Competitive Interactions and Resource Partitioning Between Northern Spotted Owls and Barred Owls in Western Oregon

by
J. David Wiens

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APPROVED:

Major Professor, representing Wildlife Science

Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

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J. David Wiens, Author

AN ABSTRACT OF THE DISSERTATION OF

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The federally threatened northern spotted owl (*Strix occidentalis caurina*) is the focus of intensive conservation efforts that have led to much forested land being reserved as habitat for the owl and associated wildlife species throughout the Pacific Northwest of the United States. Recently, however, a relatively new threat to spotted owls has emerged in the form of an invasive competitor: the congeneric barred owl (*Strix varia*). As barred owls have rapidly expanded their populations into the entire range of the northern spotted owl, mounting evidence indicates that they are displacing, hybridizing with, and even killing spotted owls. The barred owl invasion into western North America has made an already complex conservation issue even more contentious, and a lack of information on the ecological relationships between the 2 species has hampered conservation efforts. During 2007–2009 I investigated spatial relationships, habitat selection, diets, survival, and reproduction of sympatric spotted owls and barred owls in western Oregon, USA. My overall objective was to determine the potential for and possible consequences of competition for space, habitat, and food between the 2 species. My study included 29 spotted owls and 28 barred owls that were radio-marked in 36 neighboring territories and monitored over a 24-month tracking period.

Based on repeated surveys of both species, the number of territories occupied by pairs of barred owls in the 745 km^2 study area (82) greatly outnumbered those occupied

by pairs of spotted owls (15). Estimates of mean size of home-ranges and core-use areas of spotted owls (1,843 ha and 305 ha, respectively) were 2–4 times larger than those of barred owls (581 ha and 188 ha, respectively). Individual spotted and barred owls in adjacent territories often had overlapping home ranges, but inter-specific space sharing was largely restricted to broader foraging areas in the home range with minimal spatial overlap among core-use areas.

I used an information-theoretic approach to rank discrete choice models representing alternative hypotheses about the influence of forest conditions and interspecific interactions on species-specific patterns of nighttime habitat selection. Spotted owls spent a disproportionate amount of time foraging on steep slopes in ravines dominated by old (>120 yrs old) conifer trees. Barred owls used available forest types more evenly than spotted owls, and were most strongly associated with patches of large hardwood and conifer trees that occupied relatively flat areas along streams. Spotted and barred owls differed in the relative use of old conifer forest (higher for spotted owls) and slope conditions (steeper slopes for spotted owls). I found no evidence that the 2 species differed in their use of young, mature, and riparian-hardwood forest types, and both species avoided forest-nonforest edges. The best resource selection function for spotted owls indicated that the relative probability of a location being selected was reduced if the location was within or in close proximity to a core-use area of a barred owl.

I used pellet analysis and measures of food niche overlap to examine the potential for dietary competition between spatially associated pairs of spotted owls and barred owls. I identified 1,223 prey items from 15 territories occupied by pairs of spotted owls and 4,299 prey items from 24 territories occupied by pairs of barred owls. Diets of both species were dominated by nocturnal mammals, but diets of barred owls included many terrestrial, aquatic, and diurnal prey species that were rare or absent in diets of spotted owls. Northern flying squirrels (*Glaucomys sabrinus*), woodrats (*Neotoma fuscipes, N. cinerea*), and lagomorphs (*Lepus americanus, Sylvilagus bachmani*) were particularly important prey for both owl species, accounting for 81% and 49% of total dietary

biomass for spotted owls and barred owls, respectively. Dietary overlap between pairs of spotted and barred owls in adjacent territories ranged from 28–70% (mean = 42%)

In addition to overlap in resource use, I also identified strong associations between the presence of barred owls and the behavior of spotted owls, as shown by changes in space-use, habitat selection, and reproductive output of spotted owls exposed to different levels of spatial overlap with barred owls in adjacent territories. Barred owls in my study area displayed both numeric and demographic superiority over spotted owls; the annual survival probability of radio-marked spotted owls from known-fate analyses (0.81, SE = 0.05) was lower than that of barred owls (0.92, SE = 0.04), and barred owls produced over 6 times as many young over a 3-year period as spotted owls. Survival of both species was positively associated with an increasing proportion of old (>120 yrs old) conifer forest within the home range, which suggested that availability of old forest was a potential limiting factor in the competitive relationship between the 2 species. When viewed collectively, my results support the hypothesis that interference competition with a high density of barred owls for territorial space can act to constrain the availability of critical resources required for successful recruitment and reproduction of spotted owls. My findings have broad implications for the conservation of spotted owls, as they suggest that spatial heterogeneity in survival and reproduction may arise not only because of differences among territories in the quality of forest habitat, but also because of the spatial distribution of an invasive competitor.

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This research was approved by the Institutional Animal Care and Use Committee at Oregon State University (Study No. 3516). Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Competitive Interactions and Resource Partitioning Between Northern Spotted Owls and Barred Owls in Western Oregon

INTRODUCTION

Two species cannot permanently coexist unless they are doing things differently. In his classic work on *Paramecium*, Gause (1934) proposed what later became known as the 'competitive exclusion principle', one of ecology's few guiding principles. Inspired in part by the work of Gause and others (Lotka 1932, Volterra 1926), the study of interspecific competition has since become one of ecology's most central pursuits (MacArthur and Levins 1967, Schoener 1982, Connell 1983, Keddy 2001, Dhondt 2011). Interspecific competition has been defined as "an interaction between members of 2 or more species that, as a consequence of either exploitation of a shared resource or of interference related to that resource, has a negative effect on fitness-related characteristics of at least one species" (Wiens 1989:7). This definition implies that (1) a resource must be limited in supply for competition to occur, and that (2) the effects of competition operate primarily at the individual level. As the effects of competition accumulate across individuals, however, they can eventually be translated to the population or metapopulation levels, leading to overall reductions in population growth rate of 1 or both species. Competition theory further predicts that the coexistence of ecologically similar species can be maintained by niche differentiation. In a classic example, MacArthur (1958) found that 5 closely related species of *Dendroica* warblers coexisted by foraging in different portions of trees in a coniferous forest. Although there was high overlap, each species spent the majority of its foraging time in a unique portion of the trees. In England, Lack (1971) found that niche segregation in coexisting *Parus* tits in broad-leaved woodlands was mediated by differences in body size and the size and shape of the birds' beaks. These slight differences in morphology translated to differences in the size of insect prey taken and the hardness of seeds used.

In contrast to these traditional examples of niche differentiation, the invasion of an ecosystem by an alien species poses a different kind of predicament because there may not have been sufficient evolutionary time for segregation in resource use to develop. In this scenario, competitive pressure intensifies as ecologically similar species become increasingly restricted to a common set of resources, leading to reduced fecundity or survival of 1 or more species. The widespread replacement of the native Eurasian red squirrel (*Sciurus vulgaris*) throughout the British Isles by the competitively dominant North American grey squirrel (*Sciurus carolinensis*) is a well-documented example of invasion by an alien species with the subsequent loss of a native species (Gurnell et al. 2004, Tompkins et al. 2003). In the Pacific Northwest of the United States, there is increasing concern that the recent range expansion and invasion of the barred owl (*Strix varia*) may represent this type of competitive threat to the northern spotted owl (*Strix occidentalis caurina*; Kelly et al. 2003, Gutiérrez et al. 2007, Buchanan et al. 2007, Anthony et al. 2006, Forsman et al. 2011).

Conservation efforts for the northern spotted owl began as early as early as 1973 in Oregon, but the sub-species was not listed federally as threatened until 1990 (Noon and McKelvey 1996). The original listing of the sub-species was based on the owl's strong association with old conifer forest and declining trends in both old-forest habitat and owl populations (USDI 1990). The conservation and management of spotted owls has since become one of the largest and most visible wildlife conservation issues in United States history (Noon and Franklin 2002). Management of spotted owls has been an incredibly complicated interagency effort that has led to much federal land being reserved as habitat for the owl and associated wildlife species in the Pacific Northwest of the United States (USDA Forest Service and USDI Bureau of Land Management 1994). Despite these efforts, spotted owl populations have continued to decline throughout much of the sub-species' range (Forsman et al. 2011). The most recent meta-analysis of demographic rates of spotted owls on 11 study areas indicated that several populations in Washington and northern Oregon had declined by 40–60% between 1985 and 2008, but populations on federal lands in southern Oregon and northern California were relatively stationary or only slightly declining (Forsman et al. 2011). These authors concluded that an increasing number of barred owls and loss of habitat were at least partially responsible for these declines, especially in areas of Washington and northern Oregon where barred owls had been present the longest.

The barred owl invasion into the Pacific Northwest has been well documented, and the newly extended range of this species now completely overlaps that of the northern spotted owl (Kelley et al. 2003, Livezey 2009). Evidence suggests that barred owls now outnumber spotted owls in British Columbia (Dunbar et al. 1991), the Washington Cascades (Pearson and Livezey 2003, Forsman et al. 2011), and western Oregon (Wiens et al. 2011), which are areas that were colonized sequentially by barred owls as they expanded their populations southward into the Pacific Northwest (Livezey 2009). Barred owls are similar to spotted owls both morphologically and ecologically, although barred owls are slightly larger (Gutiérrez et al. 2004, Appendix A), use smaller home ranges (Hamer et al. 2007, Singleton et al. 2010), have more diverse diets (Hamer et al. 2001), and use a wider range of forest conditions for nesting (Herter and Hicks 2000, Pearson and Livezey 2003, Livezey 2007). Barred owls also appear to defend their territories more aggressively than spotted owls (VanLinen et al. 2011), which, in the most extreme cases, may result in spotted owl mortality (Leskiw and Gutiérrez 1998). When viewed collectively, the behavioral and life history traits exhibited by barred owls may give them a significant advantage over spotted owls when competing for critical resources such as space, habitat, and food.

Central to any definition of interspecific competition is the requirement that it have a detrimental effect on the population characteristics of 1 or more species (Dhondt 2012). Evidence of a negative relationship between barred owl occurrence and population characteristics of spotted owls include: 1) a decline in occupancy rates of historic spotted owl territories where barred owls were detected (Kelly et al. 2003, Olson et al. 2005, Kroll et al. 2010, Dugger et al. 2011); 2) a negative relationship between the occurrence of barred owls and apparent survival of spotted owls (Anthony et al. 2006, Glenn et al. 2011a, Forsman et al. 2011); 3) a negative relationship between the presence of barred owls and fecundity of spotted owls (Olson et al. 2004, Forsman et al. 2011); and 4) declining rates of population change in portions of the spotted owl's range where barred owls have been present the longest (Anthony et al. 2006, Forsman et al. 2011). Despite this potential for interspecific competition, all aforementioned studies that reported a negative effect of barred owls on spotted owls were based on coarse-scale measures of barred owl occurrence from incidental detections during surveys of spotted owls. Barred owls may often go undetected in surveys of spotted owls, however (Bailey et al. 2009, Wiens et al. 2011), which could lead to inaccurate estimates of occurrence of barred owls and weak inferences regarding the magnitude, mechanisms, and possible outcome of competition. Moreover, it remains unclear how joint exploitation of resources or territorial displacement (or both) may actually translate to a negative effect on the survival and fecundity of spotted owls. Ultimately, the conservation of the spotted owl and its habitats may need to be extended from ameliorating the effects of habitat loss and fragmentation to account for the impacts of an invasive competitor as well (Peterson and Robins 2003, Dugger et al. 2011). The challenges associated with preserving spotted owl habitat while accounting for the potentially overriding effects of a widespread competitor are far reaching and complex. These uncertainties have led scientists and managers to conclude that a better understanding of the ecological relationships between the 2 species is needed to better inform future decisions regarding conservation and management of the northern spotted owl and its habitat (Buchanan et al. 2007, Forsman et al. 2011, USFWS 2011). Specific information on competitive relationships between the species including partitioning of space, habitat, and food resources will be particularly relevant in guiding future management decisions.

During 2007–2009 I conducted a comprehensive investigation of the ecological relationships between sympatric northern spotted owls and barred owls in the central Coast Ranges of western Oregon, USA. The overall objective of my study was to determine the potential for and possible consequences of competition for space, habitat, and food between these previously allopatric species. Using a combination of population surveys and radio-telemetry methods, I addressed 2 primary questions: 1) What is the degree of resource partitioning between spotted and barred owls in an area where the 2 species co-occur?; and 2) Does the presence of barred owls have the potential to influence the space-use, resource selection, and fitness characteristics of spatially associated spotted owls? I examined these questions by directly monitoring spatial relationships, habitat selection, diets, survival, and reproduction of sympatric spotted owls and barred owls. I predicted that if competition between the 2 species was occurring then: 1) spotted owls should broaden their level of space use or alter selection of shared habitats in response to an escalating likelihood of encountering territorial barred owls; 2) selection of preferred foraging habitats by spotted owls should be negatively associated with the presence of barred owls; and 3) fitness potential (i.e., survival and/or reproduction) of individuals should be negatively associated with increasing levels of exposure to competitors. Herein, I characterize resource use and overlap by northern spotted owls and barred owls and their relevance to these predictions.

STUDY AREA AND METHODS

Study Area

The 975 km^2 study area was located in the central Coast Ranges of western Oregon, USA (Fig. 2.1). This area included a mixed ownership of lands administered by the U.S. Bureau of Land Management (BLM, 48%), large timber companies (47%), Oregon Department of Forestry (ODF, 3%), and small private landowners (2%). I selected this area based on many considerations, including existing data on the locations of spotted owls, year-round access to owl sites, land ownership boundaries, and the locations of ongoing demographic studies of spotted owls (where owls could not be radio-marked). Throughout the study area, square-mile sections of federal or state owned lands alternated with sections of privately owned lands, which produced a checkerboard pattern of land ownership and forest structure (Richardson 1980). Divergent forest management practices among public and private ownerships had resulted in strong contrasts in forest conditions; federal and state lands contained more mature and old forests whereas private lands managed for timber production were dominated by young (<40 yrs old) even-aged forests and recent clear-cuts (Stanfield et al. 2002, Spies et al. 2007). Forests were dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). Mixed species stands of hardwoods, especially bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*), occupied many riparian areas and recently disturbed sites. Common understory herbs and shrubs included swordfern (*Polystichum munitum*), salal (*Gaultheria shallon*), vine maple (*Acer circinatum*), and Oregon-grape (*Berberis nervosa*). Approximately 38% of the study area included patches of mature (60–120 yrs old) or old-growth (>120 yrs old) conifer forest within a matrix of recent clear-cuts and young forests growing in old clear-cuts (Appendix Fig. B-3).

The study area was bounded on the north and south by 2 long-term spotted owl demographic study areas (Oregon Coast Ranges and Tyee; Forsman et al. 2011). Based on incidental detections of barred owls during annual surveys of spotted owls, Forsman et al. (2011:80) concluded that the relative abundance of barred owls in the Coast Ranges and Tyee study areas was low during the early 1990's, but that the proportion of spotted owl territories where barred owls were detected increased steadily to a high of approximately 70% in 2008. Previous mark-recapture studies in my study area during 1990–1995 indicated that non-juvenile spotted owls had relatively high and constant survival (87%), the mean number of young produced per pair varied extensively among years (range = 0.09–1.35), and the population was declining (lambda = 0.94; Thrailkill et al. 1998:18–27).

Data Collection

Owl Surveys

I conducted annual surveys of spotted owls and barred owls between 1 March and 1 September, 2007–2009. Each year I used a 2-stage survey protocol to locate both owl species and collect information on site occupancy and reproduction. In the first stage, I used a standardized survey protocol for locating and monitoring spotted owls (Lint et al. 1999) that included ≥3 nighttime surveys of areas extending 2.0–2.5 km out from historically occupied activity centers (i.e., a nest tree, observations of fledged young, or a pair of resident owls). Annual surveys were conducted on as many as 52 territories that were historically occupied by spotted owls. Surveys of spotted owls were conducted by a combination of biologists from Oregon State University, USDA Forest Service, BLM, or contractors hired by timber companies. In the second stage, I used barred owl calls to survey territories found to be occupied by spotted owls. This stage of my survey protocol helped increase the likelihood of detecting barred owls that were spatially associated with territorial spotted owls, and it typically included 1–3 nighttime surveys of an area extending 1.5–2.0 km out from a nest or roosting location used by ≥1 spotted owl. Further details on the survey protocols I used for each owl species are described elsewhere (Lint et al. 1999, USFWS 2009, Wiens et al. 2011).

Within the broader telemetry study area I established a smaller 745 km^2 study area that I systematically surveyed for barred owls in 2009. Repeated surveys of barred owls in this year resulted in a high probability of detection (96%) and provided a measure of the occupancy patterns, distribution, and spacing among territorial pairs of barred owls in the study area (Wiens et al. 2011). I was unable to survey the entire study area for spotted owls, but estimated that >80% of suitable spotted owl habitat was surveyed in each year. Moreover, because both owl species were responsive to broadcasts of heterospecific calls, I was confident that most territories occupied by spotted or barred owls were detected during the 3-yr study. Once owls were identified as residents and radio-marked, I excluded their territories from conspecific surveys but I continued to survey their territories for heterospecifics.

Radio Marking and Tracking

I attempted to capture and attach radio transmitters to all resident spotted owls located in the study area except for banded owls that were part of adjacent studies of demography (Anthony et al. 2006, Forsman et al. 2011). I captured spotted owls with noose poles following Forsman (1983). Once the location and residency status of single or paired spotted owls were confirmed, I attempted to capture and radio-mark all neighboring barred owls identified within a 2.0 km radius. To capture barred owls, I used an amplified megaphone (Wildlife Technologies, Manchester, NH) to broadcast conspecific calls and lure owls into dho-gaza mist nets baited with a stuffed barred owl decoy or live mouse (Bierregaard et al. 2008). All owls captured were fitted with a U. S. Geological Survey (USGS) aluminum leg band. I used a Teflon tubing harness to attach a 12.5 g (with harness) backpack-style radiotransmitter to each owl (Gutterman et al. 1991). Radiotransmitters were equipped with a mortality sensor and had a 24-month life expectancy (model R1-2C, Holohil Systems Ltd., Ontario, Canada). Total mass of radio transmitters represented 2.2% and 1.9% of mean body mass for male spotted owls and barred owls, respectively. I determined sex of owls based on their vocalizations, nesting behaviors, or measurements (Forsman 1983, Appendix A). Radio-marked owls were recaptured at the conclusion of the study to remove radio-transmitters. All field activities were performed in accordance with Oregon State University's Animal Care and Use Committee (Study No. 3516).

Radio-marked owls were monitored using directional 2- or 3-element Yagi antennas (Wildlife Materials, Inc., Carbondale, IL or Telonics, Inc., Mesa, AZ) and a portable receiver (model R-1000, Communication Specialists, Inc., Orange, California). I estimated nighttime locations of each individual owl ≥2 times weekly by taking bearings on the strongest signal received from ≥3 different locations spaced >200 m apart within the shortest time possible (≤20 min), as described by Carey et al. (1989) and Glenn et al. (2004). Signal bearings were entered on site into program LOCATE III (Nams 2006) to estimate a 95% confidence ellipse for the point location based on the standard deviation of bearing intercepts. If a 95% confidence ellipse was >2 ha or if the owl moved before ≥3 bearings were taken, the location was discarded and a new location was estimated later that night. I used a rotating monitoring schedule to track owls at randomly selected times between sunset and sunrise to ensure that estimated locations were representative of all nighttime activities. I also obtained visual observations of all owls at their daytime roosting locations at least once per week to collect pellets and measure roost-site characteristics. I classified locations as either nighttime foraging locations (collected from 0.5 hr after sunset to 0.5 hr before sunrise) or daytime roosting locations, but these classes included a broad range of behaviors beyond just foraging and roosting. Each time I obtained locations of owls in one territory I attempted to locate all radio-marked owls in adjacent territories. In most situations I was able to relocate spotted and barred owl pairs occupying adjacent territories (4 individuals) within a total span of 1.0–1.5 hrs. My goal was to collect ≥50 locations per owl each season or 6-mo interval.

The extensive road system and high ridges in the study area allowed me to estimate most locations from within 250 m of radio-marked owls, which helped reduce error associated with locations estimated by triangulation (White and Garrot 1990). I estimated the accuracy of the telemetry system by placing radiotransmitters at random locations and heights (1–15 m above ground) within owl home ranges and having naïve observers locate them at night. Median linear measurement error between estimated and actual transmitter locations was 78 m (mean = 145 m, SE = 30.7 m, *n* = 32), which was comparable to error estimates in previous telemetry studies of spotted owls (range = 68–164 m; Carey et al. 1992, Zabel et al. 1995, Glenn et al. 2004, Forsman et al. 2005). I used the 95% confidence ellipse estimated for each location in LOCATE III as a measure of precision of the telemetry system. Median size of the 95% confidence ellipse for triangulated locations was 0.63 ha (mean = 0.74 ha, SD = 0.63 ha), and 99.5% of all nighttime foraging locations for both species had a confidence ellipse ≤2 ha.

Quantifying Habitat Conditions

Semantic and empirical distinctions between the terms *habitat*, *habitat use*, and *habitat selection* are often unclear (Block and Brennan 1993, Hall et al. 1997). Similar to Hall et al. (1997), I defined *habitat* as a distinctive set of resources and conditions present in an area that produce occupancy – including survival and reproduction – by spotted owls or barred owls. I referred to *habitat use* as the way in which an owl uses a collection of physical and biological resources within a defined area and time, and *habitat selection* as a hierarchical, nonrandom process involving innate and learned decisions made at different geographic scales leading to occupancy or use of a particular location (Hall et al. 1997, Manly et al. 2002). To quantify important environmental conditions used for foraging and roosting by each owl species, I compiled a series of digital maps of primary forest types and physiographic conditions in ArcGIS (version 9.3.1). The spatial extent of my maps was based on the cumulative movements of radio-marked owls (Fig. 2.1). Within this area I identified 5 general forest structural types: old conifer (>120 yrs old); mature conifer (60–120 yrs old); young conifer (<60 yrs old); riparian/hardwood forest, and nonforest (Table 2.1). Based on previous studies of habitat selection by spotted owls (Carey et al. 1992, Glenn et al. 2004, Irwin et al. 2007, 2011) and barred owls (Hamer et al. 2007, Livezey 2007, Singleton et al. 2010), I identified an additional 9 environmental covariates to include in my assessment (Table 2.1). These variables represented forest structural characteristics, physiographic conditions, and interspecific influences that were predicted to be important determinants of space-use, resource selection, and survival.

Satellite maps of forest vegetation in my study area (e.g., Ohmann and Gregory 2002) contained useful forest structural information but did not have appropriate spatial resolution to depict landscape features (e.g., stand edges) which were predicted to be important to owls and their prey. As a consequence, I developed a new map of forest types and boundaries from high-resolution (1-m) natural color orthophotographs of the study area (United States Department of Agriculture, National Agricultural Imagery Program [NAIP], Salt Lake City, Utah 2009). Specifically, I used object-based classification techniques in ENVI EX image analysis software (version 4.8, ITT Visual Information Solutions, 2009) to derive patch-scale maps of the 5 primary forest types described above. This process allowed me to segment the NAIP imagery into clusters of similar neighboring pixels (i.e., objects) and then classify each cluster according to its spatial, spectral, and textural attributes (Hay et al. 2005, Cleve et al. 2008, Blaschke 2010). Thus, contiguous stands of trees with similar size and age (i.e., patches) were represented as polygons with boundaries that matched forest edges shown by the orthorectified imagery (e.g., Appendix Fig. B-2). My minimum mapping unit was 0.5 ha, and mean patch size of the final 2009 vegetation map was 14.0 ha (SD = 41.1 ha, n = 7,091 patches). Overall accuracy of the vegetation map was 82% based on ground sampling of vegetation conditions at 141 random test plots (Appendix B). The greatest source of mapping error was in distinguishing between young and mature forest types, with mature forest being misclassified as young in 9 (38%) of 24 test plots (Table B-1). Based on these results, I concluded that the mean accuracy of triangulated telemetry locations (0.63 ha) was sufficient to assign locations to polygons with minimal error.

The vegetation map I developed provided a broad-scale representation of the spatial distribution of different forest types, but it lacked many of the fine-scale structures associated with forest patches that could be important to owls and their prey. To account for this I quantified the structural conditions of individual patches using data obtained from a map of forest vegetation that was developed using a gradient nearest neighbor (GNN) method by Ohmann and Gregory (2002). Specifically, I estimated density (no. trees ha^{-1}) of large (>50 cm dbh) confers, quadratic mean diameter of conifers, basal area of hardwoods, and canopy cover of hardwoods using the mean of 30×30 m GNN pixel values contained within each patch of my forest vegetation map. I was unable to verify forest structural covariates derived from GNN maps directly, but local-scale accuracies for these variables showed that predicted values correlated well with observed plot measurements (range of correlation coefficients = 0.53–0.71; LEMMA 2009). The GNN map was based on satellite imagery from 2006 whereas my forest cover map was based on imagery from 2009. To account for this mismatch I obtained time-specific data on timber harvests and used this information to add or subtract vegetation in the base map.

Owl Diets

I determined composition, diversity, and overlap of spotted owl and barred owl diets from regurgitated pellets collected at nesting areas and below roost sites used by radio-marked and unmarked owls in the study area. Pellets were collected from both species by: 1) tracking radio-marked owls to their roost sites and searching the ground below their roosts; 2) regularly searching areas of concentrated use by radio-marked owls; 3) searching areas immediately surrounding occupied nests; and 4) climbing nest trees to collect pellets ejected by young inside the nest cavity. To avoid double counting larger prey that appeared in >1 pellet, I combined remains from multiple pellets found at the same roost on the same date into a single sample and did the same for nest tree collections. All pellet collections were bagged, labeled (date, location, observer), and dried for later identification of prey remains. During the nonbreeding season (September–February), searches for pellets were limited to roosts of radio-marked owls because I could not be certain that pellets collected in other areas belonged to the focal owl species. Moreover, both owl species tended to roost higher in the tree canopy during winter as compared to summer, which made pellets more difficult to find during winter because they would often get stuck in the tree or break apart before reaching the ground. As a consequence, most prey remains identified in pellets of spotted owls (95%) or barred owls (94%) were from the breeding season.

Monitoring Survival and Reproduction

I recorded the fate (live or dead) of radio-marked owls by monitoring transmitter signals 2–4 times per week. Individuals that made long-distance movements in winter were generally relocated in <1 wk during expanded searches from the ground, so there were few time periods in which an owl's fate was unknown. If a transmitter signal indicated a mortality event, the carcass or remains of the owl were recovered to determine the cause of death, usually within 24 hrs. Carcasses recovered intact were submitted to the Veterinary Diagnostic Lab at Oregon State University, Corvallis, Oregon for necropsy and histopathology analysis. I estimated reproductive parameters for all spotted owls in the study area following the methods described in Lint et al. (1999). This protocol takes advantage of the fact that spotted owls are relatively unafraid of humans and will readily take live mice from observers and carry mice to their nest or fledged young (Forsman et al. 2011). Barred owls, however, did not readily take mice from observers so the standard protocol for determining nesting status and number of young fledged for spotted owls was largely ineffective for barred owls. As a consequence, I obtained nesting information on barred owls by tracking radio-marked females to their nest trees or by repeatedly locating pairs of unmarked owls during the breeding season to determine nest locations and count the number of young that left the nest. This ensured that all territories included in estimates of nesting success and productivity were regularly monitored between egg-laying (1 March) and juvenile dispersal (31 August) of each year.

Data Analysis

Spatial Relationships

Spacing and distribution of owl pairs. – I made a preliminary assessment of both interspecific and intraspecific territoriality among spotted and barred owls by calculating first-order nearest-neighbor distances between activity centers of all owl pairs identified during the 2009 breeding season, when survey coverage was most complete. Nearest neighbor distances are a commonly used measure of territoriality in raptors (Newton et al. 1977, Katzner et al. 2003, Carrete et al. 2006). I defined activity centers for resident pairs of spotted or barred owls based on the best available records for a given year, including: 1) an active nest (eggs laid); 2) the mean center of roosting locations acquired from radio-marked owls during the breeding season; 3) location of fledged young; or 4) the mean center of repeated diurnal or nocturnal survey detections of owls classified as residents (Lint et al. 1999, Forsman et al. 2011).

Space use and seasonal movements. – I defined a home range as the area regularly traversed by an individual owl during its daily activities, and I calculated home ranges over seasonal (6-mo) and annual (12-mo) time frames. Seasonal estimates were based on 2 phenological periods: the breeding season (1 March–31 August) when owls nested and fed young, and the nonbreeding season (1 September–28 February) when owls were not engaged in breeding activities. I used the *kernelUD* function in R version 2.10.1 (R Development Core Team 2010, Calenge 2006) to calculate 95% fixed-kernel home range areas (Worton 1989) for seasonal and annual time periods. Fixed-kernel home ranges represented the area, or group of areas, encompassing 95% of the probability distribution for each individual owl. I did not calculate home ranges for owls with <28 locations per season due to instability of kernel estimates with small sample sizes (Seaman et al. 1999). I used Animal Space Use 1.3 (Horne and Garton 2009) to estimate a smoothing parameter for each fixed-kernel home range using likelihood cross-validation (CV*h*; Silverman 1986, Horne and Garton 2006). I used CV*h* to estimate the smoothing parameter because simulation studies have shown that this method outperforms the more commonly used least-squares cross validation (LSCV) and produces a better fit with less variability among estimates, especially with sample sizes ≤50 (Horne and Garton 2006). Moreover, I found that home ranges estimated using LSCV tended to over-fit the data, which produced highly fragmented, discontinuous home ranges that excluded important areas (e.g., young forest or openings) that were commonly traversed, but not necessarily used by owls as they moved among discrete patches of their preferred forest types. Thus, despite the widespread use of LSCV in previous home-range studies of spotted owls, fixed-kernel estimates based on LSCV failed to satisfy my definition of a home range, whereas estimates based on CV*h* did. I also calculated 100% minimum convex polygon home ranges (MCP) using Home Range Tools for ArcGIS (Rodgers et al. 2007). The MCP method suffers from a variety of shortcomings (White and Garrott 1990, Laver and Kelly 2008), but this was the only home range estimator that has been consistently used in many previous studies of spotted and barred owls. Consequently, I relied on MCP home ranges for comparative purposes only but considered the 95% fixed-kernel smoothed with CV*h* to be the most biologically realistic approximation of each owl's space-use patterns.

I used linear mixed-models (PROC MIXED; SAS Institute, Cary, NC) to evaluate the relative importance of different biological and environmental covariates on annual movements of radio-marked owls (i.e., size of the 95% fixed-kernel home range). I treated individual owls nested within species as a repeated effect and species, sex, year, current year's nesting status, and forest composition variables as fixed effects. Prior to the modeling process, I used a separate fixed-effects analysis of variance to compare the size of home ranges between sexes and seasons for each species. My analysis was based on a set of *a priori* models containing combinations of biologically relevant covariates that were hypothesized to explain species-specific variation in annual home range size. Of particular interest were models used to examine the prediction that individual spotted owls or barred owls may alter their space-use patterns in response to an escalating likelihood of encountering the other species within their home range. To examine this prediction, I included the probability of heterospecific presence within the home range (see below) as a covariate to home range size and investigated how this effect varied between species and with habitat composition by comparing results from models with additive versus interactive effects. Alternatively, annual home range size of spotted or barred owls may be associated with the landscape distribution of preferred forest types used for foraging (Glenn et al. 2004, Forsman et al. 2005, Hamer et al. 2007). To explore this prediction I used Patch Analyst for ArcGIS (v0.9.5, Elkie et al. 1999) to estimate proportions of old conifer and riparian-hardwood forest within each owl's home range. For this analysis I also combined old and mature forest types into a single category of older forest (i.e., conifer forest >60 yrs old) to see if the combined cover of these 2 forest types influenced space-use. I used the second-order Aikaike's Information Criterion (AIC_c) to rank candidate models (Burnham and Anderson 2002), and I evaluated the degree to which 95% confidence intervals of regression coefficients (β) overlapped 0 to determine the direction, precision, and strength of covariate effects.

I estimated areas of concentrated use during the breeding season (core-use areas) for individual owls that exhibited a nonrandom pattern of space-use within their home range. I defined the core-use area as the portion of the breeding season home range in which use exceeded that expected under a null model of a uniform distribution of space-use (Bingham and Noon 1997, Powell 2000, Vander Wal and Rodgers 2012). I estimated core-use areas using Animal Space Use for ArcGIS (Horne and Garton 2007, Carpenter 2009). Core-use areas only provide a fraction of the resources required for reproduction and survival, but these areas typically contain unique structures and resources required for nesting, roosting, and provisioning young (Bingham and Noon 1997, Glenn et al. 2004). Hence, I assumed that core-use areas represented the portion of the home range that was likely to be the most heavily defended from conspecifics. In cases where both male and female members of a pair were monitored, I estimated the pair's breeding home range or core-use area as the union (total area) of female and male estimates (Bingham and Noon 1997, Forsman et al. 2005).

