

NORTHERN SPOTTED OWL AND BARRED OWL HOME RANGE SIZE AND
HABITAT SELECTION IN COASTAL NORTHWESTERN CALIFORNIA

By

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ABSTRACT

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The federally threatened northern spotted owl (*Strix occidentalis caurina*) continues to experience range-wide population declines despite two-plus decades of intensive conservation and recovery efforts. Management of the owl has been a highly contentious issue, focused primarily on setting aside critical habitat and preserving old-growth and mature forests in the Pacific Northwest. Recent evidence however, indicates that competition from the invading and closely-related barred owl (*Strix varia*) is the primary threat to northern spotted owl populations. While agonistic interactions are widely documented, there remains a lack of information on how these two species compete for ecological resources. The redwood region of coastal northwestern California, where spotted owl populations remain relatively high, offered a unique opportunity to study resource competition and partitioning between northern spotted owls and barred owls. I used radio-telemetry to locate both species at night with the objectives of (1) determining home range size of northern spotted owls and barred owls (2) determining foraging habitat selection and resource partitioning of sympatric northern spotted owls and barred owls.

Average home range size for northern spotted owls and barred owls during the breeding season was 391 ha and 303 ha, respectively, and average home range size during the nonbreeding season was 560 ha and 442 ha, respectively. I did not find a significant difference in home range size between the two species in either season. Spotted owls occupied smaller home ranges in my study area than in the northern portion of their range and both species exhibited relatively little home range size variation between seasons.

My top four models ($\Delta AIC_c < 2$) indicated that both species exhibited habitat selection for percent understory vegetation, hardwood trees (percent and basal area), and distance to nest. However, variables in my top models included the interactive effects of the owl species, providing evidence that some degree of resource partitioning may exist between northern spotted owls and barred owls in coastal northwestern California.

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INTRODUCTION

The northern spotted owl (*Strix occidentalis caurina*; “spotted owl”) was listed as a threatened subspecies under the Endangered Species Act in 1990 due to declining populations linked to habitat loss and degradation (USFWS 1990). Despite decades of intensive conservation efforts, the subspecies continues to experience range-wide population declines (Forsman et al. 2011, USFWS 2011). Until recently, recovery efforts focused almost entirely on spotted owl critical habitat areas by preserving the remaining old-growth and mature forest stands in the Pacific Northwest, USA (Courtney et al. 2004, USFWS 2011). While maintaining suitable habitat is crucial for the recovery of a species, there is increasing concern that competition from the recently colonizing and congeneric barred owl (*Strix varia*) is now the primary threat to spotted owl populations (Kelly et al. 2003, Courtney et al. 2004, Gutiérrez et al. 2004, 2007, Anthony et al. 2006, Buchanan et al. 2007, Forsman et al. 2011, USFWS 2011, Wiens et al. 2014). The range of the barred owl now completely overlaps that of the northern spotted owl (Kelly et al. 2003, Gutiérrez et al. 2004, Anthony et al. 2006, Livezey et al. 2009), creating the potential for interspecific competition between the two species. The ecological and morphological similarity of spotted and barred owls, combined with their overlap in distribution, may cause barred owls to limit or even extirpate northern spotted owls throughout their range (Kelly et al. 2003, Anthony et al. 2006, Buchanan et al. 2007, Gutiérrez et al. 2007, Forsman et al. 2011, Wiens et al. 2014).

Barred owl populations, once restricted to the eastern United States (Mazur and

James 2000, Anthony et al. 2006), have rapidly expanded in recent decades to overlap the entire range of the northern spotted owl (Dark et al. 1998, Kelly et al. 2003, Courtney et al. 2004, Gutiérrez et al. 2004, Livezey 2009). First reported in the range of the spotted owl in British Columbia in 1969 (Stirling 1970), barred owls quickly moved south through Washington, Oregon (Taylor and Forsman 1976), and finally into California, where they were first documented in Del Norte and Trinity Counties in 1981 (Evens and LeValley 1982). Evidence indicates that spotted owls are experiencing population declines concurrently with the expansion of barred owls (Anthony et al. 2006, Livezey 2009, Forsman et al. 2011), and 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. 2014). In Washington and northern Oregon, where barred owls have been present the longest and occur in the highest densities in the western US, spotted owls declined 40-60% between 1985 and 2008 (Forsman et al. 2011). In southern Oregon and northern California, where barred owl numbers are relatively low, only minor declines in spotted owl populations have been observed (Forsman et al. 2011).

