CASCADES, WASHINGTON.

ABSTRACT

Territorial interactions with recently established barred owls (*Strix varia*) are contributing to northern spotted owl (*Strix occidentalis caurina*) population declines. Although spotted owls and barred owls are morphologically and ecologically quite similar, there are also some differences in demography, behavior, space use, and landscape associations that could have important effects on spotted owl population outcomes. The overall goal of this work was to examine potential spotted owl population responses to displacement resulting from territorial interactions with barred owls under existing habitat conditions in the eastern Cascade Range, Washington. I had three specific objectives: 1) to evaluate different individual-based modeling approaches for assessing population-level effects of displacement resulting from territorial interactions with barred owls; 2) to use the models to conduct simulation experiments to explore potential effects of displacement by barred owls on spotted owl population size and distribution under a range of demographic assumptions and habitat overlap conditions; and 3) to examine changes in the distribution of the simulated spotted owl population and identify existing habitat areas that could be of increased importance for spotted owl population persistence given displacement by barred owls. I used two individual-based modeling approaches for assessing the effects of displacement by barred owls on spotted owl population outcomes: 1) a dual-species approach in which populations of both spotted owls and barred owls were explicitly modeled, and 2) a single species approach where only the spotted owl population was modeled and barred owl displacement effects were based on an empirical estimate of barred owl probability of occupancy. I evaluated 10 model scenarios to investigate potential spotted owl population outcomes under a variety of barred owl vital rate and occupancy assumptions. Despite differences in space use and landscape associations displayed by spotted owls and barred owls, displacement by barred owls had substantial detrimental impacts on spotted owl population performance in most of my modeling scenarios. The most plausible estimates of barred owl vital rates produced spotted owl population declines of approximately 60% to 80% relative to the spotted owl population estimate without barred owl displacement. These population simulations suggest that this landscape is capable of supporting at least twice as many barred owls as spotted owls, without considering the effects of inter-specific competition. When displacement effects were incorporated, this landscape supported more than seven times as many barred owls as spotted owls. These population simulations suggest that understanding patterns of barred owl distribution and abundance throughout the range of the northern spotted owl will be increasingly important for spotted owl conservation planning.

INTRODUCTION

Territorial interactions are an important mechanism structuring bird communities (Newton 1992). Understanding the implications of such interactions can be important for conservation planning, particularly when there are novel interactions between native and colonizing species (for example, Tannerfeldt et al. 2002, Gurnell et al. 2004, Stokes et al. 2009). Novel interaction with colonizing species has been ranked second only to habitat loss in contributing to species imperilment in the United States (Wilcove et al. 1998). The frequency and intensity of such interactions are projected to increase as a consequence of species range shifts due to climate change (Urban et al. 2012, Zarnetske et al. 2012). Developing tools to evaluate the population-level implications of such novel competitive interactions is likely to become increasingly important for conservation planning.

One example of a novel species interaction contributing to the decline of an imperiled species is in the Pacific Northwest, USA, where competitive interactions with recently established barred owls (*Strix varia*) are contributing to northern spotted owl (*Strix occidentalis caurina*) population declines (Olson et al. 2005, Dugger et al. 2011, Forsman et al. 2011, Wiens 2012). The northern spotted owls is a medium-sized owl found in the coniferous forests of the northwestern United States (Forsman et al. 1984, Courtney et al. 2004). The U.S. Fish and Wildlife Service listed the northern spotted owl as a threatened species under the Endangered Species Act in 1990 (USFWS 2011). The primary factor contributing to listing the northern spotted owl was on-going loss of the old forest habitat with which it is associated (Thomas et al. 2006, USFWS 2011). Over the past two decades, competitive interaction with the recently established population of barred owls has also been recognized as an important factor contributing to spotted owl population declines (Guttierez et al. 2007, Forsman et al. 2011). Prior to the turn of the twentieth century, the range of barred owls was largely restricted to areas east of the Mississippi River (Livezey 2009). Barred owls expanded their range into the boreal forest of Canada in the first half of the twentieth century, and were detected in Washington and Oregon in the 1970s (Taylor and Forsman 1976). They are now found throughout the range of the northern spotted owl, and have become abundant in some areas (Livezey 2009).

Although spotted owls and barred owls are morphologically and ecologically quite similar, there are also important ecological differences between the species, including differences in behavior, space use, and landscape associations (Hamer et al. 2001, 2007, Singleton et al. 2010, Wiens 2012). Spotted owls use much larger home ranges that can overlap with neighboring conspecifics (for example, Forsman et al. 1984, 2005). Barred owls use smaller home ranges that they aggressively defend (Hamer et al. 2007, Singleton et al. 2010, Wiens 2012). Ecological differences between spotted owls and barred owls appear to be a product of different foraging strategies. Spotted owls forage primarily on nocturnal arboreal mammals, which they traverse large areas to capture (Forsman et al. 2004, Hamer et al. 2007, Wiens 2012). Barred owls are prey generalists, feeding on a wide variety of primarily ground-dwelling vertebrate and invertebrate prey, which they capture within a more limited area (Hamer et al. 2001, Graham 2012, Wiens 2012).

Previous chapters of this dissertation have explored some of the differences in habitat and landscape associations for the two species. Chapter 2 showed that, much like spotted owls, barred owls are associated with structurally diverse forest conditions. Chapter 3 highlighted differences between spotted owl and barred owl landscape associations, showing that barred owls were more closely associated with gentle slopes in lower topographic positions compared to spotted owls. Chapter 4 showed that patterns of habitat overlap for the two species influenced spotted owl site occupancy over time.

Understanding the population-level implications of territorial interactions between spotted owls and barred owls will be important for evaluating potential spotted owl population outcomes resulting from competitive interactions with colonizing barred owls. Territoriality has long been recognized as an important mechanism regulating bird populations (Howard 1920, Newton 1992). Territorial interactions can be a particularly important determinant of community structure for large raptors (Newton 1979). For example, Craighead and Craighead (1956) found that home ranges of congeneric hawks did not overlap in their seminal study of a raptor community in Michigan.

Such territorial interactions appear to be an important mechanism contributing to on-going spotted owl population declines (Gutierrez et al. 2007, Forsman et al. 2011, Wiens 2012). Barred owls are highly territorial throughout the year (McGarigal and Fraser 1985, Nicholls and Fuller 1987, Mosher et al. 1990). Adjacent barred owl home ranges documented by Singleton et al. (2010) in the eastern Cascade Range did not overlap. Wiens (2012) found complex patterns of spatial partitioning between neighboring barred owls and spotted owls during his radio-telemetry study in the Oregon Coast Range. Spotted owls avoided entering barred owl home ranges and used larger areas to compensate for loss of access to areas occupied by territorial barred owls, and spotted owls that nested close to nesting barred owls failed to reproduce (Wiens 2012). In a recent meta-analysis of demographic monitoring across the range of the northern spotted owl, Forsman et al. (2011) concluded that “fecundity, apparent survival, and/or populations were declining on most study areas, and that increasing numbers of barred owls and loss of habitat were partly responsible for these declines” (Forsman et al. 2011, p 70). Wiens (2012) also concluded that competitive interactions with barred owls were contributing to spotted owl population declines.

One important challenge in assessing the effects of interactions with barred owls on spotted owl populations is that broad-scale population-level outcomes of territorial interactions are very difficult and expensive to observe directly. In this case, individual-based models (IBMs) are especially well-suited for exploring fundamental assumptions regarding territorial interactions given existing information on animal distribution and vital rates (Grimm and Railsback 2005, Railsback and Grimm 2012). IBMs are particularly useful for identifying critical information gaps, generating testable hypotheses, and identifying opportunities for adaptive management in relation to complex emergent ecological processes (Railsback and Grimm 2012). IBMs provide a tool to investigate potential outcomes based on empirical information regarding habitat associations and demography (for example, Heinrichs et al. 2010, Spencer et al. 2011, Wilsey 2011). IBMs are also particularly useful for examining questions of space use and interactions between populations or individuals (for example, Grimm et al. 2003, Wang and Grimm 2007, Wilsey 2011).

A large volume of information on spotted owl population dynamics has been collected (reviewed by Noon and McKelvey 1996, Noon and Franklin 2002, Gutierrez 2008). Gutierrez (2008) cited 94 peer-reviewed papers addressing spotted owl population dynamics published from 1983 to 2007, and several more have been published since that review. Past population modeling for spotted owl conservation planning has included models that contained no spatial habitat information (Marcot and Holthausen 1987, Noon and Biles 1990), assumed that the suitable habitat was arranged uniformly or distributed randomly across the landscape (Lande 1987, 1988, Lamberson et al. 1992), assumed that suitable habitat occurred in regular clusters distributed across the landscape (Doak 1989, Carroll and Lamberson 1993, Lamberson et al. 1994, Carroll et al. 1995), or used actual habitat maps (Holthausen et al. 1995). More recent population modeling efforts have emphasized assessing realistic representations of spatial landscape and population structure using spatially explicit IBM (Lamberson 2012). For example, the recent critical habitat designation for northern spotted owls was informed by an extensive IBM exercise using empirically derived habitat maps (Dunk et al. 2012, USFWS 2012a). However, none of these spotted owl population models has incorporated a spatially explicit representation of territorial interactions with barred owls.

The overall goal of this work was to examine potential spotted owl population responses to displacement resulting from territorial interactions with barred owls under existing habitat conditions in the eastern Cascade Range, Washington. I had three specific objectives: 1) to evaluate different individual-based modeling approaches for assessing population-level effects of displacement resulting from territorial interactions with barred owls; 2) to use the models to conduct simulation experiments to explore potential effects of displacement by barred owls on spotted owl population size and distribution under a range of demographic assumptions and habitat overlap conditions; and 3) to examine changes in the distribution of the simulated spotted owl population and identify existing habitat areas that could be of increased importance for spotted owl population persistence given displacement by barred owls. I developed these models as part of an on-going multi-process landscape simulation project investigating how forest growth, forest management, and disturbance patterns influence spotted owl population dynamics and interactions with barred owls (Kennedy et al. 2009). The work presented here represents an initial investigation of the projections produced by these models using a static landscape based on existing habitat conditions.

STUDY AREA

My modeling area encompassed the range of the northern spotted owl within the Okanogan-Wenatchee National Forest, Washington. This 1.62 million ha area extended from the crest of the Cascade Mountain Range on the west, to the forest – shrub-steppe ecotone on the east, and from the Canadian border on the north to the Yakama Indian Reservation on the south (Figure 5.1). The area is characterized by complex, mountainous topography. Elevation ranges from approximately 240 to 2750 m (800 to 9000 ft). Vegetation communities on the east slope of the Cascade Range are substantially influenced by the strong moisture gradients associated with the rain-shadow effect of these mountains and local topography. Forest types are a mix of moist-mesic conifer forest found in the western portion of the study area, characterized by silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) at higher elevations, and Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and western hemlock (*Tsuga heterophyla*) at lower elevations. Xeric-mesic mixed conifer forest is found at mid-elevations through the central portion of the study area, characterized by a mix of Douglas-fir, grand fir, and ponderosa pine (*Pinus ponderosa*). Dry ponderosa pine woodlands, shrublands, and grasslands are found along the eastern edge of the study area (Johnson and O'Neil 2001, Lillybridge et al. 1995).

My modeling area encompassed the Cle Elum and Wenatchee Spotted Owl Demographic Study Areas (DSAs, Anthony et al. 2006, Forsman et al. 2011). The Wenatchee DSA received consistent spotted owl call survey effort from approximately 1990 to 2003 (Anthony et al. 2006). Spotted owl demographic monitoring started in the Cle Elum DSA in 1989 and is ongoing (Forsman et al. 2011). Research on barred owls within the modeling area included a radio-telemetry study conducted from 2003 to 2006 (Singleton et al. 2010).

METHODS

Overview

The purpose of this modeling exercise was to examine potential spotted owl population responses to displacement resulting from territorial interactions with barred owls. These models focus on the effects of displacement of spotted owls by territorial barred owls. They do not address potential effects of direct mortality of spotted owls resulting from agonistic interactions with barred owls (Van Lanen et al. 2011), or potential changes in spotted owl vital rates due to interactions with neighboring barred owls (Wiens 2012). I developed single-species and dual-species variants of the population models to explore how different representations of barred owl territory occupancy influenced spotted owl population outcomes. The single-species variant provided a simpler approach that avoided explicit assumptions regarding barred owl population dynamics, whereas the dual-species variant provided opportunities to explore the effect of varying barred owl vital rates on spotted owl population outcomes. I conducted several model experiments to investigate the influence of different assumptions regarding barred owl abundance and population performance on spotted owl population size and distribution in the existing landscape. Sensitivity analysis for the spotted owl population model has been reported elsewhere (Marcot et al. in prep.).

The Population Model

I developed a suite of spatially explicit, individual-based population models using HexSim software (version 2.4, Schumaker 2012) that integrated habitat maps with information on spotted owl and barred owl population dynamics. The general model structure was based on the work of Dunk et al. (2012, also see USFWS 2011: Appendix C), but was modified extensively for my study area and questions. Breeding pairs are the fundamental unit of population function for most large raptors, including spotted owls and barred owls (Newton 1979, Anthony et al. 2006, Forsman et al. 2011). I used a female-only, single-sex model structure, where territorial females were surrogates for reproductive pairs. The landscape was represented as a grid of 86.6 ha (1000 m diameter) hexagons in these models. Each hexagon was assigned a habitat resource value based on the amount of good and moderate habitat within the hexagon. Areas of good habitat were those identified as being used in greater proportion than available based on the resource selection analysis presented in Chapter 3 of this dissertation. Moderate habitat included areas used approximately in proportion to availability. Resource values were calculated independently for each species, based on landscape-scale habitat associations observed for that species using forest vegetation conditions in 2006 (Ohmann and Gregory 2002, Appendix 5.A). The model explicitly depicted annual survival, dispersal movement, home-range establishment (i.e., resource acquisition), and reproduction for each female (Figure 5.2). Underlying habitat resource values influenced each of these model processes.

Differences in space use between barred and spotted owls were depicted in my models by the different ways that the two species accrued habitat resources. Barred owls accrued resources only within a defended core territory. Spotted owls accrued resources from a defended core and a surrounding home range area where use could overlap with neighboring spotted owl pairs. Defended core area size was 520 ha (6 hexagons) for both species. This approximates the barred owl annual pair home range size reported by Singleton et al. (2010), as well as the median spotted owl pair breeding season 75% kernel home range size from Cle Elum DSA telemetry data (Stan Sovern, Oregon State University, Cle Elum WA, unpublished data). Spotted owls also accrued resources from up to 40 additional surrounding hexagons to approximate a 4000 ha annual home range area where use could overlap with neighboring spotted owl pairs.