Measures of spatial overlap and space-use sharing. – I estimated the extent of spatial segregation and space-use sharing among radio-marked owls during annual, breeding, and nonbreeding time frames using 3 complementary overlap statistics: amount of home range overlap (*HR*), probability of spatial overlap (*PHR*), and the utilization distribution overlap index (UDOI; Fieberg and Kochanny 2005). Each measure was estimated at 2 levels of use intensity within the fixed-kernel home range (95% and 50% utilization contours). I used these measures as indicators of the extent and magnitude of space-use sharing among individual owls as well as their interaction potential. Following the notation of Kernohan et al. (2001), the proportion of owl i's home range that was overlapped by owl j's home range was calculated as $HR_{i,j} = A_{i,j} / A_i$, where A_i is the area of owl i's home range and $A_{i,j}$ is the area of overlap between the 2 owls' home ranges. I used estimates of HR to delineate the region of spatial overlap between 2 owls, but this measure did not account for the gradient in use intensity within home ranges (i.e., the utilization distribution [UD]). Thus, to provide a more accurate measure of spatial overlap that considered each owl's UD, I calculated the probability of owl j being present in owl i's home range as:

$$PHR_{i,j} = \iint\limits_{A_i} \widehat{\mathrm{UD}}_j(x,y)dxdy$$

where $\widehat{UD}_j\ (x, y)$ was the estimated value of the utilization distribution of owl j at location x, y. Estimates of PHR provided an easily interpretable, directional measure of spatial overlap that accounted for differences between individuals in the probability of use within the region of home-range overlap. Estimates of HR and PHR were directional in that they resulted in 2 values for each dyad combination (i.e., overlap of owl j on owl i's home range and overlap of owl i on owl j's home range). Thus, to quantify the level of joint space-use sharing among individual radio-marked owls and provide a symmetrical measure of space-use sharing, I calculated the utilization distribution overlap index (UDOI) described by Fieberg and Kochanny (2005):

$$\mathrm{UDOI} = A_{i,j} \iint\limits_{x,y} \widehat{\mathrm{UD}}_i(x,y) \times \widehat{\mathrm{UD}}_j\ (x,y)$$

The UDOI is a function of the product of the utilization distributions of 2 owls integrated over the spatial domain of the home range estimates and measures of the amount of spatial overlap relative to 2 individuals using the same space uniformly. Measures of UDOI range from 0 (no overlap) to 1 (complete overlap) except in cases where the 2 UDs are non-uniformily distributed and have an unusually high degree of overlap, in which case UDOI is >1. The UDOI is non-directional in that it provides a single measure of space sharing within the overlap region. High intensity use of the same area by 2 owls will result in high UDOI values. Thus, I considered the UDOI to be a good indicator of interaction potential between owls. All measures of spatial overlap were based on the assumption that the fixed-kernel UD smoothed with CV*h* was an accurate and precise estimate of each owl's space-use patterns. I used the *kerneloverlap* function for R (R Development Core Team 2010, Calenge 2006) to calculate values of *HR*, *PHR*, and UDOI for all intra-specific (paired owls, conspecific neighbors) and inter-specific (heterospecific neighbors) pairwise combinations. A mean overlap value was calculated for directional measures of overlap by using all possible dyad combinations.

Habitat Selection

I evaluated habitat selection by spotted owls and barred owls at 2 spatial scales corresponding to Johnson's (1980) second- and third-orders of selection and Block and Brennan's (1993) recommended spatial scales for avian habitat analyses. These 2 spatial scales reflected an owl's selection of forest patches within the study area (second order landscape-scale selection) and selection of patches within the home range (third order home-range scale selection), respectively. I evaluated habitat selection at both scales, but recognized that the territory or home range was the scale at which interspecific interactions were most likely to influence one or both species. Accordingly, I described general habitat characteristics used for foraging and roosting at the landscape scale and developed more detailed, species-specific resource selection functions (RSF) to explore how environmental conditions and the presence of a potential competitor may influence each owl's selection of foraging locations within the home range (third-order selection).

At the landscape scale, I compared patterns of resource selection by each species using univariate selection ratios ($\hat{w}_i$) and Bonferroni 95% confidence intervals calculated with the *widesII* function in R (R Development Core Team 2010, Calenge 2006). In this analysis I compared foraging or roosting locations of each owl (used) to 11,974 random points drawn from the analysis region (available) with a type II study design (sampling protocol A; Thomas and Taylor 1990, Manly et al. 2002). Thus, use of resources was uniquely measured for each owl but availability was measured at the population (landscape) level. Following Manly et al. (2002:65–67), I calculated selection ratios for each owl as:

$$\widehat{w}_i = {}^{o_i}/_{\pi_i}$$

where $\widehat{w}_i$ is the selection ratio for a given resource category *i*, expressed as the ratio of the sample proportion of used locations, o_i, to the sample proportion of available locations, π_i. A mean selection ratio with a confidence interval >1 indicated positive selection for a particular resource category, and a mean and confidence interval <1 indicated avoidance. I calculated selection ratios for each activity period (daytime, nighttime) using covariates for forest type, distance to edge, distance to stream, and interspecific proximity (Table 2.1). I used the Jenks natural breaks method (Jenks 1967) in ArcGIS to divide continuous variables into classes for categorical univariate analyses and plotted overlap of 95% Bonferroni confidence intervals to identify important differences in $\widehat{w}_i$ between species and activity periods. I used selection ratios with Pianka's (1973) measure of niche overlap to approximate the level of similarity among neighboring spotted owls and barred owls in their proportional use of different forest types for foraging. This symmetric index ranges from 0 (no overlap) to 1 (complete overlap) and was calculated for each radio-marked spotted owl and the nearest barred owl with sufficient data (>30 nighttime locations). High index values indicated that proportional use of different forest types by neighboring heterospecific individuals was similar. I then calculated the average pairwise overlap among neighboring spotted and barred owls to obtain an overall mean estimate.

At the home-range scale, I developed an RSF of nighttime habitat selection for each species using the discrete-choice model (Cooper and Millspaugh 1999, Manly et al.

2002, McDonald et al. 2006). Similar to logistic regression analysis, discrete-choice methods assume that animals make a series of selections from finite sets of available resources. Discrete-choice differs from other types of resource selection analyses in that: 1) the composition of choice sets may vary among choices, and 2) they estimate the relative probability of a single resource unit being selected during 1 choice rather than across multiple choices (McDonald et al. 2006). These properties of the model allowed me to account for changes in habitat conditions (e.g., timber harvests, presence of competitors) that occurred within many of the owl's home ranges during the study. The discrete-choice RSF has been applied in several previous studies of resource selection by spotted owls (McDonald et al. 2006, Irwin et al. 2007, 2011). Similar to these studies, I developed a choice set for each owl based on the collection of used and available resources measured within the 95% fixed-kernel home range. This was analogous to a type III study design in which I compared nighttime foraging locations to 4 times as many random points within the home range (Manly et al. 2002). I developed a new choice set for each owl that was monitored >1 yr to accommodate annual changes in space-use, resource availability, and location of potential competitors. I estimated log-likelihood values and parameter coefficients using a stratified Cox proportional hazards function in SAS 9.3 (PROC PHREG), which uses the same multinomial logit likelihood function as the with-replacement discrete choice model (Manly et al. 2002:208). I calculated selection ratios from model coefficients (selection ratio = exp[coefficient]) to measure the multiplicative change in the relative probability of selection when a covariate changed by 1 unit, assuming all other variables remain constant (McDonald et al 2006, Irwin et al. 2011). I originally modeled sexes separately because of a high level of home-range overlap between paired males and females. However, initial results from sex-specific analyses differed little from an analysis in which sexes were combined, so I report results from the latter method.

I used an information-theoretic approach (Burnham and Anderson 2002) to evaluate candidate models representing alternative hypotheses about the influence of environmental conditions and interspecific interactions on each species' patterns of resource selection (Appendix C). I used AIC values to rank models, and I evaluated the degree to which 95% confidence intervals for regression coefficients (β) overlapped 0 to determine the direction, precision, and strength of covariate effects. Prior to the modeling process I used a Pearson correlation matrix to screen habitat covariates for evidence of co-linearity, and I discarded models with highly correlated ($r > 0.5$) variables. I then fit a base RSF for each species using forest type, forest structure, and abiotic covariates (Table 2.1). Once a final base model was attained for each species, I used ΔAIC values to determine whether the addition of covariates related to heterospecific presence improved model fit, and hence whether heterospecifics affected resource selection. The covariates representing heterospecific presence were: 1) distance to the nearest heterospecific core-use area; and 2) a binary variable for locations inside or outside of a heterospecific core-use area (Table 2.1). Based on mean estimates from radio-marked owls, I used 620 m and 800 m radius circles centered on year-specific activity centers to represent areas of concentrated use by unmarked pairs of barred owls and spotted owls, respectively. Under a hypothesis of interspecific territoriality (Dohnt 2011), I predicted that: 1) owls would select sites more distant from a heterospecific core-use areas than expected by chance; and 2) owls would use areas more distant from their preferred forest types when heterospecifics were present (Appendix C).

In addition to modeling resource selection for each owl species separately, I also wanted to identify differences between the species in use of specific resource components and to quantify the uncertainty associated with those differences. To do this I pooled the data from both species and fit an additional 4 discrete-choice models that included the interactive effects of 'species' with environmental covariates from the best base RSF models developed for each species. Better support of models including interactive effects relative to models without interaction terms provided evidence for differential resource selection. As in previous analyses, I used AIC to rank competing models.

Dietary Analysis

Prey remains from owl pellets were identified using dichotomous keys and a reference collection of bird and mammal skeletons at the U.S. Forest Service Pacific Northwest Research Station, Corvallis, Oregon. Remains that could not be identified to species were identified to the lowest taxon possible. I quantified dietary composition using standard measures of relative frequency and biomass (Ganey and Block 2005, Marti et al. 2007). The frequency of vertebrate prey items in diets was estimated by counting skulls, mandibles, or bones of the appendicular skeleton, whichever gave the highest count (Hamer et al. 2001, Forsman et al. 2001, 2004). For non-vertebrates I estimated numbers based on fragments of the exoskeleton or shells following Graham (2012). I used owl territories as the primary sampling unit in dietary analyses to avoid biases associated with an unequal number of prey remains collected for different owl pairs and to allow estimation of the amount of dietary variation among territories (Seamans and Gutiérrez 1999, Forsman et al. 2004). Thus, I characterized dietary composition for each species by computing the percent of prey numbers and percent of prey biomass in samples from each territory and then averaging among territories. Mean estimates of dietary composition were based on territories with >20 prey items.

I subdivided diets into 30 prey types for comparisons of dietary composition between spotted and barred owls. These categories were based on those described for spotted owls in Oregon by Forsman et al. (2004) in addition to prey types that contributed >2% of total prey numbers to diets of barred owls. I estimated the percent composition of prey identified in pellets from each territory by dividing the estimated number of individuals of each prey species by the total number of prey in the sample and multiplying by 100. To estimate the percent of total biomass for each prey species in the diet of each territory, I divided the estimated total biomass of each species by the total biomass in the sample and multiplied by 100. To do this I first had to estimate the total biomass of each prey species in the diet. I used 2 different methods to do this, depending on the type of prey. For smaller prey (e.g., insects, shrews, mice, voles), I multiplied the estimated number of individuals of each species by the estimated mean mass of each species. Estimates of mean mass were obtained from a variety of sources, including Dunning (1993) for birds and Verts and Carraway (1998) for most mammals. For larger mammals and birds such as northern flying squirrels (*Glaucomys sabrinus*), snowshoe hare (*Lepus americanus*), brush rabbits (*Sylvilagus bachmani*), woodrats (*Neotoma* spp.), mountain beaver (*Aplodontia rufa*), and grouse (*Bonasa umbellus*), I estimated mass of each individual based on comparisons of bones from specimens of known mass in the reference collection. I then summed the individual estimates to get the total for each species. Mean mass of signal crayfish (*Pacifastacus leniusculus*) was estimated from samples of locally collected specimens (Graham 2012). To further evaluate potential differences in the timing and location of foraging by spotted and barred owls, I grouped prey species by their primary period of activity (nocturnal, diurnal, or both) and primary zone of activity (aerial, arboreal, semi-arboreal, terrestrial, or aquatic). Behavioral attributes of prey were based on information in Verts and Carraway (1998), Hamer et al. (2001), and Forsman et al. (2004). I used a contingency test of independence to evaluate differences between species in the average percentage of prey biomass captured in different prey categories among territories.

I used 3 standard trophic estimators for comparisons of prey numbers in diets of each owl species: food niche breadth, mean prey mass, and food niche overlap (Marti et al. 2007). Food niche breadth (FNB), an index of diversity in owl diets, was estimated using the reciprocal of Simpson's index (Simpson 1949, Levins 1968). This index was used because it incorporated both species richness (the number of prey types in the diet) and dietary evenness (how uniformly those prey types were represented in the diet) into a single measure. Values of FNB ranged from 1 to n, where n was the total number of prey types (30 in this case). I standardized FNB to a proportion following Colwell and Futuyma (1971): $FNB_{st} = (FNB–1)/(n–1)$ for comparisons between species. Values of FNB and FNB_{st} were estimated for each owl territory and then averaged among territories for interspecific comparisons. Measures of food niche breadth are dependent on sample size and how the diet data are categorized, so I used individual-based rarefaction analysis (Heck et al. 1975, Gotelli and Colwell 2001) to statistically compare differences in prey species richness between the diets of spotted and barred owls. Here, expected species richness was estimated as the mean number of prey species present over repeated randomized subsamples of the diet data for each species. I used the species diversity module in program EcoSim 7.71 to estimate mean expected prey species richness and 95% confidence intervals (Gotelli and Entsminger 2004). I estimated mean mass of prey captured by each owl pair by dividing the total biomass in the sample by the total number of prey in the sample. I estimated mean prey mass with and without insect prey included because of a high frequency of insects in diets of barred owls. For comparisons between species according to the size of prey captured, I divided prey into 7 classes according to mean mass and calculated the frequency of occurrence in each class for each owl pair.

I used Pianka's (1973) index of niche overlap as a measure of dietary overlap between each pair of spotted owls and the nearest neighboring pair of barred owls with sufficient data ($\geq$20 prey items). I used program EcoSim to generate null models of food niche overlap (Gotelli and Entsminger 2004), which provided a baseline measure in evaluating the observed level of interspecific dietary overlap. Specifically, I compared observed values of dietary overlap with the expected frequency distribution of overlap values generated from 2,000 Monte Carlo randomizations of the observed diet data. Null models provided an appropriate null hypothesis against which the observed values of food-niche overlap could be compared (Gotelli and Graves 1996). I constructed null models using Lawlor's (1980) randomization algorithm 3, which retained the realized niche breadth of each owl species while randomizing proportional use of different prey categories. In addition, I compared proportions of prey consumed by owls during breeding and nonbreeding seasons to evaluate the potential for seasonal changes in dietary composition and overlap. Seasonal analyses were based on the combined sample for all owl pairs because samples were too small to estimate diets for owl pairs in the nonbreeding season.

Trophic and Ecological Overlap

In the sections above I described how I quantified overlap between neighboring spotted owls and barred owls for the major resource dimensions of space (home ranges and core-use areas), habitat (use of primary forest types), and food (diet composition). After calculating overlap coefficients between the 2 species for each resource axis separately, I then calculated a unified measure of ecological overlap as the arithmetic mean of spatial, habitat, and dietary overlap coefficients (May 1975, Geange et al. 2011, Whitney et al. 2011). Values of ecological overlap were 0 when distributions of space-use, habitat selection, or diets were completely disjoint and 1 when they completely overlapped. I calculated trophic overlap by multiplying habitat and dietary overlap coefficients (MacArthur and Levins 1967, Pianka 1974, Whitney et al. 2011). I calculated overlap coefficients for each radio-marked spotted owl and the nearest barred owl that was concurrently radio-marked. If >1 barred owl home range overlapped with the focal spotted owl, I selected the barred owl with the highest cumulative home-range overlap. I was unable to estimate diets of individual owls directly because pellets of males and females were often mixed under roosts, so individuals assumed territory-specific values of dietary overlap in calculations of trophic and ecological overlap. Taken together, trophic and ecological overlap values provided an index of the variation among individuals in their potential exposure to exploitative competition with neighboring heterospecifics.

Estimation of Survival Probabilities and Reproduction

I used known-fate models in program MARK (White and Burnham 1999) to estimate survival probabilities of radio-marked owls and to assess the influence of time, sex, habitat conditions, and interspecific interactions on species-specific survival. Known-fate parameter estimation in program MARK uses a modification of the Kaplan-Meier product limit estimator (Kaplan and Meier 1958) that accommodates staggered entry of individuals as they are added or censored from the risk set (Pollock et al. 1989).

I conducted this analysis in 2 steps. First, I evaluated support for a set of 10 *a priori* models that considered species-and sex-specific variation in seasonal (6 mo), annual (12 mo), and cumulative (22 mo) survival probabilities (Appendix D). Second, I introduced a small number of biologically relevant covariates to the most parsimonious model from step 1. This stage of the analysis was based on a small set of models developed to examine alternative hypotheses regarding the influence of forest conditions, interspecific interactions, and a combination of these effects on survival of each species. I examined differences between species in covariate relationships by allowing slope coefficients to vary according to species via an interaction term. I selected the best models using AIC_c (Burnham and Anderson 2002). I evaluated precision of slope coefficient estimates using standard errors and 95% confidence intervals, which helped supplement AIC_c evidence of important covariate relationships based on the degree to which intervals overlapped 0.

I selected 5 spatially explicit covariates to include in known-fate models (Appendix D). Several studies have identified associations between survival of spotted owls and the amount of old forest in their territories (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). To examine how this relationship might vary between spotted and barred owls, I tabulated the proportion of old (>120 yrs) conifer forest in seasonal 95% FK home ranges and core-use areas of radio-marked owls. Similar to anecdotal evidence from previous studies in western Oregon (Forsman et al. 1984, Paton et al. 1991, Carey et al. 1992), predation by great horned owls (*Bubo virginianus*) appeared to be an important source of mortality for spotted owls in my study area (Appendix E). Great horned owls often include nonforested openings in their home ranges (James and Neal 1986, Ganey et al. 1997) and may generally prefer highly fragmented landscapes for foraging (Johnson 1993). Consequently, I hypothesized that spotted owls that spent more of their time near open areas and habitat edges may have experienced a higher risk of predation than owls that avoided these areas. To evaluate this hypothesis I calculated the mean distance from used telemetry points for each owl to the closest edge between forested and nonforested areas, and included those values as individual covariates in

Program MARK. To investigate the potential influence of spatial interactions with heterospecifics on survival, I included 2 measures of spatial overlap: 1) the mean proportion of each owl's home range that was shared with radio-marked heterospecifics in adjacent territories (*HR*); and 2) the mean probability of heterospecific presence in the home range (*PHR*). The spatial covariates I used assumed that telemetry locations represented a random sample of use within the home range and that the mean adequately represented exposure to these conditions.

I estimated reproductive output for each species as the number of young fledged (NYF) per territorial female per year following Franklin et al. (1996), Lint et al. (1999), and Glenn et al. (2011b). Estimates ranged from 0–2 for spotted owls and 0–4 for barred owls, and I included all paired owls that were monitored from 1 March–31 August in estimates. I used linear mixed-models (Littell et al. 2006) to examine evidence for a negative association between annual estimates of NYF for spotted owls and proximity to the nearest known barred owl nest or breeding activity center (PROC MIXED, SAS Institute, Cary, NC). I treated site (owl territory) and year (a categorical variable) as random effects and the nearest-neighbor distance (km) between breeding activity centers of spotted and barred owls as a fixed effect. As described above, I surveyed barred owls within all territories occupied by spotted owls in each year of the study. I therefore considered interspecific nearest-neighbor distances to be the most accurate measure of territorial relationships among both radio-marked and unmarked owl pairs. Sample sizes were small (n = 13–15 spotted owl territories per year), so I chose not to attempt to model reproduction further and considered this analysis to be exploratory rather than confirmatory. Age can have an important effect on fecundity and survival of spotted owls (Anthony et al. 2006, Forsman et al. 2011). I was unable to age barred owls in my study, but all radio-marked spotted owls were full adults (≥3 yrs old).

RESULTS

Owl Surveys and Radiotelemetry

I identified a total of 18 territories occupied by ≥1 spotted owl and 82 territories occupied by ≥1 barred owl during 2007–2009 (Table 3.1). The total number of territories occupied by spotted owls remained relatively stable during the study, ranging from 16 in 2007 to 18 in 2009. In contrast, the total number of territories with barred owls increased from 35 in 2007 to 82 in 2009, primarily as a result of annual expansions in survey effort for barred owls. By 2009 I had identified a high density of regularly spaced nesting territories occupied by barred owls (Fig. 2.1). I radio-marked a total of 29 spotted owls (14 females, 15 males) at 15 territories and 28 barred owls (13 females, 15 males) at 21 territories (Appendix E). The sample of spotted owls included 14 territories where both pair members were radio-marked and 2 territories where a single resident male was marked. The sample of barred owls included 6 territories where both pair members were radio-marked and 16 territories where only 1 member of a resident pair could be captured. Of the 57 owls that I radio-marked, 47 (24 spotted owls, 23 barred owls) were radio-marked in 2007 and 10 (5 spotted owls, 5 barred owls) were radio-marked in 2008 in areas where spotted owls had not been previously detected.

I attempted to obtain 24 months of data on owls radio-marked in 2007 but was limited by mortality or premature radio-failure (Fig. 3.1). Cumulative tracking periods averaged 565 days for spotted owls (SD = 193, range = 73–734 days) and 562 for barred owls (SD = 162, range = 109–777 days). I obtained an average of 133 locations per spotted owl (SD = 49, range = 29–201) and 145 locations per barred owl (SD = 42, range = 32–199). The total number of telemetry locations for both species combined was 7,564 (5,809 nighttime foraging locations, 1,755 daytime roost locations). I did not use home range or habitat use data from 3 spotted owls and 1 barred owl that died within the first 110 days of being radio-marked (Appendix E), but these individuals were used for estimates of survival. I also excluded a single male spotted owl from the analysis of habitat selection because he spent several months of each year beyond my study area.

Spatial Relationships

Spacing and Distribution of Owl Pairs

Based on the distribution of activity centers for owl pairs in 2009, barred owls established their nesting areas closer to activity centers occupied by spotted owls (mean nearest-neighbor distance [NND] = 1.63 km, range = 0.53–2.98 km, n = 15) than to those occupied by other barred owls in adjacent territories (NND = 2.20 km, range = 0.96–4.48 km, n = 80; t = –3.26, df = 96, P = 0.002). Compared to barred owls, territories occupied by pairs of spotted owls were sparsely distributed within the study area (NND = 4.53 km, range = 3.21–6.52 km). The minimum distance between 2 concurrently active nest trees of spotted and barred owl pairs in adjacent territories was 0.84 km, which was considerably shorter than the minimum distance between 2 active nests used by different pairs of barred owls (1.94 km).

Space Use and Seasonal Movements

Home ranges of individual spotted owls during annual, breeding, and nonbreeding periods were 2–4 times larger than those of barred owls (Table 3.2, Appendix F). This pattern was consistent among individual owls and in cases where I monitored the combined home ranges of paired males and females (Table 3.3). Although not significant (all P-values >0.13), male spotted owls tended to have smaller annual home ranges than females, whereas male barred owls tended to have larger annual home ranges than females. As a consequence, the largest difference in space-use patterns between the 2 species was for females, with female spotted owls having annual ranges that averaged 4.2 times larger than those of female barred owls. During the breeding season, proportions of different forest types within spotted and barred owl home ranges were similar except that home ranges of barred owls tended to include more hardwood forest and less old (>120 yrs old) conifer forest than those of spotted owls (Table 3.4). On an annual basis, home ranges of individual spotted and barred owls contained similar proportions of older forest (>60 yrs old; spotted owls: $\bar{x}$ = 0.41, SE = 0.02, n = 25; barred owls: $\bar{x}$ = 0.41, SE = 0.02,

$n = 26$), but home ranges of barred owls contained more hardwood forest (spotted owls: $\bar{x} = 0.05$, SE = 0.01; barred owls: $\bar{x} = 0.09$, SE = 0.01). I found no evidence that the size of annual home ranges was correlated with the number of locations for spotted owls ($r = 0.13$, $P = 0.137$) or barred owls ($r = 0.07$, $P = 0.444$).

The best model used to examine variation in size of annual home ranges included the effects of species, probability of heterospecific presence in the focal individual's breeding home range (*PHR*), and an interaction between species and *PHR* (Table 3.5). This model accounted for 88% of the AIC$_c$ weight and indicated a positive linear relationship between annual home range size of spotted owls and the probability of barred owl presence (Fig. 3.2). The 95% confidence intervals for the effects of species ($\hat{\beta} = 785$, SE = 369.5, 95% CI = 42–1528) and species × *PHR* ($\hat{\beta} = 2298$, SE = 796.8, 95% CI = 671–3925) did not overlap 0, indicating that the interaction between these variables contributed significantly to model fit. The second-best model (ΔAIC$_c$ = 5.10) included the additive effects of species, *PHR*, and amount of old (>120 yr) conifer forest in the home range. The regression coefficient for amount of old forest in this model indicated a negative relationship with home range size for both owl species, but the 95% confidence interval marginally included 0 ($\hat{\beta} = -1{,}915$, SE = 1,150.2, 95% CI = –4,265 to 433). Models containing the effects of year, nesting status, or proportion of hardwood forest in the home range were not supported by the data (AIC$_c$ wt = 0.00; Table 3.5), and regression coefficients for these effects broadly overlapped 0.

The core-use area of nearly all individual spotted and barred owls was resolved between the 45–66% fixed-kernel isopleths ($\bar{x} = 53\%$, range = 30–72%), which provided evidence of non-uniform space-use within the breeding home range for both species. One female barred owl (paired with young) and 2 male spotted owls (both single residents) exhibited space-use patterns that did not deviate from a uniform distribution so no core-use area was computed. Core-use areas of individual owls always contained nest trees or regularly used roosts and averaged 257 ha for spotted owls (SE = 29, range = 37–668 ha, $n = 22$ owls) and 136 ha for barred owls (SE = 11, range = 40–334 ha, $n = 25$

owls). Mean size of the core-use area for owl pairs was 305 ha for spotted owls (SE = 59, *n* = 13) and 188 ha for barred owls (SE = 29, *n* = 10), which represented 19% and 22% of the total breeding home range used by pairs of spotted owls and barred owls, respectively (Table 3.3). Core-use areas for each species contained similar proportions of older (>60 yr) conifer forest (Table 3.4), but barred owls tended to have more hardwood forest in their core-use areas ($\bar{x}$ = 0.12, SE = 0.02, 95% CI = 0.07–0.16) than spotted owls ($\bar{x}$ = 0.06, SE = 0.01, 95% CI = 0.04–0.09).

Both species used home ranges during the nonbreeding season that were approximately twice as large as those used during the breeding season (Table 3.2; spotted owls: $F_{1,21}$= 40.90, $P < 0.001$; barred owls: $F_{1,24}$= 15.80, $P < 0.001$). Barred owls, however, exhibited a stronger pattern of site fidelity to their nesting areas during the nonbreeding season than spotted owls. Barred owls generally remained within 1–2 km of their nest sites throughout the year, whereas spotted owls were often located 3–6 km from their breeding sites in fall and winter (Fig. 3.3). Of the 23 spotted owls that were tracked for >1 yr, 3 females and 2 males exhibited winter migration behavior in which they established a winter home range that was 7–25 km distant from their breeding range. In contrast, most barred owls (25 of 27 birds) simply expanded their use of space in late fall and winter so that the nonbreeding range largely overlapped the breeding range. The 2 exceptions were cases where individual barred owls (1 M, 1 F) left their territories in early January and moved 20–38 km away before returning to their original breeding areas in February. Such movements were uncommon and only occurred in 1 of the 2 winters in which these individuals were tracked.

Spatial Interactions among Radio-marked Owls

I observed little intraspecific overlap among home ranges of conspecific owls in adjacent territories, especially during the breeding season when owls were expected to be most strongly territorial (Table 3.6). For barred owls on adjacent territories, there were no cases of intraspecific overlap among 50% FK home ranges, and overlap among 95%

FK home ranges was low (*HR*: $\bar{x}$ = 0.10, range = 0.02–0.23; *PHR*: $\bar{x}$ = 0.08, range = 0.01–0.29; UDOI: $\bar{x}$ = 0.01, range = 0.00–0.02). Intraspecific overlap among breeding ranges of individual spotted owls on adjacent territories was also low (*HR*: $\bar{x}$ = 0.13, range = 0.01–0.44; *PHR*: $\bar{x}$ = 0.11, range = 0.04–0.73; mean UDOI: $\bar{x}$ = 0.02, range = 0.00–0.17, *n* = 39). Estimates of spatial overlap between home ranges of paired female and male barred owls were consistently high and varied little among breeding and nonbreeding periods (Table 3.6, Fig. 3.4). In contrast to barred owls, space-use sharing of paired female and male spotted owls declined during late fall and winter (Fig. 3.4).

Based on the distribution of territories occupied by marked versus un-marked barred owls (e.g., Fig. 2.1), it was clear that the actual number of barred owls that were spatially associated with radio-marked spotted owls was considerably higher than what was estimated from radio-marked owls alone. Hence, measures of interspecific overlap reported here reflect average spatial overlap among individuals in adjacent territories rather than cumulative interspecific overlap. Each individual spotted owl shared a portion of its annual home range with between 0 and 8 barred owls in adjacent territories ($\bar{x}$ = 2.4 barred owls per spotted owl). The proportion of a spotted owl's annual home range that was shared with a neighboring barred owl (*HR*) ranged from 0.01–0.56 ($\bar{x}$ = 0.10, SE = 0.01), and the proportion of a barred owl's annual home range that was shared with a spotted owl ranged from 0.01–1.00 ($\bar{x}$ = 0.35, SE = 0.03). In several cases, the smaller home ranges of barred owls were completely subsumed within the larger ranges of spotted owls. Measures of interspecific overlap of 50% home ranges were low despite a moderate to high level of overlap among 95% home ranges. Upon examination of forest composition within areas of interspecific home-range overlap during the breeding season, I found that proportions of old conifer ($\bar{x}$ = 0.29, SE = 0.03) and hardwood forest ($\bar{x}$ = 0.10, SE = 0.01) were higher than what was generally available to owls in the landscape (old conifer = 0.17, hardwood = 0.05; Table 3.4).

Probabilistic measures of spatial overlap that accounted for differences in the intensity of use within the overlap region between 2 neighboring owls indicated that the probability of locating a spotted owl within a barred owl's home range during the breeding season was considerably lower (*PHR*: $\bar{x}$ = 0.15, SE = 0.03, range = 0.00–0.84) than the probability of locating a barred owl in a spotted owl's home range (*PHR*: $\bar{x}$ = 0.39, SE = 0.04, range = 0.01–1.00). This directional pattern of interspecific overlap was consistent over all time periods at both levels of use intensity within the home range (Table 3.6). Estimates of interspecific space-use sharing (UDOI) during the breeding season were notably higher ($\bar{x}$ = 0.10, SE = 0.02, range = <0.01–0.84) than intraspecific estimates for barred owls in adjacent territories ($\bar{x}$ = 0.01, SE = 0.01, range = <0.01–0.02; Fig. 3.4). This pattern would be expected if barred owls were more likely to share their foraging areas with spotted owls than with other barred owls in adjacent territories. I did not observe a significant increase in interspecific overlap during the nonbreeding season despite the tendency for both species to expand their use of space during this time.

There were several cases in 2008 in which the level of space sharing among heterospecific individuals was markedly high (i.e., UDOI >0.30). These were situations in which newly colonizing barred owls were captured and radio-marked within the core-use areas of 2 different pairs of spotted owls (e.g., Fig. 3.5). Subsequent monitoring results demonstrated a high likelihood of locating newly colonizing barred owls within the 95% (*PHR* range = 0.55–1.00) and 50% (*PHR* range = 0.52–0.76) breeding ranges of male and female spotted owls. Interspecific territorial interactions were regularly observed in these cases, including agitated vocalizations by both species near nest sites and barred owls chasing spotted owls out of shared core-use areas. These observations provided evidence that high interspecific overlap of home ranges and core-use areas was associated with a high potential for agonistic interactions between the species.

Habitat Selection

After excluding owls that died early in the study period and those that moved beyond the extent of my study area, there were 25 spotted owls (13 F, 12 M) and 26 barred owls (12 F, 14 M) with sufficient data for analyses of habitat selection. For discrete-choice models of nighttime resource selection, there were 17 individuals of each species that were monitored for >1 yr, so I developed 2 annual choice sets for each of these owls. This resulted in a total of 42 choice sets for 25 spotted owls (2,820 used locations, 9,209 random locations) and 43 choice sets for 26 barred owls (2,799 used locations, 9,388 random locations). Sixteen spotted owls and 22 barred owls had sufficient data for the univariate analysis of daytime roost-site selection.