The ecological similarity of the two species creates high potential for interspecific competition (Lack 1946). Barred owls are closely related to spotted owls, but are more aggressive (Van Lanen et al. 2011), use smaller home ranges (Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2014), are larger (Dark et al. 1998, Gutiérrez et al. 2004, 2007), eat a wider variety of prey items (Hamer et al. 2001, Livezey 2007, Wiens et al. 2014), and potentially reproduce at a higher rate (Wiens et al. 2011, 2014). When

agonistic interactions between the two species occur, barred owls typically dominate and respond more aggressively, often leading to physical attacks and harassment of spotted owls (Gutiérrez et al. 2007, Van Lanen et al. 2011). Numerous studies indicate that barred owls are displacing (Kelly et al. 2003, Pearson and Livezey 2003, Gremel 2005, Olson et al. 2005, Hamer et al. 2007, Livezey and Fleming 2007, Dugger et al. 2011, Wiens et al. 2014), hybridizing with (Kelly and Forsman 2004), and even killing spotted owls (Leskiw and Gutiérrez 1998). Such interactions can negatively influence spotted owl vocal responses and detectability during calling surveys (Leskiw and Gutiérrez 1998, Olson et al. 2005, Crozier et al. 2006, Dugger et al. 2009, USFWS 2011, Van Lanen et al. 2011, Wiens et al. 2011). When viewed collectively, the behavioral and life history traits of barred owls give them a competitive advantage over spotted owls, likely causing reduced spotted owl site occupancy (Pearson and Livezey 2003, Gremel 2005, USFWS 2011) and reproductive success (Olson et al. 2004, Forsman et al. 2011, Wiens et al. 2014).

Barred owls appear to have a competitive advantage in habitat and resource selection as well. The species is considered a forest generalist and are known to occupy a variety of habitats in the U.S. (88Dunbar et al. 1991), including old-growth and late-successional forest types that are associated with spotted owl habitat (Hamer et al. 2007, Wiens et al. 2014). In the eastern U.S., barred owls preferred mature deciduous-coniferous forests (Dunstan and Sample 1972, Devereux and Mosher 1984, Elody and Sloan 1985, Laidig and Dobkin 1995), and bred primarily in structurally-diverse old-growth stands (>300 yrs) that were dominated by eastern hemlock (*Tsuga canadensis*;

Haney 1997). Similarly, barred owls in Oregon and Washington favored moist, low elevation mixed deciduous-coniferous and old-growth forests with high canopy cover (Herter and Hicks 2000, Pearson and Livezey 2003, Buchanan et al. 2004, Gremel 2005, Hamer et al. 2007, Wiens et al. 2014). Habitat studies in the Washington Cascades, conducted at the landscape-level or second-order habitat selection as described by Johnson (1980), showed that radio-marked barred owls tended to select older forests at lower elevations with gentle slopes (Hamer et al. 2007, Singleton et al. 2010). In the southern portion of their range in northwestern California, barred owls have displaced most historic spotted owl territories in RNSP and now occupy much of the unfragmented old-growth and mature forest stands (Schmidt 2013). Barred owls also occur in large numbers in younger forest stands that are not considered suitable spotted owl habitat in Oregon and Washington (Kelly et al. 2003), which includes a large portion of the forested areas of both states (Kelly et al. 2003, Wiens et al. 2014).