Each individual was assigned to a high, moderate, or low resource class based on the proportion of a resource target that the individual was able to accrue within its used area. Resource target settings were calculated from observed patterns of habitat distribution around spotted owl and barred owl activity centers (Appendix 5.A). Annual survival probabilities and fecundity rates differed across individuals based on those resource classes.

I used two modeling approaches for assessing the effects of displacement by barred owls on spotted owl population outcomes: a dual-species approach in which populations of both spotted owls and barred owls were modeled, and a single species approach where only the spotted owl population was explicitly modeled (Figure 5.2). In the dual-species models, areas identified as being within barred owl defended core territories were unavailable for use by spotted owls. In the single-species models, individual hexagons were attributed as occupied by barred owls or not using an empirical estimate of barred owl probability of occupancy based on the amount of good barred owl habitat within a circular area approximating the size of a barred owl annual home range (450 ha, Appendix 5.C). In both approaches, areas simulated to be occupied by barred owls were assigned a spotted owl resource value of zero for the year that they were occupied, so they did not contribute any habitat resources to resident spotted owls.

I used the Cle Elum DSA fecundity rates reported by Forsman et al. (2011) to model spotted owl fecundity (Forsman et al. 2011, Appendix 5.B). Maximum clutch size for territorial spotted owl females was two (Forsman et al. 2011). The relationship between habitat and fecundity is unclear in the spotted owl demography literature (Anthony et al. 2006, Forsman et al. 2011).

Because of this uncertainty, I did not use different fecundity rates for individuals in the high and moderate resource classes. Individuals in the low resource class did not reproduce and abandoned the territory in a subsequent movement event. This parameterization allowed territorial spotted owls to respond to displacement by barred owls by abandoning a territory and searching for another suitable area.

Specific information on barred owl fecundity rates was unavailable for my modeling area. Barred owls are widely reported to have relatively high fecundity rates (Mazur and James 2000, Johnsgaard 1988, Wiens 2012). Mazur and James (2000) reported barred owl clutch sizes ranging from one to five, with an annual average of two to three young. Wiens (2012) reported that barred owls in his study area fledged up to four young. To reflect the higher fecundity and larger clutch sizes typically reported for barred owls relative to spotted owls, I multiplied the spotted owl total fecundity rates from Forsman et al. (2011) by 1.5 and used a maximum clutch size of three as the normative settings for the barred owl population model (Appendix 5.B).

I used the Cle Elum DSA survival rates reported by Forsman et al. (2011) to model spotted owl survival (Appendix 5.B). The normative survival settings for the barred owl population were based on the spotted owl rates, but adjusted down 10% on the assumption that increased fecundity could contribute to lower survival rates. Such fecundity/survival trade-offs are a basic tenet of life history theory and have been observed for a number of species (Roff 1992, Ghalambor and Martin 2001). I adjusted annual survival probabilities for both species to differ across age and resource classes to reflect the relationship between amount of habitat and survivorship documented in the spotted owl literature (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005, Forsman et al. 2011). Wiens (2012) reported similar positive effects of increasing amounts of old forest habitat on survival rates for both spotted owls and barred owls. I assumed that resource and age class effects on survival were proportionately the same for both species (Appendix 5.B).

Movement parameters for dispersing individuals were also the same for both species. There were two movement events for each population in each year, one after reproduction to represent juvenile dispersal, and another prior to breeding territory establishment. These events reflect the two-stage movement patterns described for spotted owls by Forsman et al. (2002) and settings were based on the Dunk et al. (2012) model. Only non-territorial individuals that had failed to acquire adequate resources to establish a territory moved in these events. Dispersal path length was set to minimum 25 and maximum 250 hexagons. Movement direction was moderately auto-correlated (50% over five hexagons). The landscape was uniformly permeable to movement for all hexagons with values corresponding to areas used equal to or greater than availability (resource value >20, Appendix 5.A). Probability of movement into a hexagon decreased linearly as hexagon resource values declined from 20 to 0. Hexagons with no habitat had a resource value of 2 so modeled individuals could move through such areas, though the probability of movement into those hexagons was much lower than for movement into hexagons with higher resource values. Hexagons with value 0 (including study area boundaries and hexagons occupied by barred owls) were completely impermeable to movement. High elevation areas (>1700 m) dominated by non-forest cover types (predominantly rock and ice) and a large lake (Lake Chelan) were also identified as impermeable movement barriers within my modeling landscape (Figure 5.2). Individuals stopped moving when they encountered three consecutive hexagons with a mean resource value of 30 (corresponding to areas used in proportion to availability, Appendix 5.A). At the end of each movement event, the individuals explored the surrounding 92 hexagons (7967 ha, approximating the size of two spotted owl annual home ranges) to identify the best available area for territory establishment.

Each model was run for a total of 150 years, including a 50 year “burn-in” period followed by a 100 year simulation period. The model simulations started with 250 individuals of each species randomly located in hexagons with resource values corresponding to areas used equal to or greater than available for that species (resource value > 20). The “burn-in” period allowed populations to approach equilibrium in the landscape and develop a representative distribution of age classes prior to the simulation period used in the population analysis. Modeled individuals were assigned to four age classes: juvenile (age <1 year), first-year (age 1 year), second-year (age 2 years), and adult (age >2 years). Survival and reproduction varied by age class, but other parameter values (e.g., resource thresholds and movements) were the same across age classes. I used a 100 year simulation period to capture the range of variation in population performance the landscape supported based on different model parameter settings. Numbers of individuals and their status (territorial or floater) were recorded at the end of the annual sequence for each yearly time step. The distribution of individuals as well as location and number of births and deaths was summarized for the 100-year simulation period.

It is important to note that these models are not realistic simulations of population performance through time because the population simulations were based on an un-changing habitat map derived from landscape conditions in 2006 (Appendix 5.A). Outputs from these population simulation models are best interpreted as indices of habitat carrying capacity under current conditions, given the model assumptions. Simulations to evaluate potential population performance through time will need to incorporate habitat changes resulting from forest growth and disturbance processes (as proposed by Kennedy et al. 2009).

Model Experiments

I evaluated ten model scenarios to investigate potential spotted owl population outcomes under a variety of barred owl vital rate and occupancy assumptions (Table 5.1). I evaluated four model scenarios using the single-species spotted owl population modeling framework to evaluate effects of displacement under different barred owl occupancy estimates. I modeled the spotted owl population without barred owl displacement effects to provide a baseline estimate of spotted owl carrying capacity and distribution without barred owl impacts (the single-species normative scenario: S_Norm). I evaluated the effects of varying barred owl occupancy probability in three additional scenarios. I set the barred owl probability of occupancy to the empirical estimate observed during systematic barred owl call surveys conducted in 2009 (the single-species observed barred owl occupancy scenario: S_BDO,

Appendix 5.C), and adjusted the occupancy estimate plus or minus one standard error (the single-species high and low barred owl occupancy scenarios: S_BDH and S_BDL, Appendix 5.D).

I developed six model scenarios with the dual-species modeling framework to investigate the influence of varying barred owl vital rates on spotted owl population outcomes. Model scenarios were based on my normative estimate of barred owl survival and fecundity (the dual-species normative scenario: D_Norm), as well as adjusting survival up or down 10% (the dual-species high and low barred owl survival scenarios: D_SVH and D_SVL) and adjusting fecundity up or down 15% (the dual-species high and low barred owl reproduction scenarios: D_RPH and D_RPL, Appendix 5.D). I also evaluated a modeling scenario in which barred owl resource values were derived from the spotted owl habitat map to investigate potential population outcomes if spotted owl habitat was equally suitable for barred owls (the dual-species complete habitat overlap scenario: D_HAB).

I ran 25 population simulation replicates for each modeling scenario. Preliminary analysis indicated that 25 replicates were adequate to capture the variability in annual population size and distribution estimates produced by a very large number of repeated simulations. I evaluated model outcomes with three metrics of spotted owl and barred owl population performance: 1) ending population size; 2) decadal lambda; and 3) simulation-duration lambda. I estimated ending population size by recording the number of territorial and non-territorial (floater) females in the last decade of the simulation (years 91-100), and calculated means and 90% quantile ranges across simulation replicates for each scenario. I calculated decadal lambda (i.e., the decadal rate of change in the number of territorial pairs) for the 100-year simulation period using the equation $(N_t+1)/(N_{t-10}+1)$, where N_t was the number of territorial females at each yearly time step. Adding one to each population estimate ensured that the calculation returned a real number when N_{t-10} was zero. I calculated simulation-duration lambda (i.e., the rate of change in the number of territorial pairs over the entire 100-years of the simulation) using the equation $(N_{t(91to100)}+1)/(N_{t(1to10)}+1))$, where $N_{t(91to100)}$ was the mean of the number of territorial females in the last decade of the simulation period and $N_{t(1to10)}$ was the mean number of territorial females in the first decade of the simulation period. I evaluated whether populations consistently increased or decreased over the entire simulation period for each scenario using a student's t-test to calculate the probability that the mean of the estimates of simulation duration lambda across the 25 simulation replicates was drawn from a population with a mean of one.

Because of the single-sex structure of these models, they do not address important processes that contribute to extinction risk in small populations, including Allee effects and stochastic variation in sex ratios (Lacy 2000). To account for this and provide a relative index of extinction risk for comparison across the different modeling scenarios, I calculated pseudo-extinction rates based on the proportion of simulation replicates during which the number of spotted owl territorial pairs fell below 10% or 20% of the habitat carrying capacity. I calculated habitat carrying capacity based on the median of last-decade estimates of territorial spotted owl females from the spotted owl population simulations without barred owl displacement effects. I calculated randomized 95% confidence intervals for the pseudo-extinction rates by randomly sampling 17 (approximately two-thirds) of the 25 pseudo-extinction observations, calculating the pseudo-extinction rate, repeating the process 100 times, and calculating the 95% quantile range for the resulting values (Manly et al. 2007).

I summarized patterns of spatial distribution of the modeled populations across the analysis area by calculating the annual mean number of territorial females by sub-basin. I also calculated the number of births minus the number of deaths recorded within each sub-basin for the simulation duration to assess spatial patterns of demography across the analysis area. To spatially display this information, I aggregated the 86.6 ha hexagon-scale records of occupancy, births, and deaths to 4000 ha hexagons to capture processes at a scale that approximated a single spotted owl annual home range. All model output compilation, statistical analysis, and mapping were conducted using R software (version 2.15.1, R Development Core Team, Vienna Austria).

RESULTS

Despite differences in space use and landscape associations displayed by spotted owls and barred owls (Figure 5.3), displacement by barred owls had substantial detrimental impacts on spotted owl population performance in most model scenarios. Spotted owl population outcomes ranged from nearly deterministic extinction of the spotted owl population under assumptions of complete habitat overlap with barred owls or high barred owl occupancy, to larger and more broadly distributed spotted owl populations under assumptions of low barred owl survival or low barred owl occupancy.

Poor outcomes for the spotted owl population were not due to spotted owls having more limited habitat resources than barred owls. Approximately twice as much moderate or high habitat resource value area was available for spotted owls compared to barred owls (Figure 5.3, Appendix 5.A). There were 315,224 ha (3640 hexagons) of high spotted owl resource value (>40), and 297,471 ha (3435 hexagons) of moderate spotted owl resource value (20-40). For barred owls, 152,329 ha (1759 hexagons) had high resource value (>40), and 145,921 ha (1685 hexagons) had moderate resource value (20-40). The smaller territory size used by barred owls in my simulations allowed for much higher densities of barred owls, thereby supporting many more barred owl than spotted owl pairs, even though barred owl habitat was more limited in area.

The spotted owl landscape carrying capacity was approximately 200 pairs based on population simulations without barred owl displacement effects. Spotted owl ending population sizes ranged from approximately 35 to 80 pairs for scenarios with barred owl displacement effects. The barred owl population estimates ranged from approximately 450 to 500 pairs, depending on assumptions regarding reproduction and survival (Table 5.2, Figure 5.4). Adjusting barred owl reproduction up or down (scenarios D_RPH and D_RPL) and increasing survival (D_SVH) had relatively small effects on the abundance and distribution of territorial barred owl females, but numbers of non-territorial floaters varied substantially across these scenarios (Table 5.2). The distribution of spotted owl population estimates overlapped for these scenarios (ranging from 35 to 80 pairs). Two of the dual-species model scenarios had substantially different barred owl and spotted owl population outcomes. For the complete habitat overlap scenario (D_HAB), the number of barred owl pairs nearly doubled when spotted owl habitat was assumed to be equally suitable for barred owls. The spotted owl population went extinct during the burn-in period or the first 10 years of the simulation period for all complete habitat overlap (D_HAB) simulation replicates. In contrast, far fewer barred owls were supported under low survival assumptions (D_SVL), resulting in a substantially larger and much more widely distributed spotted owl population. Dual-species scenarios resulted in nearly twice as many spotted owl pairs as the single-species scenario with observed barred owl occupancy (S_BDO). Spotted owl population sizes for the single-species model were substantially different depending on assumptions regarding barred owl occupancy probability.

Barred owl simulation-duration lambda did not significantly differ from 1 for any of the scenarios, though lambda for the low barred owl survival scenario (D_SVL) was lower and more variable than the others (Table 5.3). The spotted owl population showed declines across the simulation period (simulation-duration lambda significantly less than 1) for the complete habitat overlap (D_Hab), low barred owl reproduction (D_RPL), and the observed and high barred owl occupancy (S_BDO, S_BDH) scenarios. Even though the ending spotted owl population size was slightly higher for the low barred owl reproduction scenario (D_RPL) compared to the other dual-species scenarios, the spotted owl simulation-duration lambda for this scenario (D_RPL) was low because it took longer for the barred owl population to reach equilibrium during the burn-in period, so the spotted owl population was still responding to displacement effects during the simulation period. The spotted owl population had simulation-duration lambda estimates slightly greater than 1 for the simulation without barred owl displacement (S_Norm), low barred owl survival (D_SVL), and low barred owl occupancy (S_BDL) scenarios. Decadal lambda rates were highly variable across simulations, especially when population sizes were relatively small, but did not differ substantially from one under any of the scenarios for barred owls and only differed from one for spotted owls under the two scenarios where spotted owls went to extinction (Figure 5.5).

Decadal lambda rates were generally more variable for spotted owl populations than for barred owl populations due to the smaller spotted owl population sizes (Figure 5.5). Mean decadal barred owl lambda rates equaled one for all of the dual-species scenarios, and standard deviations of the means were < 0.03 for all scenarios excepting the low barred owl survival scenario (D_SVL, SD = 0.29). Mean spotted owl decadal lambda rates equaled one, with standard deviations ranging from 0.1 to 0.2, for all of the scenarios excepting the high barred owl occupancy scenario (S_BDH, mean = 0.92, SD = 0.37) and complete habitat overlap (D_HAB, mean = 0.98, SD = 0.12) scenarios.