Influence of Forest Conditions and Topography

At the landscape scale (second-order selection), the 2 species displayed broadly similar patterns of habitat selection (Table 3.7). Mean selection ratios indicated that both species selected patches of old (>120 yrs old) conifer forest in proportions 2–3 times greater than their availability in the landscape (Fig. 3.6). Based on overlap of 95% Bonferroni confidence intervals, use of old forest for foraging was similar for the 2 species, but spotted owls used old forest in higher proportions for roosting ($\widehat{w}_i$ = 3.74, 95% CI = 3.23–4.25) than barred owls ($\widehat{w}_i$ = 2.49, 95% CI = 1.79–3.19). Barred owls showed strong positive selection for hardwood forest, especially for foraging ($\widehat{w}_i$ = 2.96, 95% CI = 1.39–4.54). In contrast, spotted owls used hardwood forest in similar proportions to its availability in the landscape. Both species used patches of mature conifer forest in proportions equal to their availability, and both species avoided patches of young forest and open areas. Both species selected foraging and roosting locations at intermediate distances from high contrast edges, with selection ratios and confidence intervals being negative for distances <135 m from edges and positive for distances of 490–800 m from edges (Fig. 3.6). Both species also selected locations ≤150 m from streams. Relative to random landscape locations, both species selected patches of forest that were characterized by larger quadratic mean diameter (42–60 cm) with a higher density of conifers >50 cm dbh (15–25 trees ha^{-1}; Table 3.7). Based on Pianka's measure of niche overlap estimated for 24 pairwise combinations of neighboring heterospecific owls (48 individuals), mean similarity between spotted and barred owls in proportional use of different forest types for foraging was 0.809 (SE = 0.022, range = 0.306–0.990). This index indicated moderate to high overlap in habitat use by the 2 species.

At the home-range scale (third-order selection), the best base RSF model for spotted owls included the effects of forest type, distance to nest, slope, and distance to streams (Table 3.8, Appendix G). A closely competing model included a quadratic term for distance to high contrast edge, but the 95% confidence interval for this effect included 0 ($\hat{\beta}$ = 0.18, SE = 0.14, 95% CI = –0.10 to 0.46). Under the base RSF for spotted owls, old conifer was >5 times as likely to be selected for foraging as the nonforest reference category (selection ratio [exp($\hat{\beta}$)] = 5.3, 95% CI = 4.4–6.4), followed by riparian-hardwood (4.3, 95% CI = 3.5–5.4), mature conifer (3.4, 95% CI = 2.8–4.1), and young conifer forest (1.9, 95% CI = 1.6–2.4). The base RSF for spotted owls also indicated positive selection for steeper slopes and a negative effect on selection as distance from nest sites and streams increased.

Similar to spotted owls, the best RSF model for barred owls included the effects of forest type, slope, distance to nest, and distance to streams (Table 3.8). In contrast to spotted owls, however, there was strong support for a quadratic effect of high contrast edges on nighttime resource selection by barred owls (Table 3.9). Also in contrast to spotted owls, barred owls tended to avoid steep slopes. Under the overall best RSF developed for barred owls, riparian-hardwood forest was >3 times as likely to be selected for foraging as the nonforest reference (selection ratio = 3.2, 95% CI = 2.5–4.0), followed by old conifer (2.9, 95% CI = 2.3–3.5), mature conifer (2.6, 95% CI = 2.1–3.1), and young conifer forest (1.7, 95% CI = 1.4–2.1). Thus, similar to results from the landscape-scale analysis, barred owls showed a more even distribution of use of available forest types than spotted owls. Base models that included forest structural covariates from GNN maps were not competitive with those containing the categorical effect of forest type (Appendix G). Nonetheless, there was some support for a nonlinear effect of quadratic mean diameter of conifers (QMD) on foraging site selection by both species, as indicated by 95% confidence intervals that did not overlap 0. The best models that included the QMD effect indicated that the relative probability of selection was maximized in patches of forest with average QMD of 40–65 cm for both species.

When data from both species were combined, the best model was the most complex structure with all interactions between species and environmental covariates (AIC weight = 1.0; Appendix G). This model was >257 AIC units lower than a model without species effects, thereby providing strong evidence of differential selection of foraging conditions by spotted owls and barred owls. As indicated by parameter coefficients and 95% confidence intervals for species-specific interaction terms, the 2 species differed significantly in their relative use of old conifer forest (higher for spotted owls), distance to nest, and slope conditions (Table 3.10, Fig. 3.8). I found no evidence that the 2 species differed in their use of young, mature, or riparian-hardwood forest.

Influence of Heterospecifics

At the landscape-scale, spotted owls showed negative selection for locations within 1,000 m of barred owl activity centers ($\hat{w}_i$ = 0.61, 95% CI = 0.30–0.92 for distances <500 m; $\hat{w}_i$ = 0.69, 95% CI = 0.42–0.95 for distances of 500–1,000 m; Fig. 3.6). Foraging locations of barred owls were generally closer to areas used by spotted owls ($\bar{x}$ = 2.7 km, SE = 0.3 km) than to random landscape locations ($\bar{x}$ = 3.8 km, SE = 0.2 km), but proportional use of different distance classes surrounding spotted owl activity centers did not deviate from availability. This was likely due to the fact that spotted owls were sparsely distributed across the landscape, which contributed to a high level of variation among individual barred owls in their exposure to spotted owls.

At the home-range scale, spatial covariates related to areas of concentrated use by barred owls contributed further in explaining resource selection by spotted owls. The addition of covariates representing core-use areas of barred owls (HETcore) or proximity to a barred owl core-use area (dHET) resulted in models that were 14.3–31.4 AIC units lower than the base RSF model without heterospecific effects, respectively (Table 3.8). Parameter coefficients from the best model with HETcore indicated that the relative probability of a spotted owl selecting a location at night was reduced if the location was within a core-use area of barred owls (selection ratio = 0.72, 95% CI = 0.61–0.85). The best RSF model for spotted owls, however, included the effect of proximity to barred owls plus an interaction between riparian-hardwood forest and proximity to barred owls (Table 3.9). This model accounted for 90% of the AIC weight and indicated that use of different forest types varied with an increasing likelihood of encountering barred owls. As proximity to a barred owl's core-use area increased, a spotted owl's affinity for old, mature, and young conifer forest types was gradually replaced by selection for riparian-hardwood forest (Fig. 3.7). For barred owls, inclusion of covariates representing spatial overlap with spotted owls failed to substantially improve upon a RSF model without these effects (Table 3.8), and the 95% confidence intervals for interspecific covariates effects broadly overlapped 0.

Diets and Foraging Behavior

I identified a total of 1,223 prey items from 15 territories occupied by spotted owls and 4,299 prey items from 24 territories occupied by barred owls. The number of prey items from each territory ranged from 20–173 for spotted owls ($\bar{x}$ = 81.5, SE = 11.8) and 28–441 for barred owls ($\bar{x}$ = 179.1, SE = 26.2). Diets of spotted and barred owls included at least 51 and 95 prey species, respectively (Appendix H). The diet of spotted owls was dominated by mammals, which comprised an average of 95.7% of total prey numbers and 97.4% of total prey biomass (Table 3.11). In comparison, mammals comprised 66.0% of prey numbers and 89.2% of prey biomass in diets of barred owls, with the remainder being composed of birds, frogs, salamanders, lizards, snakes, crayfish, snails, fish, millipedes, and insects. Based on percent biomass contributions to diets, the 5 most important prey species for spotted owls were (in descending order): flying squirrels (50.0%), woodrats (17.4%), lagomorphs (13.3%), deer mice (*Peromyscus maniculatus*; 4.9%), and red tree voles (*Arborimus longicaudus*; 4.4%). In comparison, the 5 most important prey for barred owls were: flying squirrels (24.3%), lagomorphs (17.4%), moles (14.8%), Douglas' squirrels (*Tamiasciurus douglasii*; 6.9%), and woodrats (6.8%). Thus, flying squirrels, woodrats, and lagomorphs were particularly important prey for both owl species, accounting for 80.7% and 48.5% of total dietary biomass for spotted owls and barred owls, respectively. No single bird species accounted for >2.0% of dietary biomass for either species. I found no evidence of intraguild predation between the 2 species based on the absence of spotted or barred owl remains in owl pellets.

The majority of prey consumed by both species were nocturnal, but barred owls also consumed a high proportion of diurnal prey (e.g., squirrels, birds, reptiles) that were rare or absent in diets of spotted owls (χ^2= 324.7, df = 3, $P < 0.001$; Fig. 3.9). Both owls fed upon similar proportions of semi-arboreal species, but within this prey group spotted owls fed more heavily on nocturnal woodrats and barred owls fed more heavily on diurnal squirrels. Diets of spotted owls contained a notably higher proportion of arboreal prey (e.g., flying squirrels, red tree voles) than those of barred owls. Conversely, barred owl diets contained a higher proportion of prey associated with terrestrial and aquatic environments (χ^2= 827.37, df = 6, $P < 0.001$; Fig. 3.9).

Mean food-niche breadth (FNB) was 4.44 for spotted owls (SE = 0.25, range = 2.11–6.12, n = 15 territories) and 8.40 for barred owls (SE = 0.39, range = 3.63–12.40, n = 24). Standardized measures of food-niche breadth indicated that diets of barred owls were considerably more diverse (FNBst = 0.26, SE = 0.01) than those of spotted owls (FNBst = 0.12, SE = 0.01). This result was supported by the rarefaction analysis, which illustrated that diets of barred owls consistently contained a higher diversity of prey than diets of spotted owls over a range of simulated sampling frequencies (Fig. 3.10). Although estimates of dietary breadth for barred owls were high relative to spotted owls, values for both species were near the lower end of the scale of possible values (1–30) which indicated that proportional use of different prey types was uneven.

The average size of individual prey captured by barred owls was smaller than prey captured by spotted owls. When insects were included, mean mass of prey was 91.0 g for spotted owls (SE = 6.2, 95% CI = 77.7–104.2) and 60.2 g for barred owls (SE = 3.1, 95% CI = 53.7–66.6). Mean mass of non-insect prey was 92.5 g for spotted owls (SE =

6.4, 95% CI = 78.8–106.1) and 68.8 g for barred owls (SE = 3.0, 95% CI = 62.7–74.9 g). Both species captured prey in a variety of sizes ranging from *Hymenopterid* bees (0.1 g) to adult snowshoe hares (~1,200 g). Diets of spotted owls, however, were dominated by prey in the 11–40 g and 81–160 g size classes whereas diets of barred owls were more evenly distributed among prey-sizes (Fig. 3.11). Unlike spotted owls, barred owls consumed a high proportion of very small (≤10 g) prey that included at least 14 species of insects, 4 species of snails, 4 species of shrews, and 5 species of small birds (Appendix H). Barred owls also took a disproportionately greater number of prey items within the size range of 50–90 g, which included coast moles (*Scapanus orarius*), Townsend's chipmunks (*Tamias townsendii*), and large salamanders (*Ambystoma* or *Dicamptodon* spp.).

Mean dietary overlap between pairs of spotted owls and barred owls in adjacent territories was 0.42 (SE = 0.03, range = 0.28–0.70; Table 3.12). Mean overlap in the proportional use of mammals alone was 0.51 (SE = 0.03, range = 0.34–0.73). Estimates of interspecific overlap from null model simulations were lower than those observed (range = 0.14–0.27), but observed values of dietary overlap deviated from random expectations in only 2 of 15 cases (*P*-values < 0.05; Table 3.12). Based on data pooled over all territories, dietary overlap increased from 0.45 during the breeding season to 0.68 in the nonbreeding season when amphibians, reptiles, crayfish, and insects were less available and both species were more strongly restricted to mammalian prey. Proportional use of mammals by spotted owls was similar during breeding (94.1%) and nonbreeding (95.6%) periods. In contrast, the frequency of mammals in the diet of barred owls increased from 63.5% in the breeding season to 71.3% in the nonbreeding season with a concomitant increase in the mean mass of prey captured (Table 3.13). Seasonal changes in diets of barred owls were most strongly related to increases in the proportional use of flying squirrels, red tree voles, and lagomorphs during fall and winter.

Trophic and Ecological Overlap

A comparison of mean overlap coefficients estimated for each of the 3 resource dimensions showed that neighboring spotted owls and barred owls were most similar in their use of primary forest types ($\bar{x}$ = 0.81, SE = 0.04), followed by diets ($\bar{x}$ = 0.43, SE = 0.02) and spatial distributions ($\bar{x}$ = 0.17, SE = 0.04; Table 3.14). Trophic overlap estimated for neighboring spotted and barred owls ranged from 0.09 to 0.50 ($\bar{x}$ = 0.35, SE = 0.02; Table 3.14), indicating that interspecific similarities in the use of available forest types and prey varied considerably among individuals examined. Ecological overlap based on the arithmetic mean of space, habitat, and dietary overlap coefficients also varied widely among individuals, ranging from 0.23 to 0.69 ($\bar{x}$ = 0.47, SE = 0.02). With few exceptions, measures of ecological overlap generally fell below 0.50, with 0.54 considered by some authors as the critical limit to similarity for coexisting species (MacArthur and Levins 1967). These measures were likely underestimated because they did not account for cumulative overlap among all heterospecific neighbors or for potential seasonal or annual variation in prey availability.

Survival and Reproduction

Causes of Mortality and Survival Probabilities

I documented a total of 13 mortalities of radio-marked owls (9 spotted owls, 4 barred owls) over a 22-month tracking period (Table 3.15). Nine carcasses (5 spotted owls, 4 barred owls) were recovered fully intact and submitted for necropsy. Necropsy results showed no injuries directly attributable to radio-transmitters, and all owls tested negative for West Nile Virus (*Flavivirus*). Based on necropsy results and evidence collected at recovery sites, causes of death included severe bacterial infections associated with endoparasitism (6 cases), disease (1 case), emaciation (1 case), and avian predation (5 cases). Avian predation was identified as the primary cause of death in spotted owls, whereas severe bacterial infection associated with heavy infestations of parasitic worms (e.g., *Acanthocephala* spp.) was the primary cause of death in barred owls. One male spotted owl was found dead of emaciation just 9 days after the death of his mate, who died of a possible pneumonia infection shortly after a failed nesting attempt. Avian predation was linked with 5 (56%) of 9 spotted owl deaths, but I found no evidence that predation was a factor in the death of any barred owl. The remains of 2 spotted owls were located (in different years) at a perch where great horned owls had been observed. In both cases I found the radio-transmitter along with scattered feathers, whitewash, and large owl pellets containing remains of the spotted owls. The other 2 spotted owls were found partially eaten and cached beneath fallen logs shortly after their mortality sensors activated. These owls had wounds consistent with those inflicted by a large raptor and were recovered in areas where both great horned owls and barred owls had been detected. Although I could not rule out the possibility that barred owls were responsible for these deaths, I found no evidence to support this.

I partitioned survival of radio-marked spotted owls and barred owls by 6-month time intervals to provide estimates of seasonal, annual, and cumulative survival probabilities over a 22-month period (May 2007–Feb 2009). The number of owls included in each 6-month time interval ranged from 21–26 (Table 3.15). There were no cases of data censoring because the fate of all owls was known (no undetected emigration), and there were no cases of radio-failure during the time intervals in which survival was estimated. Consequently, my estimates of survival were free of bias due to right-censoring (i.e., confounding of mortality with transmitter failure or emigration; Murray 2006, Franklin et al. 2006). The best model from the initial analysis, *S*(Spp), indicated that survival differed between species (higher for barred owls) and was constant between sexes and over time (Table 3.16). The 95% confidence interval for the effect of species in this model narrowly included 0 ($\hat{\beta}$ = –0.92, SE = 0.62, 95% CI = –2.14 to 0.30), indicating weak support for species-specific differences in survival. The derived estimate of annual survival under this model was 0.81 for spotted owls (SE = 0.05, 95% CI = 0.68–0.90) and 0.92 for barred owls (SE = 0.04, 95% CI = 0.80–0.97). Models containing the effects of sex, year, or season were not supported by the data (AIC$_c$ wt = 0; Appendix I), and 95% confidence intervals for these effects broadly overlapped 0.

The best model for survival included the additive effect of species, mean proportion of old conifer forest in the home range, and the probability of heterospecific presence in the home range (Table 3.16). The slope coefficient for the effect of old forest in this model ($\hat{\beta}$ = 10.15, SE = 3.92, 95% CI = 2.46–17.84) indicated a strong positive relationship with survival of both species. This model indicated that survival was highest for owls with >35% of old forest in their home range (Fig. 3.12). Moreover, models that included the effect of old forest consistently outperformed those without this covariate (Table 3.16, Appendix I). On average, owls that survived had greater proportions of old forest in their home ranges (spotted owls: $\bar{x}$ = 0.20, SE = 0.02; barred owls: $\bar{x}$ = 0.23, SE = 0.03) than owls that died (spotted owls: $\bar{x}$ = 0.14, SE = 0.03; barred owls: $\bar{x}$ = 0.11, SE = 0.04). The negative and additive effect of the probability of heterospecific presence in the home range was also included in the top model, but the 95% confidence interval for this effect overlapped 0 slightly ($\hat{\beta}$ = –1.98, SE = 1.35, 95% CI = –4.62 to 0.66), indicating a relatively weak relationship with survival. Models containing the effects of high-contrast edges (dedge), proportion of old conifer in the breeding season core-use area (old_core), and proportion of the home range shared with heterospecific neighbors (*HR*) were not supported by the modeling results and data.

Nesting Success and Productivity

There was a dramatic difference in annual measures of nesting success and productivity between spotted owls and barred owls (Table 3.17). In general, barred owls nested more often, had fewer nest failures, and produced over 6-times as many young over a 3-year period as spotted owls. Over 3 breeding seasons combined (2007–2009), spotted owls produced a total of 13 fledglings during 21 nesting attempts at 15 occupied territories. In contrast, barred owls produced a total of 80 fledglings during 45 breeding attempts at 20 occupied territories. Barred owls also fledged more young per successful nest ($\bar{x}$ = 2.0, range = 1–4 young) as compared to spotted owls ($\bar{x}$ = 1.86, range = 1–2 young). All 13 female barred owls that were radio-marked attempted to nest each year they were monitored, and 12 of these females (92%) successfully fledged a total of 49 young. Conversely, 10 (71%) of 14 female spotted owls that were radio-marked attempted to nest at least once during the study, but only 4 (29%) of these females successfully fledged a total of 7 young. In addition to differences in reproductive output between the species, I also observed a marked difference between the 2 species in the estimated date of egg-laying, with barred owls initiating nesting an average of 1 month prior to spotted owls in all years of the study (Fig. 3.13). The estimated mean date of clutch initiation was 12 March for barred owls (range = 3 March–25 March, n=13) and 12 April for spotted owls (range = 31 March–1 May, n=10).

Based on a limited sample size, the number of young fledged per pair per year by spotted owls increased linearly with increasing distance from the nearest barred owl nest or territory center ($F_{1,19}$= 9.50, P = 0.006; slope coefficient [$\hat{\beta}$] = 0.387, SE = 0.125, 95% CI = 0.124–0.649). Five of 15 pairs of spotted owls attempted to nest within 1.5 km of an active barred owl nest during the study, but none of these nesting attempts were successful.

DISCUSSION

The recent colonization of the entire range of the northern spotted owl by barred owls provided a unique situation where I was able to identify emergent behaviors of resource partitioning which may mediate competitive interactions between these 2 species. By directly monitoring spatial relationships, habitat selection, diets, survival, and reproduction of sympatric spotted owls and barred owls I was able to identify a high potential for interspecific competition. I found a moderate to high level of overlap in use of space, habitat, and food resources between the 2 species. Spotted owls shared 10–56% of their seasonal and annual home ranges with individual barred owls in adjacent territories, and the 2 species displayed broadly similar patterns of habitat selection. Flying squirrels, woodrats, lagomorphs, tree voles, and deer mice were particularly important prey for both owl species, but barred owls captured large numbers of small-sized terrestrial and aquatic prey that were rare or absent from the diets of spotted owls. In addition to overlaps in resource use, I also identified strong associations between the presence of barred owls and the behavior of spotted owls, as shown by changes in space-use, habitat selection, and reproductive output of spotted owls exposed to varied levels of spatial overlap with barred owls. Both predators often used old conifer forest for foraging and the survival rates of both species were positively associated with the percent cover of old forest in their home ranges, which suggests that old forest is a potential limiting factor in the competitive relationship between these species. Collectively, my results suggest that interference competition with a high density of barred owls for territorial space can act to constrain the availability of critical resources for spotted owls.

Spatial Relationships

Understanding spatial relationships between interacting species requires primary information on the spatial ecology and individual life-history traits of each species. In particular, information on space-use, site fidelity, and the level of spatial overlap is required to assess potential segregation between species at the individual level, which in turn can determine species distributions at the population level. This is especially true in birds of prey, where spacing among well-defined territories is often maintained by intra- and inter-specific territoriality (Newton 1979, Solonen 1993, Katzner et al. 2003). Based on species-specific surveys of spotted owls and barred owls, there were >4.5 times as many territories occupied by barred owls than spotted owls in my study area. Territories with pairs of spotted owls were sparsely distributed with a mean nearest-neighbor distance of 4.5 km (0.02 pairs per km^2), which was nearly twice that reported for the same region in the 1970s (2.6 km; Forsman et al. 1984). This change in the density of spotted owl pairs most likely reflected recent declines in spotted owl populations in the Oregon Coast Ranges (Anthony et al. 2006, Forsman et al. 2011). The density of territories with pairs of barred owls was considerably greater, with a mean nearest-neighbor distance of 2.2 km (0.11 pairs per km^2). The different spacing patterns among conspecific versus heterospecific owl pairs suggested that barred owls had a higher tolerance for spotted owls within their home ranges than for other barred owls. For example, nests used by barred owls in adjacent territories were always >1.9 km apart, whereas spotted owls sometimes nested (unsuccessfully) within 530 m of concurrently active barred owl nests. This pattern, which was also noted in western Washington (Hamer 1988), might be expected if intraspecific interactions had a stronger influence on spatial distribution of barred owls than interspecific interactions with spotted owls.

Mean (2,872 ha) and median (1,997 ha) estimates of annual home-range size (100% MCP) of individual spotted owls in my study were similar to those reported in the more fragmented landscapes of the central and southwest portions of the Oregon Coast Ranges by Forsman et al. (1984: $\bar{x}$ = 1,913 ha) and Carey et al. (1992: $\bar{x}$ = 2,908 ha). However, my estimates tended to be larger than for spotted owls in areas covered by more extensive and less fragmented old forests in western Oregon (Forsman et al. 1984: $\bar{x}$ = 1,177; Carey et al. 1990: $\bar{x}$ = 1,580 ha). Several previous studies of spotted owls in western Oregon have reported that home range size can be influenced by the spatial distribution of old and mature forests, with larger home ranges found in more fragmented landscapes with limited availability of mature and old forest (Forsman et al. 1984, Carey et al. 1992, Carey and Peeler 1995, Glenn et al. 2004). My results were consistent with these previous studies in that annual home range size of spotted owls and barred owls was negatively associated with cover of old forest in the home range, but this relationship was highly variable among individuals and relatively weak. Instead, the most strongly supported predictor of annual home range size for spotted owls was the probability of barred owl presence in the breeding season home range, as determined by overlap of utilization distributions of radio-marked owls in adjacent territories. This result supported my prediction that spotted owls would respond to an increasing likelihood of space sharing with barred owls by expanding their movements to include other areas. This response may have important negative consequences for a central-place forager like the spotted owl, as the ability to increase the size of the home range and maintain territory ownership is likely limited by energetic and social constraints (Carey et al. 1992, Ward et al. 1998, Newton 1998).

Estimates of mean (841 ha) and median (701 ha) annual home range size (100% MCP) of barred owls in my study were similar to those reported for the north Cascades of Washington (Hamer et al. 2007; $\bar{x}$ = 781 ha, n = 22 owls, 95% adaptive fixed-kernel) and Saskatchewan (Mazur et al. 1998; $\bar{x}$ = 971 ha, n = 6, 100% MCP), but nearly twice as large as those reported in the eastern Cascades of Washington (Singleton et al. 2010; $\bar{x}$ = 416–477 ha, n = 9; 100% MCP). Comparisons of home range size among these studies were somewhat confounded by differences in sample sizes and sampling intervals, but radio-telemetry studies that have been conducted on barred owls clearly show that, relative to spotted owls, they have small home ranges in most areas in which they occur (see reviews by Courtney et al. 2004, Hamer et al. 2007, and Livezey 2007). Similar to spotted owls in my study, there was a weak negative association between annual home range sizes of barred owls and amount of old forest in home range. None of the other environmental covariates I examined, including the level of spatial overlap with spotted owls, explained a significant amount of variation in annual home range size of barred owls. The striking disparity in space-use between the 2 species in my study is best explained by differences in the scale of resource use by a generalist (barred owl) versus specialist (spotted owl) predator. For example, diets of the 2 species indicated that barred owls foraged opportunistically across a broad range of prey types and sizes, whereas spotted owls specialized on arboreal mammals associated with older conifer forest. These observations support the hypothesis that barred owls have smaller home ranges relative to spotted owls because of interspecific differences in prey selection and foraging strategies (Hamer et al. 2001, 2007).

Both species used home ranges during the nonbreeding season that were approximately twice as large as those used during the breeding season. As in most previous studies of spotted owls (e.g., Forsman et al. 1984, 2005, Carey et al. 1992, Glenn et al. 2004, Hamer et al. 2007) and barred owls (Elody and Sloan 1985, Hamer et al. 2007), patterns of home range expansion during fall and winter reflected a variety of behaviors, including a general expansion in space use, a slight shift to a winter range that partially overlapped the breeding range, or a winter migration to an entirely separate range that was some distance from the breeding range. In my study, 21% of individual spotted owls exhibited winter migration behavior. Such movements were uncommon in barred owls and most individuals remained within 1–2 km of their nesting sites throughout the year. These species-specific differences in seasonal movements may reflect differences in territorial behavior or dissimilar responses to seasonal changes in prey availability and weather. Regardless, the high density of barred owls in my study area, their strong year-round fidelity to nesting sites, and the low spatial overlap among seasonal home ranges of conspecifics were all indicators that barred owls maintained well-defined territories throughout the year. These observations are consistent with studies that monitored year-round movements of barred owls elsewhere (Nicholls and Fuller 1987, Hamer et al. 2007).

My study confirmed that neighboring pairs of spotted and barred owls not only co-existed in close proximity but also shared the same broader foraging areas within their home ranges. In some cases they occasionally shared the same patch of trees within overlapping core-use areas (e.g., Fig. 3.4), but this was usually directional in that barred owls were more likely to be located within spotted owl core-use areas. I used 3 different measures of home-range overlap to examine spatial interactions among radio-marked owls. Regardless of which measure was used, they were all consistent in indicating greater interspecific than intraspecific overlap among home ranges and core-use areas. Thus, if any form of interspecific territoriality was operating, it did not result in complete interspecific exclusion at the home-range scale. Based on overlap of 50% fixed-kernel utilization distributions for owls in adjacent territories, I found that the probability of locating a barred owl within a neighboring spotted owl's core-use area (0.09) was greater than the probability of locating a spotted owl within a barred owl's core-use area (0.03). For the most part, however, interspecific spatial overlap was low and most spotted and barred owls did not share areas of concentrated use (i.e., core-use areas) during breeding or nonbreeding periods. This was an important result because core-use areas were likely to be the most heavily defended area of both species home ranges, and it suggests some degree of interspecific territoriality between the species.

When space sharing did occur between spotted owls and barred owls, it was almost always limited to the outer portion of home ranges and beyond an individual's center of activity. Because overlap among core-use areas can indicate a greater potential for competition than home-range overlap (Pita et al. 2010, Robinson and Terborgh 1995, Katzner et al. 2003), non-overlapping core-use areas of the 2 species suggested that interspecific competition may have influenced their spatial distributions. Nonetheless, in order to demonstrate that differences in the spatial distributions of 2 species are due to interspecific territoriality, it is necessary to show not only that 1 species defends its territories against the other and the 2 do not have overlapping nesting territories, but also that the subordinate species would occupy habitat used by the dominant species if it were not prevented from doing so (Dhont 2012). I investigated this issue in greater detail in my analysis of habitat selection (see below), where selection of foraging sites by spotted owls or barred owls could be examined relative to the known spatial distribution of each species in the landscape.

Habitat Selection

Old conifer forest was the only forest type used by spotted owls for both foraging and roosting in greater proportions relative to its availability at the landscape scale. This result is similar to that observed in previous analyses of habitat selection by spotted owls in the Douglas-fir/western hemlock zone of the central Oregon Coast Ranges (Forsman et al. 1984, Carey et al. 1992). Within their home ranges, spotted owls most often selected locations within patches of old conifer forest for foraging that were within 2–3 km of nest sites, had steep (40–50°) slopes, and were within 300–400 m of a stream. Spotted owls were occasionally located in young forest and along edges of recent clear-cuts, but this was uncommon and these conditions were generally avoided. Rather, spotted owls spent a disproportionate amount of time foraging in steep ravines within patches of old conifer forest. Spotted owls in my study also showed strong selection for riparian-hardwood forest along low-order streams. Solis and Guitierrez (1990), Carey and Peeler (1995), Hamer et al. (2007), and Irwin et al. (2007, 2011) reported similar patterns of habitat selection by northern spotted owls (but see Forsman et al. 2005). My results also parallel those of Glenn et al. (2004), who reported that resource selection by spotted owls in younger forests of western Oregon was associated with hardwood (broadleaf) trees and riparian areas.

Habitat associations of barred owls have been described in a variety of different forest conditions throughout much of their geographic range. In eastern deciduous forests, they typically selected mature and old mixed-forests in swamps and lowland riparian areas (Elody and Sloan 1985, Bosakowski et al. 1987). In boreal forests of Saskatchewan (Mazur et al. 1998) and in Alberta (Takats 1998, Olsen and Hannon 2006), barred owls selected older mixed-conifer forests with trembling aspen (*Populus tremuloides*), but avoided young (<50 yrs old) forest and recent clear-cuts. Consistent with these descriptions, barred owls in my study used a broad mixture of forest types but were most strongly associated with gentle slopes in patches of structurally diverse mature and old conifer forests and lowland riparian areas containing large hardwood trees. Use of older forest in combination with moist, valley-bottom forest was consistent with habitat associations described for barred owls in Washington (Herter and Hicks 2000, Gremel 2003, Pearson and Livezey 2003, Buchanan et al. 2004, Hamer et al. 2007, Singleton et al. 2010). Although there was a high level of variation among individuals, barred owls were equally likely to be found foraging in riparian areas dominated by red alder and bigleaf maple trees or in patches of old conifer forest within 1.0 km of nests. In the eastern Cascades of Washington, radio-marked barred owls selected areas that had larger tree-crown diameters, lower topographic positions, and gentler slopes relative to a set of random landscape locations (Singleton et al. 2010). My findings that habitat use was most strongly associated with large conifer trees (>90 cm dbh) and hardwood trees along streams were consistent with that pattern.

I observed a minor difference in the proportions of different forest cover types within home ranges and core-use areas of spotted and barred owls, with home ranges of barred owls including slightly more riparian-hardwood forest than home ranges of spotted owls. Barred owls were more strongly associated with riparian-hardwood forest at the landscape scale than spotted owls, but this difference diminished at finer scales of investigation. In contrast to spotted owls, foraging barred owls showed equally strong selection for both old conifer and riparian-hardwood forest types and negative selection for steep slopes. Individual spotted and barred owls were occasionally located in young conifer forests at night, and young forests were used significantly more often than nonforested openings by both species. I found no evidence that barred owls used young conifer, nonforest, or riparian-hardwood forest disproportionately more or less than spotted owls did. The best model of nighttime resource selection indicated that individual spotted owls and barred owls differed only in the relative use of distance to nest, old conifer forest, and slope conditions. Models that included a polynomial term for distance to nests were strongly supported for both species, which indicated that owls in my study area selected foraging sites based on proximity to nest, at least during the breeding season. Consistent with the differences I observed in home range size and seasonal movements, barred owls selected foraging sites that were considerably closer to their nests than spotted owls did. I also found strong evidence that the 2 species differentially used slope conditions within shared forest cover types across both spatial scales of analysis. This result was similar to previous studies showing that barred owl nests were located on gentler slopes than those used by spotted owls (Herter and Hicks 2000, Gremel 2003, Buchanan et al. 2004, Pearson and Livezey 2003).