While information exists on the broad habitat use patterns of barred owls across the landscape, data are lacking at the finer scale of habitat selection. Studying resource use at the home range level may reveal patterns in habitat selection and partitioning not detected at the landscape level (Wiens et al. 2014). For example, radio-marked spotted and barred owls monitored in western Oregon displayed similar patterns of habitat selection at the second order or landscape level, but differed at the third order or home range level (Wiens et al. 2014). At the third order, spotted owls were more likely to select riparian hardwood, old and mature conifer, and young conifer forest patches in comparison to barred owls (Wiens et al. 2014). However, few studies have directly

examined the resource selection of barred owls in the Pacific Northwest (Marzur and James 2000, Gutiérrez et al. 2004, 2007, Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2011, 2014), and most information reporting the negative effects of barred owl occurrence on spotted owls has been collected incidentally during spotted owl surveys (Livezey and Flemming 2007). In contrast, the spotted owl has been widely studied throughout its range (Courtney et al. 2004, Buchanan et al. 2004, Gutiérrez et al. 2007), but recovery efforts are limited by the lack of data on barred owls and information on resource competition between the two species (Gutiérrez et al. 2007, Livezey and Flemming 2007).

As apex predators, competition for resources is driven by habitat selection and strongly influenced by prey availability and abundance on the landscape. The redwood region of northwestern California offered a unique opportunity to study the habitat selection of the two species in an area of co-occurrence, because barred owl numbers are still relatively low and spotted owl numbers remain relatively stable (Forsman et al. 2011). Unlike the northern portion of their range, spotted owls typically select young forest stands and edge habitat for foraging in northwestern California, which is likely a reflection of prey availability (Zabel et al. 1995, Ward et al. 1998, Franklin et al. 2000). In this region, the primary prey by biomass is the dusky-footed woodrat (*Neotoma fuscipes*; Hamm 1995, Ward et al. 1998, Franklin et al. 2000), which are most abundant in early-seral forests (Fitts and Northen 1991, Sakai and Noon 1993, Hamm and Diller 2009). Edge habitat that contains structurally-complex forests in close proximity to early-seral forest stands is likely most beneficial for spotted owls (Zabel et al. 1995,

Ward et al. 1998, Glenn et al. 2004, Franklin et al. 2000, 2004), because such heterogenic habitat provides both shelter, maneuverability, and an abundant source of prey (Ward et al. 1998). Other variables suggested to affect spotted owl habitat selection through woodrat prey density include the amount of shrub layer vegetation (Sakai and Noon 1993, Hamm 1995, Hamm and Diller 2009) and proximity to streams and riparian areas (Anthony et al. 2003, Carey et al. 1999).

Barred owl habitat selection in coastal northwestern California remains largely unclear, so I examined habitat variables shown to influence spotted owls. Based on previous studies that examined spotted owl fitness and occupancy in northern California (e.g., Franklin et al. 2000), I predicted that foraging habitat selection of spotted owls in northwestern California would be positively influenced by vegetation variables and physical environmental factors including: percent understory vegetation, tree basal area (the cross sectional area m^2/ha of trees), hardwoods, quadratic mean diameter (QMD), distance to nest, distance to streams, distance to young forest stands, slope, and elevation. I also predicted that barred owls would be positively influenced by the same habitat variables, excluding distance to young forest stands, but would exhibit stronger habitat selection for areas with higher basal area, gentler slopes, and lower elevation. I also predicted that barred owls would have smaller home ranges than spotted owls based on previous studies (Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2014).

STUDY AREA

The study was conducted in coastal northwestern California on lands owned by Redwood National and State Parks (RNSP), Green Diamond Resource Company (GDRC), and the City of Arcata (Figure 1). All sites were located within Humboldt and Del Norte counties and contained similar vegetative communities that were dominated by coast redwood (*Sequoia sempervirens*) forests. Other dominant tree species in the study area included Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), and western red cedar (*Thuja plicata*). Secondary tree composition consisted primarily of deciduous trees including, tanoak (*Lithocarpus densiflorus*), red alder (*A. rubra*), Pacific madrone (*Arbutus menziesii*), California bay (*Umbellularia californica*), and bigleaf maple (*A. macrophyllum*; Diller and Thome 1999). Common understory vegetation included sworn fern (*Polystichum munitum*), salal (*Gaultheria shallon*), Oregon grape (*Berberis nervosa*), salmonberry (*Rubus spectabilis*), huckleberry (*Vaccinium spp.*), and redwood sorrel (*Oxalis oregana*). The study area was strongly influenced by the Pacific Ocean and experienced mild temperatures throughout the year ranging from an average of 7.2° C in the winter to 20.5° C in the summer (Schmidt 2013). Annual precipitation averaged 175 cm across the region (Schmidt 2013).