The spotted owl population dropped below the 20% of carrying capacity (40-pair) pseudo-extinction threshold in more than one of the simulation replicates for all of the dual-species scenarios excepting the low barred owl survival scenario (D_SVL, Table 5.4). Spotted owl populations did not drop below the 10% of carrying capacity (20-pair) pseudo-extinction threshold for any of the dual-species model scenarios, excepting the complete habitat overlap scenario (D_HAB), for which the spotted owl population went extinct in all of the simulation replicates. Under the single-species simulations, the spotted owl population never dropped below the 20% of carrying capacity pseudo-extinction threshold for the simulations without barred owl displacement (S_Norm) or with low barred owl occupancy (S_BDL). It dropped below the 10% of carrying capacity pseudo-extinction threshold for 24% of the simulations using observed barred owl occupancy rates (S_BDO) and for all of the simulations using high barred owl occupancy rates (S_BDH).

Spatial patterns for spotted owl occupancy and population sources were generally consistent across the model variants that included barred owl displacement in that similar areas were identified as having relatively high occupancy or population source rates, but the extent and intensity of those measures did vary across the model scenarios (Figures 5.6 and 5.7). Spotted owls were most abundant in the Wenatchee and Yakima sub-basins across all scenarios (Table 5.5). The Wenatchee sub-basin was the most consistent spotted owl population source (Table 5.6). Without barred owl displacement, the Chiwawa River / Lake Wenatchee area (Wenatchee sub-basin), the Yakima River valley (Yakima sub-basin), and the Naches River valley (Naches sub-basin) had high spotted owl occupancy rates and served as population sources (Figure 5.6). The Swauk Creek / Mission Mountains area (along the divide between the Wenatchee and Yakima sub-basins) continued to display relatively high occupancy as well as functioning as a population source under all of the displacement scenarios (Figures 5.6 and 5.7). Spotted owl population sources in other areas were greatly constrained by barred owl displacement effects

(Figure 5.7). For the barred owl population, the Wenatchee, Yakima, and Naches sub-basins supported substantially more pairs of barred owls than other portions of the analysis area under all of the scenarios (Table 5.5, Figure 5.6). The models highlighted four potential population sources for barred owls: the Methow River Valley (Methow sub-basin), the Chiwawa River Valley (Wenatchee sub-basin), the Cle Elum area (including areas surrounding the Yakima River, Swauk Creek, and Teanaway River in the Yakima sub-basin), and the Naches River Valley (Naches sub-basin, Table 5.6, Figure 5.7). The Chelan and Entiat sub-basins were population sinks for both spotted owls and barred owls across all of the scenarios (Table 5.6).

DISCUSSION

Territorial displacement by barred owls had a substantial impact on spotted owl abundance and distribution in my population simulations. The most plausible estimates of barred owl vital rates produced spotted owl population declines of approximately 60% to 80% relative to the spotted owl population estimate without barred owl displacement. Simulated spotted owl population levels fell below the 20% of carrying capacity (40-pair) pseudo-extinction threshold for all but the most optimistic scenarios incorporating barred owl displacement. Modeling the spotted owl population without displacement effects or with more limited displacement effects (as in the low barred owl survival and low barred owl occupancy scenarios) resulted in larger and more broadly-distributed spotted owl populations relative to the other scenarios.

These population simulations suggest that this landscape is capable of supporting at least twice as many barred owls as spotted owls, not considering the effects of inter-specific competition. When displacement effects are taken into consideration, this landscape may support more than seven times as many barred owls as spotted owls. Despite the ecological differences displayed by spotted owls and barred owls, territorial displacement by barred owls has the potential to have substantial detrimental impacts on spotted owl population performance. Many of those impacts may already have been realized in the eastern Cascades, as reflected by the declining number of spotted owls within the Cle Elum DSA (Forsman et al. 2011). Detrimental effects could be even more substantial than indicated by my population simulations if other impacts, such as direct mortality during agonistic interactions or reduced vital rates, are a consequence of interactions between the species (e.g., Lourenco et al. 2011).

Assumptions regarding barred owl probability of occupancy or degree of habitat overlap between the species had substantial influence on spotted owl population outcomes during my population simulations. Assuming complete habitat overlap caused spotted owl populations to become extinct relatively rapidly. Changing assumptions regarding barred owl probability of occupancy within the plausible range from my barred owl occupancy modeling resulted in substantially different outcomes for the spotted owl population. The barred owl occupancy estimates for this study were based on a relatively limited barred owl survey effort (Appendix 5.C). In this study, I have demonstrated how such estimates can be used for evaluating potential spotted owl population responses. Improving the precision of those occupancy estimates through expanded systematic survey efforts for barred owls would improve confidence in the modeling results. Accurate spatially-explicit estimates of barred owl probability of occupancy will be particularly important if these models are to be used for management decision support.

One of the notable results of these models was that barred owls were quite abundant and had a substantial impact on spotted owl populations even though their habitat was more limited. Even with twice as much high and moderate resource value area for spotted owls as for barred owls, my modeled spotted owl populations performed poorly for most scenarios. The space-use patterns of barred owls allowed their populations to become relatively large and dense, even with constrained habitat distribution. These patterns should not be interpreted to suggest that spotted owls are not habitat limited, or that additional habitat would not improve spotted owl population function. The degree of habitat overlap between spotted owls and barred owls appears to be an important limiting factor for spotted owl populations (Wiens 2012). Reduced habitat area, including loss of areas that are more likely to be occupied by territorial barred owls, could increase negative impacts of competition by reducing resource availability for both species, and forcing barred owls into areas that may otherwise be available to spotted owls (Dugger et al. 2011, Forsman et al. 2011, Wiens 2012).

It is important to note that these models are based on fixed assumptions regarding barred owl and spotted owl distribution. The ecological relationships between colonizing and native species can be very dynamic as the colonizing species adapts to a new environment and as the native species adapts to the presence of a new competitor or predator (Cox et al. 2004). Much of the observed difference in landscape associations for the two species could be an artifact of displacement processes that were already in effect when the spotted owl activity center locations were recorded. I evaluated spotted owl habitat based on the observed distribution of spotted owl activity centers from approximately 1990 to 2003. Displacement by barred owls may have been at its peak during that time (after barred owls had become common in the study area, but before the spotted owl numbers had declined substantially), and areas observed to be used by spotted owls during that period may not reflect optimal spotted owl habitat conditions (Van Horne 1983). If this is the case, and areas identified as high quality habitat in my analysis do not in fact provide adequate resources to sustain spotted owls, spotted owl populations may perform even more poorly than indicated in these models.

The distribution and abundance of barred owls may also continue to change through time as barred owls adapt to this landscape and population dynamics associated with colonization play out. For example, colonizing species often undergo a period of rapid adaptation in response to novel habitat and food resources (Cox et al. 2004, Lockwood et al. 2007). These models may under-estimate barred owl impacts on spotted owl populations if barred owls expand the range of habitat conditions that they occupy. The sensitivity of these models to assumptions regarding barred owl occupancy indicates that such changes in barred owl behavior could have important impacts on spotted owl populations. On the other hand, spotted owls could also adapt to the presence of barred owls by becoming more stealthy and/or territorially aggressive, thereby performing better than predicted in these models. Providing spotted owls with opportunities to adapt to the presence of barred owls may be an increasingly important concept for spotted owl conservation planning. Areas once considered to be marginal spotted owl habitat may have increasing importance for spotted owl population persistence if these areas provide the best opportunity for spotted owls to avoid encounters with territorial barred owls. On-going monitoring of the distribution and abundance of both spotted owls and barred owls may provide important insights into ecological changes both species may be experiencing.

The relative consistency of my spotted owl population outcomes across the most plausible modeling scenarios indicated that my models were relatively robust to uncertainty regarding barred owl vital rates. Different barred owl fecundity settings did not substantially influence the population size or distribution of barred owl territories, though they did have substantial influence on the number of non-territorial floaters. Uncertainty regarding barred owl fecundity rates does not seem to be a major concern for evaluating territorial displacement, but it could be important if agonistic encounters between resident spotted owls and non-territorial barred owls are detrimental to spotted owls (e.g., Walters and James 2010, Penteriani et al. 2011).

As typical for a long-lived species, reduced survival did have substantial influence on barred owl population outcomes. The normative setting for barred owl survival assumed lower survival for barred owls than for spotted owls. This setting does not reflect recently observed patterns. Wiens (2012) reported that survival of barred owls was higher than for spotted owls in his study area in western Oregon. However, my survival setting was intended to be a conservative assumption and I believe it contributes to the robustness of the normative dual-species model findings. The relatively high barred owl survival rates documented by Wiens (2012) may have been associated with a recently established colonizing population, and survival rates may go down as the population ages and effects of intra-specific competition are realized (Lockwood et al. 2007). Even with the lower normative survival settings for barred owls, the barred owl population reached habitat carrying capacity (i.e., the number of territorial barred owl pairs did not increase substantially when survival or reproduction settings were higher) and spotted owl population outcomes were quite similar when barred owl survival rates were set to equal spotted owl survival.

The single-species model structure that I used avoided uncertain assumptions regarding barred owl vital rates and demonstrated how empirical estimates of barred owl probability of occupancy could be used to represent effects of displacement by barred owls on spotted owl populations, while the dual-species modeling framework provided a structure for addressing a wider variety of questions, including investigating the effects of different assumptions regarding barred owl vital rates. I believe that these are complementary approaches that provide different insights into potential interactions between spotted owls and barred owls. There were specific differences in population size and distribution estimates under the two approaches. In particular, spotted owl populations were larger for the normative dual-species model than for the single-species model with observed barred owl occupancy. It appears that spotted owl populations were projected to be larger when barred owl movements and home range establishment were explicitly simulated (as in the dual-species models) than it was when individual hexagons were simply attributed as occupied by barred owls or not based on occupancy probability estimates (as in the single-species models). However, the general trends in terms of spotted owl population declines and displacement patterns were similar for both approaches.

Both my models and the demographic monitoring data showed substantial declines in the spotted owl population for the Cle Elum DSA (Forsman et al. 2011). My modeled population declines of 60-80% relative to habitat carrying capacity corresponded to the approximately 60% decline from 1994 to 2006 reported for the Cle Elum DSA by Forsman et al. (2011). On-going monitoring within the Cle Elum DSA has documented a continuing decline in the number of spotted owl pairs in recent years (Stan Sovern pers. comm.). Annual lambda for the Cle Elum DSA from 1990 to 2006 was estimated to be 0.937 (Forsman et al. 2011). In contrast, my models simulated populations that achieved equilibrium because vital rate settings for good habitat were high enough that population stability could be achieved based on the refugia provided by areas of good spotted owl habitat where barred owls were unlikely to occur.

Much of my modeling approach was drawn from the spotted owl population modeling work conducted to support spotted owl critical habitat planning by Dunk et al. (2012). For example, the basic model structure for the spotted owl population simulation event sequence was similar, and we used similar approaches to calculate habitat resource values based on maximum entropy modeling. The fundamental difference between our population simulation models was that we were addressing different questions at different scales. Dunk et al. (2012) were focused on addressing range-wide reserve design questions to support regulatory critical habitat designation decisions (USFWS 2012a), whereas my analysis was focused on exploring the potential consequences of local population interactions within a much smaller area. Because of these differences, I was able to take advantage of local information on barred owl distribution and habitat associations to develop a spatially explicit representation of barred owl territorial displacement effects. In the Dunk et al. (2012) models, barred owl effects were non-spatial. Spotted owls had uniform probabilities of encountering barred owls within modeling regions or across the entire range, and consequences of those encounters were expressed as changes in survival rates. Their model structure appropriately reflected the study area-scale barred owl covariates used in the Forsman et al. (2011) spotted owl demography meta-analysis, but it could not capture finer-scale displacement effects. My models used a spatially explicit representation of displacement, and barred owl occupancy did not directly influence spotted owl vital rates, though there were important secondary effects on spotted owl survival and reproduction as access to habitat resources was limited by displacement. I was unable to directly compare my population outcome estimates to those of Dunk et al. (2012) because my analysis area was just a subset of one of their modeling regions and they did not report specific population outcome estimates based on the existing conditions for this region (USFWS 2011). Their representation of range-wide barred owl impacts produced a 50% decline in the spotted owl population relative to estimates without barred owl effects (USFWS 2011), less than the 60% to 80% decline from my models.

The U.S. Fish and Wildlife Service made three overarching recommendations in the recent recovery plan for the northern spotted owl (USFWS 2011): 1) to protect the best of the spotted owl’s remaining habitat, 2) revitalize forest ecosystems through active management, and 3) reduce competition from barred owls. Individual-based models that explicitly address territorial displacement of spotted owls by barred owls could provide important information for addressing all of these recommendations. For example, the results of these models could contribute to identifying the “best remaining spotted owl habitat” from the perspective of spotted owl population function and barred owl displacement effects, and those areas could become the focus of landscape-scale management approaches designed to enhance habitat resilience and sustainability.

Much of the emphasis in management to address competition from barred owls has been on implementing experimental removal of barred owls to test the feasibility and effectiveness of barred owl control (USFWS 2012b). Dual-species models like those I have presented here could be used for spatial study design, hypothesis development, power analysis, and cost projections for removal experiments. For example, dual-species models could be used to identify experimental treatment and control areas, develop cost estimates for removal treatments in those areas based on modeled density of barred owls, virtually apply those treatments, investigate the range of plausible population responses under a variety of modeling assumptions, and simulate field survey effort required to detect modeled changes in populations. One important insight from these simulations is that some areas not occupied by spotted owls, and not considered to be typical spotted owl habitat (e.g., riparian forests on private lands), may serve as important sources for the barred owl population. Such insights on the spatial structure of the barred owl population may be particularly important for the development and implementation of effective removal experiments. Information from removal experiments could also contribute to population model parameterization by providing an empirical basis for estimates of spotted owl vital rates with and without barred owls (i.e., addressing the question of whether agonistic interactions with neighboring barred owls result in changes in vital rates for territorial spotted owl pairs). However, removal experiments would not provide information on effects of direct mortality for non-territorial spotted owls (e.g., effects of encounters with barred owls during dispersal), nor will they improve our understanding of barred owl distribution and abundance at a broader scale.