High contrast edges, mostly associated with clear-cuts, were an important landscape feature that influenced selection of foraging sites by both owl species at both scales of investigation. Although the effect was slightly stronger for barred owls, I found that the relative probability of a particular location being selected at night increased in a unimodal (convex) relationship with increasing distance to a forest-nonforest edge. Thus, both species appeared to prefer foraging within the interior of forest patches, usually 300–500 m from edges. This finding is in slight contrast to other studies of resource selection by spotted owls in the southern part of their geographic range where they foraged disproportionately along or near edges of forest openings, perhaps in response to high densities of woodrats (Ward et al. 1998, Franklin et al. 2000). In northwestern Washington where woodrats are less abundant, Hamer et al. (2007) evaluated use of forest-nonforest edges by spotted owls and barred owls but found no clear relationship for either species. I had no evidence to suggest that woodrats were more or less abundant near forest edges, but in several cases I did observe individual spotted owls and barred owls foraging along newly created edges bordering active timber harvests. These observations were uncommon and may reflect a short-term response of owls taking advantage of vulnerable prey animals displaced by ongoing timber harvest activities.

Spotted owls and barred owls in my study selected foraging sites that were closer to streams than random locations, and the relative probability of selection decreased linearly with increasing distance to a stream for both species. This result was in contrast to studies conducted in the Washington Cascades, which showed no strong association between resource use by barred owls within their home ranges and proximity to water (Hamer et al. 2007, Singleton et al. 2010). In my study area, small low-order streams were common in lower elevation riparian-hardwood zones and steep, narrow ravines in patches of mature and old conifer trees. Strong selection for habitats near riparian zones has at least 3 explanations. First, cool microclimates associated with stream drainages may be favorable for thermoregulatory purposes during hot, dry summers (Forsman 1976, Barrows 1981). Second, and perhaps more importantly, productive vegetation conditions near streams are likely to support a rich diversity of prey used by both owl species, including woodrats (Carey et al. 1999, Anthony et al. 2003), flying squirrels (Meyer et al. 2005, Wilson 2008), deer mice, and shrews (Verts and Carroway 1998). Stream habitats also provided a diversity of aquatic prey used by barred owls that were rare or absent from diets of spotted owls, such as salamanders, frogs, crayfish, snails, and fish. A third reason that riparian areas were selected may be due to their complex canopy structures that resulted from past fires that burned less intensively along stream corridors than in upslope areas (Reeves et al. 1989, Kauffman et al. 2001). Such structures may provide good perching opportunities for hunting terrestrial or arboreal prey.

Resource selection functions based on marked individuals have recently been used to show how the distribution of prey species can be shaped by predation risk from a dominant predator (Creel et al. 2005, Fortin et al. 2005, Hebblewhite et al. 2005), but few studies have used this approach to examine the functional relationship between the presence of a dominant competitor and patterns of resource selection by its subordinate. Results from my analysis provided strong evidence that descriptions of forest vegetation and physiographic conditions were not always sufficient in characterizing selection of foraging sites by spotted owls, as the presence of barred owls was also an important factor. I found strong support for models that accounted for the locations of barred owl core-use areas, which supported my initial hypothesis that the presence of barred owls would alter resource selection by spotted owls. In contrast, there was little evidence that resource selection by barred owls was influenced by the presence of core-use areas of spotted owls. The best model of resource selection indicated that spotted owls responded to an increased likelihood of encountering core-use areas of barred owls by decreasing the time spent in mature and old forest and intensifying use of riparian-hardwood forests. Additionally, I found that when spotted owls did enter a core-use area of barred owls they were located more frequently within riparian-hardwood forest than other forest types. A possible explanation for the increased use of riparian-hardwood forest by spotted owls in the vicinity of barred owls was that dietary segregation between the 2 species was most apparent in riparian-hardwood forests, as these areas contain a greater diversity of moisture-dependent or aquatic prey species for barred owls that were rarely used by spotted owls.

Spatial avoidance of a dominant competitor by a subordinate is a common feature of many species interactions (Palomares and Caro 1999, Dhondt 2012). I found no direct evidence that spotted owls were injured or killed by barred owls, although I was unable to rule out this possibility in a few cases. The strong support for the covariate representing proximity to barred owls in the best model for habitat selection of spotted owls indicated that the influence of barred owls on resource selection extended beyond the core-use area and into the home range. Risk-sensitive resource selection by spotted owls may represent an attempt to partition resource use spatially, as would be expected if barred owls excluded spotted owls from their core-use areas via territorial aggression (or mutual avoidance), a form of interference competition. Rather than avoiding areas used by barred owls altogether, spotted owls appeared to alter resource selection to balance the probability of agonistic interactions with the potential for energetic benefit. This behavior was consistent with many other studies that show spatial segregation as an important form of niche partitioning among closely related bird species that occupy the same habitats (Cody 1974, Newton 1979, Jaksic 1985, Gerstell and Bednarz 1999, Robinson and Terborgh 1995). Based on these findings, I suggest that the presence of territorial barred owls rendered the preferred habitats of spotted owls less suitable in a manner similar to that of intraspecific territoriality among conspecifics. Competition for space through territorial behavior is a clear example of interference competition (Dhondt 2012).

Diets and Foraging Behavior

As apex predators, spotted owls and barred owls are closely tied to the distribution and availability of their prey. Any explanation of differences in spatial distributions or habitat selection between the species is, therefore, largely dependent on understanding the diets and foraging requirements of each species. Ecological separation of coexisting raptor species is often associated with differences in diet (Steenhof and Kochert 1985, Bosadowski and Smith 1992, Bilney et al. 2011), and diet appeared to be a major contributor to niche differentiation between spotted owls and barred owls for a portion of the year in my study. Although the 2 species broadly overlapped in the suite of mammalian prey used, which represented the majority of dietary biomass, there were distinct differences in the sizes and activity behaviors of their most common prey. Spotted owls primarily captured arboreal and semi-arboreal prey such as flying squirrels, tree voles, and woodrats, whereas barred owls took more terrestrial and aquatic prey such as moles, shrews, salamanders, and crayfish. In addition, a greater proportion of diurnal animals (e.g., Douglas squirrels, birds, reptiles) in diets of barred owls (18%) as compared to spotted owls (4%) suggested that barred owls were more active in the day. Differences in diets of spotted owls and barred owls can only be partially explained by differential habitat use because the 2 species selected broadly similar forest conditions for foraging. Rather, segregation in diets must largely be explained by fundamental differences in foraging behavior between the 2 species, as shown by the high level of separation in the percent contributions of arboreal (52% vs. 26%), terrestrial (26% vs. 48%), and aquatic (0% vs. 4%) prey to dietary biomass of spotted owls and barred owls, respectively. This pattern of food-niche partitioning according to habitat strata was strikingly similar to that reported in a previous study of dietary overlap between spotted and barred owls in northwestern Washington (Hamer et al. 2001). Similar food-niche partitioning according to habitat strata has recently been described for other specialist-generalist owl species that co-occupy similar habitats, including sooty owls (*Tyto tenebricosa*) and powerful owls (*Ninox strenua*) in southeastern Australia (Bilney et al. 2011), and the elegant scops-owl (*Otus elegans*) and Japanese scops-owl (*O. semitorques*) in Japan (Toyama and Saitoh 2011). Collectively, these studies and mine suggest that fine-scale partitioning of vertical space may be an important mechanism contributing to ecological separation between closely related owl species.

Diet composition of spotted owls in my study was similar to that reported for northern spotted owls throughout much of their geographic range in that diets were dominated by flying squirrels, woodrats, tree voles, deer mice, and lagomorphs (Forsman 1976, Barrows 1980, Forsman et al. 1984, 2001, 2004, Ward 1990, Hamer et al. 2001). Diets of spotted owls in my study were also similar to diets described in previous studies conducted in my study area during 1970–1980 (Forsman et al. 1984) and 1990–1995 (Thrailkill et al. 1998). These studies provided a unique historical perspective of spotted owl diets before barred owls had reached high densities in the region. For example, the relative occurrence of flying squirrels in diets of spotted owls remained fairly constant across the 3 different study periods spanning a 39-yr period (1970–1980: 35%; 1990–1995: 44%; 2007–2009: 38%; Forsman et al. 1984, Thrailkill et al. 1998, and my study, respectively), and proportions of other mammal species captured were similar as well.

Barred owls in my study captured a wide diversity of prey species at relatively low frequencies as has been reported elsewhere for this species (Elderkin 1987, Bosakowski and Smith 1992, Hamer et al. 2001). Despite the substantial use of insects, snails, shrews, and other small prey, however, the majority (89%) of biomass in the diets of barred owls was composed of mammals. Particularly important mammals for barred owls in terms of biomass were flying squirrels, lagomorphs (brush rabbits, snowshoe hares), moles, Douglas squirrels, and woodrats. Other important prey items for barred owls in terms of numbers or biomass were red tree voles, deer mice, and salamanders. This was in slight contrast to diets of barred owls in northwestern Washington where the most important prey were snowshoe hares, flying squirrels, Douglas squirrels, and birds (Hamer et al. 2001). Also unlike Hamer et al. (2001), barred owls in my study captured a large number of moles, small- to large-sized salamanders, crayfish, snails, millipedes, and ground beetles.

Although the distribution of prey species in diets of barred owls was considerably more diverse and more even than that of spotted owls, a moderate level of dietary overlap among heterospecific neighbors (42%) and higher level of overlap in use of mammal prey (61%) suggested that the 2 species may compete for food, especially in situations where both species shared the same foraging areas within overlapping home ranges. Flying squirrels, woodrats, and lagomorphs were particularly important prey for both owl species, as these species alone accounted for 81% and 49% of total dietary biomass for spotted owls and barred owls, respectively. Flying squirrels and hares were also identified as important prey for both spotted and barred owls in Washington (Hamer et al. 2001). The degree of dietary overlap between spotted owls and barred owls in my study (42%) was lower than in northwestern Washington during the 1980s (76%; Hamer et al. 2001). Differences in time frames, sample sizes, prey availability, and the manner in which prey species were categorized makes direct comparisons difficult, but these studies do indicate that the level of dietary overlap between these species can vary regionally. In this case, however, differences in dietary overlap may have been partly due to differences in availability of prey, as woodrats have a restricted distribution, and red tree voles do not occur in northwestern Washington (Verts and Carraway 1998).

In my study, indices of dietary overlap were lowest during the breeding season when many barred owls captured large numbers of insects, amphibians, crayfish, or chipmunks that were only seasonally available. When these prey became less available during fall and winter, both spotted owls and barred owls converged on more similar sized prey such as flying squirrels and tree voles, and both species used larger areas, as shown by an increase in home range size. Sample sizes were limited during the nonbreeding season, suggesting that caution in warranted when interpreting the seasonal changes in diets I observed. Nonetheless, an increased level of dietary overlap during the nonbreeding season was consistent with anticipated seasonal changes in prey availability. I also found that spatial overlap between the species varied little among seasons. When viewed collectively my observations suggested that seasonal changes in prey availability may result in changes in the potential for both interference and exploitative competition between the species. For example, a reduced level of interspecific territoriality during winter may decrease direct aggression near nest sites, but additional food constraints may increase exploitation competition for prey. Relative to spotted owls, the larger variety of prey used by barred owls may allow them to take better advantage of daily or seasonal variations in prey availability. The greater dietary diversity of barred owls may also give them a significant advantage over spotted owls during periods of low prey abundance.

I found differences between spotted owls and barred owls in timing and location of foraging activities as well as in the size distribution of prey captured. Despite this evidence of dietary segregation, neighboring barred owls and spotted owls were similar in that: 1) they both captured predominantly nocturnal prey; 2) they both spent much of their time foraging in old conifer forest and riparian areas; and 3) they both relied on many of the same mammal prey for the bulk of their dietary biomass (e.g., flying squirrels, woodrats, lagomorphs, red tree voles, and deer mice); and 4) their foraging areas often overlapped spatially. These similarities indicate a high potential for exploitative competition between the species. The specializations particular to each species and the seasonal differences I observed in dietary overlap further suggested that the intensity of exploitative competition may vary seasonally or spatially with changes in prey availability. The consequences of similar diets associated with older forests is that barred owls may sufficiently reduce the density of spotted owl prey such that space-sharing spotted owls cannot find sufficient food for maintenance and reproduction.

Niche Relationships and Interspecific Territoriality

Species may reduce the potentially adverse effects of interspecific competition in a variety of different ways. For example, they may decrease spatial overlap in resource use with dominant competitors, change their diet, or change their habitat utilization. Coexistence among closely related owl species is often thought to be sustained by separation of diets, space, foraging periods, foraging habitat, or a combination of these factors (see review by Gutiérrez et al. 2007). Measures of niche overlap in my study calculated for neighboring spotted owls and barred owls along space, habitat and food resource dimensions showed that the 2 species were most similar in their use of forest types and habitat selection (81%), followed by diets (43%) and then spatial distributions (18%). Data on habitat selection and dietary composition suggested that riparian-hardwood forests may be an important aspect of resource partitioning between the species, but that selection of mature and old forests was similar as was the use of mammalian prey. The measures of niche overlap I used cannot be used to estimate the intensity of competition; however, they can be used to describe the potential for competition if resources that limit survival or reproduction are in short supply (Abrams 1980, Krebs 1998). Spotted owls and barred owls used patches of old conifer and riparian-hardwood forest in proportions 2–4 times their availability, and the survival rates of both species were positively associated with the proportion of old forest within the home range. These lines of evidence suggest that old conifer forest may represent a limiting resource for both owl species, especially when considered in the context of a high density of territorial barred owls in the study area. In addition, the fact that spotted owls do not breed every year suggests that annual variation in prey abundance limits reproduction, as in many other northern-latitude owl species (Korpimäki 1987, Brommer et al. 2004).

Aside from the minor differences I observed in proportional use of old forest, slope conditions, and riparian areas, spotted owls and barred owls displayed broadly similar patterns of habitat selection at both the landscape and home range scales of investigation. By linking data on habitat selection with concurrent information on owl diets, it was apparent that the 2 species focused on different habitat strata, with barred owls preying more heavily on terrestrial species and spotted owls preying more heavily on arboreal mammals. This finding suggested that segregation in habitat use may have been operating along vertical space (e.g., canopy or understory height), a dimension of resource partitioning that I was unable to examine. This form of trophic partitioning may not have been particularly effective in my study area, however, given the high density of barred owls and constrained availability of the most commonly used forest types.

Spatial segregation between spotted and barred owls, as shown by the general lack of significant overlap among core-use areas, provided additional insight on the niche relationships between these species. When resources are limiting, many bird species will defend their breeding territories not only against conspecifics, but also against individuals of different species (Newton 1979, Jaksic 1985, Van Lanen et al. 2011). The broad similarity in patterns of resource selection in my study suggested that spatial segregation among core-use areas was most likely a result of territorial interactions (interference competition) rather than differences in the way individuals utilized available forest conditions. Spatial avoidance of barred owl nesting areas by spotted owls in my study most likely reflected a combination of indirect (e.g., territorial calling) and direct (e.g., being chased) interactions. The potential for barred owls to physically exclude spotted owls from their territories was demonstrated by Van Lanen et al. (2011), who used a call playback experiment to quantify aggressive vocal and physical behavior of spotted and barred owls during territorial defense. Barred owls in their study responded with higher levels of vocal and physical aggression than did spotted owls when artificial agonistic interspecific interactions occurred, suggesting that barred owls assumed the dominant role during territorial interactions. Van Lanen et al. (2011) concluded that interspecific interference competition was likely occurring in the system and that spotted owls may attempt to reduce the frequency of agonistic interactions with barred owls through spatial avoidance. This appeared to be the case in my study where the smaller subordinate species (spotted owls), appeared to reduce the potential for agonistic interactions through spatial avoidance of core-use areas of barred owls. A high density of barred owls that locate and defend their territories within habitats historically used by spotted owls could be a major obstacle for newly colonizing spotted owls, as has been indicated by several studies of occupancy dynamics (Olson et al. 2005, Kroll et al. 2010, Dugger et al. 2011).

Survival and Reproduction

Although my estimate of annual survival of spotted owls (0.81, SE = 0.05) was lower than that of barred owls (0.92, SE = 0.04), there was only weak support for species-specific differences in survival probabilities. Known-fate estimates of annual survival for spotted owls were within the range of estimates of apparent survival ($\hat{\varphi}$ = true survival × [1 – the probability of permanent emigration]) reported for adult (≥3 yrs old) spotted owls in 2 adjacent demographic study areas in the Oregon Coast Range (Coast Ranges: $\hat{\varphi}$ = 0.86, SE = 0.01; Tyee: $\hat{\varphi}$ = 0.86, SE = 0.01; Forsman et al. 2011:32). Known-fate and apparent survival estimates are typically not comparable (i.e.; $\hat{\varphi} = \hat{S}$ only when permanent emigration is 0), but this comparison was useful because: 1) permanent emigration observed in long-term demographic studies of color-marked spotted owls is typically low (2–3% per year; Forsman et al. 2002); and 2) I had no cases of data censoring due to unknown mortality or emigration of radio-marked owls. I found no published estimates of survival for barred owls, but annual survival of barred owls in my study was slightly higher than what has been reported for adult spotted owls from capture-recapture studies (range = 0.82–0.87; Forsman et al. 2011:32).

In my analysis of factors influencing survival of spotted owls and barred owls, models that included the mean amount of old forest in seasonal home ranges received the strongest support from the data, whereas models that included the effects of sex, time, and spatial overlap with neighboring heterospecifics received considerably less support. The best model of survival suggested that increasing proportions of old forest within the home range had a positive influence on adult survival of both spotted owls and barred owls, an essential component of fitness (Noon and Biles 1990, Sæther and Bakke 2000). Specifically, survival of spotted owls and barred owls declined when the percentage of old forest in seasonal home ranges was <35%, but increases in the cover of old forest above that point had little influence. This finding is similar to the results of Franklin et al. (2000), Olson et al. (2004) and Dugger et al. (2005), who found that apparent survival of spotted owls was positively associated with cover of older forest within concentric circles surrounding nest trees or territory centers. The primary mechanisms through which this relationship is likely to arise is that the structural diversity of old forests may: 1) provide more optimal structure for pursuing and capturing prey; 2) provide greater densities of mammalian prey such as flying squirrels (Carey et al. 1992, Halloway and Smith 2011) and red tree voles; and 3) provide refuges and escape routes from large avian predators (Forsman et al. 1984, Franklin et al. 2000, Hakkarainen et al. 2008).

Despite the uncertainty associated with predation events of spotted owls, I did not find any direct indication that spotted owls were wounded or killed by barred owls. Rather, great horned owls likely predated at least 2 spotted owls in my study. Great horned owls have been identified as a source of mortality for spotted owls in western Oregon (Forsman et al. 1984, Carey et al. 1990). Although great horned owls are also a common predator of barred owls (Mazur and James 2000), predation was not a cause of death for barred owls in my study. Great horned owls were regularly observed within more open habitats or near forest edges in my study area during nighttime surveys and radio-telemetry monitoring activities. Great horned owls are known to include open habitats in their home ranges (Ganey et al. 1997, Grossman et al. 2008), and may prefer highly fragmented landscapes for foraging (Johnson 1993, Rohner and Krebs 1996). In my study area, forest fragmentation was primarily a result of clear-cutting which could increase predation rates on spotted owls by favoring predators that use edges or more open landscapes, such as great horned owls and red-tailed hawks (*Buteo jamaicensis*). Despite this potential, I found no evidence that the amount of time radio-marked owls spent near forest edges was associated with survival for either species.

Barred owl pairs in my study produced over 6 times as many young over a 3-year period than spotted owls. The mean percentage of spotted owl pairs that nested during 2007–2009 (50%, n = 42 nesting opportunities) was similar to previous estimates obtained in my study area during 1990–1995 (44%, *n* = 117 nesting opportunities; Thrailkill et al. 1998:17). However, the mean percentage of nesting pairs that successfully produced young was substantially lower in my study (33%) as compared to this historical study (64%; Thrailkill et al. 1998:17), which reflected a greater nest failure rate in my study. My estimates of the mean number of young fledged per pair of spotted owls ranged from 0.14 in 2008 to 0.54 in 2007, which was at the lower end of historical values reported in the study area before barred owls had reached high numbers (range = 0.09 –1.35; Thrailkill et al. 1998:18). During the first 2 years of the study, the proportion of spotted owl and barred owl pairs that attempted to nest was similar. Thus, the marked difference in fledgling production between species in these years was largely due to a greater rate of nesting failure of spotted owls, as 32–90% of pairs that attempted to nest failed to produce any young. In the third year of the study, the percentage of spotted owls that attempted to nest dropped to 20% whereas the proportion of barred owls that nested increased to 85%. The cause of nesting failures in both species was generally unknown, but in 1 case a radio-marked spotted owl male with nestlings was predated by a great horned owl and the female spotted owl (also radio-marked) subsequently abandoned the nest. In 2 other cases of failed nesting attempts by spotted owls I documented barred owls from adjacent territories within 100 m of active nest trees of spotted owls. In both cases the female spotted owls were recorded off nests during the incubation stage, apparently in response to the presence of a vocalizing barred owl. Whether barred owls were the cause of nest failures of spotted owls was ultimately unknown, but due to the mismatch in the timing of egg-laying between the species it was common for nesting pairs of spotted owls to still be incubating while their nearby barred owl neighbors already had nestlings.

Experimental evidence has shown that interspecific interactions among raptors can influence species-specific reproduction. Krüger (2002), for example, showed that an experimentally increased artificial goshawk (*Accipiter gentilis*) threat near the nests of common buzzards (*Buteo buteo*) substantially decreased reproductive output. Buzzards failing under artificial predation risk also abandoned their territories frequently (Krüger 2002). In my study, inferences concerning the effects of barred owls on reproduction of spatially associated spotted owls were limited by small sample sizes. Moreover, I did not evaluate other factors that can influence reproductive output of spotted owls such as habitat and weather (Franklin et al. 2000, Olson et al. 2004, Glenn et al. 2011b). Despite these potential limitations, I found strong evidence that the number of young fledged by spotted owls decreased with increasing proximity to the nearest barred owl nest or territory center. All spotted owls that attempted to nest within 1.5 km of a concurrently active barred owl nest failed to successfully produce young. Intra-guild predation did not explain this pattern because I found no evidence of predation of adult or nestling spotted owls by barred owls. Rather, joint use of common resources leading to food depletion in combination with territorial interactions with neighboring barred owls during critical stages of nesting may have jointly affected breeding performance of spotted owls, as has been demonstrated for diurnal raptors (Krüger et al. 2002; Carete et al. 2006) and long-eared owls (*Asio otus*; Nilsson 1984). This finding has broad implications for the future conservation of spotted owls, as it suggests that spatial heterogeneity in productivity may not arise solely because of differences among territories in the quality of forest conditions or landscape configurations (e.g., Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005), but also because of the spatial distribution of a now widespread competitor.

Conclusions

Inferences to populations and larger areas beyond my study are somewhat limited by small sample sizes inherent to radio-telemetry research of wide-ranging predatory birds. In addition, the ecological relationships I observed between spotted owls and barred owls within the highly fragmented matrix of federal and industrial forests of western Oregon may not be representative of relationships between these species in more contiguous or drier forests, or in areas where owl densities are different. Despite these potential limitations, my observations of the ecological relationships between spotted owls and barred owls satisfy several of the most stringent criteria proposed for establishing the existence of interspecific competition in birds (MacNally 1983, Wiens 1989, Newton 1998, Dhondt 2012), including: 1) resource use between potential competitors must overlap; 2) resource use of 1 species affects the resource use (availability) of the other; and 3) the fitness potential of individuals is reduced by the presence of individuals of another species. The determination of cause-effect relationships between the presence of barred owls and population declines of spotted owls was not possible with an observational study like mine. Such a determination would have required experimental removal of barred owls from the study area to observe the demographic response by spotted owls (Gutiérrez et al. 2007, Buchanan et al. 2007). Nonetheless, I was able to identify a strong potential for interspecific competition by directly monitoring spatial relationships, habitat selection, diets, survival, and reproduction of sympatric spotted owls and barred owls.

All lines of evidence from my study supported the hypothesis that interference competition with barred owls can interact with other limiting factors to influence vital rates of spotted owls. Both species used patches of older conifer forest for roosting and foraging, both species relied on similar prey associated with these forest types, and the survival of both species was associated with the amount of old forest in their home ranges. These findings highlight the significance of old forest as a potential limiting factor in the competitive relationship between the 2 species. My analyses of species-specific variation in home range size and nighttime resource selection further suggested that barred owls altered patterns of space-use and habitat selection of spotted owls, which may have both direct and indirect consequences to fitness of spotted owls. These results are consistent with reports of a reduction in site occupancy, survival, and fecundity of spotted owls when barred owls were detected in their territories (Kelly et al. 2003, Olsen et al. 2004, 2005, Anthony et al. 2006, Kroll et al. 2010, Glenn et al. 2011a, 2011b, Dugger et al. 2011, Forsman et al. 2011). I also found a high potential for exploitation competition among individual spotted owls and barred owls, as shown by their broadly overlapping spatial distributions and similarities in habitat selection and use of mammalian prey.

Despite a moderate to high level of ecological overlap, spotted owls and barred owls differed in terms of their space-use, habitat selection, foraging strategies, and diets. Patterns of resource selection by spotted and barred owls in my study likely reflected trade-offs between individual goals, such as the need to occupy certain forest types yet avoid obstacles like competitors and predators. Spotted owls may attempt to reduce competitive interactions with barred owls by spatial avoidance, but in doing so they probably limit the amount of resources available to them and may experience increased predation risk. Ultimately, spatial segregation among core-use areas and differences in foraging strategies between spotted owls and barred owls may only be effective mechanisms of resource partitioning in situations where resources are not strongly limiting, or when densities of barred owls are at lower levels that what I observed. With interspecific territoriality acting in conjunction with exploitative competition for a common set of limited resources, high densities of barred owls are likely to have a significant impact on spotted owl populations that are already in flux due to climatic variation or habitat loss. I therefore conclude that an increasing population of invasive barred owls could affect viability of spotted owls both directly (via spatial exclusion from critical resources) and indirectly (via joint exploitation of high-biomass prey and changes in habitat selection that lead to increased risk of mortality).

MANAGEMENT IMPLICATIONS

The addition of species to landscapes is as important to consider in managing wildlife populations as is species loss. Non-native species are second only to direct habitat loss as a threat to imperiled species in the United States (Wilcove et al. 1998), and the combined constraint these stressors can place on wildlife populations has been exemplified by challenges associated with the conservation and management of northern spotted owl populations (Noon and Franklin 2002, Buchanan et al. 2007, Gutiérrez et al. 2007, USFWS 2011). The causes of the barred owl range expansion into western North America are ultimately unknown, but some authors have suggested that landscape changes caused by humans (Livezey 2009) or historical changes in climate (Monahan and Hijmans 2007) enabled barred owl populations to expand beyond their historical geographic range in eastern North America. Clearly, the importance of interspecific competition in natural communities will be an increasingly important consideration in the management of wildlife populations as species' distributions are modified by habitat loss or gain caused by changes in land use and climate (Walther et al. 2002). My results emphasize the value of older conifer forests, large hardwood trees, and moist bottomland riparian areas to resource partitioning between spotted owls and barred owls in the central Oregon Coast Ranges. These findings provide support for the conclusions of Dugger et al. (2011) and Forsman et al. (2011) in that the existence of a new and potential competitor like the barred owl makes the protection of old forest habitat even more important because any loss of habitat will likely further constrain the 2 species to the same set of limited resources, thereby increasing competitive pressure and leading to further negative impacts on spotted owls. In addition, my analyses suggested that old forests represented high quality habitat for both owl species in terms of its influence on adult survival, which is the demographic parameter that most strongly influences population growth rate of spotted owls (Noon and Biles 1990). This finding, along with evidence that the presence of barred owls reduced the amount of old forest available to spotted owls, suggests that spatially structured social aspects such as the presence and distribution of a widespread competitor constitutes an emergent and critically relevant aspect of habitat quality for spotted owls.

Managers should be cautious about extrapolating my results beyond the central Oregon Coast Ranges, where I estimated that barred owls outnumbered spotted owls by more than 4:1. In areas where barred owls currently occur at lower density (e.g., southern Oregon, northern California), it is possible that they are still in the early colonization phase of invasion and their presence may have negligible effects on spotted owls. Alternatively, there is a continuum of mesic and xeric forest types within the range of the spotted owl which some authors have suggested may inhibit barred owls from attaining high densities in the drier forests occupied by spotted owls (Peterson and Robins 2003, Gutiérrez et al. 2004). Patterns of resource partitioning are likely to be different in dry forests as compared to those observed in my study, and no information currently exists on resource selection by barred owls within the southern portion of the spotted owl's range. I recommend a stronger research emphasis on resource partitioning in these regions. In addition, based on differences between spotted and barred owls in their use of prey associated with different habitat strata, it appeared that segregation in habitat use may have been operation along vertical space (e.g., canopy or understory height). Future studies could examine the relative importance of vertical forest structure to spotted owls and barred owls by using remote sensing technologies that characterize above-ground forest structure (e.g., light detection and ranging [LiDAR]).

Barred owls in my study area exhibited numeric and demographic superiority over spotted owls. Under these circumstances, the level of ecological segregation I observed may not be effective in allowing sustained coexistence between the 2 species in my study area. As outlined by Buchanan et al. (2007), there are clear limitations to the actions that can be taken to control barred owls and their negative impact on spotted owls. While it unknown if removal of barred owls is an effective and feasible means of reducing competitive pressure, it is clear from my analyses and others (e.g., Dugger et al. 2011) that further loss of contiguous older forests on the landscape with an increasing population of barred owls can act synergistically to increase competitive pressure and negatively affect spotted owls. My finding that older riparian-hardwood forests played an important role in niche segregation between the 2 species emphasizes the need to consider these forest conditions within a management context, as these forests are likely to promote a wide diversity of prey for both species but are shorter-lived than conifer forests due to normal succession. Results from my study indicated a strong potential for interference competition between spotted owls and barred owls, and that high quality habitat and associated prey species are likely to be the most strongly limiting factors in the competitive relationship. Experimental control of the barred owl population in at least 1 study area is required to verify my results and to test the hypothesis that the presence of barred owls limits the population growth rate of spotted owls. My analyses suggest that competitive release from barred owls should result in subsequent decreases in space use and energy expenditure and increases in site occupancy and reproductive output, but only if sufficient nesting, roosting, and foraging habitats are available for re-occupancy by spotted owls and their prey. Experimental removal of barred owls may also provide an answer to whether there are sufficient numbers of nonbreeding spotted owls available in landscapes to re-colonize historical nesting territories. Landscape-scale experiments could be designed to determine whether population control of barred owls at high densities is even possible, and if so what level of control would be required to maintain different levels of population growth for spotted owls.

As a generalist predator and fiercely territorial invader, barred owls at high densities have the potential to affect a variety of native wildlife through competition, niche displacement, and predation. Total impact of an invasive predator on native species might be a function of both increased predator abundance and prey susceptibility as habitats are modified (Didham et al. 2007). Land managers and researchers should be aware of the potentially cascading effects that increasing populations of barred owls may have on the native wildlife community beyond spotted owls, and my study provides a baseline sample of prey species in western Oregon that could be susceptible.

SUMMARY

1. Repeated surveys of spotted owls and barred owls in a 975 km^2 forested study area in western Oregon, USA, showed that the number of territories occupied by pairs of barred owls (82) greatly outnumbered those occupied by pairs of spotted owls (15).
2. Home ranges of spotted owls estimated for breeding, nonbreeding, and annual time periods were 2–5 times larger than those estimated for barred owls.
3. Inter-specific home range overlap was higher than intra-specific home range overlap among owls radio-marked in adjacent territories. I observed a moderate to high level of interspecific space-use sharing within home ranges of neighboring pairs of spotted and barred owls, but minimal spatial overlap among core-use areas.
4. The probability of locating a barred owl in the home range of a neighboring spotted owl was higher than the probability of locating a spotted owl within the home range of a neighboring barred owl. This directional pattern of spatial overlap was consistent among sexes, seasons, and years. Spatial segregation between the 2 species' core-use areas was suggestive of interference (territorial) competition.
5. I found a strong, positive association between annual home range size of spotted owls and the probability of barred owl presence within the home range, suggesting that spotted owls responded to an increased likelihood of space-use sharing with neighboring barred owls by expanding their movements to include other areas.
6. Both species used patches of old (>120 yrs old) conifer forest in proportions 2–5 times greater than their availability, and both species showed strong selection for riparian-hardwood forest along streams, especially for foraging. Barred owls used available forest types more evenly than spotted owls, but were most strongly associated with patches of large hardwood and conifer trees that occupied relatively flat areas. Conversely, spotted owls spent a disproportionate amount of time foraging and roosting in large (>50 cm dbh) conifer trees along steep slopes in ravines. Mean overlap among spotted and barred owls in proportional use of different forest types was high (81%, range = 30–99%).