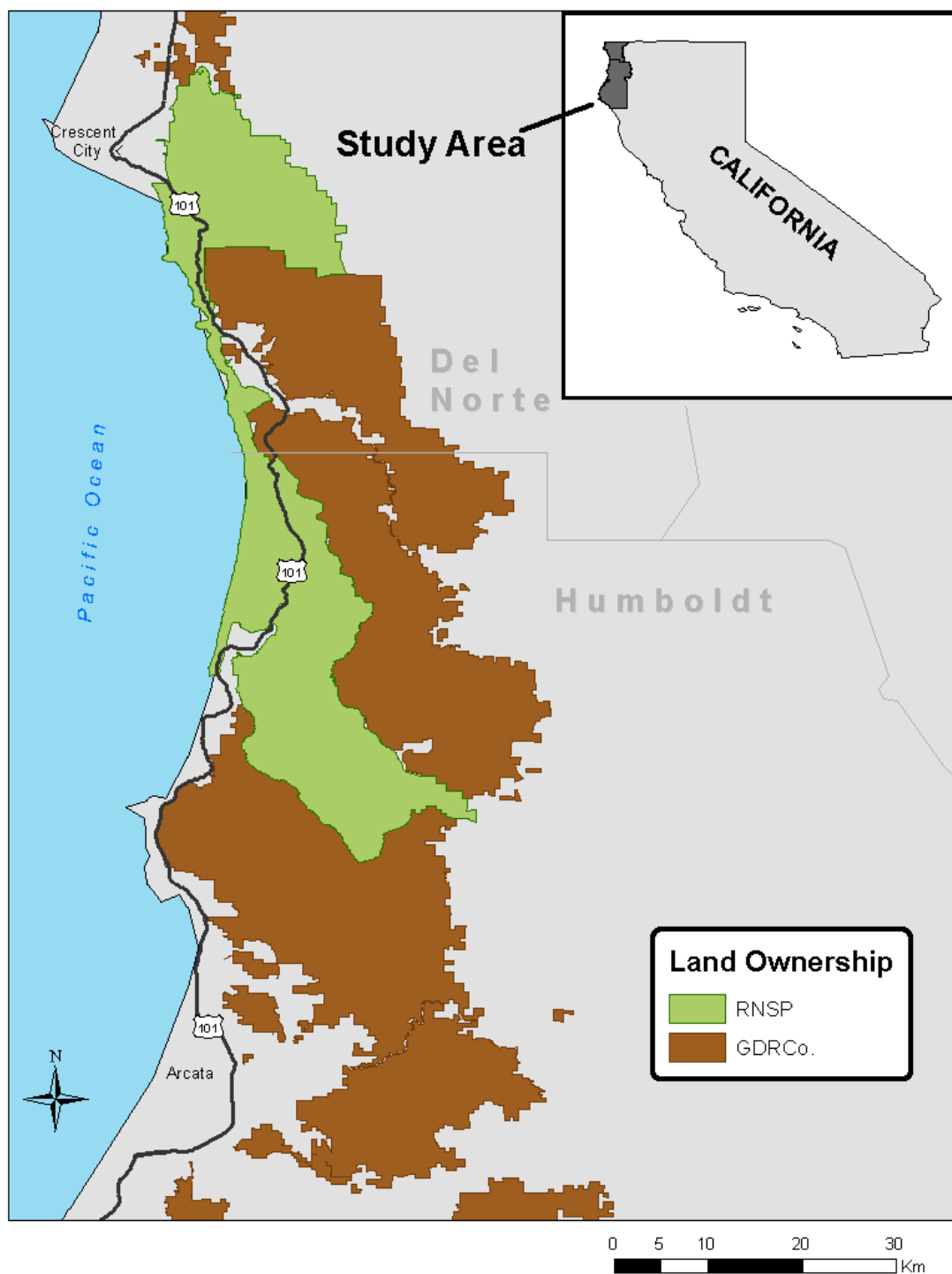


Figure 1. Land ownership across the study area displayed as Green Diamond Resource Company land in brown and Redwood National and State Parks land in green. All sites were located Humboldt and Del Norte Counties, California, USA.