Through these population simulations, I have demonstrated that territorial interactions with barred owls could result in substantial negative consequences for spotted owl populations, even with a relatively restricted representation of barred owl habitat. These simulations also highlight some important information gaps for furthering our understanding of interactions between spotted owls and barred owls. In addition to territorial displacement, effects of other barred owl interactions including direct mortality during agonistic encounters and effects of harassment on spotted owl vital rates remain unknown. Quantifying and incorporating such interaction effects into future population modeling efforts could improve the realism of population simulations. Small population processes, including Allee effects, stochastic variation in sex ratios, and loss of the non-territorial floater component of the population, could become increasingly important as spotted owl populations decline. Dual-sex, dual-species modeling could better address small population dynamics and direct mortality issues, but will require many more assumptions regarding movement and mate-finding behavior. My models assess the effects of interference competition as manifested by territorial displacement. Other model structures that address resource competition, by incorporating prey populations and predator-prey dynamics, could be considered. This may be feasible for spotted owls, which are more reliant on a few prey species with relatively well-documented habitat associations; however quantifying prey availability for barred owls would be particularly challenging because they are prey generalists. Perhaps most important is that these population simulations indicate that understanding patterns of barred owl distribution and abundance throughout the range of the northern spotted owl will be increasingly important for spotted owl conservation planning. Efforts to quantify the distribution and abundance of barred owls should not be focused exclusively on occupied spotted owl habitat because areas that are currently occupied by few or no spotted owls may function as important barred owl population sources.

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Table 5.1. Population simulation experimental scenarios for examining the effects of territorial displacement by barred owls on the spotted owl population in the eastern Cascade Range, Washington.

Code	Type[1]	Parameters Changed[2]	Description
S_Norm	Single	None	SPOW population only with normative parameter settings, no BDOW.
S_BDO	Single	None	Normative model, with observed barred owl occupancy
S_BDL	Single	BDOW occupancy probability - 1 SE	Low BDOW occupancy
S_BDH	Single	BDOW occupancy probability + 1 SE	High BDOW occupancy
D_Norm	Dual	None	Dual species model with normative parameter settings
D_RPL	Dual	BDOW Reproduction rates – 15%	Low BDOW reproduction
D_RPH	Dual	BDOW Reproduction rates + 15%	High BDOW reproduction
D_SVL	Dual	BDOW Survival rates -10%	Low BDOW survival (BDOW survival 20% less than SPOW survival)
D_SVH	Dual	BDOW Survival rates +10%	High BDOW survival (BDOW survival equal to SPOW survival)
D_HAB	Dual	BDOW use SPOW habitat map	Assumes complete habitat overlap for SPOW and BDOW

[1] Single: single-species model, simulating only the spotted owl population. Dual: dual-species model, simulating both spotted owl and barred owl populations.

[2] SPOW: spotted owl, BDOW: barred owl

Table 5.2. Median (and 90% quantile range) of the estimated number of territorial females (Pairs) and non-territorial females (Floaters) during the last decade of the simulations for barred owl and spotted owl populations in the eastern Cascade Range, Washington. Medians and quantile ranges were drawn from 25 replicates of 10 population simulation scenarios (Table 5.1).

	Barred Owls		Spotted Owls	
Scenario	Pairs	Floaters	Pairs	Floaters
D_Norm	469 (454.4-480.0)	313.0 (241.2-362.1)	61 (40.0-81.0)	31 (18.0-45.0)
D_HAB	981 (962.0-998.0)	496.5 (406.8-570.5)	0 (0.0-0.0)	0 (0.0-0.0)
D_RPH	482 (465.5-494.0)	420.5 (331.4-484.0)	60 (34.5-78.0)	30 (15.5-43.0)
D_RPL	443 (425.0-463.5)	201.0 (141.7-252.0)	65 (45.5-79.0)	34 (21.0-48.0)
D_SVH	503 (492.4-512.0)	748.0 (682.9-811.5)	57 (34.0-73.5)	28 (14.0-42.0)
D_SVL	95 (24.0-183.2)	3.0 (0.0-22.0)	159 (131.0-182.5)	78 (59.5-102.5)
S_Norm			200 (180.0-219.5)	101 (84.0-117.0)
S_BDO			33 (15.0-46.5)	17 (6.0-27.0)
S_BDH			0 (0.0-9.5)	0 (0.0-6.5)
S_BDL			137 (120.0-157.0)	70 (54.5-88.0)

Table 5.3. Population rates of change (lambda) over the 100-year simulation duration for 10 scenarios simulating spotted owl and barred owl populations in the eastern Cascade Range, Washington, including the mean simulation period lambda for 25 simulation replicates (Mean), t-test p value evaluating the probability that those estimates were drawn from a population with a mean of 1 (p), and 95% confidence intervals of the mean (LCI, UCI).

	Barred Owls				Spotted Owls			
Scenario	Mean	p	LCI	UCI	Mean	p	LCI	UCI
D_Norm	1.00	0.24	0.99	1.00	0.97	0.54	0.88	1.06
D_HAB	1.01	0.01	1.00	1.01	0.93	0.02	0.86	0.99
D_RPH	1.00	0.66	0.99	1.00	0.94	0.19	0.86	1.03
D_RPL	1.00	0.69	0.99	1.01	0.89	0.00	0.82	0.95
D_SVH	1.00	0.86	0.99	1.01	0.91	0.07	0.80	1.01
D_SVL	0.84	0.07	0.66	1.01	1.07	0.00	1.03	1.12
S_Norm					1.05	0.00	1.02	1.07
S_BDO					0.78	0.00	0.70	0.86
S_BDH					0.36	0.00	0.23	0.48
S_BDL					1.04	0.09	0.99	1.09

Table 5.4. Mean and randomized 95% confidence intervals of spotted owl pseudo-extinction rates for thresholds approximating 10% (20 pairs) and 20% (40 pairs) of the landscape carrying capacity without barred owl displacement effects in the eastern Cascade Range, Washington.

Scenario	20 Pairs	40 Pairs
D_Norm	0.00 (0-0)	0.36 (0.30-0.45)
D_HAB	1.00 (1-1)	1.00 (1-1)
D_RPH	0.00 (0-0)	0.36 (0.25-0.45)
D_RPL	0.00 (0-0)	0.08 (0-0.10)
D_SVH	0.00 (0-0)	0.40 (0.30-0.48)
D_SVL	0.00 (0-0)	0.00 (0-0)
S_Norm	0.00 (0-0)	0.00 (0-0)
S_BDO	0.24 (0.15-0.30)	1.00 (1-1)
S_BDH	1.00 (1-1)	1.00 (1-1)
S_BDL	0.00 (0-0)	0.0 (0-0)

Table 5.5. Annual mean and standard error of the number of spotted owl and barred owl pairs (territorial females) during the 100-year simulation period for 10 modeling scenarios within six sub-basins in the eastern Cascade Range, Washington.

	Methow		Chelan		Entiat		Wenatchee		Yakima		Naches		
Scenario	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Total
Barred Owls													
D_Norm	53.9	0.3	12.0	0.1	8.2	0.0	116.7	0.3	156.4	0.3	122.4	0.2	469.6
D_HAB	120.4	0.3	55.6	0.2	36.7	0.1	290.8	0.3	256.8	0.2	218.2	0.3	978.5
D_RPH	56.9	0.2	12.3	0.1	8.3	0.0	119.4	0.2	159.3	0.2	124.4	0.2	480.6
D_RPL	47.7	0.6	11.3	0.1	7.9	0.0	110.3	0.5	150.0	0.4	118.0	0.3	445.2
D_SVH	61.6	0.1	12.6	0.1	8.5	0.1	125.1	0.2	165.8	0.3	129.9	0.3	503.5
D_SVL	3.1	0.9	2.2	0.3	1.9	0.2	21.0	2.3	42.2	3.3	40.5	3.4	110.9
Spotted Owls													
D_Norm	5.5	0.6	5.1	0.3	3.0	0.1	21.5	0.6	21.2	0.5	5.9	0.5	62.2
D_HAB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
D_RPH	3.8	0.7	3.9	0.4	2.6	0.2	21.4	0.7	20.5	0.4	6.8	0.5	59
D_RPL	6.5	0.7	4.7	0.3	2.8	0.1	22.6	0.6	21.8	0.4	7.6	0.5	66
D_SVH	3.7	0.5	4.2	0.2	2.8	0.1	19.6	0.5	20.2	0.4	6.5	0.4	57
D_SVL	16.1	0.8	8.7	0.2	4.9	0.1	52.0	0.8	42.3	0.8	30.6	1.1	154.6
S_Norm	18.8	0.5	10.0	0.1	5.8	0.1	61.3	0.5	54.6	0.4	45.8	0.4	196.3
S_BDO	1.9	0.4	2.2	0.2	1.6	0.1	14.2	0.5	14.0	0.6	3.3	0.3	37.2
S_BDH	0.1	0.0	0.1	0.0	0.2	0.1	1.8	0.4	2.7	0.5	0.5	0.1	5.4
S_BDL	12.9	0.4	7.6	0.2	4.5	0.1	44.3	0.4	38.1	0.3	27.7	0.5	135.1

Table 5.6. Mean and standard error of the total number of births minus the total number of deaths over the 100-year simulation period for 10 modeling scenarios within six sub-basins in the eastern Cascade Range, Washington. Sub-basins with positive values function as population sources, those with negative values function as population sinks.

	Methow		Chelan		Entiat		Wenatchee		Yakima		Naches	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Barred Owls												
D_Norm	133.0	7.2	-402.0	6.9	-172.4	7.3	237.0	11.9	115.4	14.6	82.3	8.8
D_HAB	169.6	9.2	-373.8	10.1	-233.3	12.5	398.3	20.1	-16.9	18.6	87.1	13.7
D_RPH	186.5	8.6	-524.0	8.5	-200.9	6.8	253.2	15.1	163.5	16.1	133.7	10.8
D_RPL	73.5	5.6	-269.9	5.5	-129.0	7.4	167.6	12.5	125.5	14.6	52.5	8.9
D_SVH	263.2	8.1	-751.2	8.5	-246.8	6.4	417.3	17.0	160.8	18.3	165.8	11.6
D_SVL	-16.7	7.8	-24.4	3.3	-22.5	3.4	-47.3	20.7	14.2	19.9	57.4	15.5
Spotted Owls												
D_Norm	3.8	2.0	-8.9	2.2	-1.2	1.6	12.7	4.3	4.4	2.8	-9.9	1.9
D_HAB*	-0.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
D_RPH	-0.8	2.1	-10.7	1.8	-4.3	1.3	14.3	3.2	-2.5	3.2	-9.0	2.4
D_RPL	0.6	2.1	-14.2	1.9	-1.9	2.0	9.0	3.5	-1.7	3.4	-10.7	3.1
D_SVH	-0.9	1.6	-7.7	1.3	-4.0	1.9	9.3	3.0	-5.2	2.9	-4.4	2.1
D_SVL	13.6	2.7	-21.5	2.1	-14.7	2.2	29.6	3.7	13.4	4.1	1.8	3.5
S_Norm	15.8	3.0	-20.2	2.6	-15.1	2.8	20.8	5.1	7.4	5.1	2.1	2.9
S_BDO	-1.1	1.2	-6.1	1.2	-4.8	1.0	6.3	2.7	-1.6	2.7	-9.9	1.7
S_BDH*	-0.5	0.1	-1.0	0.3	-0.8	0.5	-3.4	1.2	-5.1	1.3	-1.4	0.7
S_BDL	9.2	3.2	-15.2	1.7	-9.4	2.0	17.1	3.2	10.0	4.3	0.6	3.0

*Spotted owl populations went to complete extinction for many of the simulations under these scenarios.

Figure 5.1. Modeling area for individual-based population simulations investigating effects of territorial displacement by barred owls on the spotted owl population in the eastern Cascade Range, Washington.

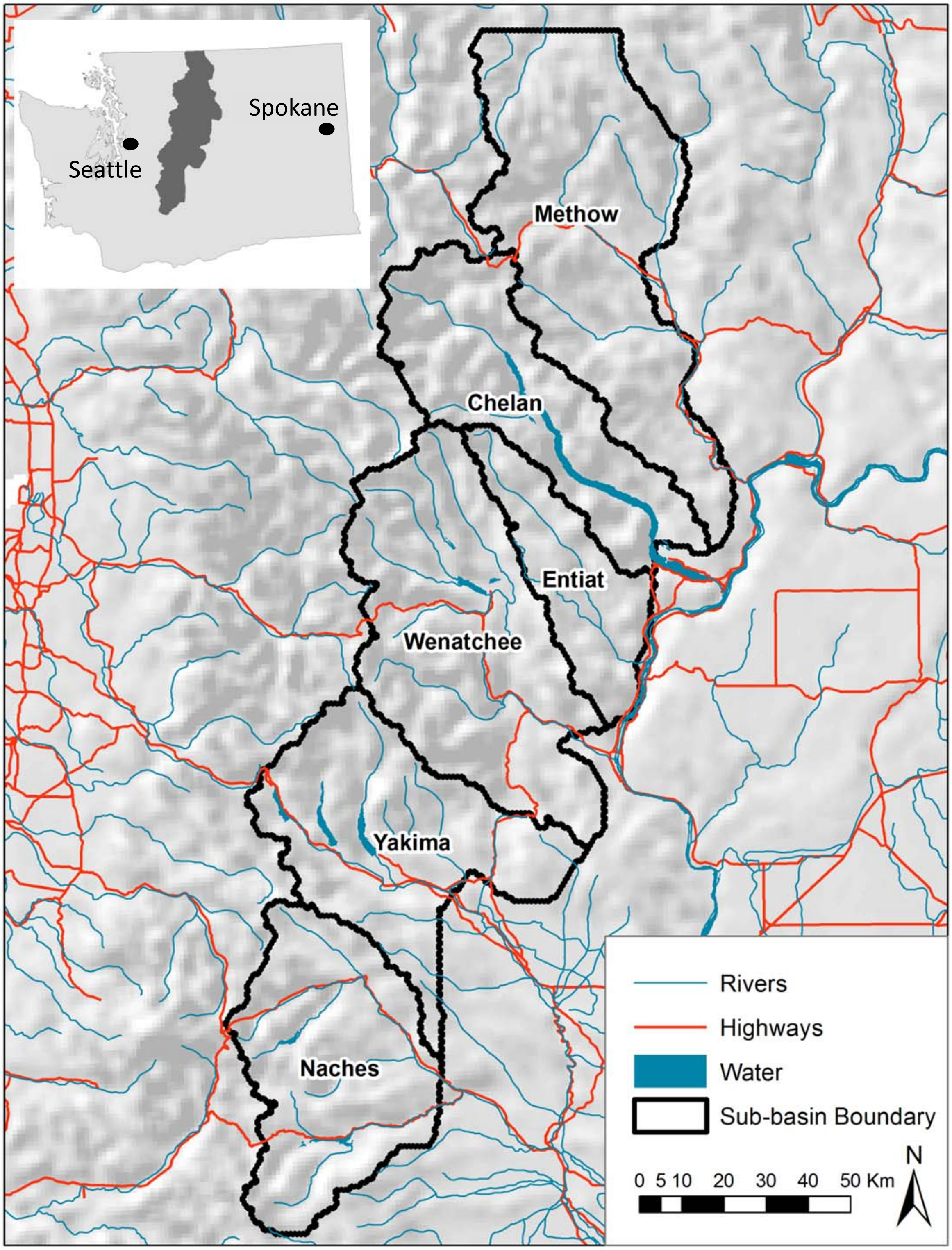
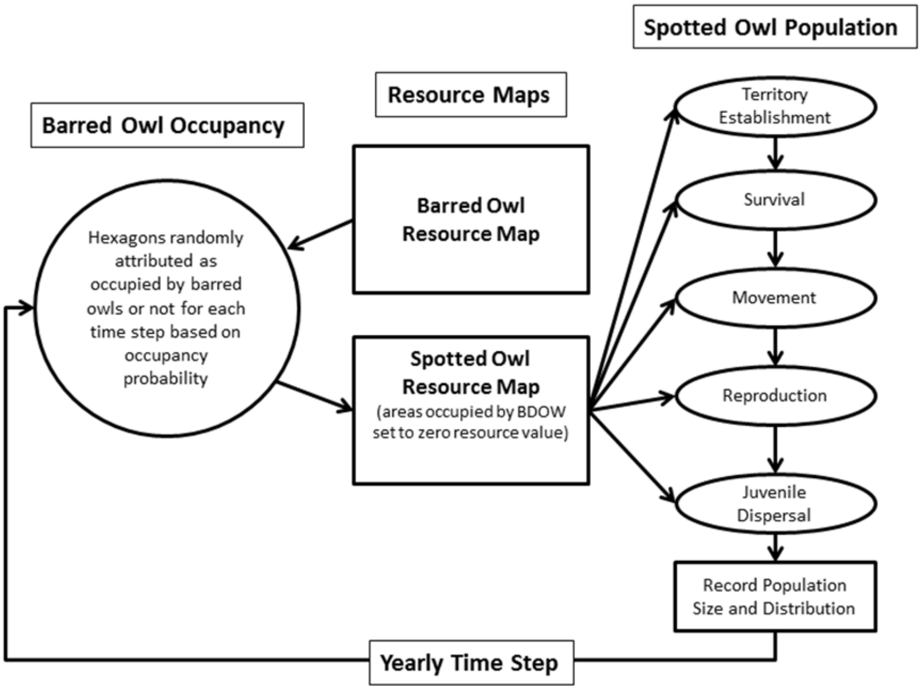