7. Spotted owls generally avoided areas that were heavily used by barred owls while foraging, as shown by a decline in the relative probability of selection as the distance to the nearest barred owl core-use area decreased.
8. Barred owls foraged opportunistically across a broad range of prey sizes and types, whereas spotted owls specialized on arboreal mammals associated with mature and old forests. Flying squirrels, woodrats, and lagomorphs were among the most important prey items for both owl species in terms of dietary biomass. Mean interspecific dietary overlap among neighboring pairs of spotted and barred owls was moderate (42%; range = 28–70%).
9. Barred owls exhibited demographic superiority over spotted owls; the estimated annual survival probability was greater for barred owls (0.92, SE = 0.04) than for spotted owls (0.81, SE = 0.05), and annual reproductive output of barred owls was 6–9 times greater than that of spotted owls.
10. The percent cover of old forest habitat within the home range was positively associated with seasonal (6-mo) survival probabilities of both owl species. I found no evidence that spotted owls were killed or predated by barred owls, and survival probabilities of spotted owls were not strongly influence by the amount of spatial overlap with barred owls in adjacent territories.
11. The number of young fledged per pair per year by spotted owls decreased linearly with decreasing nearest-neighbor distances between the nest sites of the two species, and no spotted owls that attempted to nest within 1.5 km of a concurrently active barred owl nest successfully produced young.
12. My study provided strong support for predictions concerning a negative effect of barred owls on movements, resource selection, and reproduction of spotted owls. My study cannot be used by itself to directly assess whether barred owls are responsible for ongoing declines in spotted owl populations, but my results can be considered in concert with well-designed experiments to help inform decisions regarding the future management of spotted owls and their habitats.

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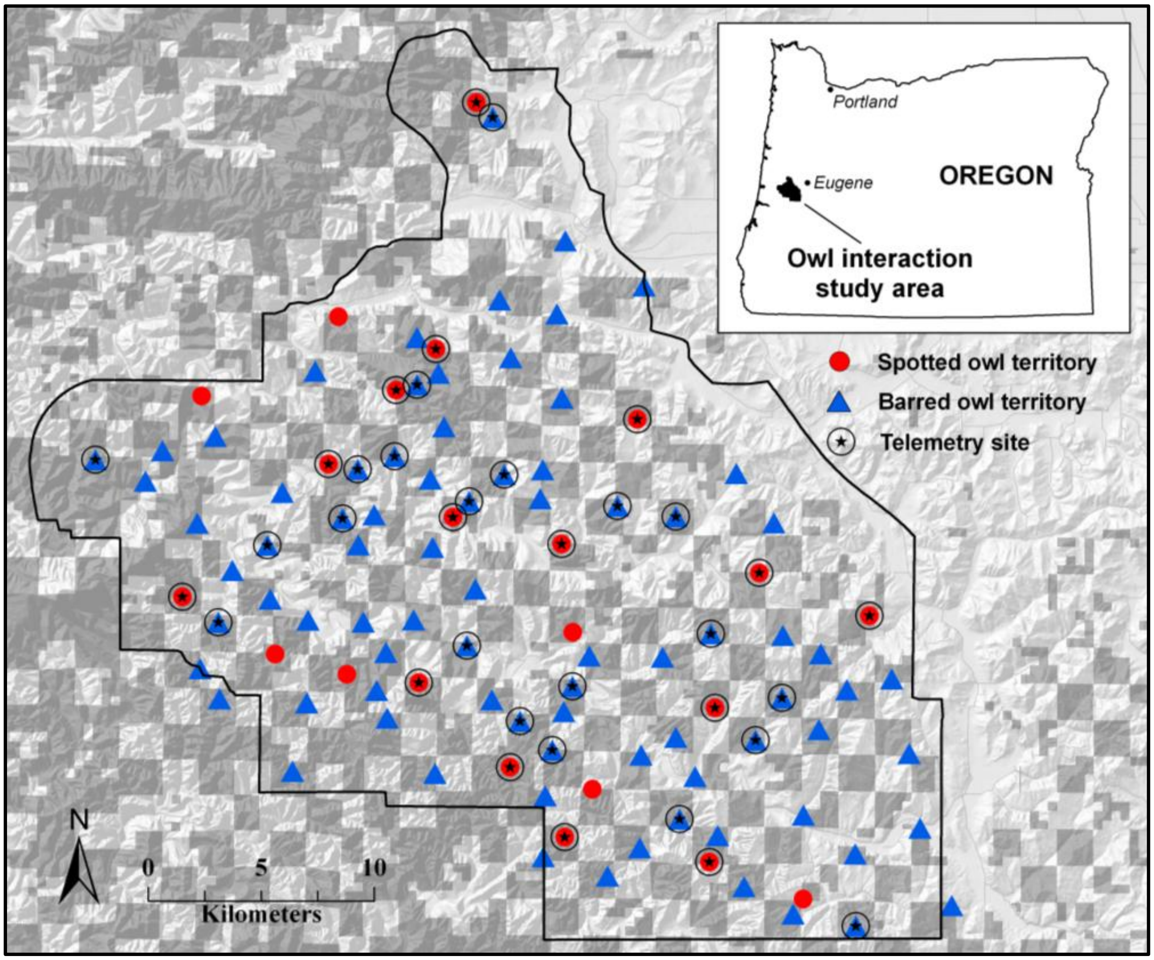

Figure 2.1. Distribution of territories occupied by northern spotted owls and barred owls on the owl interaction study area in western Oregon, USA, 2007–2009. Also shown are sites where ≥1 owl was radio-marked. Dark grey areas indicate federal or state ownership and light grey areas indicate private or county lands.

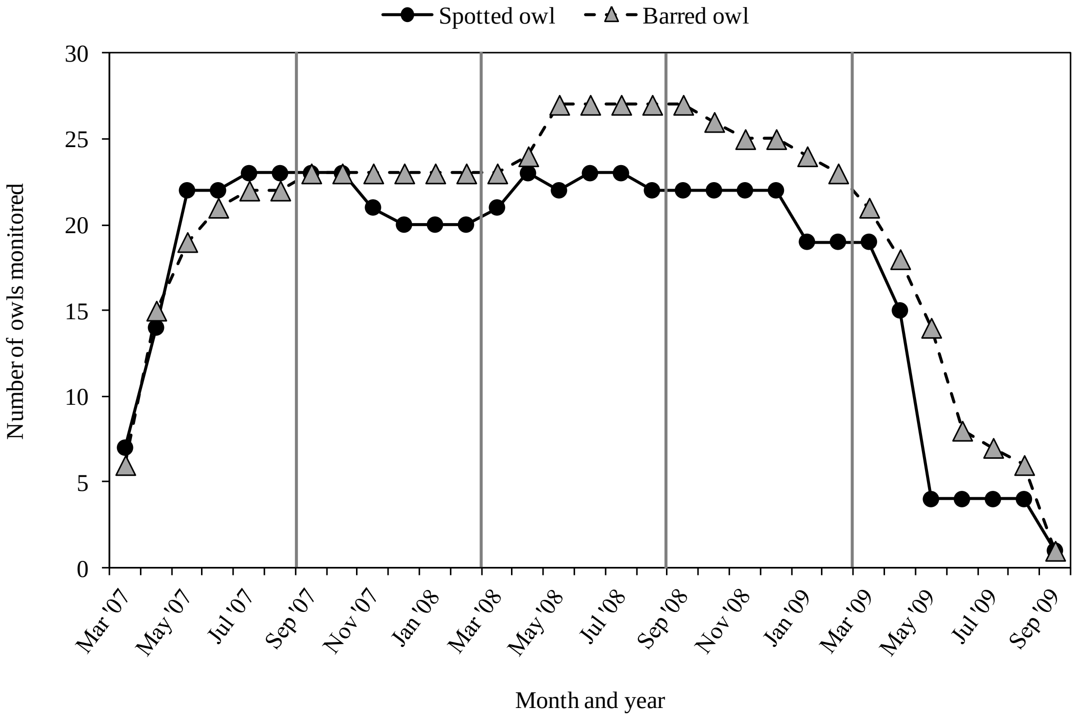

Figure 3.1. Tracking periods for 28 northern spotted owls and 29 barred owls radio-marked in western Oregon during March 2007–September 2009. Vertical lines indicate 6-month time intervals used to distinguish between breeding and nonbreeding seasons of each year.

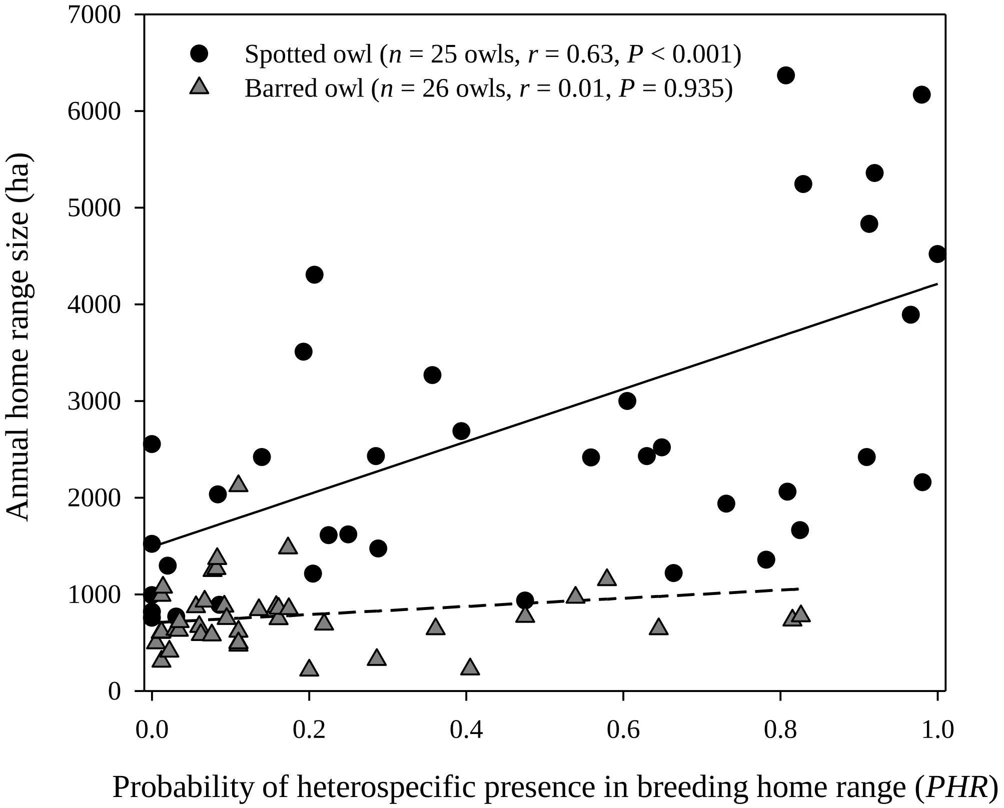

Figure 3.2. Annual home range size of individual northern spotted owls was positively associated with the probability of barred owl presence within their breeding season home range in western Oregon, 2007–2009. This relationship was neutral for barred owls. Prediction lines are from the best-fitting model (Table 3.5) used to examine variation in annual home range size, Spp + *PHR* + (spp × *PHR*).

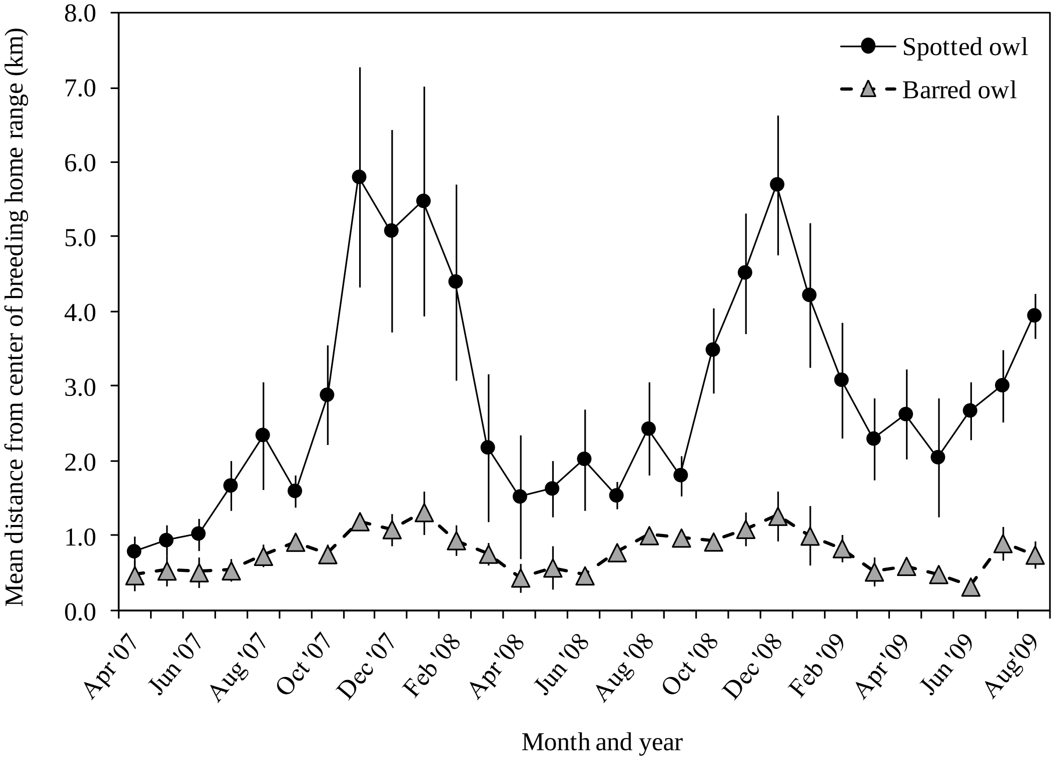

Figure 3.3. Monthly variation in the mean distance between foraging locations used by radio-marked northern spotted owls or barred owls and the center of each owl's breeding home range in western Oregon, 2007–2009. Shown are weighted means and standard errors (vertical bars) estimated from individual spotted and barred owls, subdivided by month. The center of each owl's breeding home range was the current year's nest location or the mean center of roosting locations used during 1 March–31 August of each year. Estimates do not include incubating females.

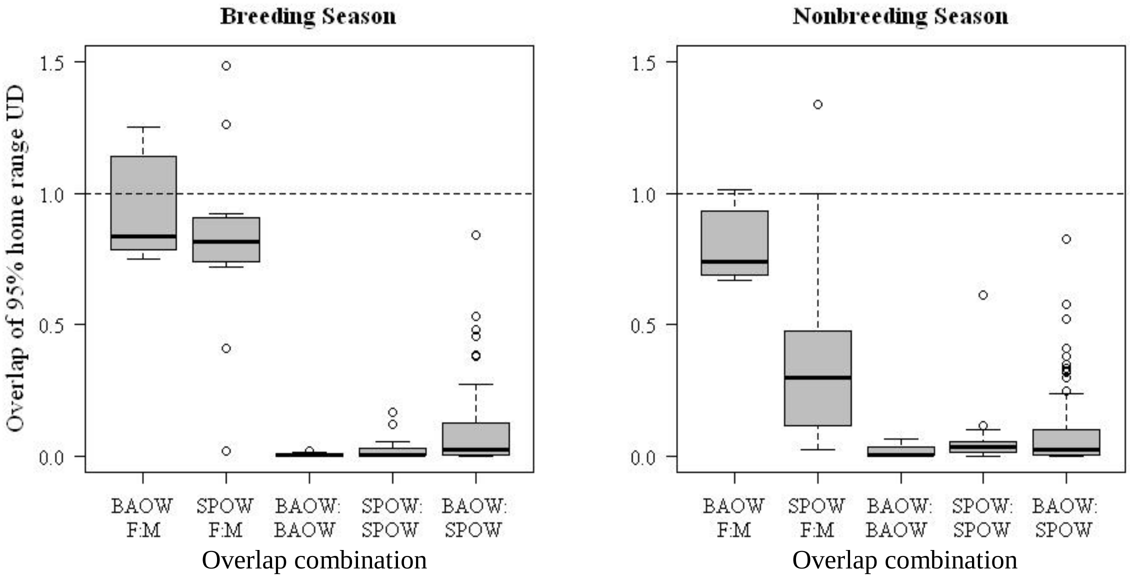

Figure. 3.4. Seasonal estimates of intra- and inter-specific overlap among the 95% fixed-kernel utilization distributions (UD) of space-sharing northern spotted owls (SPOW) and barred owls (BAOW) in western Oregon, 2007–2009. Overlap combinations included paired females and males (F:M), conspecific neighbors (BAOW:BAOW, SPOW:SPOW), and heterospecific neighbors in adjacent nesting territories (BAOW:SPOW). Values range from 0 (no overlap) to 1 (100% overlap), except in cases where the 2 UDs have an unusually high degree of overlap, in which case the value is >1. Boxes bound the 25th and 75th percentiles of the overlap statistic, solid line within the box indicates the median, and the whiskers extend to 1.5 times the interquartile range of the observations. Dots indicate extreme values.

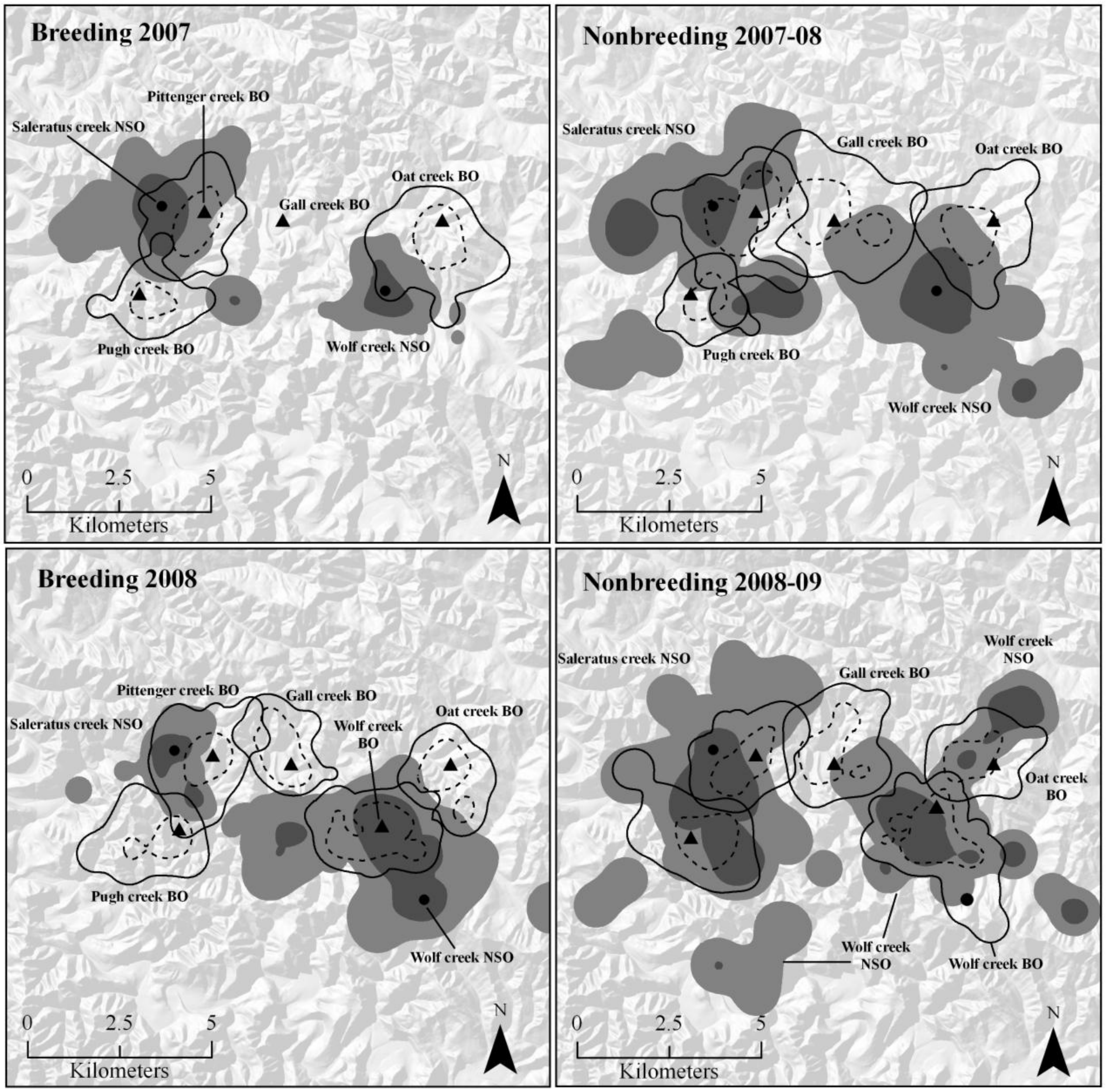

Figure. 3.5. Example of spatial overlap among 2 pairs of northern spotted owls and 5 pairs of barred owls radio-marked in western Oregon from March 2007–August 2009. The 95% fixed-kernel home ranges and core-use areas of spotted and barred owls are indicated by shaded and open polygons, respectively. Also shown is the current year’s nest location or breeding season activity center for each pair of owls (dots = spotted owls, triangles = barred owls). Note change in location of the activity center for the Wolf creek spotted owl pair before (2007) and after the arrival of the Wolf creek barred owl pair in early spring of 2008.

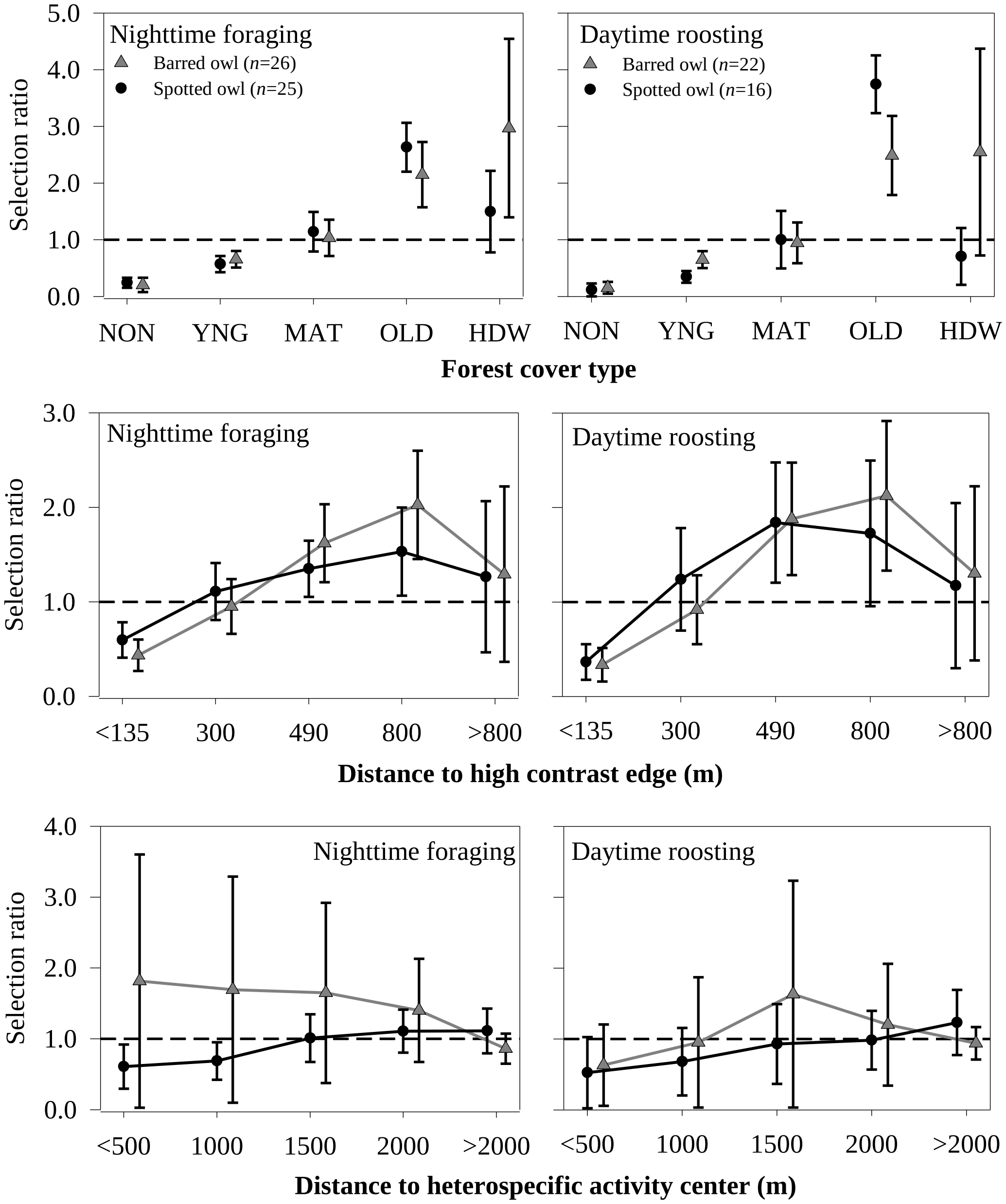

Figure 3.6. Mean landscape-scale selection ratios ($\hat{w}_i$ ± 95% Bonferroni confidence interval) for different environmental conditions used for foraging or roosting by sympatric northern spotted owls and barred owls in western Oregon, 2007–2009. The dashed horizontal line indicates the level at which use is equal to availability; values with confidence intervals >1 indicate positive selection, values with confidence intervals <1 indicate avoidance. Forest types were nonforest (NON), young conifer (YNG), mature conifer (MAT), old conifer (OLD), and riparian-hardwood (HWD).

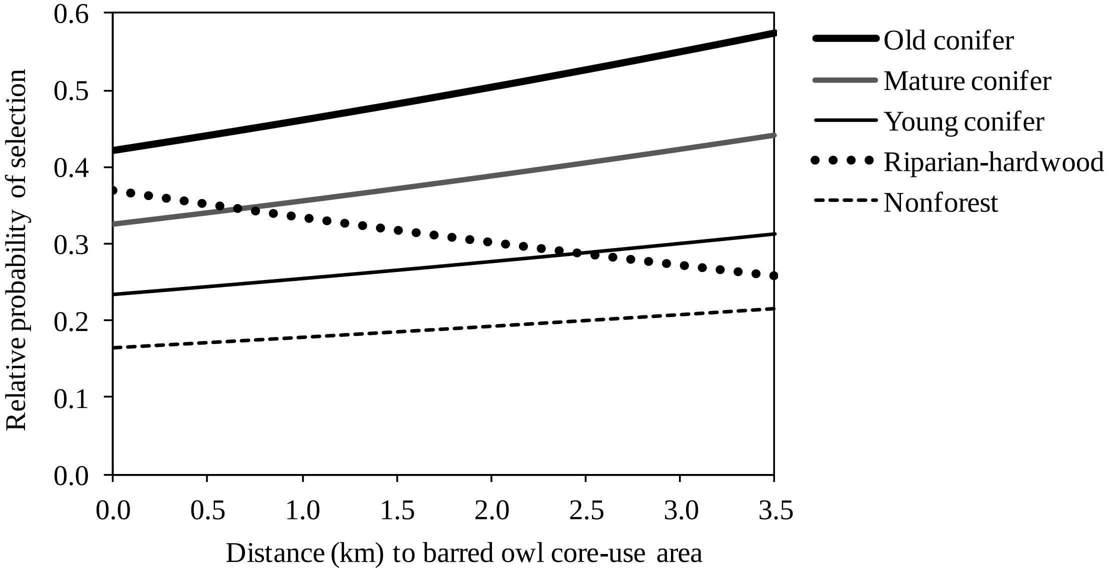

Figure 3.7. Relative probability of a location being selected at night by a northern spotted owl as a function of forest type and proximity to the nearest barred owl core-use area in western Oregon, 2007–2009. Predicted values are from the best discrete-choice model of resource selection for spotted owls. Covariates not plotted were held constant at their median values.

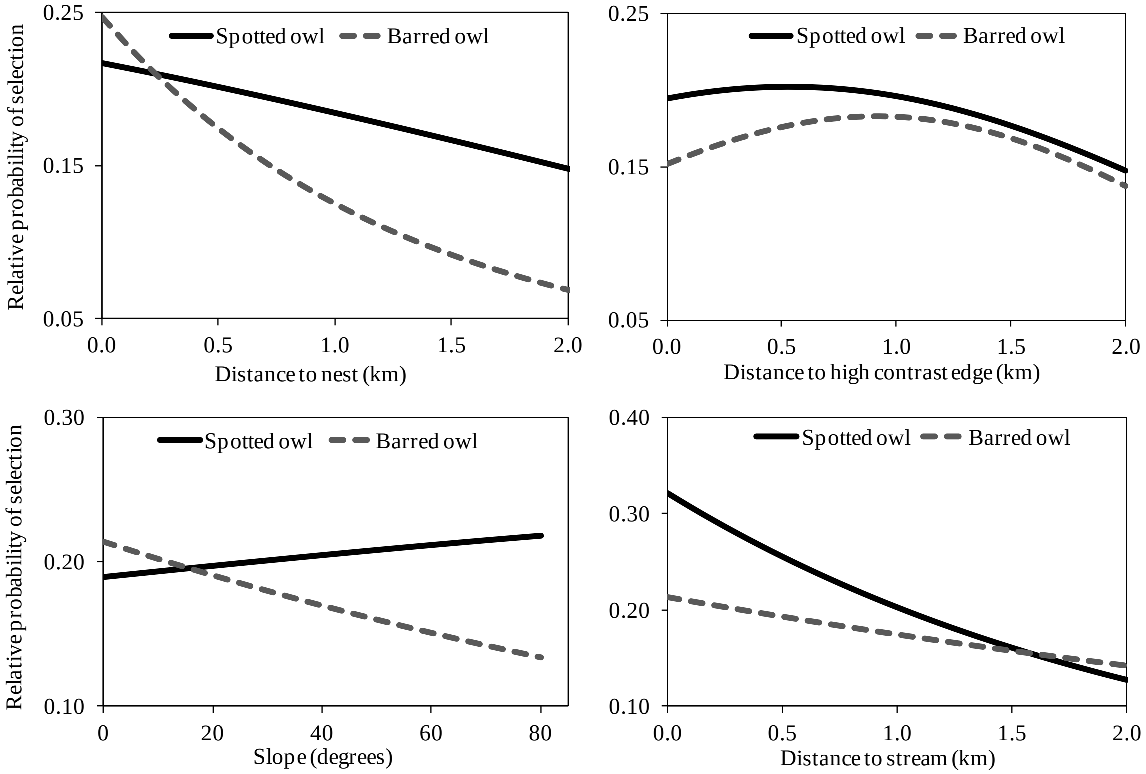

Figure 3.8. Predicted relationships for environmental covariates included in the best discrete choice model of nighttime resource selection within the home range by sympatric northern spotted owls and barred owls in western Oregon, 2007–2009. Predicted values are shown for the old conifer forest type; variables not plotted were held constant at their median values.

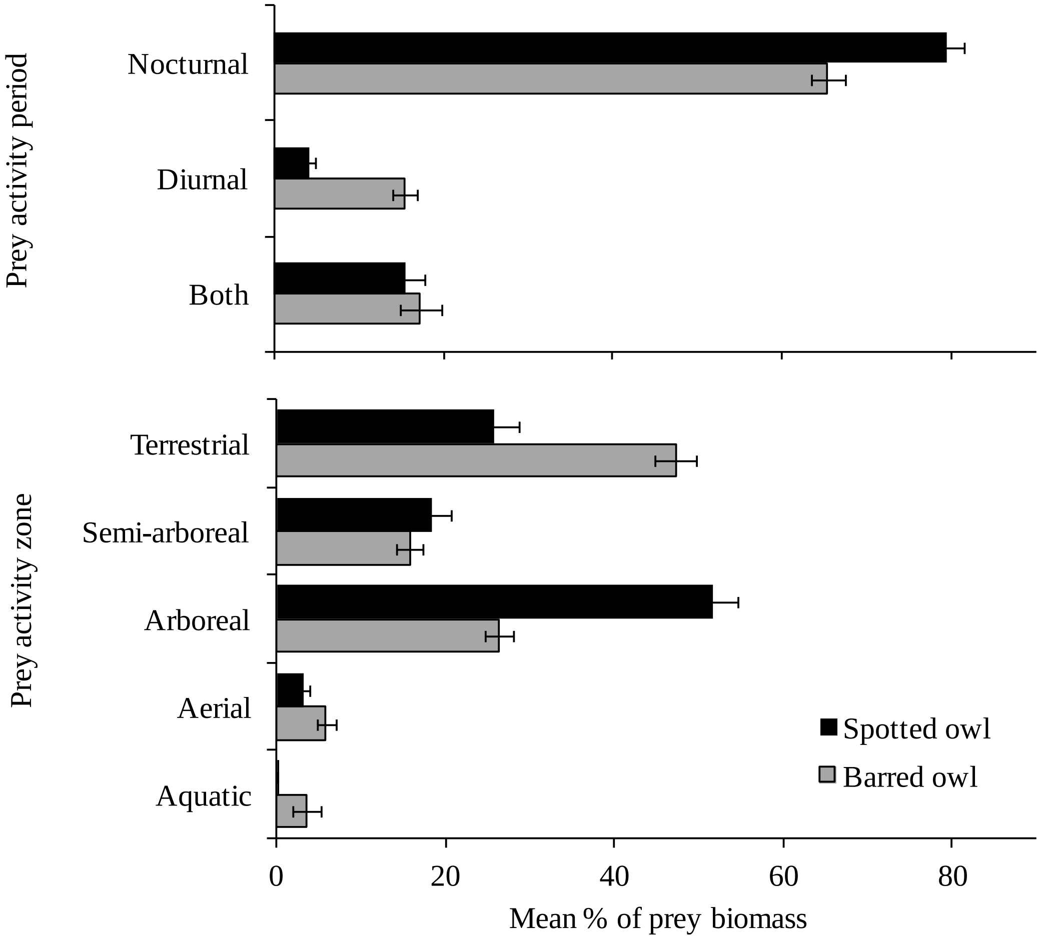

Figure 3.9. Diets (mean percent of prey biomass per territory ± SE) of northern spotted owls and barred owls in western Oregon, 2007–2009, categorized by the primary activity period and activity zone of prey species identified in owl pellets. Diets were estimated from pellets collected at 15 and 24 territories occupied by spotted and barred owls, respectively.