Although the vegetation types throughout the study area were similar, forest structure and land management practices differed among land owners. Approximately 30% of RNSP reserved land was old-growth forest (Schmidt 2013), whereas City of Arcata land and managed timberlands owned by GDRC contained almost no old-growth (>180 years; Diller et al. 2014). GDRC practiced almost entirely clear-cut logging (Thome et al. 1999); the oldest forest stands on GDRC land were approximately 80-90 years old (Thome et al. 1999), but ranged from recently cut to 120 years (Diller et al. 2014). The City of Arcata did not clear cut, but used selective harvesting techniques since 1980 to promote the structural characteristics found in old growth forests (City of Arcata 1994). Thus, the study area included a wide range of habitat conditions that spotted and barred owls inhabit in coastal northwestern California.

METHODS

Field Methods

Capture Methods

I captured territorial spotted owls and barred owls at known locations identified from previous demographic studies conducted in Redwood National and State Parks and on Green Diamond Resource Company land. Capture efforts were limited to sites that had sufficient road or trail access for collecting night time telemetry locations and were logistically efficient to monitor based on proximity to other monitored owl sites. Spotted owls were captured according to standard protocols described by Forsman (1983). Barred owls were captured using an amplified megaphone (Wildlife Technologies, Manchester, NH) to play conspecific calls and a plastic barred owl decoy to lure owls into break-away dho-gaza nets. Captured spotted and barred owls were then fitted respectively with a 6.5 g or 12.5 g (Holohil Inc., Woodlawn, ON, Canada) backpack-mounted radio transmitter attached with Teflon ribbon (Guetterman et al. 1991, Wiens et al. 2014). Owls were also banded with a uniquely numbered U.S. Geological Survey (USGS) aluminum band on one leg and a color band on the opposing leg. Radio transmitters plus attachment harnesses were all <3% of the adult spotted and barred owl body mass for both males and females. I determined the sex of the owls based on their weight and vocalizations or the presence of a brood patch on nesting females (Forsman 1983, Wiens et al. 2014). Follow-up surveys were conducted after attaching radio

transmitters by locating the owl during daylight hours to visually assess behavior and monitor overall health.

Telemetry Methods

Telemetry locations were gathered throughout the year using the standard triangulation method approximately 1-3 times per week at night (Carey et al. 1989, Guetterman et al. 1991, Millspaugh and Marzluff 2001). We used a minimum of 24 hours between tracking periods to minimize autocorrelation between owl locations. Locations were obtained using a hand-held, 3-element Yagi directional antenna (Telonics, Mesa, AZ or Communication Specialists, Inc., Orange, CA) and a portable telemetry receiver (model R-1000, Communication Specialists, Inc., Orange, CA). Each owl location consisted of ≥ 3 azimuths taken consecutively at geo-referenced stations (Trimble Geo XT, Sunnyvale, CA), within the shortest amount of time possible (usually 10-15 min) as described by Carey et al. (1998), Glenn et al. (2004), and Wiens et al. (2014) to create a polygon. Polygons were recorded in the field on 1:24,000 topographic maps. Triangulation (error) polygons estimated in the field as being ≥ 2 ha were discarded and another location, preferably during the same night, was gathered. Triangulation polygons were typically much less than 2 ha, however. Owl locations were assumed to be the center of the polygon and calculated using the arithmetic mean estimator in LOAS software (Ecological Software Solutions, LLC, Tallahassee, FL). Locations were gathered from 0.5 hours after sunset to 0.5 hours before sunrise. I rotated the order of tracking at each site every week to ensure that locations were obtained during different sampling periods. I attempted to replace radio-transmitters before the battery

life ended, which was approximately 12 months for spotted owls and 24 months for barred owls. If transmitters failed prematurely, I attempted to recapture the owl and replace the transmitter.