Figure 5.2. Individual-based population model event sequences for simulating effects of territorial displacement by barred owls on the spotted owl population in the eastern Cascade Range, Washington.

Single-species approach (spotted owl population only):



Dual-species approach (spotted owl and barred owl populations):

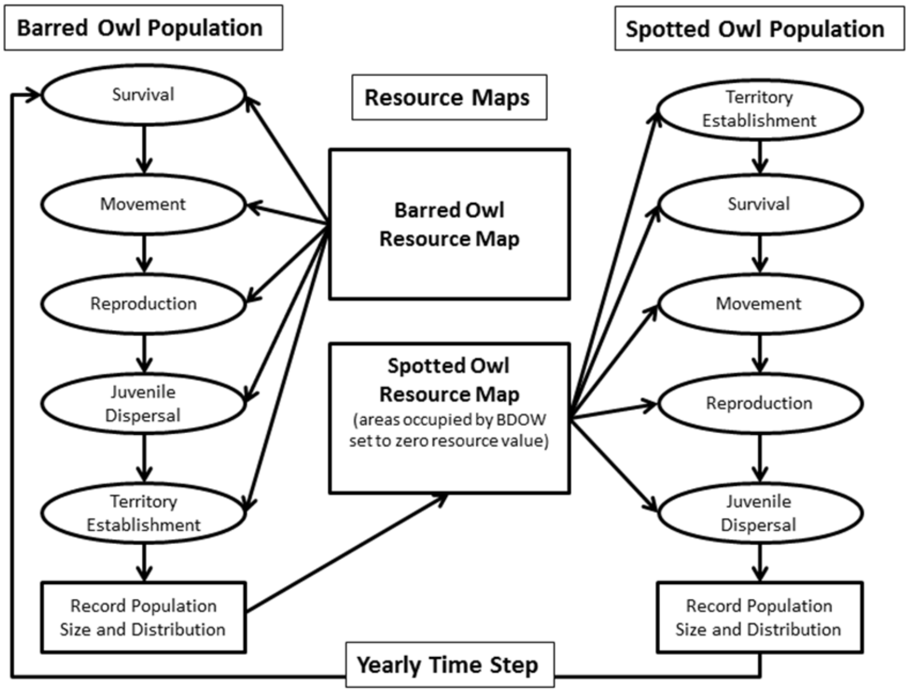
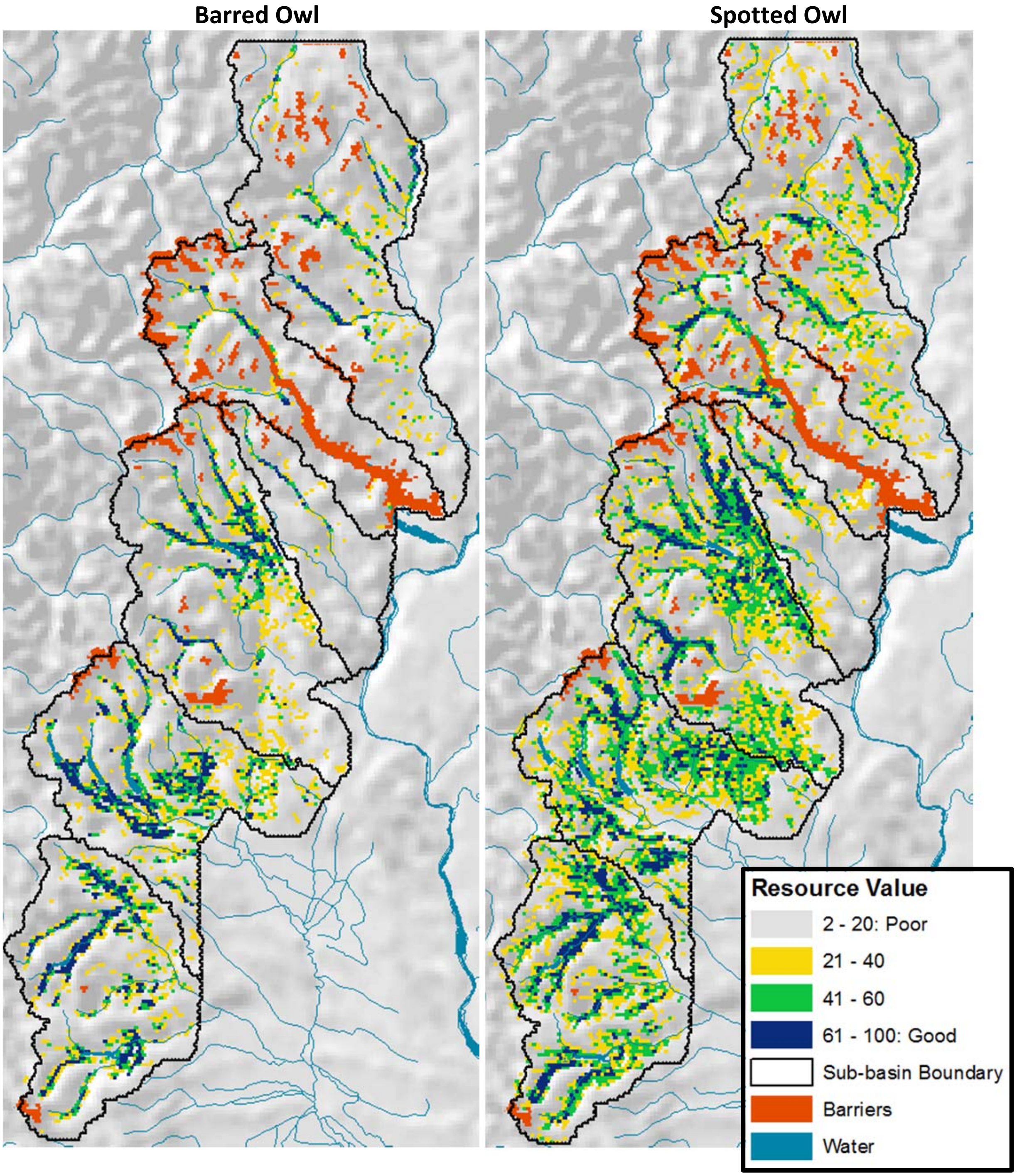


Figure 5.3. Spotted owl and barred owl habitat resource value maps, showing individual hexagon resource values, movement barriers, and sub-basin boundaries for barred owl and spotted owl population simulation modeling in the eastern Cascade Range, Washington.


Barred Owl

Spotted Owl

Figure 5.4. Population outcomes from 25 replicates of 10 modeling scenarios for spotted owl and barred owl populations in the eastern Cascade Range, Washington. (a) Median (solid lines) and 90% quantile range (dashed lines) of the number of barred owl and spotted owl territorial females by scenario (shown in different colors), including six dual-species models (Dual Spp.) and four single-species scenarios (Single Sp.). (b) Boxplots of the estimated number of barred owl and spotted owl territorial females for the last ten years of the 100-year simulation period for each scenario.

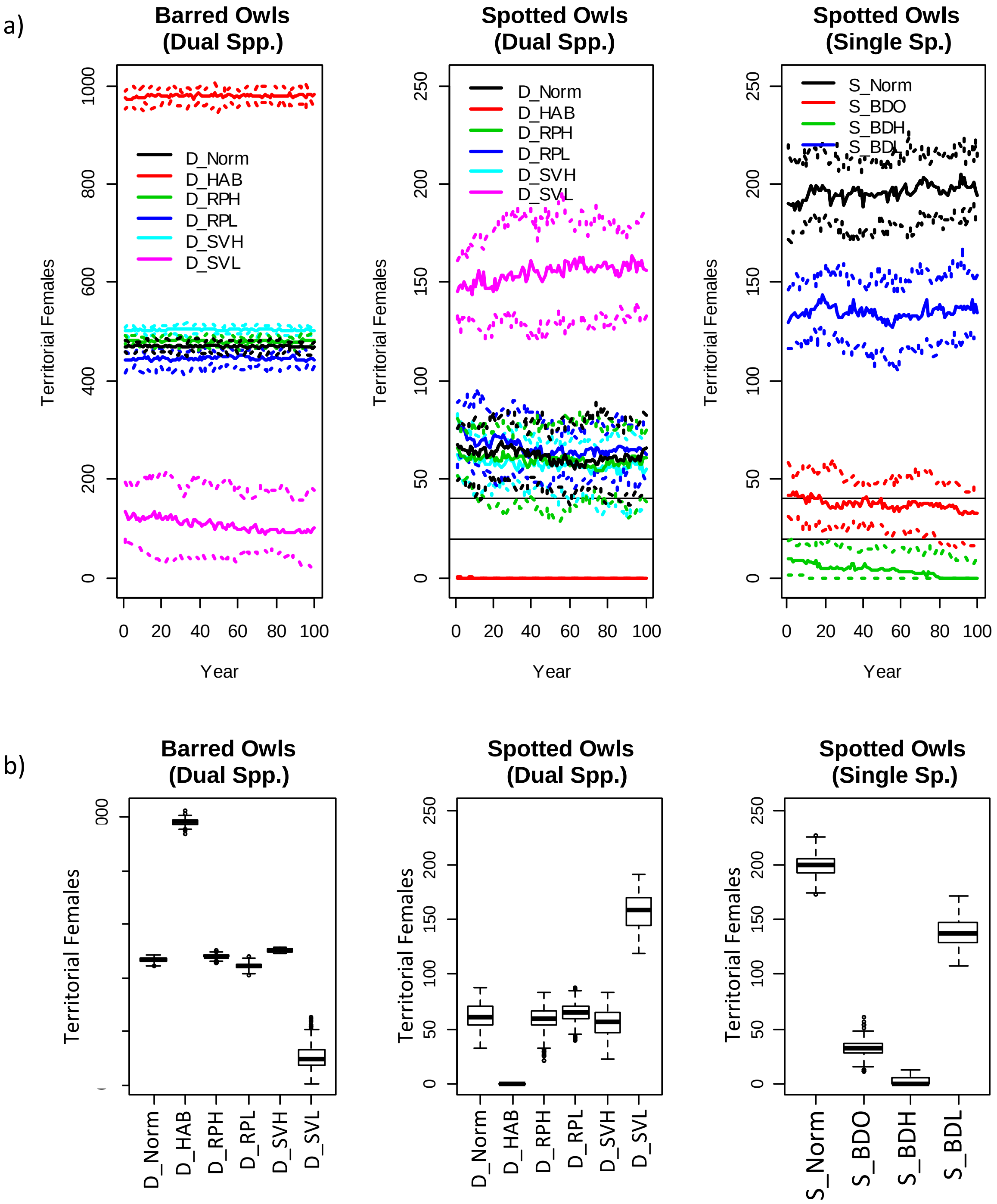


Figure 5.5. Decadal lambda for spotted owl populations in each year during the simulation period for ten population simulation scenarios in the eastern Cascade Range, Washington. Center lines indicate the median decadal lambda for 25 simulation replicates, outer lines indicate the 90% quantile range.