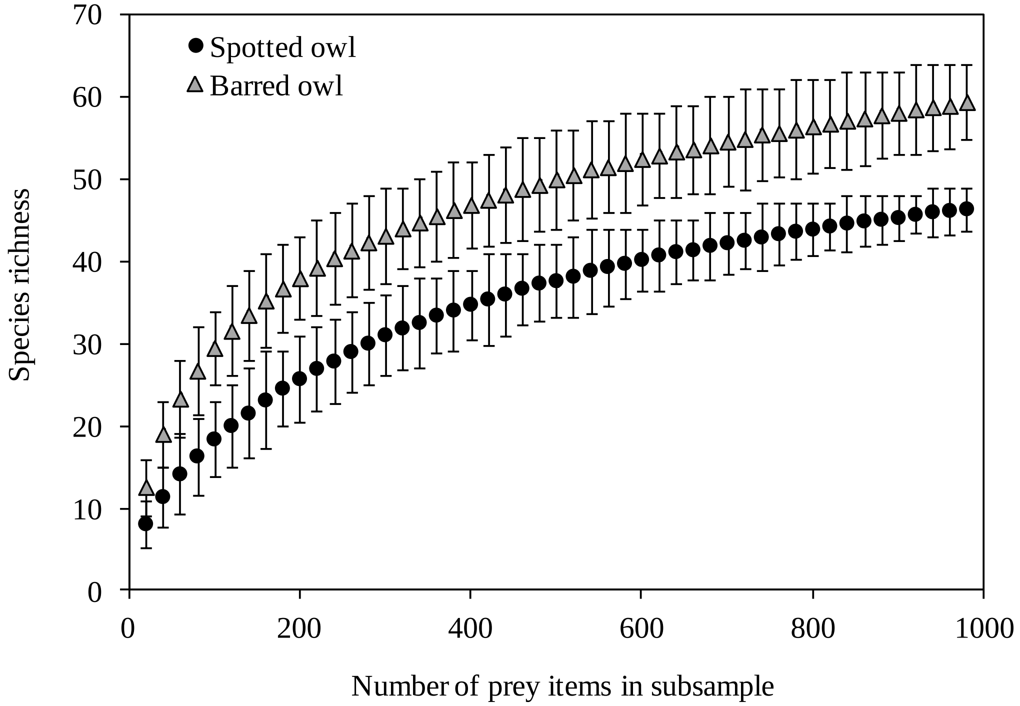

Figure 3.10. Rarefaction curves illustrating differences in expected number of prey species captured by northern spotted owls or barred owls over a range of simulated sample sizes. Point estimates and 95% confidence intervals were estimated from 2,000 repeated randomizations of observed diets in western Oregon, 2007–2009.

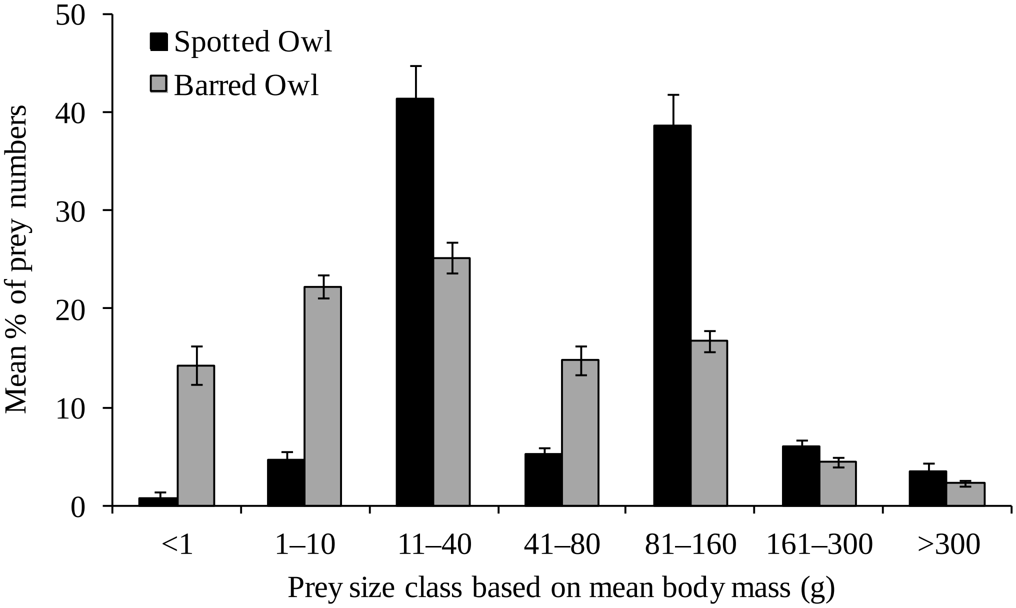

Figure 3.11. Dietary overlap between neighboring pairs of northern spotted owls (*n* = 15) and barred owls (*n* = 24) in western Oregon, 2007–2009, based on the mean percentage (±SE) of prey captured in different size classes.

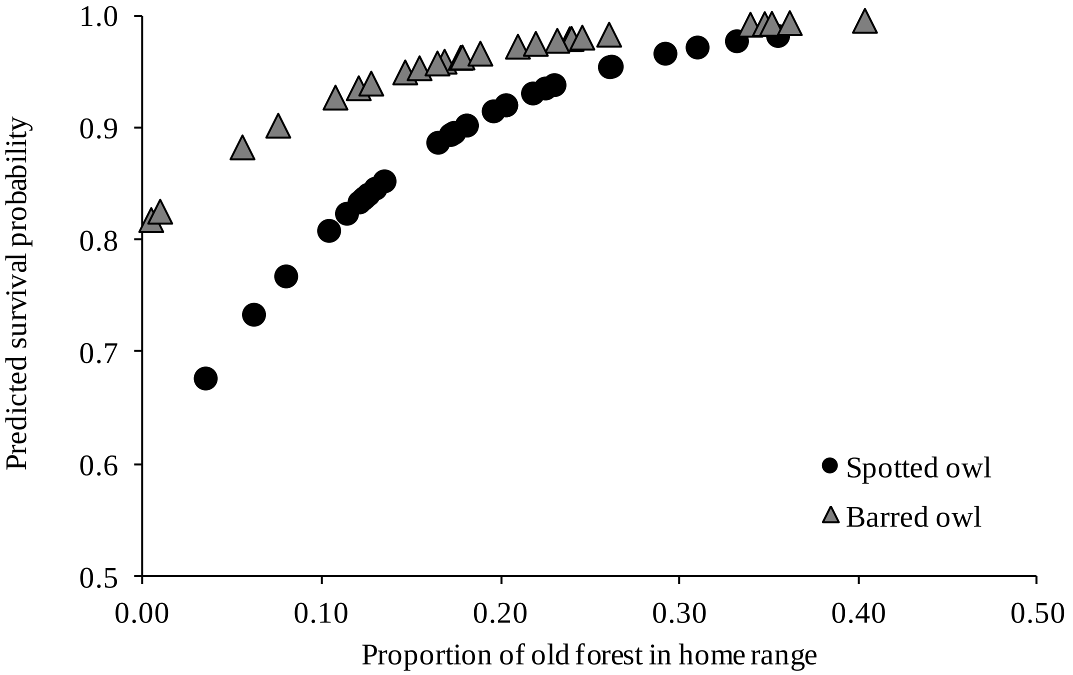

Figure 3.12. Predicted relationship between mean proportion of old conifer forest within the home range and survival probabilities of radio-marked northern spotted owls (n = 29) and barred owls (n = 28) in western Oregon, 2007–2009. Survival estimates were based on 6-mo time intervals; point estimates are from the best-supported model of survival, {*S*(Spp+old)}.

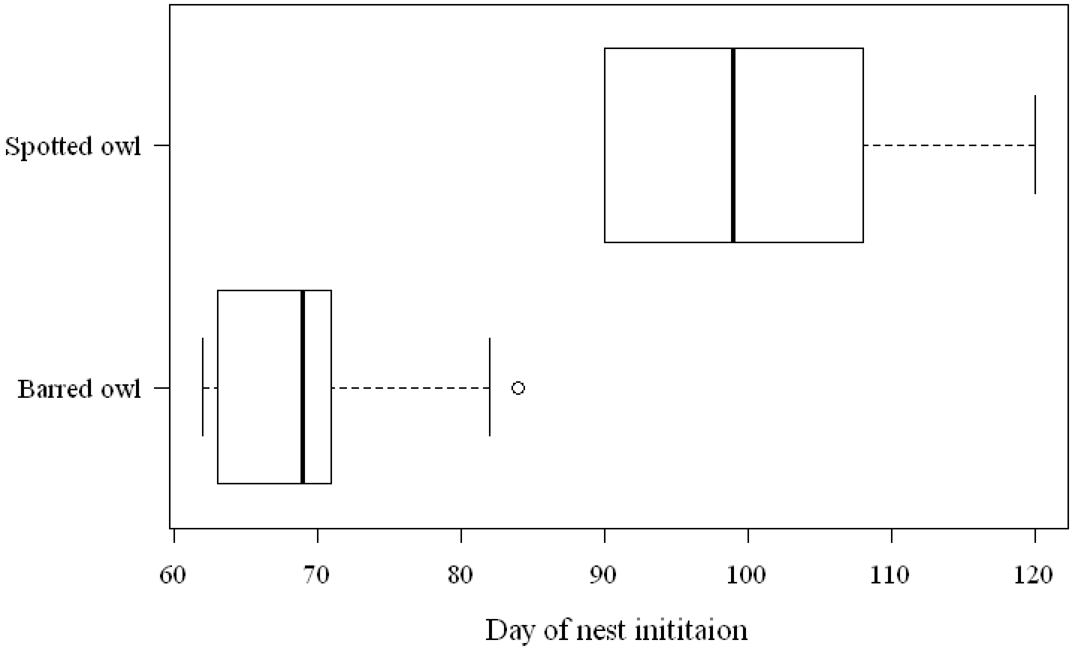

Figure 3.13. Ordinal date (day 1 = 1 January) of nest initiation for radio-marked northern spotted owls (*n* = 10) and barred owls (*n* = 13) in western Oregon, 2007–2009. The date of nest initiation was the first day in which a radio-marked female was detected on a nest. Boxes bound the 25th and 75th percentiles, solid line within the box indicates the median, and the whiskers extend to 1.5 times the interquartile range of the observations. Dots indicate extreme values.

Table 2.1. Forest cover types, environmental conditions, and interspecific covariates used to characterize resource selection by sympatric northern spotted owls and barred owls in western Oregon, 2007–2009.

Covariate	Abbreviation	Description
Forest cover type[a]		
Old conifer	OLD	Multilayered forests of large to giant-sized Douglas-fir, western hemlock, and western redcedar with dominant overstory trees >120 yrs old and >90 cm dbh.
Mature conifer	MAT	Forests of medium-sized Douglas-fir, western hemlock, and western redcedar with dominant overstory trees 60–120 yrs old and 50–90 cm dbh.
Young conifer	YNG	Single-layered forests of small-sized Douglas-fir, western hemlock, and western redcedar trees <60 yrs old and 2.5–50 cm dbh. Included even-aged stands managed for timber production on private ownership.
Riparian/hardwood	HDW	Riparian forests dominated by red alder, bigleaf maple, and variable amounts of western redcedar and Douglas-fir. Also included patches of lowland forest with >60% cover by hardwood trees and shrubs.
Nonforest	NON	Recent clear-cuts dominated by bare soil, grasses, shrubs, or seedling trees <2.5 cm dbh. Also included roads, meadows, agricultural lands, and residential areas.
Forest structural covariates[b]		
Density of large conifers	TPHcon50	Density of all live conifers ≥50 cm dbh (trees/ha).
Basal area of hardwoods	BAhdw	Basal area of all live hardwoods ≥2.5cm dbh (m^2/ha).
Quadratic mean diameter	QMDcon	Quadratic mean diameter of dominant and co-dominant conifers (cm).
Canopy cover of hardwoods	CANCOVhdw	Canopy cover of all hardwood species ≥2.5 cm dbh (%).

Table 2.1 (Continued)

Abiotic covariates		
Slope	slope	Slope gradient in degrees, derived from a 10-m resolution digital elevation model using ArcGIS spatial analyst (version 9.3.1).
Distance to high contrast edge	dedge	Distance (km) to nearest edge between mature or old conifer forest and nonforest.
Distance to stream	dstream	Distance (km) to nearest permanent stream or river extracted from the United States Geological Survey National Hydrography Dataset for the state of Oregon (USGS 2010).
Distance to nest	dnest	Distance (km) to nest tree or center of roost locations used during the breeding season. This year-specific variable was used to account for non-uniform use of space within the home range (Rosenberg and McKelvey 1999).
Interspecific covariates		
Proximity to heterospecific core-use area	dHET	Distance to nearest heterospecific neighbor's breeding season core-use area (km). Core-use areas were delineated as the area of concentrated use by radio-marked owls, or the area within a 620 m (barred owls) or 800 m (spotted owls) radius of the activity center used by a pair of unmarked owls.
Heterospecific core-use area	HETcore	Discrete variable for locations that were inside (1) or outside (0) the perimeter of a heterospecific neighbor's core-use area.

[a] Forest cover types were derived from an object-based classification of 1-m resolution aerial imagery taken in 2009 (see Appendix B for details).

[b] Forest structural covariates were derived from the 2006 regional gradient nearest neighbor (GNN) maps of vegetation composition and structure (Ohmann and Gregory 2002; www.fsl.orst.edu/lemma). Values were calculated as the mean of 30×30m pixel values contained within forest patches derived using object-based classification methods (see Appendix B for details).

Table 3.1. Results of annual surveys conducted for northern spotted owls and barred owls in western Oregon, 2007–2009, including the number of territories and individual owls under radio-telemetry study.

	Survey results					Radio-telemetry monitoring	
Year and species[a]	Historical territories surveyed[b]	No. with pairs (%)[c]	No. with single owls	Additional territories[d]	Total territories occupied by ≥1 owl	Territories with ≥1 owl radio-marked	Owls with radio-transmitters
2007							
Spotted owl	42	14 (33)	2	0	16	13	24
Barred owl	42	27 (64)	2	6	35	19	23
2008							
Spotted owl	49	12 (25)	3	2	17	14	23
Barred owl	49	31 (63)	0	9	40	19	24
2009							
Spotted owl	52	15 (29)	2	1	18	12	18
Barred owl	52	48 (92)	2	32	82	19	23

[a] Annual time periods are from 1 March–28 February. Survey effort for barred owls increased each year and included the entire study area in 2009.

[b] Historical territories were areas that were historically occupied by a pair of spotted owls at least once during 1969–2006.

[c] Percentage of historical territories surveyed that were occupied by owl pairs.

[d] Additional territories were those identified with pairs of owls in areas >2.5 km from the center of historical territories.

Table 3.2. Home range size (ha) of individual northern spotted owls and barred owls in western Oregon, 2007–2009. Home ranges were calculated using the 95% fixed-kernel estimator with likelihood cross-validation.

		All owls			Females			Males		
Time period[a]	*n* (F, M)[b]	Mean	SE	(Min.–max.)	Mean	SE	(Min.–max.)	Mean	SE	(Min.–max.)
Annual										
Spotted owl	26 (12, 14)	2,813	290	(754–8,040)	3,165	490	(767–8,040)	2,507	332	(754–6,470)
Barred owl	27 (13, 14)	879	110	(213–4,887)	737	77	(213–1,367)	1,015	201	(496–4,887)
Breeding										
Spotted owl	23 (10, 13)	1,620	193	(217–4,880)	1,508	288	(217–4,880)	1,712	265	(341–4,615)
Barred owl	26 (12, 14)	556	41	(143–1,416)	487	57	(143–1,111)	614	57	(265–1,416)
Nonbreeding										
Spotted owl	24 (12, 12)	2,688	273	(237–7,458)	3,008	450	(237–7,458)	2,351	292	(725–4,808)
Barred owl	26 (12, 14)	1,028	139	(275–5,999)	874	114	(275–2,144)	1,168	243	(450–5,999)

[a] Annual=1 Mar–28 Feb; breeding=1 Mar–31 Aug; nonbreeding=1 Sep–28 Feb.

[b] Number of owls (females, males).

Table 3.3. Mean size (ha) of combined male and female home ranges and core-use areas for territorial pairs of northern spotted owls and barred owls during the breeding season (1 March–1 September) in western Oregon, 2007–2009.

		100% MCP[a]			95% fixed kernel[a]			Core-use area[a]			
Species	*n*[b]	Mean	SE	(Min.–max.)	Mean	SE	(Min.–max.)	Mean	SE	(Min.–max.)	Proportion[c]
Spotted owl	13	1,881	291	(482–4,103)	1,843	295	(534–4,106)	305	59	(74–668)	0.19
Barred owl	10	581	74	(277–1,155)	846	72	(556–1,318)	188	29	(85–347)	0.22

[a] Estimated as the union (total area) of the minimum convex polygon (MCP), 95% fixed-kernel, or core-use area estimated for male and female members of each pair. Core-use areas were estimated as the overused portion of the breeding home range relative to a uniform distribution of space-use (Bingham and Noon 1997).

[b] Number of owl pairs.

[c] Size of the core-use area divided by the size of the 95% fixed-kernel home range.

Table 3.4. Mean proportion of different forest cover types in the breeding season core-use area, 95% fixed-kernel home range, and the region of spatial overlap for space-sharing northern spotted owls and barred owls in western Oregon, 2007–2009.

		Proportion of area occupied by forest type[a]					
		Core-use area		Home range		Overlap region	
Forest type	Species	Mean	SE	Mean	SE	Mean	SE
Old conifer	Spotted owl	0.396	0.026	0.223	0.015	0.293	0.026
	Barred owl	0.335	0.027	0.230	0.019		
Mature conifer	Spotted owl	0.199	0.026	0.213	0.019	0.161	0.016
	Barred owl	0.215	0.023	0.190	0.015		
Young conifer	Spotted owl	0.259	0.029	0.345	0.021	0.368	0.024
	Barred owl	0.299	0.026	0.362	0.023		
Riparian-hardwood	Spotted owl	0.063	0.011	0.055	0.006	0.101	0.014
	Barred owl	0.115	0.020	0.107	0.013		
Nonforest	Spotted owl	0.083	0.094	0.169	0.015	0.080	0.015
	Barred owl	0.036	0.063	0.121	0.016		

[a] See table 2.1 for a description of forest types. Proportional forest composition of the study area in 2009 was 0.170 (old conifer), 0.223 (mature conifer), 0.340 (young conifer), 0.048 (riparian-hardwood), and 0.208 (nonforest).

Table 3.5. Ranking of models used to examine variation in the size of annual home ranges of northern spotted owls and barred owls in western Oregon, 2007–2009.

Model[a]	K^c	$-2\log L^b$	$\Delta \text{AIC}_c{}^c$	AIC_c wt[c]
Spp + *PHR* + (spp × *PHR*)	8	1,350.6	0.0	0.88
Spp + OLD + *PHR*	7	1,355.8	5.1	0.07
Spp + *PHR*	6	1,358.5	5.5	0.06
PHR	4	1,382.6	18.8	0.00
Spp + yr + (spp × yr)	11	1,382.7	32.0	0.00
Spp	5	1,390.0	34.2	0.00
Spp + OLDER + (spp × OLDER)	8	1,385.5	34.8	0.00
Spp + yr	7	1,387.9	34.9	0.00
Spp + OLD + HDW	7	1,385.8	35.1	0.00
Spp + OLD	6	1,388.4	35.3	0.00
Spp + OLDER	6	1,388.6	35.6	0.00
Spp + HDW	6	1,388.7	35.7	0.00
Spp + OLD + (spp × OLD)	8	1,386.4	35.7	0.00
Spp + sex	7	1,389.1	36.1	0.00
Spp + nest	7	1,389.6	36.6	0.00
Spp + sex + (spp × sex)	11	1,387.5	36.8	0.00
Spp + HDW + (spp × HDW)	8	1,388.2	37.5	0.00
Spp + OLD + HDW + (spp × OLD) + (spp × HDW)	11	1,383.8	38.0	0.00
Spp + nest + (spp × nest)	11	1,389.2	38.6	0.00
Spp + sex + nest + (sex × nest)	13	1,388.5	40.2	0.00
Null model (no fixed effects)	3	1,415.0	57.5	0.00
Yr	5	1,413.1	57.9	0.00
Nest	5	1,413.5	58.2	0.00
Sex	4	1,414.4	59.1	0.00
OLDER	4	1,414.4	59.2	0.00

[a] Model effects included species (spp), sex, year (yr), proportion of the home range with: conifer forest >60 yrs (OLDER), conifer forest >120 yrs (OLD), or riparian-hardwood forest (HDW), current year's nesting status (nest), and probability of locating a radio-marked heterospecific within the focal individual's home range (*PHR*).

[b] Value of the maximized log-likelihood function.

[c] K = number of parameters in model (includes intercept and 2 covariance parameters), ΔAIC_c = difference between the AIC_c value of each model and the lowest AIC_c model, AIC_c wt = Akaike weight.

Table 3.6. Seasonal measures of intra- and inter-specific home range overlap among sympatric northern spotted owls (SPOW) and barred owls (BAOW) in western Oregon, 2007–2009.

			Overlap of 95% fixed kernel home ranges[a]				Overlap of 50% fixed kernel home ranges[a]			
			HR		*PHR*		*HR*		*PHR*	
Overlap type	Time period[b]	*n*[c]	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Intraspecific										
SPOW:SPOW (paired female and male)	Breeding	26	0.55	0.05	0.71	0.05	0.63	0.06	0.41	0.04
	Nonbreeding	30	0.47	0.05	0.53	0.05	0.30	0.06	0.23	0.04
BAOW:BAOW (paired female and male)	Breeding	18	0.68	0.05	0.81	0.03	0.58	0.07	0.42	0.05
	Nonbreeding	14	0.68	0.06	0.80	0.04	0.42	0.08	0.36	0.05
SPOW:SPOW (conspecific neighbors)	Breeding	39	0.13	0.02	0.11	0.02	0.01	0.01	0.01	0.01
	Nonbreeding	74	0.14	0.02	0.15	0.02	0.05	0.02	0.04	0.01
BAOW:BAOW (conspecific neighbors)	Breeding	20	0.10	0.02	0.08	0.02	0.00	0.00	0.00	0.00
	Nonbreeding	48	0.15	0.02	0.11	0.02	0.00	0.00	0.00	0.00
Interspecific										
BAOW:SPOW (heterospecific neighbors)	Breeding	71	0.38	0.04	0.15	0.03	0.11	0.03	0.03	0.01
	Nonbreeding	115	0.33	0.03	0.11	0.01	0.07	0.02	0.02	0.01
SPOW:BAOW (heterospecific neighbors)	Breeding	66	0.14	0.02	0.39	0.04	0.04	0.01	0.09	0.02
	Nonbreeding	110	0.11	0.01	0.34	0.03	0.03	0.01	0.06	0.01

[a] *HR* = proportion of owl *i*'s home range that is overlapped by the home range of owl *j*; *PHR* = probability of owl *j* being present in the home range of owl *i*. Mean estimates for intraspecific overlap types were calculated using all possible dyad combinations.

[b] Breeding = 1 Mar–31 Aug; nonbreeding = 1 Sep–28 Feb.

[c] Number of observed overlap combinations used to calculate means.

Table 3.7. Mean values of environmental covariates measured at foraging and roosting locations used by individual northern spotted owls or barred owls as compared to a set of random landscape locations in the western Oregon study area, 2007–2009. Forest types are expressed as the mean percentage of total foraging, roosting, or random locations. Sample sizes (number of individual owls or random points) are shown in parentheses.

	Spotted owl				Barred owl					
	Foraging (*n*=25)		Roosting (*n*=16)		Foraging (*n*=26)		Roosting (*n*=22)		Random (*n*=11,974)	
Covariate	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Forest type										
Old conifer (%)	38.3	3.2	60.0	3.2	35.0	3.8	41.1	4.4	16.2	0.8
Mature conifer (%)	28.9	3.2	21.9	3.7	23.2	2.9	19.3	3.0	20.9	0.8
Young conifer (%)	17.8	1.6	11.5	1.3	21.9	2.0	22.2	2.1	34.9	0.7
Riparian/hardwood (%)	10.0	1.9	3.8	1.1	15.7	3.0	13.8	3.6	5.4	0.9
Nonforest (%)	5.0	0.6	2.9	1.1	4.2	0.9	3.7	0.9	22.7	0.8
Quadratic mean diameter of conifers (cm)	44.3	1.3	49.7	0.6	42.6	1.8	44.8	0.6	32.4	0.2
Density of conifers >50 cm dbh (no./ha)	17.0	0.6	20.1	0.4	15.4	0.7	16.4	0.3	10.9	0.1
Canopy cover of hardwoods (%)	20.7	0.7	19.7	0.2	19.0	0.8	18.5	0.2	19.2	0.1
Basal area of hardwoods (m^2/ha)	5.4	0.2	5.0	0.1	4.7	0.2	4.6	0.1	5.0	0.1
Slope (degrees)	46.6	1.3	50.1	0.6	39.7	1.7	41.4	0.6	44.3	0.2
Distance to high contrast edge (m)	470.3	49.3	478.3	16.3	500.0	56.5	535.4	13.8	401.1	4.9
Distance to stream (m)	387.3	18.8	398.2	11.6	360.4	37.9	374.1	10.7	453.1	3.2
Distance to nest (m)	2,879.1	428.5	2,868.1	159.3	963.0	71.1	831.3	34.0	3,674.0	42.7

Table 3.8. Ranking of top five discrete-choice models used to characterize nighttime resource selection within home ranges of sympatric northern spotted owls and barred owls in western Oregon, 2007–2009. The base model without interspecific effects is in boldface, and the null model without covariates is shown for comparisons.

Species and model[a]	*K*[b]	-2log*L*[c]	AIC[d]	ΔAIC[d]	AIC wt[d]
Spotted owl (*n* = 25 owls, 42 choice sets)					
Fortype + dnest^2 + slope + dstream + dHET + (HDW × dHET)	10	30,994.2	31,014.2	0.00	0.90
Fortype + dnest^2 + slope + dstream + dHET	9	31,001.8	31,019.8	5.53	0.06
Fortype + dnest^2 + slope + dstream + dHET + (OLD × dHET)	10	31,000.4	31,020.4	6.14	0.04
Fortype + dnest^2 + slope + dstream + HETcore	9	31,013.3	31,031.3	17.07	0.00
Fortype + dnest^2 + slope + dstream	8	31,029.6	31,045.6	31.38	0.00
Null model (no effects)	0	31,964.5	31,964.5	950.31	0.00
Barred owl (*n* = 26 owls, 43 choice sets)					
Fortype + dnest^2 +slope + dedge^2 + dstream	10	30,653.3	30,673.3	0.00	0.41
Fortype+ dnest^2 + slope + dedge^2 + dstream + dHET + (OLD × dHET)	12	30,651.0	30,675.0	1.72	0.17
Fortype+ dnest^2 + slope + dedge^2 + dstream + HETcore	11	30,653.2	30,675.2	1.96	0.15
Fortype+ dnest^2 + slope + dedge^2 + dstream + dHET	11	30,653.3	30,675.8	2.55	0.12
Fortype+ dnest^2 + slope + dedge^2 + dstream + dHET + (HDW × dHET)	12	30,652.5	30,676.5	3.23	0.08
Null model (no effects)	0	31,625.4	31,625.4	952.16	0.00

[a] Forest type (fortype) was a categorical variable with 5 levels: old conifer (OLD), mature conifer (MAT), young conifer (YNG), riparian/hardwood (HDW), and nonforest (NON). Other model covariates included slope, distance to nest (dnest), distance to stream (dstream), distance to high contrast edge (dedge), proximity to heterospecific core-use area (dHET), and area within a heterospecific neighbor's core-use area (HETcore).

[b] *K* = number of covariates in model.

[c] Value of the maximized log-likelihood function.

[d] ΔAIC = difference between the AIC value of each model and the lowest AIC model; AIC wt = Akaike weight.

Table 3.9. Parameter estimates ($\hat{\beta}$) from the best discrete-choice resource selection functions developed for sympatric northern spotted owls and barred owls in western Oregon, 2007–2009. The reference level for forest type was nonforest.

			Approximate 95% CI[a]	
Covariate	$\hat{\beta}$	SE	Lower	Upper
Spotted owls				
Old conifer	1.694	0.095	1.508	1.881
Mature conifer	1.210	0.095	1.024	1.397
Young conifer	0.697	0.098	0.506	0.889
Riparian-hardwood	1.618	0.121	1.380	1.856
Distance to nest (km)	–0.140	0.015	–0.168	–0.111
Distance to nest^2 (km)	0.004	0.001	0.003	0.006
Slope (degrees)	0.002	0.001	0.000	0.005
Distance to stream (km)	–0.489	0.064	–0.615	–0.362
Proximity to barred owl (km)	0.100	0.018	0.065	0.134
Riparian-hardwood × proximity to barred owl	–0.100	0.042	–0.181	–0.018
Barred owls				
Old conifer	1.050	0.108	0.837	1.262
Mature conifer	0.938	0.106	0.729	1.147
Young conifer	0.516	0.109	0.302	0.729
Riparian-hardwood	1.155	0.115	0.930	1.380
Distance to nest (km)	–0.808	0.045	–0.897	–0.720
Distance to nest^2 (km)	0.070	0.006	0.059	0.081
Slope (degrees)	–0.006	0.001	–0.009	–0.004
Distance to edge (km)	0.454	0.159	0.142	0.766
Distance to edge^2 (km)	–0.226	0.098	–0.419	–0.033
Distance to stream (km)	–0.222	0.079	–0.377	–0.067

[a] Approximate 95% confidence interval calculated as: coefficient ± 1.96(coefficient standard error).

Table 3.10. Parameter estimates ($\hat{\beta}$) from the best model of differential resource selection between sympatric northern spotted owls and barred owls in western Oregon, 2007–2009. The reference level for forest type was nonforest and the reference level for species was barred owl.

			Approximate 95% CI[a]	
Covariate	$\hat{\beta}$	SE	Lower	Upper
Old conifer (OLD)	1.050	0.108	0.837	1.262
Mature conifer (MAT)	0.938	0.106	0.729	1.147
Young conifer (YNG)	0.516	0.109	0.302	0.729
Riparian-hardwood (HDW)	1.155	0.115	0.930	1.380
Distance to nest (km)	–0.808	0.045	–0.897	–0.720
Distance to nest^2 (km)	0.070	0.006	0.059	0.081
Slope (degrees)	–0.006	0.001	–0.009	–0.004
Distance to edge (km)	0.454	0.159	0.142	0.766
Distance to edge^2 (km)	–0.226	0.098	–0.419	–0.033
Distance to stream (km)	–0.222	0.078	–0.376	–0.069
Species-specific interactions				
Species × OLD	0.598	0.147	0.309	0.887
Species × MAT	0.264	0.146	–0.023	0.551
Species × YNG	0.150	0.150	–0.144	0.444
Species × HDW	0.294	0.162	–0.023	0.611
Species × dnest	0.664	0.048	0.571	0.757
Species × dnest^2	–0.063	0.006	–0.074	–0.052
Species × slope	0.009	0.002	0.005	0.012
Species × dedge	–0.301	0.215	–0.722	0.119
Species × dedge^2	0.093	0.131	–0.163	0.350
Species × dstream	–0.265	0.102	–0.465	–0.065

[a] Approximate 95% confidence interval calculated as: coefficient ± 1.96(coefficient standard error).

Table 3.11. Dietary composition of sympatric northern spotted owls and barred owls in western Oregon, 2007–2009. Diets are expressed as the mean percent of the total number and total biomass of prey identified in owl pellets. Sample sizes (number of owl pairs with >20 prey items) are in parentheses.