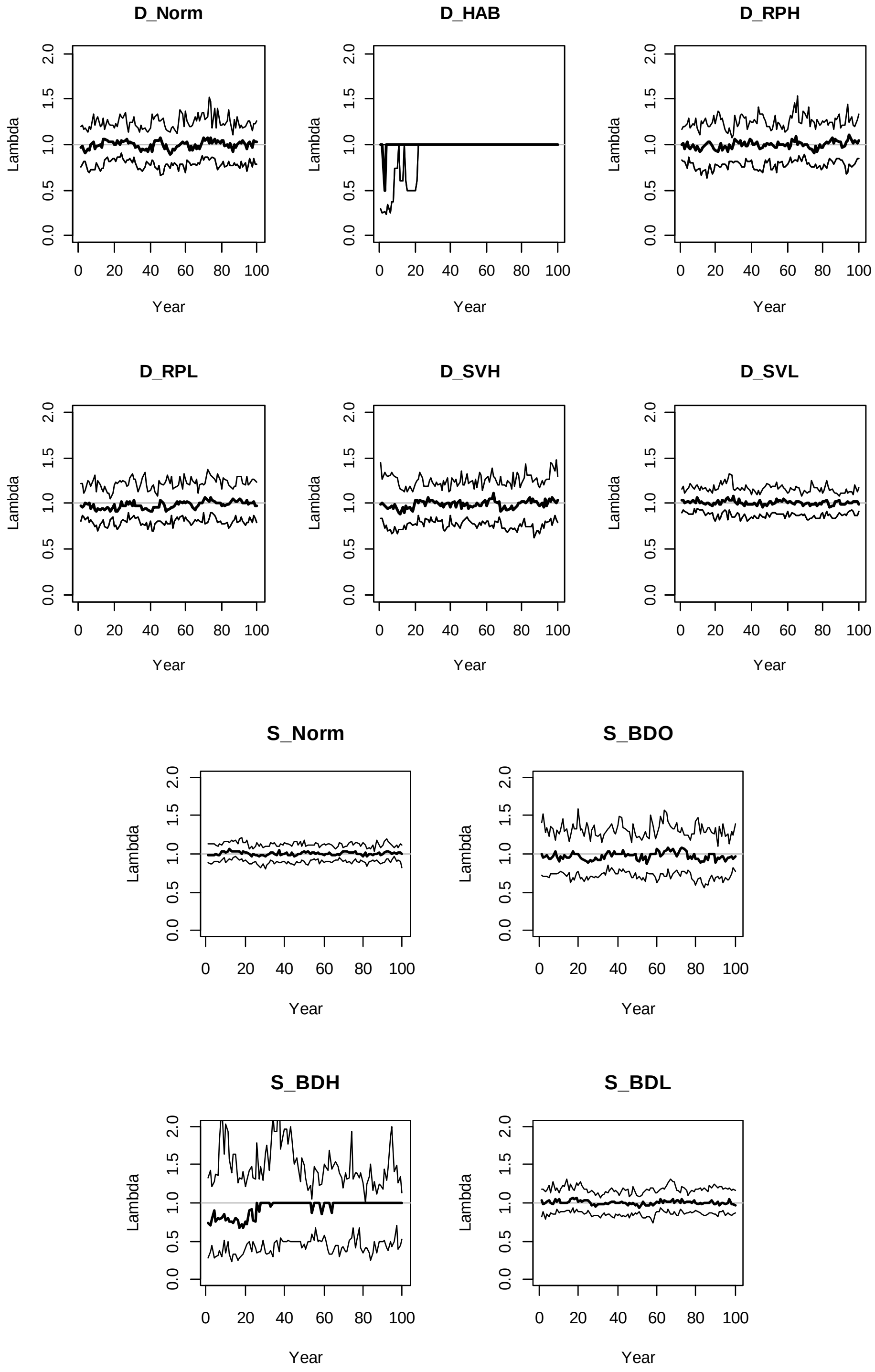
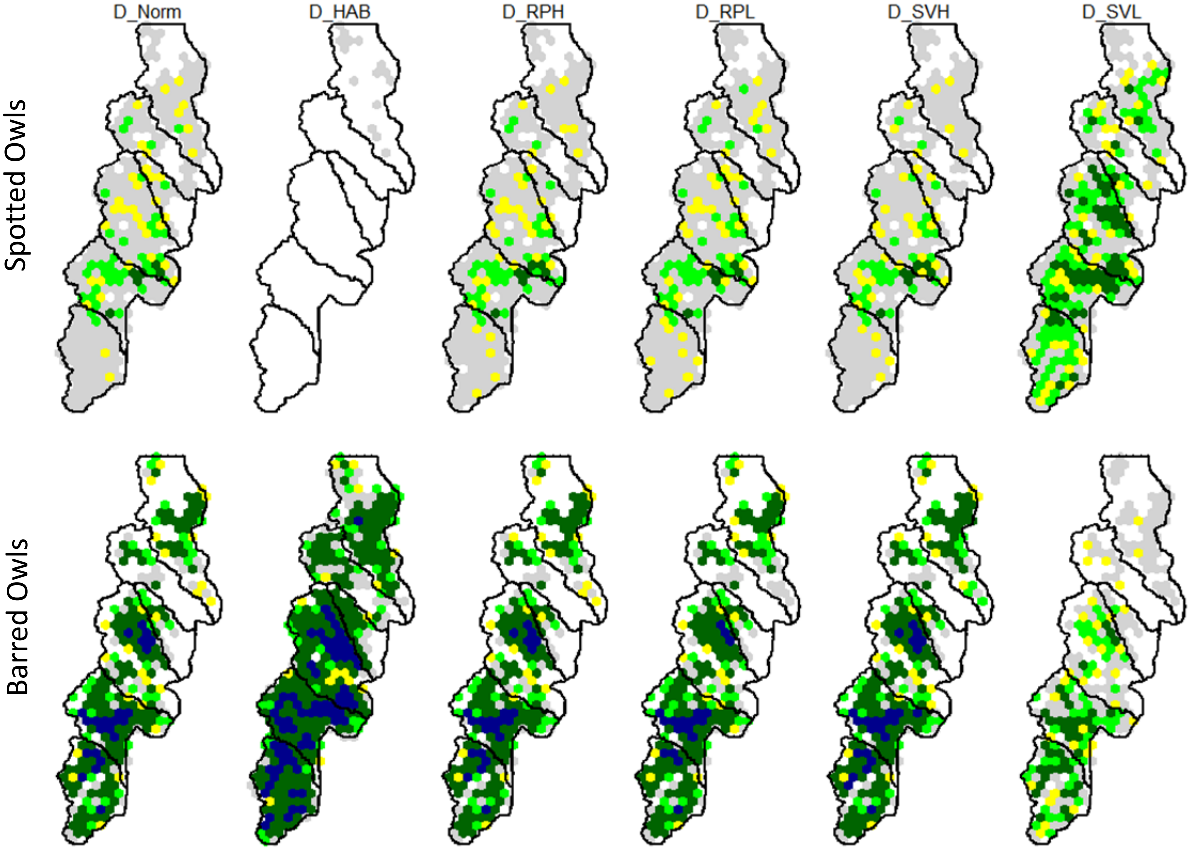


Figure 5.6. Maps of mean annual spotted owl and barred owl pair occupancy rate (mean number of territorial females per year within each 4000 ha hexagon) for ten population simulation scenarios for spotted owls and barred owls in the eastern Cascade Range, Washington.

a. Dual-species scenarios:



b. Single-species scenarios:

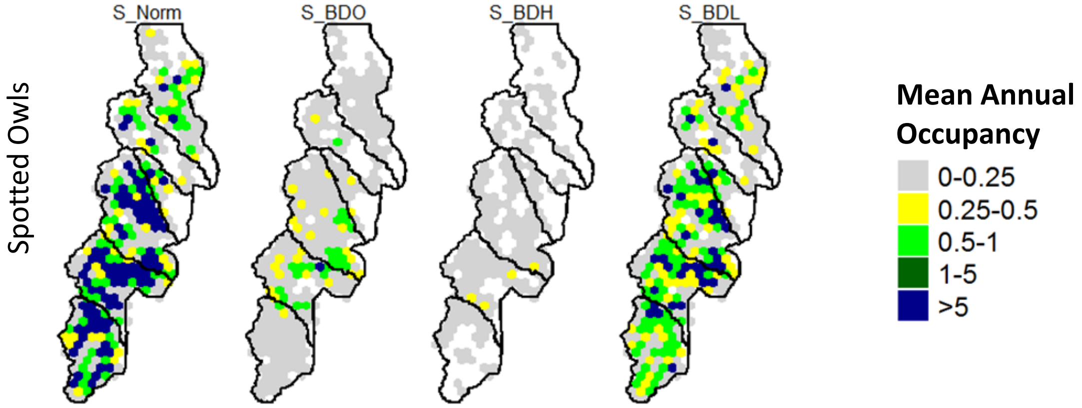
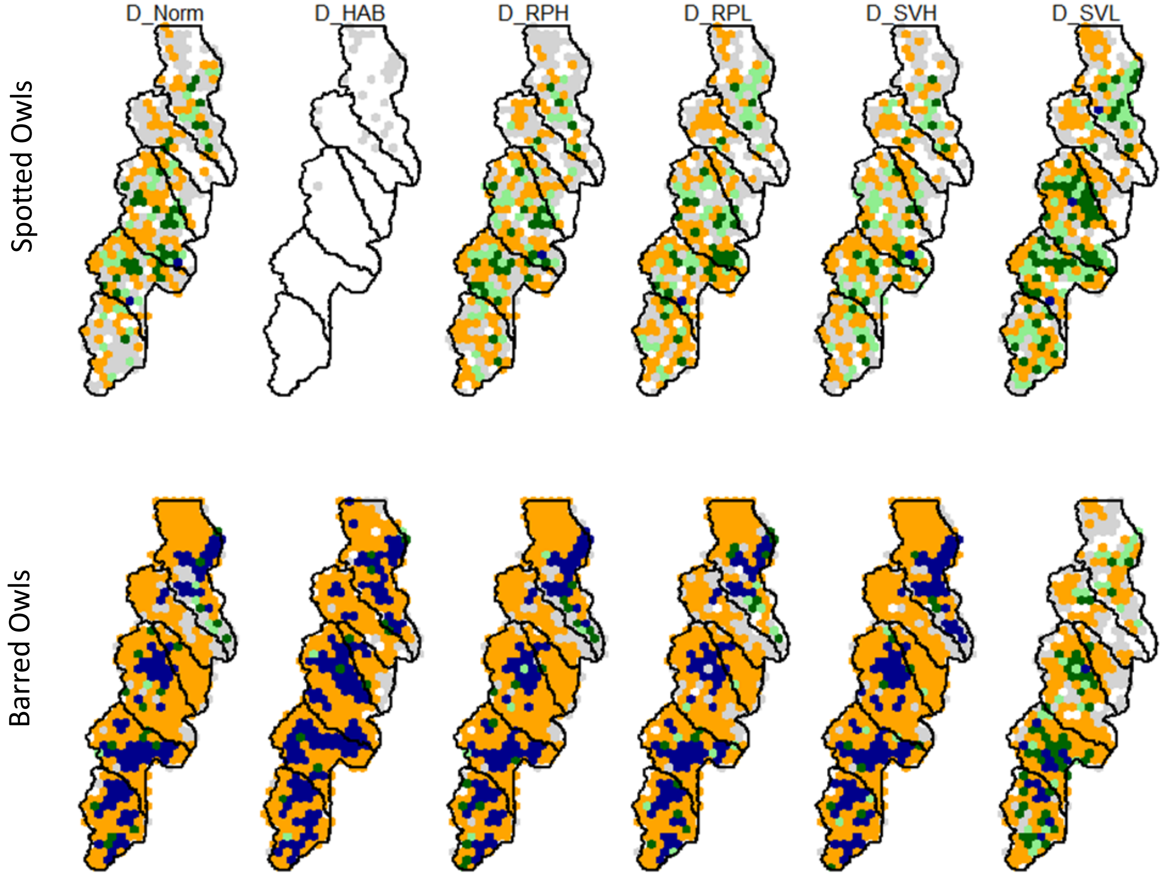
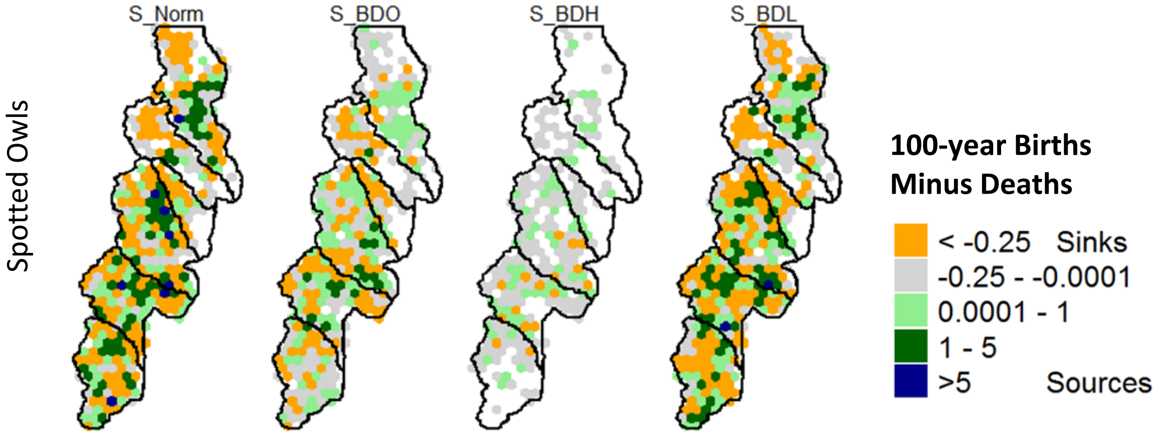


Figure 5.7. Maps of source-sink dynamics (total births minus total deaths over 100 years, summarized to 4000 ha hexagons) for ten population simulation scenarios for spotted owls and barred owls in the eastern Cascade Range, Washington. Areas with positive values are population sources, areas with negative values are population sinks.

a. Dual-species scenarios



b. Single-species scenarios



APPENDIX 5.A: RESOURCE VALUE AND THRESHOLD SETTINGS FOR POPULATION SIMULATIONS.

This appendix presents my methods and results for analyzing habitat amounts observed around spotted owl and barred owl activity centers, translating those patterns into resource values for input into the HexSim population models, and identifying resource thresholds for HexSim simulations.

METHODS

The spatial extent of this analysis was the portion of the Okanogan-Wenatchee National Forest (OWNF) south of Lake Chelan, below 1700 m. This area was within the Cle Elum and Wenatchee Spotted Owl Demographic Study Areas, and received consistent spotted owl call survey effort from 1989 to 2003 (Anthony et al. 2006, Forsman et al. 2011). More limited systematic barred owl call surveys were conducted within this area in 2009 (Appendix 5.C).

Habitat analysis and classification for this area were described in Chapter 3 of this dissertation. Briefly, I derived habitat selection maps based on binomial generalized linear mixed model analysis of 50 points from five ha surrounding activity centers for spotted owls (n=214) and barred owls (n=41), compared to three times as many random points taken from the OWNF analysis area. Activity centers were located during species-specific call surveys for both spotted owls and barred owls to avoid potential bias associated with barred owl detections recorded incidental to spotted owl survey efforts. Model covariates included forest characteristics (canopy cover, tree size, and species composition from GNN classified satellite imagery for 2006, Ohmann and Gregory 2002) and topographic characteristics derived from a 10 m digital elevation model (slope, solar radiation, and topographic position). Areas over 1700 m elevation were considered to be unavailable to both species of owl based on the observed distribution of the owl sites, and were excluded from the habitat selection analysis.