	% of prey numbers[a]				% of prey biomass[b]			
	Spotted owl (*n*=16)		Barred owl (*n*=25)		Spotted owl (*n*=16)		Barred owl (*n*=25)	
Prey species[c]	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Mammals	95.7	1.1	66.0	2.9	97.4	0.7	89.2	1.2
Shrews, shrew-moles (*Sorex* spp., *Neurotrichus gibbsii*)	1.9	0.9	13.8	0.9	0.2	0.1	1.4	0.1
Moles (*Scapanus orarius, S. townsendii*)	0.8	0.3	17.9	1.5	0.2	0.1	14.8	1.7
Mountain beaver (*Aplodontia rufa*)	0.9	0.4	1.0	0.3	1.9	0.7	5.5	1.5
Bats (*Eptesicus fuscus, Myotis* spp.)	0.3	0.1	0.3	0.2	0.0	0.0	0.0	0.0
Rabbits, hares (*Sylvilagus bachmani, Lepus americanus*)	3.4	0.6	2.5	0.4	13.3	2.5	17.4	3.0
Northern flying squirrel (*Glaucomys sabrinus)*	37.8	3.4	11.6	1.2	50.0	3.3	24.3	1.8
Douglas' squirrel (*Tamiasciurus douglasii)*	0.8	0.3	2.0	0.3	1.4	0.5	6.9	0.8
Western gray squirrel (*Sciurus griseus)*			0.1	0.1			0.3	0.2
Townsend’s chipmunk (*Tamias townsendii*)	0.5	0.2	1.2	0.3	0.3	0.2	1.7	0.5
Western pocket gopher (*Thomomys mazama*)	0.7	0.3	0.3	0.1	0.9	0.5	0.5	0.2
Western spotted skunk (*Spilogale gracilis)*			0.4	0.2			2.8	1.5
Woodrats (*Neotoma fuscipes, N. cinerea*)	8.1	1.4	1.5	0.3	17.4	2.5	6.8	1.3
Pacific jumping mouse (*Zapus trinotatus)*	0.4	0.2	0.7	0.2	0.1	0.1	0.3	0.1
Deer mouse (*Peromyscus maniculatus)*	17.3	2.6	3.5	0.6	4.9	1.0	1.3	0.2
Red tree vole (*Arborimus longicaudus)*	14.7	2.2	3.4	0.6	4.6	0.8	1.5	0.3
Western red-backed vole (*Myodes californicus)*	2.8	0.8	1.3	0.3	0.9	0.3	0.5	0.1
Other voles (*Microtus* spp.)	0.9	0.3	2.0	0.4	0.3	0.1	1.1	0.3

Table 3.11 (continued)

Unidentified vole or mouse *(Muridae* spp.)	4.0	0.9	0.3	0.1	1.0	0.3	0.1	0.0
Black rat (*Rattus rattus)*			<0.05	0.0			0.2	0.2
Common muskrat (*Ondatra zibethicus)*			<0.05	0.0			0.7	0.7
Ermine (*Mustela erminea)*	0.3	0.2	0.2	0.1	0.1	0.1	0.2	0.1
Unidentified weasel (*Mustela* spp.)			1.6	0.3			0.8	0.2
Birds	3.1	0.6	2.8	0.3	3.1	0.6	4.3	0.9
Amphibians	0.1	0.1	8.0	0.9	0.1	0.1	2.8	0.3
Frogs (*Rana* spp.)			1.0	0.6			0.4	0.1
Salamanders	0.1	0.1	7.0	0.7	0.1	0.1	2.5	0.4
Reptiles	0.0	0.0	1.1	0.3	0.0	0.0	1.5	0.4
Insects, millipedes, and springtails	1.0	0.5	12.5	2.0	0.0	0.0	0.1	0.0
Signal crayfish (*Pacifastacus leniusculus*)	0.1	0.1	2.6	1.3	<0.1	0.0	1.1	0.7
Snails	0.2	0.1	6.9	1.8	<0.1	0.0	0.7	0.1
Fish (small salmonids)			0.2	0.1			0.2	0.1

[a] Total number of prey items was 1,238 for spotted owls and 4,299 for barred owls.

[b] Total prey biomass was 112,661 g for spotted owls and 258,598 g for barred owls.

[c] See Appendix H for a complete list of prey species identified in owl diets.

Table 3.12. Observed versus simulated estimates of dietary overlap between neighboring pairs of northern spotted owls and barred owls in western Oregon, 2007–2009.

	Number of prey items[a]				
Overlap no.	Spotted owl	Barred owl	Observed dietary overlap[b]	Mean of simulated overlaps (SE)[b]	*P*[c]
1	67	94	0.411	0.220 (0.020)	0.106
2	146	439	0.505	0.188 (0.022)	0.032
3	32	90	0.411	0.169 (0.023)	0.086
4	72	352	0.277	0.191 (0.022)	0.175
5	110	439	0.393	0.156 (0.021)	0.077
6	42	215	0.392	0.143 (0.022)	0.122
7	173	274	0.470	0.237 (0.018)	0.070
8	59	185	0.380	0.266 (0.019)	0.179
9	56	90	0.472	0.203 (0.019)	0.056
10	94	94	0.312	0.223 (0.021)	0.218
11	20	65	0.283	0.184 (0.021)	0.242
12	55	378	0.373	0.230 (0.019)	0.178
13	60	255	0.696	0.268 (0.021)	0.005
14	82	57	0.363	0.171 (0.021)	0.087
15	155	171	0.531	0.257 (0.017)	0.059
Mean (SE)	82 (12)	213 (35)	0.418 (0.028)	0.207 (0.010)	

[a] Total number of prey items in the dietary sample from neighboring pairs of spotted and barred owls.

[b] Pianka’s index of niche overlap (Pianka 1973).

[c] Probability that the observed value of dietary overlap is greater than or equal to the mean of simulated overlaps generated from 2,000 Monte Carlo randomizations of the observed diet data.

Table 3.13. Seasonal changes in diet composition (% of total prey numbers) and mean mass of prey (g) of sympatric northern spotted owls and barred owls in western Oregon, 2007–2009. The breeding season was 1 March–31 August and the nonbreeding season was 1 September–28 February. Numbers of prey items are in parentheses.

	Spotted owl		Barred owl	
Prey species	Breeding season (*n*=1,156)	Nonbreeding season (*n*=67)	Breeding season (*n*=4,048)	Nonbreeding season (*n*=251)
Mammals	94.2	95.5	63.5	71.3
Shrews, shrew moles	2.1	3.0	13.0	13.6
Moles	0.9	1.5	18.4	8.4
Rabbits, hares	3.8	4.5	1.9	2.8
Mountain beaver	0.9	0.0	0.9	0.0
Northern flying squirrel	36.5	25.4	11.0	19.1
Douglas' squirrel	0.9	1.5	2.0	3.6
Woodrats	7.2	9.0	1.4	2.0
Deer mouse	18.2	19.4	3.5	2.8
Red tree vole	14.2	18.0	3.5	5.2
Other mammals	9.5	13.2	7.9	13.8
Birds	4.0	1.5	3.0	5.6
Amphibians	0.1	0.0	9.3	5.6
Reptiles	0.1	0.0	0.9	0.8
Insects	1.5	1.5	13.0	9.5
Snails	0.1	1.5	6.5	3.2
Fish	0.0	0.0	0.2	1.6
Crayfish	<0.01	0.0	5.7	0.8
Mean mass (g) of prey (SE)	91.3 (3.1)	84.0 (14.2)	59.0 (1.7)	78.8 (6.8)
Interspecific dietary overlap[a]	0.446	0.676	0.446	0.676

[a] Pianka's index of food niche overlap (Pianka 1973) with data pooled across territories.

Table 3.14. Trophic and ecological overlap indices for individual northern spotted owls and barred owls that were radio-marked in adjacent territories in western Oregon, 2007–2009.

Spotted owl ID[a]	Barred owl ID[a]	Spatial overlap (S)[b]	Habitat overlap (H)[c]	Dietary overlap (D)[c]	Trophic overlap (H × D)	Ecological overlap (S+H+D)/3
BUL_SF	PAT_BF	0.056	0.877	0.411	0.360	0.448
BUL_SM	PAT_BF	0.163	0.902	0.411	0.371	0.492
CC_SF	EC_BF	0.124	0.905	0.505	0.457	0.511
CC_SM	EC_BM	0.149	0.859	0.505	0.434	0.504
DC_SF	SF_BF	0.094	0.306	0.277	0.085	0.226
DC_SM	SF_BF	0.134	0.575	0.277	0.159	0.329
EC_SF	EC_BF	0.155	0.829	0.393	0.326	0.459
HC_SF	SC_BM	0.102	0.956	0.392	0.375	0.483
HC_SM	SC_BM	0.129	0.925	0.392	0.363	0.482
IM_SF	IM_BF	0.032	0.987	0.470	0.464	0.496
IM_SM	IM_BF	0.107	0.967	0.470	0.454	0.515
LEO_SF	KLI_BF	0.168	0.493	0.380	0.187	0.347
LEO_SM	KLI_BF	0.130	0.736	0.380	0.280	0.415
LM_SF	SG_BM	0.033	0.914	0.472	0.431	0.473
PAT_SM	PAT_BF	0.579	0.795	0.312	0.248	0.562
PAT_SM2	PAT_BF	0.144	0.819	0.312	0.256	0.425
SAL_SF	UPC_BF	0.328	0.846	0.373	0.316	0.516
SAL_SM	UPC_BM	0.702	0.986	0.373	0.368	0.687
SCW_SF	LBC_BF	0.003	0.448	0.696	0.312	0.382
SCW_SM	LBC_BF	0.000	0.509	0.696	0.354	0.402
WC_SF	WC_BF	0.475	0.990	0.363	0.359	0.609
WC_SM	WC_BM	0.361	0.971	0.363	0.352	0.565
WP_SF	HP_BM	0.008	0.873	0.531	0.464	0.471
WP_SM	HP_BM	0.000	0.938	0.531	0.498	0.490
	Mean	0.174	0.809	0.429	0.345	0.470
	Median	0.130	0.875	0.393	0.360	0.483
	SE	(0.037)	(0.039)	(0.022)	(0.021)	(0.019)

[a] First 2–3 letters indicate site name, second to last letter indicates species, last letter indicates sex.

[b] Estimated as the proportion of a spotted owl's 95% fixed-kernel home range that was overlapped by the home range of the nearest neighboring barred owl.

[c] Calculated using Pianka's (1973) measure of niche overlap. Dietary overlap was based on proportional use of 30 prey categories and habitat overlap was based on proportional use of 5 forest cover types. Values of habitat overlap incorporated availability of each forest type in the study area.

Table 3.15. Causes of death and estimates of model-averaged survival probabilities ($\hat{\bar{S}}$) for radio-marked northern spotted owls (*n*=29) and barred owls (*n*=28) in western Oregon, 2007–2009.

			Cause of death[a]			Survival probability	
Species and time interval	Owls at risk	Deaths (females, males)	Avian predation	Endoparasitism or bacterial infection	Disease or starvation	$\hat{\bar{S}}$	SE
Spotted owl							
May–Aug 2007	24	1 (0, 1)	1	0	0	0.903	0.040
Sep 2007–Feb 2008	23	3 (1, 2)	1	0	2	0.896	0.044
Mar–Aug 2008	25	3 (3, 0)	1	2	0	0.904	0.039
Sep 2008–Feb 2009	21	2 (0, 2)	2	0	0	0.897	0.043
Cumulative (22 months)	29	9 (4, 5)	5	2	2	0.681	0.102
Barred owl							
May–Aug 2007	22	1 (0, 1)	0	1	0	0.947	0.029
Sep 2007–Feb 2008	22	1 (1, 0)	0	1	0	0.943	0.029
Mar–Aug 2008	26	0	0	0	0	0.948	0.029
Sep 2008–Feb 2009	26	2 (2, 0)	0	2	0	0.944	0.029
Cumulative (22 months)	28	4 (3, 1)	0	4	0	0.815	0.075

[a] Cause of death was determined by necropsy or evidence collected at recovery sites if remains were insufficient for necropsy analysis.

[b] Weighted average of survival probabilities and unconditional standard errors (SE) estimated from all models with time effects (models 1-10; Appendix D). Cumulative survival was derived from seasonal estimates.

Table 3.16. Ranking of top 10 known-fate models used to examine variation in survival (*S*) of radio-marked northern spotted owls and barred owls in western Oregon from 1 May 2007 to 28 February 2009. The intercept-only model without covariates, *S*(.), and the fully parameterized global model, *S*(Spp × t), are shown for comparisons.

Model[a]	K^b	$AIC_c{}^b$	$\Delta AIC_c{}^b$	AIC_c wt[b]	Deviance[b]
S(Spp + old + *PHR*)	4	89.57	0.00	0.32	81.35
S(Spp + old)	3	89.60	0.03	0.32	83.47
S(Spp + dedge + old)	4	91.64	2.07	0.12	83.42
S(Spp × old)	4	91.68	2.11	0.11	83.47
S(Spp)	2	95.77	6.20	0.01	91.71
S(Spp + old_core)	3	95.93	6.36	0.01	89.80
S(Spp + *PHR*)	3	96.00	6.43	0.01	89.87
S(.) – no effects model	1	96.09	6.52	0.01	94.07
S(Spp + dedge)	3	96.97	7.40	0.01	90.84
S(Spp + *HR*)	3	97.02	7.45	0.01	90.89
S(Spp + edge + old_core)	4	97.27	7.69	0.01	89.05
S(Spp × t) – global model	8	104.85	15.28	0.00	88.05

[a] The top 10 covariate models are shown in addition to the intercept-only and global models (see Appendix D for the full set of models considered). Time effects modeled as constant (.) or varying among 6-mo time intervals (t). Model covariates include species (Spp; spotted owl or barred owl), proportion of old conifer forest in the home range (old), proportion of old conifer forest in the breeding core-use area (old_core), mean distance to high-contrast edge (edge), proportion of the 95% fixed-kernel home range shared with heterospecific neighbors (*HR*), and probability of heterospecific presence within the 95% fixed-kernel home range (*PHR*).

[b] K = number of parameters; AIC*c* = Akaike's Information Criterion adjusted for small sample size; ΔAIC_c=difference between the AIC_c value of each model and the lowest AIC_c model; AIC_c wt = Akaike weight of each model; deviance = difference in –2log(likelihood) of the current model and –2log (likelihood) of the fully saturated model.

Table 3.17. Measures of nesting success and productivity of sympatric northern spotted owls and barred owls in western Oregon, 2007–2009. Estimates are based on territorial pairs for which reproductive status was monitored from 1 Mar to 31 August of each year.

Year and species	Number of pairs	Number nesting (%)[a]	Number successful (%)[b]	Total young fledged	Young fledged per pair (SE)
2007					
Spotted owl	13	8 (62)	4 (50)	7	0.54 (0.24)
Barred owl	19	13 (68)	12 (92)	25	1.32 (0.27)
2008					
Spotted owl	14	10 (71)	1 (10)	2	0.14 (0.14)
Barred owl	20	15 (75)	14 (93)	26	1.30 (0.23)
2009					
Spotted owl	15	3 (20)	2 (67)	4	0.27 (0.18)
Barred owl	20	17 (85)	14 (82)	29	1.45 (0.27)
3-yr means					
Spotted Owl	14	7 (50)	2.3 (33)	4.3	0.31 (0.11)
Barred Owl	20	15 (75)	13.3 (89)	26.7	1.36 (0.14)

[a] Percentage of pairs that attempted to nest.

[b] Percentage of nesting pairs that successfully fledged ≥1 young.

APPENDICES

Appendix A. Morphometric measurements of northern spotted owls and barred owls captured in western Oregon during 2007–2009 (*n* = number of individuals).

	Spotted owls				Barred owls			
Measurement	*n*	Mean	SD	Min. – Max.	*n*	Mean	SD	Min. – Max.
Mass (g)								
Females	14	691.3	56.0	613.0 – 795.0	16	780.6	57.5	670.0 – 895.0
Males	16	576.8	49.3	490.0 – 680.0	15	667.1	24.7	630.0 – 702.0
Tail length (mm)[a]								
Females	11	184.8	5.8	173.0 – 193.0	13	212.7	8.3	201.0 – 230.0
Males	12	182.8	13.9	159.0 – 218.0	12	212.9	6.2	202.0 – 221.0
Wing chord (mm)[b]								
Females	13	321.7	21.4	307.0 – 390.0	14	340.8	14.2	316.0 – 359.0
Males	11	305.4	12.4	285.0 – 330.0	12	321.5	12.2	299.0 – 333.0
Foot length (mm)[c]								
Females	14	60.5	6.4	46.6 – 69.2	15	59.0	8.6	43.0 – 71.9
Males	14	60.0	7.5	45.2 – 70.1	13	63.2	8.8	42.8 – 74.4
Hallux length (mm)[d]								
Females	14	19.8	0.8	18.1 – 21.0	14	19.0	1.3	16.5 – 20.6
Males	15	18.1	0.6	17.0 – 19.2	13	17.6	0.9	16.2 – 19.4
Bill length (mm)[e]								
Females	12	23.2	1.5	21.0 – 26.7	15	27.9	3.0	23.6 – 32.9
Males	15	24.0	3.4	19.9 – 31.2	13	27.3	4.1	21.6 – 36.2
Bill width (mm)[f]								
Females	12	13.1	1.5	10.8 – 15.9	15	14.5	2.5	9.2 – 19.0
Males	12	12.9	2.1	9.7 – 16.4	12	13.5	2.2	10.4 – 18.2

[a] From point between central pair of retrices where they emerge from skin to tip of longest retrix.
[b] From carpal joint to tip of longest primary; measured when wing is relaxed.
[c] By opening diagonal toes flat and measuring from tips of pads.
[d] From tip of hallux to where it emerges from toe-pad.
[e] From tip of bill to culmen.
[f] From left to the right side of culmen.

Appendix B. Development of vegetation maps representing primary forest types, stand edges, and forest structural conditions in the northern spotted owl and barred owl study area of western Oregon.

Image segmentation and classification of primary forest types

I used regional forest vegetation maps based on satellite imagery (Ohmann and Gregory 2002) in combination with image segmentation and object-based classification techniques to develop forest vegetation maps of primary forest types and forest structural conditions. I conducted image segmentation and classification in 6 steps (Fig B-1): 1) segmentation of the NAIP imagery into regions of pixels with similar characteristics; 2) computation of a set of spatial, spectral, and texture attributes for each segmented region; 3) creation of a nonforest mask using rule-based feature extraction; 4) supervised classification of 4 primary forest types (old conifer, mature conifer, young conifer, hardwood) using the attribute values calculated in step 2 and a training sample of polygons; 5) manual refinement of forest types and boundaries by on-screen interpretation; and 6) field sampling to determine map accuracy (Table B-1). The imagery analyzed (referred to as the NAIP image in the flowchart) was a United States Department of Agriculture, National Agriculture Imagery Program image database of 1-m resolution, multispectral natural color orthophotograph acquired in September, 2009. I completed all analysis steps using ENVI EX image analysis software and the ENVI EX toolset for ArcGIS (ITT Visual Information Solutions, 2009). The distribution of patches of different forest types based on the 2009 NAIP imagery is illustrated in Fig. B-3.

Forest structural characteristics

In addition to classification of the 5 primary forest types I also assigned each segmented region (patch) a small set of forest structural characteristics derived from a regional forest vegetation map developed for the Northwest Forest Plan Effectiveness Monitoring Program (Lint et al. 1999, Davis et al. 2011). This classified Landsat (ETM+) map of forest composition and structure was developed using Gradient Nearest Neighbor (GNN) imputation (image year: 2006; Ohmann and Gregory 2001, 2002), and was obtained from the Landscape Ecology Mapping, Modeling, and Analysis group website. Using patch analyst for ArcGIS, I estimated the density of large (>50 cm dbh) conifers (TPHcon50; no./ha), quadratic mean diameter of conifers (QMDcon; cm), basal area of hardwoods (BAhdw; m^2/ha), and canopy cover of hardwoods (CANCOVhdw; %) as the mean of 30×30 m GNN pixel values within each segmented region (e.g., Fig. B-2, D).

Accuracy assessment

Accuracy of the classified forest map was based on ground sampling completed at 141 random test plots within the analysis region. Forest vegetation measurements at reference plots used for the accuracy assessment were obtained from 2 sources: 1) visits to randomly selected grid coordinates in the analysis region to measure size (dbh), species, and composition of dominant and codominant trees (BLM lands; *n*=47); and 2) forest vegetation inventory plot measurements obtained from private timber companies (private lands; *n*=94). I estimated accuracy of each forest type classification by comparing predicted and observed conditions at random landscape locations using a using a standard error matrix (Congalton and Green 1999; Table B-1). I was unable to verify forest structural covariates derived from GNN maps directly, but local-scale accuracies reported for the GNN map showed that predicted values correlated well with observed plot measurements (range of correlation coefficients = 0.53–0.71; LEMMA 2009).

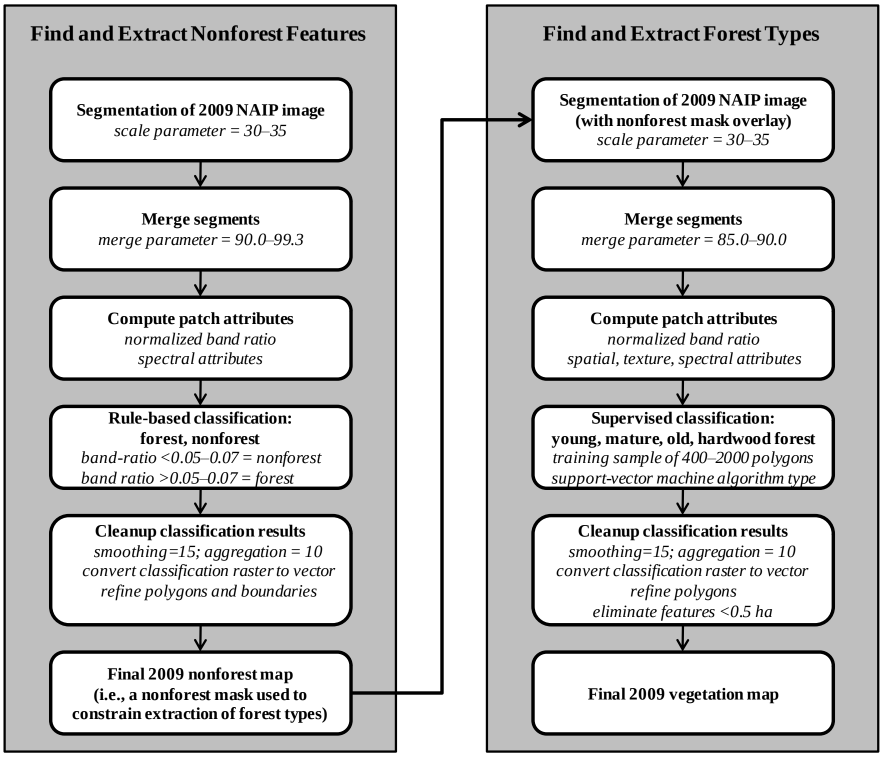

Figure B-1. Flowchart illustrating the analysis steps and parameterization of the object-based classification process used to develop patch-scale maps of primary forest types and stand edges. All analyses were conducted using ENVI EX image analysis software.

Table B-1. Error matrix of class-specific prediction accuracies of the final 2009 vegetation map based on ground sampling at 141 test plots. Reference plots that were mapped correctly fall along the diagonal in grey.

	Observed forest type[a]						
Predicted forest type	Young conifer	Mature conifer	Old conifer	Riparian-hardwood	Open	Total	*User's (%)*
Young conifer	55	2		1		58	94.8
Mature conifer	9	12	3			24	50.0
Old conifer		2	16			18	88.9
Riparian-hardwood	1			6	1	8	75.0
Nonforest	4	1		1	27	33	81.8
Total	69	17	19	8	28	141	
							Overall accuracy
Producer's (%)	79.7	70.6	84.2	75.0	96.4		**82.3%**

[a] Producer's accuracy measures the error of exclusion, user's accuracy measures the error of inclusion.

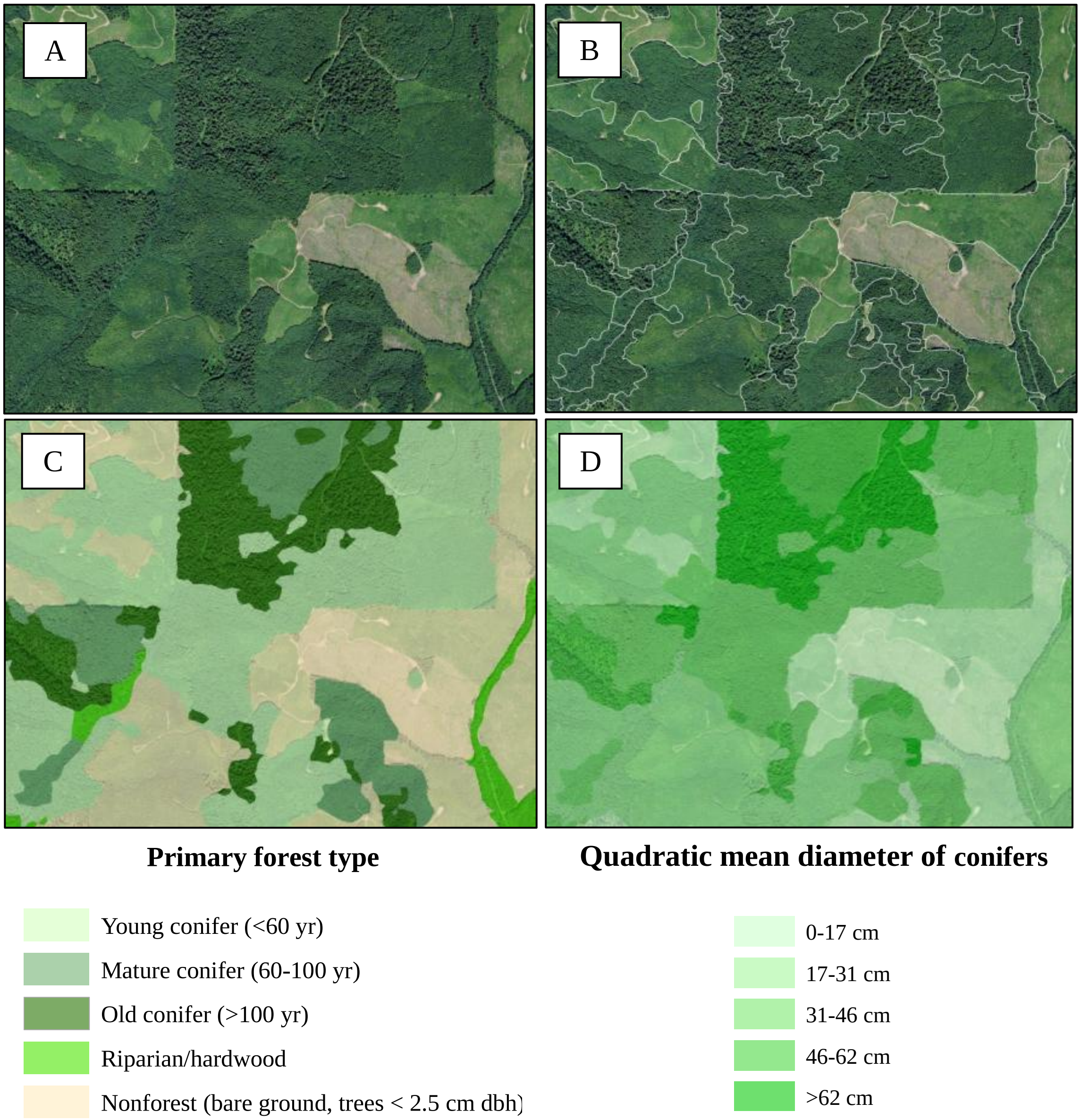

Figure B-2. An example of (A) the 1-m resolution natural color aerial photograph used as a base image for feature extraction; (B) results of the image segmentation process; (C) the classified forest vegetation map; and (D) quadratic mean diameter of all live conifers imputed from the GNN forest vegetation map (Ohmann and Gregory 2002).

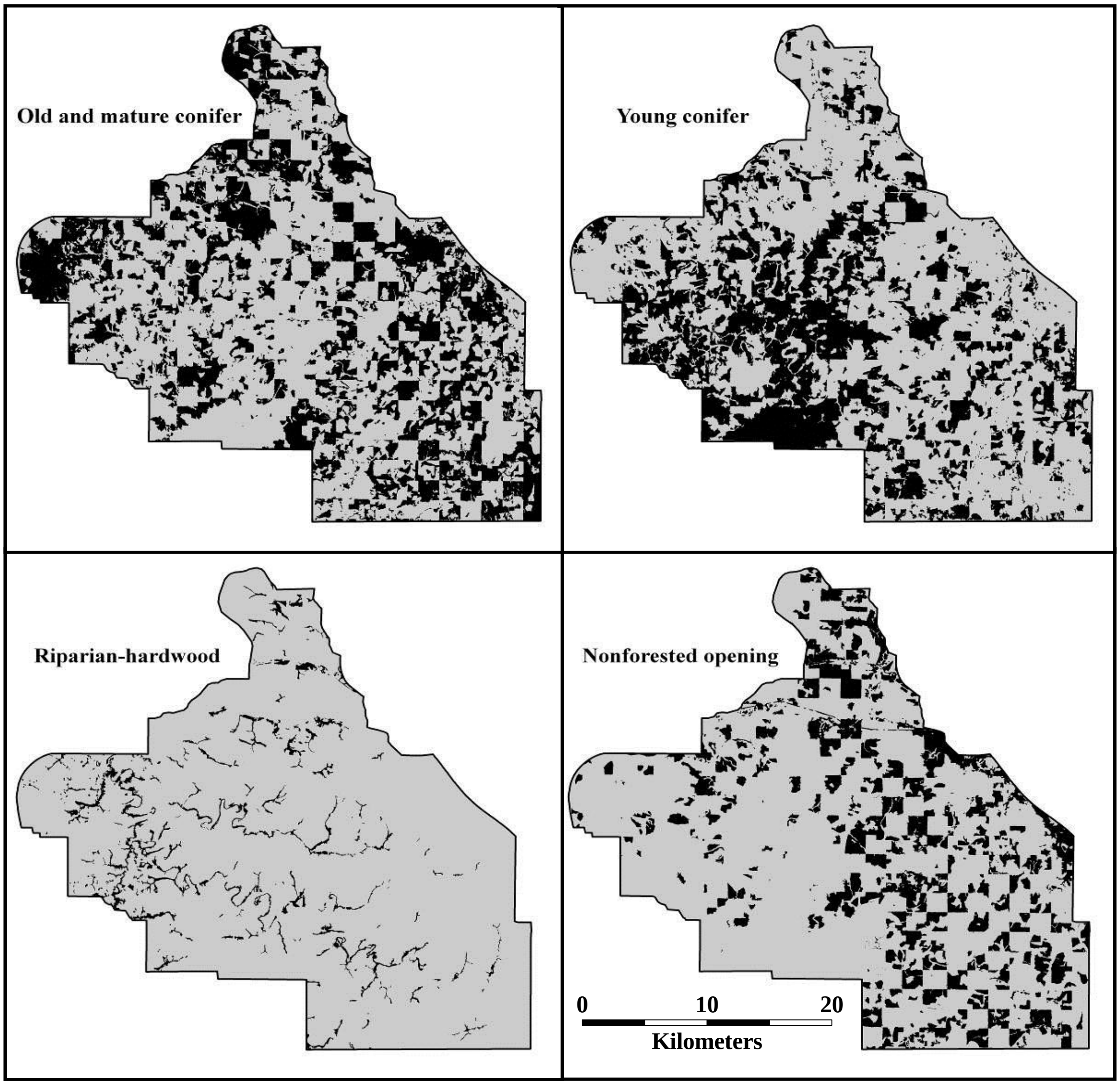

Figure B-3. Distribution of primary forest types on the western Oregon study area in 2009. Forest types and their proportional representation on the study area were: old conifer (16,873 ha, 17%), mature conifer (20,953 ha, 21.1%), young conifer (33,796 ha, 34%), riparian-hardwood (4,800 ha, 4.8%), and nonforest (20,673 ha, 20.8%).

Appendix C. *A priori* models used to characterize nighttime habitat selection within the home range by northern spotted owls and barred owls in western Oregon, 2007–2009.

Description of hypothesized effects	Model[a]
Influence of forest type and central place foraging	
1. Null model (resource selection is random)	No effects model
2. Resource selection is dependent on forest type only	Fortype
3. Additive effect of forest type and distance to nest	Fortype + dnest
4. Effect of forest type and distance to nest (polynomial)	Fortype + dnest + dnest^2
Influence of patch-scale forest structural conditions	
5. Effect of density of large (>50 cm dbh) conifers	TPHcon50
6. Effect of quadratic mean diameter of conifers	QMDcon
7. Non-linear effect of quadratic mean diameter of conifers	QMDcon + QMDcon^2
8. Effect of basal area of hardwoods	BAhdw
9. Non-linear effect of basal area of hardwoods	BAhdw + BAhdw^2
10. Effect of canopy cover of hardwoods	CANCOVhdw
11. Non-linear effect of canopy cover of hardwoods	CANCOVhdw + CANCOVhdw^2
12. Non-linear effect of quadradic mean diameter of conifers and canopy cover of hardwoods	QMDcon + QMDcon^2 + CANCOVhdw + CANCOVhdw^2
13. Non-linear effect of quadradic mean diameter of conifers with linear effect canopy cover of hardwoods	QMDcon + QMDcon^2 + CANCOVhdw
14. Best forest structure model with additive effect of distance to nest (polynomial)	(best from 5–13) + dnest^2
Influence of slope, edge, and moisture	
15. Best structure from 1–14 above with effect of slope	(best from 1–14) + slope
16. Best structure from 1–14 above with additive effect of distance to high contrast edge	(best from 1–14) + dedge
17. Best structure from 1–14 above with quadratic effect of distance to high contrast edge	(best from 1–14) + dedge + dedge^2
18. Best structure from 1–14 above with additive effect of distance to stream	(best from 1–14) + dstream
19. Best structure from 1–14 above with quadratic effect of distance to edge and distance to stream	(best from 1–14) + dedge + dedge^2 + dstream
20. Best structure from 1–14 above with additive effect of slope and distance to stream	(best from 1–14) + slope + dstream
21. Best structure from 1–14 above with additive effect of slope and quadratic distance to edge	(best from 1–14) + slope + dedge^2
22. Best structure from 1–14 above with additive effect of slope, quadratic distance to edge, and distance to stream	(best from 1–14) + slope + dedge^2 + dstream
Influence of heterospecifics	
23. Best structure from 1–22 above with additive effect of proximity to heterospecific core-use area	(best from 1–22) + dHET

Appendix C (continued)

24.	Best structure from 1–22 above with additive effect of area within heterospecific core-use area	(best from 1–22) + HETcore
25.	Best structure from 1–22 above with an interaction between proximity to heterospecific core use area and old conifer forest type.	(best from 1–22) + dHET + (OLD × dHET)
26.	Best structure from 1–22 above with an interaction between proximity to heterospecific core use area and riparian-hardwood forest type.	(best from 1–22) + dHET + (HDW × dHET)

[a] See table 2.1 for a description of covariates included in models.

Appendix D. *A priori* hypotheses and models used to examine variation in survival (*S*) of radio-marked northern spotted owls and barred owls in western Oregon, 2007–2009.

Description of hypothesized effects	Model[a]
Species, sex, and time effects	
1. Survival differs between species and among 6-mo time intervals	*S*(Spp × t) – global model
2. Survival is constant between species and over time	*S*(.) – no effects model
3. Survival differs between species but is constant over time	*S*(Spp)
4. Survival differs between species and among 6-mo time intervals	*S*(Spp + t)
5. Survival differs between species and among seasons	*S*(Spp + season)
6. Survival differs between species and years	*S*(Spp + yr)
7. Survival differs between species and years with an interaction	*S*(Spp × yr)
8. Additive effect of species and sex with constant time	*S*(Spp + sex)
9. Interactive effect of species and sex	*S*(Spp × sex)
10. Additive effect of species, sex, and season	*S*(Spp + sex + season)
Influence of habitat	
11. Survival is dependent on species and distance to edge	*S*(Spp + edge)
12. Interactive effect of species and distance to high-contrast edge	*S*(Spp × edge)
13. Effect species and mean proportion of old forest in home range	*S*(Spp + old)
14. Interactive effect of species and mean proportion of old forest	*S*(Spp × old)
15. Survival is dependent on species and mean proportion of old forest in the breeding season core-use area	*S*(Spp + old_core)
16. Interactive effect of species and mean proportion of old forest in the breeding core area	*S*(Spp × old_core)
17. Additive effect of species, ditance to edge, and mean proportion of old forest in the home range	*S*(Spp + edge + old)
18. Interactive effect of species, distance to edge, and mean proportion of old forest in breeding core area	*S*(Spp + edge + old_core)
Influence of spatial overlap with competitors	
19. Survival is dependent on species and mean proportion of the home range shared with heterospecific neighbors	*S*(Spp + *HR*)
20. Interactive effect of species and mean proportion of the home range shared with heterospecific neighbors	*S*(Spp × *HR*)
21. Survival is dependent on species and probability of heterospecific presence within the home range	*S*(Spp + *PHR*)
22. Interactive effect of species and probability of heterospecific presence within the home range	*S*(Spp × *PHR*)
Combined effect of habitat and spatial overlap with competitors	
23. Combine best time and sex model from 1–10 above with best habitat model from 11–18 and best interspecific model from 19–22	*S*(best from 1–18 + best from 19–22)

[a] Time effects modeled as constant (.), varying between years (yr), varying among 6-mo time intervals (t), or varying between breeding and nonbreeding seasons (season). Model covariates included owl species (Spp), proportion of old conifer forest in the home range (old), proportion of old conifer forest in the breeding core area (old_core), mean distance to high-contrast edge (edge), proportion of home range shared with heterospecifics (*HR*), and probability of heterospecific presence within the home range (*PHR*).

Appendix E. Tracking summaries and fates of 29 northern spotted owls (14 females, 15 males) and 28 barred owls (13 females, 15 males) radio-marked in western Oregon between 1 March 2007 and 31 August 2009.

Species and owl ID[a]	Capture date	End date[b]	Tracking days	Total locations	Fate[c]
Spotted Owls					
BUL_SF	6 Jun 2007	3 Apr 2008	297	69	Mortality (disease)
BUL_SM	29 May-2007	26 Nov 2007	177	39	Mortality (avian predation)
CC_SF	31 May 2007	7 Jul 2008	397	85	Mortality (endoparasitism)
CC_SM	23 Mar 2007	17 Mar 2009	714	178	Radio removed
DC_SF	12 Apr 2007	8 Apr 2009	716	191	Radio removed
DC_SM	17 Apr 2007	26 Mar 2009	699	170	Radio removed
EC_SF	8 Mar 2007	13 Mar 2009	725	168	Radio removed
EC_SF2	19 Mar 2008	6 Apr 2008	17	5	Mortality (avian predation)
EC_SM	8 Mar 2007	21 May 2007	73	29	Mortality (avian predation)
HC_SF	29 Mar 2007	6 Apr 2009	727	169	Radio removed
HC_SM	29 Mar 2007	30 Mar 2009	721	161	Radio removed
IM_SF	24 May 2007	27 Mar 2009	663	123	Radio removed
IM_SM	24 May 2007	10 Dec 2008	556	115	Mortality (avian predation)
LEO_SF	30 Apr 2007	11 Apr 2009	701	162	Radio removed
LEO_SM	30 Apr 2007	13 Apr 2009	703	154	Radio removed
LM_SF	22 May 2008	19 Aug 2009	447	81	Radio removed
PAT_SF	31 Jul 2007	1 Oct 2007	77	20	Mortality (endoparasitism)
PAT_SM	4 Apr 2007	21 Oct 2007	197	53	Mortality (unknown)
PAT_SM2	1 Apr 2008	4 Aug 2009	483	95	Radio removed
PT_SM	15 May 2007	16 Dec 2008	571	123	Radio removed
SAL_SF	24 Apr 2007	1 Mar 2009	667	170	Radio removed
SAL_SM	24 Apr 2007	1 Apr 2009	697	168	Radio removed
SCW_SF	18 May 2007	9 Apr 2009	681	177	Radio removed
SCW_SM	18 May 2007	27 Apr 2009	699	151	Radio removed
SHA_SM	9 May 2007	2 Dec 2008	563	145	Mortality (avian predation)
WC_SF	12 Mar 2007	26 Mar 2009	734	201	Radio removed
WC_SM	3 Mar 2007	10 Mar 2009	727	196	Radio removed
WP_SF	4 Jun 2008	31 Aug 2009	447	113	Radio removed
WP_SM	29 Apr 2008	31 Aug 2009	482	128	Radio removed

Appendix E (continued)

Barred owls					
BC_BM	4 Mar 2007	25-Apr 2009	771	100	Radio removed
DH_BM	24 Apr 2007	17 Mar 2009	683	170	Radio failure
EC_BF	28 May 2007	5 Feb 2009	607	137	Radio failure
EC_BM	29 Mar 2007	10 Apr 2009	731	194	Radio removed
ELK_BF	5 Jul 2007	4 Aug 2009	749	158	Radio removed
ELK_BM	29 May 2007	26 Jul 2009	777	182	Radio removed
FC_BF	19 Jun 2007	17 Oct 2008	478	132	Mortality (endoparasitism)
FC_BM	23 Apr 2007	30 Mar 2009	697	174	Radio removed
GC_BM	28 Mar 2007	1 May 2009	753	111	Radio removed
HP_BM	12 Apr 2007	8 May 2009	746	199	Radio failure
IM_BF	19 Jun 2007	24 Mar 2009	635	141	Radio failure
KLI_BF	9 May 2007	30 Apr 2009	711	171	Radio removed
LBC_BF	22 May 2007	3 May 2009	701	183	Radio removed
LOC_BF	30 Apr 2007	5 May 2009	725	149	Radio removed
PAT_BF	19 Jun 2007	12 Feb 2008	233	61	Mortality (endoparasitism)
PC_BF	19 Apr 2007	3 Apr 2009	704	155	Radio removed
PG_BM	14 Sep 2007	1 Jun 2009	617	158	Radio failure
RC_BM	21 Mar 2007	11 Dec 2008	620	171	Radio failure
SC_BM	3 Apr 2007	28 Feb 2009	685	162	Radio removed
SF_BF	27 Mar 2007	12 Jan 2009	645	196	Radio failure
SG_BF	28 May 2008	17 Sep 2008	109	32	Mortality (bacterial infection)
SG_BM	28 May 2008	31 Aug 2009	453	100	Radio failure
UPC_BF	24 Apr 2007	1 May 2009	727	168	Radio failure
UPC_BM	24 Apr 2007	1 May 2009	727	182	Radio removed
WC_BF	18 Apr 2008	31 Aug 2009	493	112	Radio removed
WC_BM	5 Apr 2007	26 Apr 2007	21	13	Mortality (bacterial infection)
WC_BM2	11 Mar 2008	31 Aug 2009	530	110	Radio failure

[a] First 2-3 letters indicate site name, second to last letter indicates species, last letter indicates sex.

[b] Date of mortality or when the radio transmitter was either removed or stopped transmitting.

[c] Cause of death determined by necropsy analysis (conducted by the Veterinary Diagnostic Lab, Oregon State University, Corvallis, Oregon) or by evidence collected at recovery sites in cases where remains were insufficient for necropsy analysis.

Appendix F. Seasonal home range areas (ha) estimated for northern spotted owls (*n*=26) and barred owls (*n*=27) in western Oregon during March 2007–September 2009. Estimates are based on the 95% fixed-kernel (FK) and the 100% minimum convex polygon (MCP); *n* = number of locations included in estimates.

	Season and year														
	Breeding 2007			Nonbreeding 2007–2008			Breeding 2008			Nonbreeding 2008–2009			Breeding 2009		
Owl ID[a]	95% FK	100% MCP	*n*	95% FK	100% MCP	*n*	95% FK	100% MCP	*n*	95% FK	100% MCP	*n*	95% FK	100% MCP	*n*
Spotted owls															
BUL_SF				4070	3636	45									
BUL_SM				1610	1233	39									
CC_SF				5312	4229	42									
CC_SM	341	307	51	1314	897	40	810	382	45	1645	1455	39			
DC_SF	1518	1205	42	2519	1814	49	1722	1476	49	3162	3442	44			
DC_SM				912	467	60	975	8373	40	2382	3293	41			
EC_SF	1055	1431	52	2329	2065	44	1565	824	30	3496	2000	39			
HC_SF	2584	1457	31	7377	7829	58	4880	5370	30	7458	5150	43			
HC_SM	4615	4116	40	3118	3218	40	3542	5370	40	4788	3088	35			
IM_SF				4182	2882	42	2498	1453	29	4253	2470	38			
IM_SM				2366	1496	43	509	789	35						
LEO_SF	381	287	37	845	605	40	659	440	40	1363	860	36			
LEO_SM	2443	1610	34	2988	1982	41	2392	1880	37	2392	1912	33			
LM_SF										1041	2796	40			
PAT_SM	1333	841	40												
PAT_SM2							2175	2121	36	4583	4360	40			
PT_SM	1310	804	29	4808	2112	41	4484	3407	34						
SAL_SF	1348	1109	38	2445	2337	47	517	600	45	2142	1990	39			
SAL_SM	1073	817	38	1180	871	45	449	386	40	1643	1357	38			
SCW_SF	317	261	26	1430	1437	58	217	230	28	237	130	47			
SCW_SM	453	355	26	725	1083	48	726	3484	34	1761	1212	43			
SHA_SM	2032	1352	28	1587	1301	51	1540	1317	44						
WC_SF	316	265	58	1141	1848	48	1524	1677	50	1792	2484	41			
WC_SM	588	701	58	2068	1426	45	2211	1651	49	2346	3355	41			

Appendix F (continued)

WP_SF							1213	1335	33	3557	3118	43	3491	3830	36
WP_SM							1341	1252	42	1456	1273	47	2333	3275	38
Barred owls															
BC_BM	475	333	47	450	264	37									
DC_BM							927	466	34	5999	4753	41	265	105	28
DH_BM	345	239	41	886	694	43	351	261	50	721	368	34			
EC_BF	1111	700	29	1901	1204	44	754	368	30	2144	1073	33			
EC_BM	315	244	52	763	751	49	645	455	43	632	427	44			
ELK_BF				1208	933	48	723	608	37	989	649	41			
ELK_BM	265	229	30	1261	905	52	1120	869	46	1109	684	34			
FC_BF	352	163	28	658	487	48	510	399	44						
FC_BM	652	426	43	753	470	38	514	409	49	731	431	38			
GC_BM	1416	1089	47	2733	1528	42									
HP_BM	423	325	48	1975	1047	43	331	227	55	933	767	43			
IM_BF				279	182	46	166	89	35	275	189	38			
KLI_BF	190	128	39	696	698	44	431	294	40	880	624	40			
LBC_BF	237	187	34	539	375	61	286	186	39	311	188	49			
LOC_BF	920	897	39	871	1112	45	539	321	27	598	467	38			
PAT_BF				1131	921	44									
PC_BF	471	418	37	455	292	46	681	428	33	856	568	36			
PG_BM				1330	926	48	486	398	57	774	439	39			
RC_BM	621	754	55	845	557	46	869	633	45	557	295	25			
SC_BM	826	641	44	760	589	42	855	593	43	824	406	33			
SF_BF	143	99	59	1744	1081	57	155	107	47	717	572	33			
SG_BF							553	261	32						
SG_BM							358	172	31	626	431	39	594	340	30
UPC_BF	547	351	39	857	677	48	403	197	34	312	259	39			
UPC_BM	565	324	40	922	744	48	758	449	47	703	391	39			
WC_BF							665	570	45	935	809	40	381	205	28
WC_BM2							665	570	45	570	469	35	829	491	26

[a] Second to last letter indicates species, last letter indicates owl's sex.

Appendix G. Ranking of *a priori* models used to characterize nighttime resource selection by northern spotted owls and barred owls in western Oregon, 2007–2009.

Model	*K*	AIC	ΔAIC	AIC wt
Spotted owl (*n* = 25 owls, 42 choice sets)				
Fortype+dnest^2+slope+dwater+dBO+(HDW×dBO)	10	31,014.2	0.00	0.90
Fortype+dnest^2+slope+dwater+dHET	9	31,019.8	5.53	0.06
Fortype+dnest^2+slope+dwater+dBO+(OLD×dBO)	10	31,020.4	6.14	0.04
Fortype+dnest^2+slope+dwater+HETcore	9	31,031.3	17.07	0.00
Fortype+dnest^2+slope+dwater	8	31,045.6	31.38	0.00
Fortype+dnest^2+slope+dedge^2+dwater	10	31,046.1	31.86	0.00
Fortype+dnest^2+dwater	7	31,046.7	32.51	0.00
Fortype+dnest^2+dedge^2+dwater	9	31,047.5	33.25	0.00
Fortype+dnest^2	6	31,101.1	86.83	0.00
Fortype+dnest^2+slope	7	31,101.7	87.42	0.00
Fortype+dnest^2+dedge	7	31,101.9	87.62	0.00
Fortype+dnest^2+dedge^2	8	31,103.0	88.77	0.00
Fortype+dnest^2+slope+dedge^2	9	31,103.4	89.16	0.00
Fortype+dnest	5	31,173.1	158.84	0.00
Fortype	4	31,199.8	185.54	0.00
QMDcon+QMDcon^2+CANCOVhdw+dnest^2	5	31,249.9	235.66	0.00
QMDcon+QMDcon^2+CANCOVhdw	3	31,351.9	337.70	0.00
QMDcon+QMDcon^2+CANCOVhdw+CANCOVhdw^2	4	31,353.9	339.65	0.00
QMDcon+QMDcon^2	2	31,441.1	426.88	0.00
QMDcon	1	31,461.9	447.68	0.00
TPHcon50	1	31,584.7	570.44	0.00
CANCOVhdw+CANCOVhdw^2	2	31,889.8	875.61	0.00
CANCOVhdw	1	31,899.7	885.47	0.00
BASALhdw^2	2	31,905.7	891.50	0.00
BASALhdw	1	31,911.0	896.74	0.00
Null model	0	31,964.5	950.31	0.00
Barred owl (*n* = 26 owls, 43 choice sets)				
Fortype+dnest^2+slope+dedge^2+dwater	10	30,673.3	0.00	0.41
Fortype+dnest^2+slope+dedge^2+dwater+dHET+ (OLD×dHET)	12	30,675.0	1.72	0.17
Fortype+dnest^2+slope+dedge^2+dwater+HETcore	11	30,675.2	1.96	0.15
Fortype+dnest^2+slope+dedge^2+dwater+dHET	11	30,675.8	2.55	0.12

Appendix G (continued)

Fortype+dnest^2+slope+dedge^2+dwater+dHET+ (HDW×dHEt)	12	30,676.5	3.23	0.08
Fortype+dnest^2+slope+dwater	8	30,677.9	4.66	0.04
Fortype+dnest^2+slope+dedge2	9	30,679.2	5.96	0.02
Fortype+dnest^2+slope	7	30,684.6	11.30	0.00
Fortype+dnest^2+dedge^2+dwater	9	30,703.2	29.96	0.00
Fortype+dnest^2+dwater	7	30,705.9	32.59	0.00
Fortype+dnest^2+dedge^2	8	30,712.9	39.66	0.00
Fortype+dnest^2+dedge	7	30,715.1	41.82	0.00
Fortype+dnest^2	6	30,716.1	42.82	0.00
Fortype+dnest	5	30,809.5	136.27	0.00
QMD^2+CANCOVhdw^2+dnest^2	6	30,931.1	257.82	0.00
Fortype	4	31,131.8	458.48	0.00
QMDcon+QMDcon^2+CANCOVhdw+CANCOVhdw^2	4	31,375.0	701.77	0.00
QMDcon+QMDcon^2+CANCOVhdw	3	31,378.6	705.27	0.00
QMDcon+QMDcon^2	2	31,380.6	707.29	0.00
QMDcon	1	31,388.3	715.03	0.00
TPHcon50	1	31,451.2	777.90	0.00
CANCOVhdw	1	31,622.9	949.65	0.00
CANCOVhdw+CANCOVhdw^2	2	31,623.9	950.57	0.00
BASALhdw	1	31,623.9	950.64	0.00
Null model (no effects)	0	31,625.4	952.16	0.00
BASALhdw^2	2	31,625.9	952.64	0.00
Species combined (*n* = 51 owls, 85 choice sets)				
Fortype+dnest^2+slope+dstream+dedge^2+(spp×fortype)+ (spp×dnest^2)+(spp×slope)+(spp×dstream)+ (spp×dedge^2)	20	61,719.38	0.00	1.00
Fortype+dnest^2+slope+dstream+dedge^2+(spp×dnest^2)+ (spp×slope)+ (spp×dstream)+(spp×dedge^2)	16	61,758.09	38.71	0.00
Fortype+dnest^2+slope+dstream+dedge^2	10	61,976.75	257.38	0.00
Null model (no effects)	0	63,589.98	1,870.61	0.00

[a] Forest type was a categorical variable with 5 levels: old conifer, mature conifer, young conifer, riparian-hardwood, and nonforest. Other model covariates included slope, distance to nest (dnest), distance to stream (dstream), distance to high contrast edge (dedge), proximity to heterospecific core-use area (dHET), and area within a heterospecific neighbor's core-use area (HETcore).

[b] *K* = number of parameters; ΔAIC = difference between the AIC value of each model and the lowest AIC model; AIC wt = Akaike weight.

Appendix H. Mean mass, behavioral attributes, and frequency of occurrence (*n*) of prey species identified in pellets of sympatric northern spotted owls and barred owls in western Oregon, 2007–2009.

Prey species	Mean mass (g)[a]	Activity code[b]	Spotted owl *n*	Barred owl *n*
Mammals			1,133	1,446
Fog shrew (*Sorex sonomae*)	9 (1)	N, T	—	87
Pacific marsh shrew (*Sorex bendirii*)	18 (1)	N, T	—	6
Trowbridge's or vagrant shrew (*S. trowbridgii/vagrans*)	5 (1)	N, T	8	375
Trowbridge's shrew (*Sorex trowbridgii*)	5 (1)	N, T	4	39
Unidentified shrew (*Sorex* spp.)	5 (1)	N, T	10	2
Vagrant shrew (*Sorex vagrans*)	5 (1)	N, T	6	34
Coast mole *(Scapanus orarius*)	56 (1)	N, T	4	508
Shrew mole (*Neurotrichus gibbsii*)	9 (1)	N, T	7	169
Townsend's mole (*Scapanus townsendii*)	130 (1)	N, T	—	90
Big brown bat (*Eptesicus fuscus*)	15 (1)	N, F	4	1
Unidentified bat (*Myotis* spp.)	6 (4)	N, F	2	6
Brush rabbit (*Sylvilagus bachmani*)	50-750 (3)	B, T	—	19
Snowshoe hare (*Lepus americanus*)	50-1400 (3)	B, T	—	11
Unidentified rabbit or hare	50-900 (3)	B, T	49	54
Mountain beaver (*Aplodontia rufa*)	100-550 (3)	N, T	12	36
Douglas' squirrel (*Tamiasciurus douglasii*)	221 (1)	D, S	11	89
Northern flying squirrel (*Glaucomys sabrinus*)	40-150 (3)	N, A	445	493
Townsend's chipmunk (*Tamias townsendii*)	83 (1)	D, S	6	46
Western gray squirrel (*Sciurus griseus*)	450 (1)	D, S	—	6
Western pocket gopher (*Thomomys mazama*)	95 (1)	N, T	9	20
Western spotted skunk (*Spilogale gracilis*)	606 (1)	N, T	—	10
Western red-backed vole (*Myodes californicus*)	23 (1)	N, T	36	67
Red tree vole (*Arborimus longicaudus*)	26 (1)	N, A	179	155
Creeping vole (*Microtus oregoni*)	20 (1)	N, T	14	54
Long-tailed vole (*Microtus longicaudus*)	56 (1)	N, T	—	9
Townsend's vole (*Microtus townsendii*)	54 (1)	N, T	2	14
Unidentified vole (*Microtus* spp.)	30 (4)	N, T	1	18
Unidentified vole or mouse (*Muridae* spp.)	25 (4)	N, T	41	17
Common muskrat (*Ondatra zibethicus*)	1,169 (1)	B, Q	—	3
Pacific jumping mouse (*Zapus trinotatus*)	24 (1)	N, T	6	35

Appendix H (continued)

Black rat (*Rattus rattus*)	250 (3)	N, T	—	1
Deer mouse (*Peromyscus maniculatus*)	22 (1)	N, T	223	149
Unidentified woodrat (*Neotoma fuscipes* or *N. cinerea*)	285 (4)	N, S	91	63
Ermine (*Mustela erminea*)	55 (1)	N, T	2	14
Unidentified weasel (*Mustela* spp.)	25 (3)	N, T	—	54
Unidentified mammal	30-400 (3)	U, U	—	2
Birds			49	134
Band-tailed Pigeon (*Patagioenas fasciata*)	392 (2)	D, F	—	7
Steller's Jay (*Cyanocitta stelleri*)	128 (2)	D, F	5	7
Gray Jay (*Perisoreus canadensis*)	73 (2)	D, F	2	1
Dark-eyed Junco (*Junco hyemalis*)	18 (2)	D, F	1	9
Spotted Towhee (*Pipilo maculatus*)	40 (2)	D, F	—	1
Mountain Quail (*Oreortyx pictus*)	224 (2)	D, F	1	3
Chestnut-backed Chickadee (*Poecile rufescens*)	10 (2)	D, F	—	4
Unidentified Warbler (*Dendroica* spp.)	8 (4)	D, F	1	1
Ruffed Grouse (*Bonasa umbellus*)	514 (3)	D, F	—	6
Blue Grouse (*Dendragapus obscurus*)	1,050 (3)	D, F	—	1
Unidentified grouse spp.	350 (4)	D, F	—	1
Northern Flicker (*Colaptes auratus*)	142 (2)	D, F	2	4
Pileated Woodpecker (*Dryocopus pileatus*)	287 (2)	D, S	—	2
Hairy Woodpecker (*Picoides villosus*)	66 (2)	D, S	2	1
Red-breasted Sapsucker (*Sphyrapicus ruber*)	49 (2)	D, F	1	2
Golden-crowned Kinglet (*Regulus satrapa*)	6 (2)	D, F	3	1
Red-breasted Nuthatch (*Sitta canadensis*)	10 (2)	D, F	2	3
Northern Saw-whet Owl (*Aegolius acadicus*)	83 (2)	N, F	2	8
Northern Pygmy Owl (*Glaucidium gnoma*)	68 (2)	N, F	4	1
Western Screech Owl (*Megascops kennicottii*)	169 (2)	N, F	4	9
Western Tanager (*Piranga ludoviciana*)	28 (2)	D, F	—	2
Pacific Wren (*Troglodytes pacificus)*	9 (2)	D, F	4	27
Swainson's Thrush (*Catharus ustulatus*)	31 (2)	D, F	2	2
Varied Thrush (*Ixoreus naevius*)	78 (2)	D, F	6	6
American Robin (*Turdus migratorius*)	77 (2)	D, F	3	3
Unidentified Flycatcher (*Empidonax* spp.)	11 (4)	D, F	—	1
Unidentified medium-size bird	60-299 (3)	D, F	—	5
Unidentified small bird	5-59 (3)	D, F	4	16

Appendix H (continued)

Amphibians			1	389
Unidentified frog (*Rana* spp.)	30 (6)	B, Q	—	24
Large salamander (*Ambystoma* or *Dicamptodon* spp.)	23-114 (3)	N, T	1	55
Unidentified medium-size salamander	22-23 (3)	N, T	—	186
Unidentified small salamander	6-21 (3)	N, T	—	124
Reptiles			2	37
Northern alligator lizard (*Elgaria coerulea*)	35 (7)	D, T	—	4
Western fence lizard (*Sceloporus occidentalis*)	10 (7)	D, T	1	3
Garter snake (*Thamnophis* spp.)	100 (7)	D, T	1	28
Racer (*Coluber constrictor*)	77 (8)	D, T	—	1
Unidentified snake	200 (4)	D, T	—	1
Mollusks – Gastropoda			2	271
Robust lancetooth snail (*Haplotrema vancouverense*)	7 (7)	B, T	2	55
Pleurocerid snail (*Juga* spp.)	0.02 (6)	B, Q	—	63
Pacific sideband snail (*Monadenia fidelis*)	10.4 (6)	B, T	—	149
Unidentified snail	5 (4)	B, T	—	4
Crustaceans			1	157
Signal crayfish (*Pacifastacus leniusculus*)	23.8 (6)	B, Q	1	157
Fish				
Unidentified fish (*Osteichthyes* spp.)	51 (9)	B, Q	—	10
Insects, millipedes, and springtails			19	552
Tiger beetle (*Omus audouini*)	0.3 (5)	U, U	—	9
Ground beetle (*Pterostichus lama*)	0.3 (5)	U, U	11	89
Unidentified ground beetle (*Pterosticus* spp.)	0.3 (5)	U, U	—	26
Unidentified ground beetle (*Carabidae* spp.)	0.3 (5)	U, U	1	300
Ponderosa wood borer (*Ergates spiculatus*)	2.4 (5)	U, S	5	6
Weevil (*Dyslobus lecontei*)	0.3 (5)	U, U	—	19
Unidentified ant (*Formica* spp.)	0.1 (5)	U, U	—	56
Carpenter ant (*Camponotus* spp.)	0.1 (5)	U, U	—	9
Stink bug (*Hemiptera* spp.)	0.3 (5)	U, U	—	5
Unidentified bee (*Hymenoptera* spp.)	0.1 (5)	U, U	1	3
Ichnemon wasp (*Ichneumonid* spp.)	0.1 (5)	U, U	—	1
Braconid wasp (*Braconidae* spp.)	0.1 (5)	U, U	—	1
Unidentified large insect	2.0 (5)	U, U	—	1

Appendix H (continued)

Unidentified small insect	0.3 (5)	U, U	1	18
Yellow-spotted millipede (*Harpaphe haydeniana*)	0.4 (5)	U, U	—	8
Unidentified springtail (*Entomobryid* spp.)	0.1 (5)	U, U	—	1
Totals			1,246	4,306

[a] Source of mass estimate is in parentheses: 1 = Verts and Carraway 1998; 2 = Dunning 1993; 3 = mass of each individual estimated based on comparison with reference specimen of known mass; 4 = mean of all species in group; 5 = mass based on estimates from similar species in this genus or group; 6 = estimated from local specimens; 7 = Forsman et al. 2004, 8 = Steenhof 1983, 9 = Behnke 2002.

[b] Following Forsman et al. (2004), first letter indicates primary period of activity (D = diurnal, N = nocturnal, B = active both day and night, U = unknown), second letter indicates primary area of activity (T = terrestrial, A = arboreal, S = semi-arboreal, F = flying or aerial animal, Q = aquatic, U = unknown).

Appendix I. Ranking of *a priori* models used to examine variation in survival (*S*) of radio-marked northern spotted owls (*n*=29) and barred owls (*n*=28) in western Oregon from May 2007 to February 2009.

Model[a]	*K*	AIC_c	ΔAIC_c	AIC_c wt	Deviance
S(Spp + OLD + *PHR*)	4	89.57	0.00	0.32	81.35
S(Spp + OLD)	3	89.60	0.03	0.32	83.47
S(Spp + EDGE + OLD)	4	91.64	2.07	0.12	83.42
S(Spp × OLD)	4	91.68	2.11	0.11	83.47
S(Spp)	2	95.77	6.20	0.01	91.71
S(Spp + OLDc)	3	95.93	6.36	0.01	89.80
S(Spp + *PHR*)	3	96.00	6.43	0.01	89.87
S(.) - intercept only	1	96.09	6.52	0.01	94.07
S(Spp + EDGE)	3	96.97	7.40	0.01	90.84
S(Spp + *HR*)	3	97.02	7.45	0.01	90.89
S(Spp + EDGE + OLDc)	4	97.27	7.69	0.01	89.05
S(Spp + season)	3	97.36	7.79	0.01	91.23
S(Spp + sex)	3	97.66	8.09	0.01	91.53
S(Spp + yr)	3	97.83	8.26	0.01	91.70
S(Spp × OLDc)	4	98.01	8.44	0.00	89.79
S(Spp × *PHR*)	4	98.03	8.46	0.00	89.81
S(Spp × sex)	4	98.56	8.99	0.00	90.34
S(Spp × EDGE)	4	98.98	9.41	0.00	90.77
S(Spp × *HR*)	4	99.10	9.53	0.00	90.88
S(Spp + season + sex)	4	99.26	9.69	0.00	91.04
S(Spp × yr)	4	99.79	10.22	0.00	91.58
S(Spp + t)	5	101.55	11.98	0.00	91.22
S(Spp × t) - global model	8	104.85	15.28	0.00	88.05

[a] Time effects modeled as constant (.), varying between years (yr), varying among categorical 6-mo time intervals (t), or varying in an even-odd fashion between breeding (1 Mar-31Aug) and nonbreeding (1 Sep-28Feb) seasons (season). Covariates included owl species (Spp), proportion of old conifer forest in the home range (old), proportion of old conifer forest in the breeding core area (old_core), mean distance to high-contrast edge (edge), proportion of home range shared with neighboring heterospecifics (*HR*), and probability of heterospecific presence within the home range (*PHR*).