My HexSim population simulation models used an 86.6 ha hexagonal grid to represent landscape-scale habitat patterns for spotted owls and barred owls. Following the approach of Dunk et al. (2012), I used maximum entropy models (calculated with Maxent software, Phillips et al. 2008) to derive resource value scores for each hexagon. I calculated the proportion of good or moderate habitat for each species within each hexagon and multiplied that proportion by 1000 to derive an integer value for Maxent input. I attributed hexagons as "used" or not for each species according to whether there was an owl activity center located within the hexagon. Since many of the spotted owl activity centers were documented several years prior to the date of the habitat maps, I excluded activity centers within hexagons impacted by disturbance between 1989 and 2006 from the "used" sample. Disturbance within hexagons was assessed using *landtrendr* disturbance maps (Kennedy et al. 2010). I used Maxent to compare the "used" hexagons to the population of all hexagons within the analysis area and calculate a relative resource value for each hexagon. The linear, quadratic, and product features were included for consideration in the Maxent modeling (hinge and threshold features were excluded). The maximum entropy logistic model calculation produces values ranging from 0 to 1 that approximate the relative probability of use, based on the sample and background data. I used area under the receiver operating characteristics curve (AUC) and regularized training gain to assess model fit (Phillips et al. 2006, 2008). I used percent contribution and permutation importance to evaluate contributions of individual variables to the models (Phillips et al. 2006, 2008). I multiplied the Maxent relative probability of use estimate by 100 to derive an integer resource value for each hexagon.

I identified appropriate values for resource thresholds by evaluating resource values within hexagons surrounding owl activity centers and comparing those values to the analysis area using selection ratios (Manley et al. 2002). I calculated the sum of resource values in the hexagons closest to activity centers at the scale of the defended core area for barred owls and spotted owls (the closest six hexagons) and the broader home range scale for spotted owls (the closest 46 hexagons). I randomly selected 500 hexagons from the analysis area and duplicated the process to estimate resource availability at the core and home range scales. I used selection ratios to identify resource value thresholds which represented use less than availability, equal to availability, or greater than availability at the individual hexagon, core area, and home range scales. I calculated selection ratios with the *Wides* functions in the *AdehabitatHS* package in R (Calenge et al. 2006), using the *WidesI* function for comparing sums of resource values around activity centers to background measures, and the *WidesII* function for comparing the sample of multiple hexagon values around activity centers to background values.

RESULTS

Maxent estimates of spotted owl resource value were influenced by the amount of both good and moderate habitat within a hexagon (good habitat had 78.5% contribution, and permutation importance = 85, moderate habitat had 21.5% contribution, and permutation importance = 15; Figure 5.A.2). Maximum entropy model fit for the six hexagon-scale spotted owl model comparing 214 spotted owl activity centers to background conditions was AUC=0.78, with regularized training gain = 0.56.

Maxent estimates of barred owl resource value were primarily influenced by the amount of good habitat within the hexagon (good habitat had 98.7% contribution and permutation importance = 100). The amount of moderate habitat within the hexagon contributed little to barred owl resource value estimates (1.3% contribution, and permutation importance = 0; Figure 5.A.1). Maximum entropy model fit for the model comparing the amount of habitat within hexagons at 41 barred owl activity centers (six hexagon-scale) to 500 background hexagons was AUC=0.88, with regularized training gain = 0.90.

For both species, individual hexagons with resource values less than 20 were used substantially less than expected based on availability at the core area (six hexagon) scale (Table 5.A.1). Hexagons with resource values 20 to 40 were used in proportion to availability, and hexagons with resource values greater than 40 were found adjacent to activity centers substantially more often than expected based on availability (Table 5.A.1). For barred owls, six hexagon core area-sized regions were used less than available when the sum of resource values was less than 144, and use was greater than availability when the sum of resource values was greater than 186 (Table 5.A.2). For spotted owls, core area-sized regions were used less than available when the sum of resource values was less than 212, and use was greater than availability when the sum of resource values was above 292 (Table 5.A.2). At the 46 hexagon home range-scale, spotted owls used areas where the sum of resource values was less than 1572 less than expected based on availability, and areas where the sum was greater than 2213 more than expected based on availability (Table 5.A.3).

I calibrated the spotted owl resource threshold settings by comparing the estimated number of pairs of spotted owls from a preliminary version of the spotted owl-only model to the maximum spotted owl population recorded within the Cle Elum demographic study area (approximately 40 pairs). I adjusted the resource threshold down to 1992 so that the spotted owl model without barred owl displacement produced approximately 40 territorial spotted owl females within the Cle Elum DSA and to allow for shared resources within home ranges of adjacent spotted owls.

Table 5.A.1. Individual hexagon-scale selection ratio tables comparing resource values for six individual hexagons in the vicinity of each owl activity center to 500 available hexagons randomly selected from the analysis area landscape. The table indicates the upper limit of resource values within the class (Limit), the proportion of used hexagons in that class (Used), the proportion of available hexagons within that class (Avail), the ratio of used to available (Wi), the standard error of that ratio (SE), and the lower and upper 95% confidence intervals (CILower and CIUpper).

Barred Owls

Limit	Used	Avail	Wi	SE	CILower	CIUpper
20	0.20	0.72	0.28	0.05	0.15	0.42
40	0.25	0.14	1.82	0.28	1.10	2.53
60	0.22	0.07	3.27	0.43	2.17	4.37
80	0.28	0.06	4.41	0.66	2.72	6.10
100	0.05	0.01	5.05	1.47	1.27	8.83

Spotted Owls

Limit	Used	Avail	Wi	SE	CILower	CIUpper
20	0.07	0.47	0.16	0.03	0.09	0.23
40	0.20	0.23	0.90	0.07	0.72	1.08
60	0.39	0.20	1.98	0.10	1.73	2.22
80	0.33	0.11	3.15	0.21	2.63	3.67

Table 5.A.2. Core area-scale selection ratio tables comparing the sum of resource values for six hexagons adjacent to each owl activity center to a similar summation for six hexagons adjacent to 500 available hexagons randomly selected from the analysis area landscape. The table indicates the upper limit of resource values within the class (Limit), the proportion of used sites in that class (Used), the proportion of available sites within that class (Avail), the ratio of used to available (Wi), the standard error of that ratio (SE), and the Chi-square probability that the ratio equals one (P).

Barred Owls

Limit	Used	Avail	Wi	SE	P
144	0.08	0.74	0.10	0.06	0.00
186	0.12	0.09	1.45	0.61	0.46
282	0.33	0.09	3.45	0.79	0.00
414	0.47	0.08	5.64	0.94	0.00

Spotted Owls

Limit	Used	Avail	Wi	SE	P
212	0.15	0.65	0.23	0.04	0.00
254	0.11	0.11	1.03	0.22	0.88
292	0.14	0.10	1.38	0.26	0.14
414	0.60	0.14	4.40	0.28	0.00

Table 5.A.3. Home range-scale selection ratio tables comparing the sum of resource values for 46 hexagons in the vicinity of each spotted owl activity center to a similar summation of 46 hexagons adjacent to 500 available hexagons randomly selected from the analysis area landscape. The table indicates the upper limit of resource values within the class (Limit), the proportion of used sites in that class (Used), the proportion of available sites within that class (Avail), the ratio of used to available (Wi), the standard error of that ratio (SE), and the Chi-square probability that the ratio equals one (P).

Spotted Owls

Limit	Used	Avail	Wi	SE	P
1572	0.10	0.47	0.21	0.05	0.00
2213	0.40	0.33	1.23	0.11	0.05
3070	0.50	0.20	2.49	0.19	0.00

Figure 5.A.1. Maximum entropy model predicted barred owl resource values based on the proportion of good (bd_good) and moderate (bd_mod) barred owl habitat within the 86.6 ha hexagon. Resource value at hexagon (x) was calculated as: $raw_x = \exp((4.281 * (bd\_good_x/976)) + (0.769 * (bd\_mod_x/733)) + (0.405 * ((bd\_good_x*bd\_mod_x)/230585)) – 4.281) / 776.7$, and transformed to a range from 0 to 1 with the logistic transformation: Resource Value = $(raw_x * \exp(8.35)) / (1 + raw_x * \exp(8.35))$. Habitat proportions were multiplied by 1000 to provide integer input for Maxent.

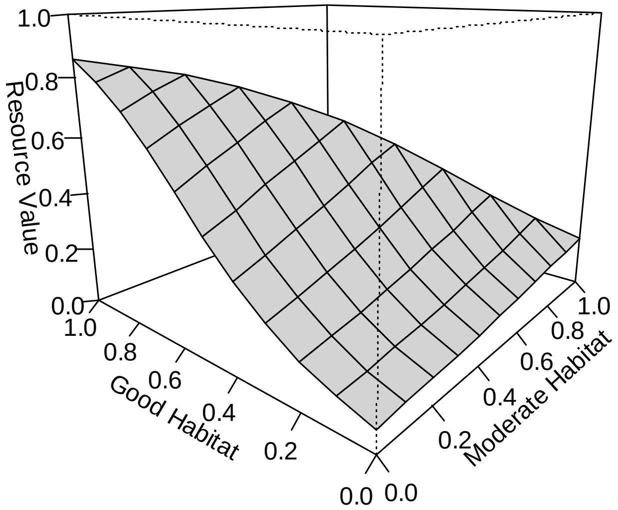
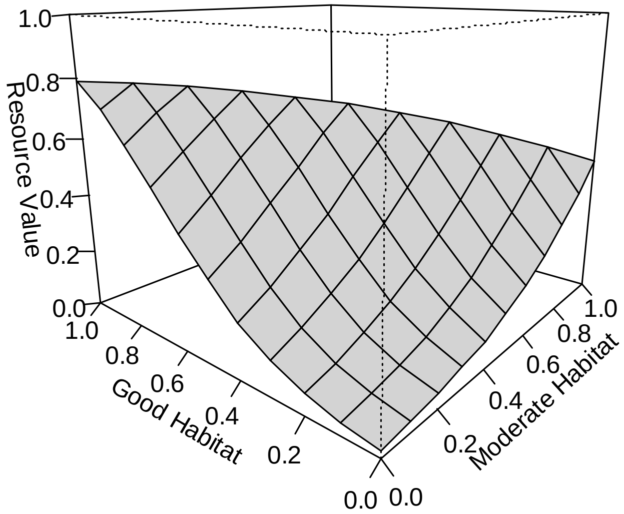


Figure 5.A.2. Maximum entropy model predicted spotted owl resource values based on the proportion of good (sp_good) and moderate (sp_mod) spotted owl habitat within the 86.6 ha hexagon. Resource value at hexagon (x) was calculated as: $raw_x = \exp((5.756 * (sp\_good_x/950)) + (3.447* (sp\_mod_x/944)) + (-0.905 * (sp\_good_x^2/902500)) + (-0.003 * ((sp\_good_x*sp\_mod_x)/ 236769)) – 4.950) / 1764.5$, and transformed to a range from 0 to 1 with the logistic transformation: Resource Value = $(raw_x * \exp(8.69)) / (1 + raw_x * \exp(8.69))$. Habitat proportions were multiplied by 1000 to provide integer input for Maxent.



APPENDIX 5.B: HEXSIM NORMATIVE PARAMETER SETTINGS.

This appendix presents the specific HexSim parameter settings for the barred owl and spotted owl population simulation models. Spotted owl parameter settings were largely based on rates for the Cle Elum Demographic Study Area (DSA) reported by Forsman et al. (2011). Detailed descriptions of the parameter functions within the HexSim software are available in the HexSim Users Guide (http://www.hexsim.net/guide/help.htm).

Table 5.B.1. Summary of the event sequence and normative parameter settings for the barred owl (BDOW) and spotted owl (SPOW) HexSim population simulation models.

Event	Parameter	BDOW	SPOW	BDOW Description	SPOW Description
Population Settings: Range Data	Max Range Area (hexagons)	6	6	Based on BDOW annual home range size of 450 ha (Singleton et al. 2010), rounded up to 6 hexes (520 ha).	Core area size approximates mean Cle Elum breeding season 75% kernel home range (Stan Sovern unpublished data).
	Hex Range-Eligible if (resource value)	20	20	Hexagons <20 were used less than available and were not eligible to be included in core areas (Table 5.A.3).	Hexagons <20 were used less than available and were not eligible to be included in core areas (Table 5.A.3).
	Min Range Resource (resource value)	144	212	Cores with 6 hex sum <144 were avoided (Table 5.A.4).	Core areas with 6 hex sum <212 were avoided (Table 5.A.4).
	Resource Target (resource value)	275	1992	The median of the core area 6 hex resource value sum at used sites was 275, cores with sum >282 were used substantially more than available (Table 5.A.4).	Home range-scale areas with resource value sums >2213 were used more than available (Table 5.A.5), adjusted down to 1992 to match Cle Elum DSA maximum observed population size.
Population Settings: Traits	Resource Class: Low (percent of target)	0	0	Ranges with resource value <52% of 275 (<144) were used less than available (Table 5.A.4).	Ranges with resource value <25% of 1992 (<498) were considered low.
	Resource Class: Mod (percent of target)	52	25	Ranges with resource value 144-186 (52%-67% of 275) were used in proportion to availability (Table 5.A.4).	Ranges with resource value 498-996 (25%-50% of 1992) were moderate.
	Resource Class: High (percent of target)	67	50	Ranges with resource value >186 were used more than available (Table 5.A.4).	Home Ranges >996 (50% of 1992) were good. This setting allows for complete home range overlap with one other SPOW pair.
Survival	Survival Table	See Table	See Table	BDOW survival rates were set 10% lower than SPOW, to represent a fecundity / survival trade-off.	Survival rates were based on Forsman et al. (2011).
Movement - Dispersal	Path Length (hexagons)	250	250	BDOW movements were set equal to SPOW movements.	Adapted from Dunk et al. (2012).
Movement – Stopping Rules	Mean Res Quality (resource value)	30	30	Approximate value of hexagons used in proportion to availability.	Approximate value of hexagons used in proportion to availability.
	Stopping Criteria Length (hexagons)	3	3	Movement stops and adjacent areas are explored when an individual encounters 3 hexagons (half a core area) of mean value 30 (the approximate value of hexagons used in proportion to availability).	Movement stops and adjacent areas are explored when an individual encounters 3 hexagons (half a core area) of mean value 30 (the approximate value of hexagons used in proportion to availability).
	Repulsion Max to Min (resource value)	0 to 20	0 to 20	Hexagons with resource value = 0 were impermeable to movement. Permeability increased linearly to resource value = 20.	Hexagons with resource value = 0 were impermeable to movement. Permeability increased linearly to resource value = 20.
	Repulsion Min (resource value)	20	20	Hexes >20 were used equal to or greater than available and were attributed as being equally permeable to movement.	Hexes >20 were used equal to or greater than available and were attributed as being equally permeable to movement.
Movement - Exploration	Max Explored Area (hexagons)	92	92	The area equivalent to two SPOW home ranges was explored.	The area equivalent to two SPOW home ranges was explored.
	Resource Threshold (percent of target)	100	100	Individuals explore with the objective of acquiring 100% of the resource target.	Individuals explore with the objective of acquiring 100% of the resource target.
Reproduction	Max Births (females only)	3	2	Maximum clutch size of 3 females.	Maximum clutch size of 2 females.
	Reproduction Table	See Table	See Table	BDOW fecundity was set at one and a half times SPOW fecundity.	Fecundity rates based on Forsman et al. (2011).

Table 5.B.1 (continued). Summary of the event sequence and normative parameter settings for the barred owl (BDOW) and spotted owl (SPOW) HexSim population simulation models.

Event	Parameter	BDOW	SPOW	BDOW Description	SPOW Description
Floater Creation: Global				Low Resource individuals always disperse, Mod & High individuals never disperse.	Low Resource individuals always disperse, Mod & High individuals never disperse.
Movement - Dispersal	Path Length (hexagons)	250	250	BDOW movements were set equal to SPOW movements.	Adapted from Dunk et al. (2012).
	Mean Res Quality (resource value)	30	30	Approximate value of hexagons used in proportion to availability.	Approximate value of hexagons used in proportion to availability.
	Stopping Criteria Length (hexagons)	3	3	Movement stops and adjacent areas are explored when an individual encounters 3 hexagons (half a core area) of mean value 30 (the approximate value of hexagons used in proportion to availability).	Movement stops and adjacent areas are explored when an individual encounters 3 hexagons (half a core area) of mean value 30 (the approximate value of hexagons used in proportion to availability).
	Repulsion Max to Min (resource value)	0 to 20	0 to 20	Hexagons with resource value = 0 were impermeable to movement. Permeability increased linearly to resource value = 20.	Hexagons with resource value = 0 were impermeable to movement. Permeability increased linearly to resource value = 20.
	Repulsion Min (resource value)	20	20	Hexes >20 were used equal to or greater than available and were attributed as being equally permeable to movement.	Hexes >20 were used equal to or greater than available and were attributed as being equally permeable to movement.
Exploration	Max Explored Area (hexagons)	92	92	The area equivalent to two SPOW home ranges was explored.	The area equivalent to two SPOW home ranges was explored.
	Resource Threshold (percent of target)	100	100	Individuals explore with the objective of acquiring 100% of the resource target.	Individuals explore with the objective of acquiring 100% of the resource target.
Movement - Set Home Ranges:	Max Explored Area (hexagons)	-	46	BDOW only accrue resources from within the defended core area.	SPOW acquire resources from the home range area set to approximately 4000 ha to approximate a typical home range area from Cle Elum telemetry data (Stan Sovern unpublished data).
	Resource Threshold (percent of target)	-	100		Individuals attempt to acquire 100% of the resource target within the home range.

Table 5.B.2. Normative survival rates for spotted owl and barred owl HexSim population simulation models. Age indicates the age class of the simulated individual: 0 = fledgling (age <1 year), 1 = juvenile (age 1 year), 2 = sub-adult (age 2 years), 3 = adult (age >2 years). Resource value thresholds are presented in Table 5.B.1 and described in Appendix 5.A. Spotted owl sub-adult and adult survival rates for the moderate resource class are based on Cle Elum DSA rates reported by Forsman et al. (2011, p 32). The spotted owl juvenile moderate resource class survival rate was based on the range-wide estimate from Forsman et al. (2002). Spotted owl survival rates were adjusted up (25% for juveniles and 10% for sub-adults and adults) or down (25%, 20%, 10%, and 5% for age classes 0 through 3 respectively) to capture expected effects of habitat quality on survival (Anthony et al. 2006, Forsman et al. 2011, and others). Barred owl survival rates were set to equal spotted owl survival rates minus 10% to represent a survival – fecundity trade-off relative to spotted owls (Ghalambor and Martin 2001).

Spotted Owl Annual Survival

Resource	Age			
Class	0	1	2	3
Low	0.375	0.635	0.738	0.778
Mod	0.500	0.794	0.820	0.819
High	0.625	0.873	0.902	0.901

Barred Owl Annual Survival

Resource	Age			
Class	0	1	2	3
Low	0.338	0.572	0.664	0.700
Mod	0.450	0.715	0.738	0.737
High	0.563	0.786	0.812	0.811

Table 5.B.3. Normative fecundity rates for spotted owl and barred owl HexSim population simulation models. Fecundity rates indicate the number of female young expected for each female in a given age class each year. Age indicates the age class of the simulated individual: 0 = fledgling (age <1 year), 1 = first-year sub-adult, 2 = second-year sub-adult, and 3 = adult (age >2 years). Spotted owl total fecundity rates by age class were based on those reported for the Cle Elum DSA by Forsman et al. (2012, p. 24). Barred owl fecundity rates were set to 150% of spotted owl survival rates to represent relatively high fecundity rates widely reported for barred owls (e.g. Mazur and James 2000, Johnsgaard 1998). Fecundity rates were evenly distributed across clutch sizes of one or two for spotted owls, and one to three for barred owls.

Spotted Owl Annual Fecundity

	No. Females/Year			
Age	0	1	2	Total
0	1.000	0.000	0.000	0.000
1	0.923	0.039	0.038	0.115
2	0.655	0.173	0.172	0.517
3	0.631	0.185	0.184	0.553

Barred Owl Annual Fecundity

	No. Females/Year				
Age	0	1	2	3	Total
0	1.000	0.000	0.000	0.000	0.000
1	0.914	0.029	0.029	0.029	0.173
2	0.612	0.129	0.129	0.129	0.776
3	0.585	0.138	0.138	0.138	0.830

APPENDIX 5.C: BARRED OWL OCCUPANCY PROBABILITY ESTIMATION.

This appendix presents the analysis and results used to develop an empirical estimate of barred owl occupancy probability based on habitat conditions that could be used for depicting barred owl displacement in individual-based spotted owl population simulations with HexSim. I used presence-absence data collected during barred owl call surveys to estimate the probability of barred owl occupancy based on the amount of good barred owl habitat within 450 ha using a single-season occupancy model (MacKenzie et al. 2006).

METHODS

I conducted call surveys for barred owls within the OWNF in 2009 using a randomized stratified sampling design based on three classes of predicted barred owl resource selection. To stratify call survey sampling effort, I extrapolated the Singleton et al. (2010) barred owl resource selection function (RSF) to the extent of the OWNF. I re-calculated the RSF parameter values by overlaying the Singleton et al. (2010) telemetry data on GNN vegetation data (Ohmann and Gregory 2002), an NDVI layer I derived from *landsat* imagery, and a digital elevation model that encompassed the entire forest. I split the resulting map into four classes: non-habitat, poor habitat, moderate habitat, and good habitat based on use-availability analysis of data from Singleton et al. (2010). I selected 91 call survey stations, approximately evenly divided between the poor, moderate, and good habitat classes. I did not place call survey stations in areas identified as non-habitat. Each station was surveyed three times between June 15 and August

31, 2009. Survey visits involved playing recorded barred owl eight-note hoot calls and agitated calls using an amplified animal calling device (Foxpro FX3, Foxpro Inc., Lewiston PA). Recorded calls were played at approximately one minute intervals for 20 minutes at all stations. Calling was not terminated early when a single barred owl or pair responded to ensure equal sampling effort at all stations. All owl responses to the recorded calls were documented.

To develop an empirical estimate of barred owl pair probability of occupancy, I used a single-species occupancy modeling approach to estimate barred owl pair probability of occupancy based on the habitat maps described in Chapter 3. I calculated the proportion of good or moderate barred owl habitat within 450 ha across the analysis area (using the *focalmean* function in ArcGIS). I evaluated a suite of single-season occupancy models based on this data (MacKenzie et al. 2006). Single-season occupancy models evaluate two model components using a multinomial likelihood approach: the probability of occupancy (Ψ), and the probability of detection (p). I used the proportion of good or moderate barred owl habitat within 450 ha of the call station as covariates to estimate Ψ. I used parameters for date (calculated as week with decimal values, centered on August 1) and time of day (hours before or after midnight) as covariates to estimate p. I used an information theoretic approach with model selection based on sample size corrected Akaike Information Criterion (AICc) to identify the best model using all combinations of the above covariates.

RESULTS

Barred owl pairs were detected at 17 of the 91 call survey stations (Table 5.C.1). Preliminary examination of habitat patterns around call survey stations showed no discernable difference in the amount of moderate barred owl habitat around sites with and without barred owl pair detections, and preliminary models incorporating the amount of moderate habitat either failed to converge or produced unreliable parameter estimates, so I included only the amount of good habitat surrounding the site as the covariate in the occupancy model component for the final model selection (Table 5.C.2). Probability of detection components including the decimal week of the survey and including both week and time of the survey were both competitive (Table 5.C.2). The coefficient for time was very close to zero and the standard error of that coefficient was greater than the estimate, so I chose the model incorporating only week in the probability of detection component. Probability of occupancy increased rapidly with increasing amounts of good barred owl habitat surrounding the calling station (Table 5.C.3). Sites with 40% or more of the surrounding 450 ha identified as good barred owl habitat had high probability of occupancy (Figure 5.C.1).

Table 5.C.1. Summary of barred owl call survey results for 91 stations surveyed three times in 2009. The table indicates the number of stations within each habitat class where no barred owls (None), a single barred owl (Single), or a barred owl pair (Pair) were detected. Predicted habitat classes for stratifying the call survey effort were mapped based on the barred owl resource selection function from Singleton et al. (2010).

	Maximum Barred Owl Response:			Total
Habitat Class:	None	Single	Pair	Stations
Poor	29	4	1	34
Moderate	18	7	4	29
Good	6	10	12	28
Grand Total	53	21	17	91

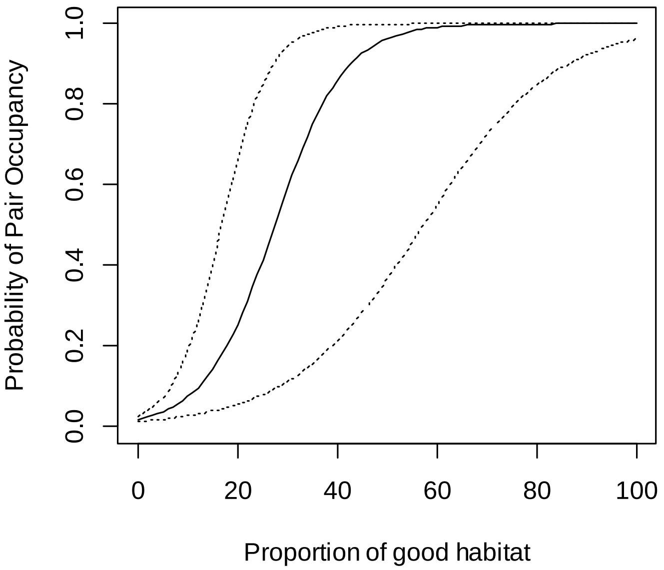
Table 5.C.2. Barred owl pair occupancy AICc model selection table. Single-season occupancy models include model components for probability of detection (*p*) and probability of occupancy (*Ψ*). The table indicates the model formula, number of parameters (K), AICc score, AICc model weight (AICcWt), cumulative model weight (CumWt), and log-likelihood (LL) for each model.

Formula	K	AICc	ΔAICc	AICcWt	CumWt	LL
p(week),*Ψ*(good)	4	123.76	0.00	0.69	0.69	-57.65
p(week+time),*Ψ*(good)	5	125.37	1.61	0.31	1.00	-57.33
p(time),*Ψ*(good)	4	136.16	12.40	0.00	1.00	-63.85
p(1),*Ψ*(1) – Null model	2	140.77	17.00	0.00	1.00	-68.32

Table 5.C.3. Parameter estimates for the best barred owl pair occupancy model. Parameters included in this model were the amount of good barred owl habitat within a 450 ha circular area (Good) in the probability of occupancy model component (*Ψ*) and an index of the date of the survey represented as the decimal week, centered on August 1 (Week) in the probability of detection model component (*p*). The table indicates the model component, the parameter, the coefficient estimate, the standard error of the estimate, and the p-value for the estimate (P).

Component	Parameter	Estimate	SE	P
Ψ	(Intercept)	-3.97	2.08	0.06
Ψ	Good	14.47	6.93	0.04
p	(Intercept)	-2.538	0.36	<0.01
p	Week	0.424	0.13	<0.01

Figure 5.C.1. Probability of occupancy by barred owl pairs based on the proportion of good barred owl habitat within a 450 ha circular area. The solid line indicates the model estimate. The dashed lines indicate the estimate plus or minus one standard error.



APPENDIX 5.D: VITAL RATE SETTINGS FOR POPULATION MODEL EXPERIMENTS.

This appendix presents vital rate settings used for HexSim population simulation model experiments (Table 5.1).

Table 5.D.1. Barred owl survival rate settings for HexSim population simulation model experiments.

Normative Settings: D_Norm
(spotted owl minus 10%)

	Stage			
Resources	0	1	2	3
Low	0.338	0.572	0.664	0.700
Mod	0.450	0.715	0.738	0.737
High	0.563	0.786	0.812	0.811

High Barred Owl Survival Settings: D_SVH
(D_Norm plus 10%)

	Stage			
Resources	0	1	2	3
Low	0.375	0.635	0.738	0.778
Mod	0.500	0.794	0.820	0.819
High	0.625	0.873	0.902	0.901

Low Barred Owl Survival Settings: D_SVL
(D_Norm minus 10%)

	Stage			
Resources	0	1	2	3
Low	0.300	0.508	0.590	0.622
Mod	0.400	0.635	0.656	0.655
High	0.500	0.698	0.722	0.721

Table 5.D.2. Barred owl fecundity rate settings for HexSim population simulation model experiments.

Normative Settings: D_Norm
(1.5 times spotted owl rate, with potential clutch size = 3)

	No. Young				
Stage	0	1	2	3	Expected
0	1.000	0.000	0.000	0.000	0.000
1	0.914	0.029	0.029	0.029	0.173
2	0.612	0.129	0.129	0.129	0.776
3	0.585	0.138	0.138	0.138	0.830

Low Barred Owl Reproduction Settings: D_RPL
(D_Norm minus 15%)

	No. Young				
Stage	0	1	2	3	Expected
0	1.000	0.000	0.000	0.000	0.000
1	0.927	0.024	0.024	0.024	0.147
2	0.670	0.110	0.110	0.110	0.659
3	0.647	0.118	0.118	0.118	0.705

High Barred Owl Reproduction Settings: D_RPH
(D_Norm plus 15%)

	No. Young				
Stage	0	1	2	3	Expected
0	1.000	0.000	0.000	0.000	0.000
1	0.901	0.033	0.033	0.033	0.198
2	0.554	0.149	0.149	0.149	0.892
3	0.523	0.159	0.159	0.159	0.954