The accuracy of owl locations was determined by having naïve observers triangulate on radio-transmitters placed approximately 2-3 m above the forest floor in random locations throughout the study area. Transmitters were geo-referenced using a Garmin GPS at the time of placement. The average telemetry error, determined by comparing the GPS location to the triangulated location was 84 m (SE = 12). Previous telemetry studies indicated an error range of 68-164 m (Carey et al. 1992, Zabel et al. 1995, Glenn et al. 2004, Forsman et al. 2005, Wiens et al. 2014).

Habitat Assessment

I conducted habitat inventory sampling during the spring, summer, and fall of 2011 (Approved 6 May 2011 under IACUC Protocol No. 10/11.W.73) immediately following the completion of the telemetry portion of the study. Areas of habitat data sampling were identified using a 95% minimum convex polygon (MCP) home range for each owl or mated pair of owls calculated using BIOTAS (Ecological Software Solutions, LLC). Data collection occurred within cumulative individual 95% MCP home ranges and served to estimate available foraging habitat conditions. Each MCP home range was then overlaid with grid of points spaced evenly at 120 m apart. Each point on the grid represented a vegetation sampling plot, and was used to characterize both the used habitat points (telemetry locations) and the available habitat within each owl's home range.

Habitat variables were collected using a grid or transect of points to reduce the amount of intensive on-the-ground data collection while providing accurate data that accounted for forest stand variation in variable-radius plots. Using the grid method to sample vegetation plots was most efficient for this study, because owls are “central place foragers (Carey and Peeler 1995, Rosenberg and McKelvey 1999),” and concentrate their activities around a nest or roost site that is centrally located within their home range. Therefore spotted and barred owls are likely to use the same area(s), or “plots,” multiple times for foraging, and collecting habitat variables at every used location would likely result in duplicate sampling. Using a grid also increased the chance that owls used a small proportion of available habitat units.

Owl telemetry points (used locations) were assigned habitat data from the closest vegetation plot on the grid determined using the Near tool in ArcMap 10.0 (ESRI, Redlands, CA). Telemetry points that fell outside the sample area or 95% MCP home range were discarded, and not included in the habitat analysis. Similarly, telemetry points that occurred more than 120 m from a vegetation (or grid) point were discarded. Following recommendations by Manly et al. (2002), I aimed for a ratio of available to used habitat plots to be 4:1 for each estimated home range.

Five types of data were collected at each grid point: general plot information, trees, snags, and understory vegetative cover. The habitat plots were centered on each grid point and included variable and fixed-radius plots to measure forest stand structure and composition, amount of understory vegetation, and abiotic variables predicted to influence owl foraging behavior (see Table 1 for habitat variables and descriptions). At

the center of each vegetation point, I used a 40 basal area factor (BAF) relaskop prism to determine the number of trees inside the variable-radius plot and subsequently calculate basal area of each plot. Trees determined to be within the variable-radius plot were identified to species and dbh measurements (≥ 10 cm) were taken. The dbh measurements were used to compute the quadratic mean diameter (QMD) or the mean central tendency tree diameter within a plot.

I used 16.1 m fixed-radius circular plots to measure understory vegetative cover, abiotic variables, and snags (Bell and Dilworth 1990). Understory vegetation was identified to species and recorded in 5% increments and consisted of tree saplings (≤ 5 m in height), tree seedlings, shrubs, and herbaceous plants. The dbh of snags (≥ 10 cm) was also measured by species if possible. At the center of every vegetation plot I measured aspect, elevation, and slope using a compass, Garmin GPS, and relaskop prism. Map-based variables that could not be identified in the field were determined using a geographic information system (GIS) in ArcMap 10.0 or 10.1 (ESRI, Redlands, CA). These variables included distance to the nest or center of activity (center of the owl's 50% home range or core-use area) and distance to perennial streams. Heatload was included as measure of solar radiation at each plot and was calculated as a function of aspect and slope (Stage 1976). Edges comprised of young forests and other forest types likely provide beneficial foraging habitat for spotted owls in northwestern California (Zabel et al. 1995, Ward et al. 1998, Franklin et al. 2000). I therefore identified plots that contained only small diameter trees (10-25 cm dbh) to include as a variable.

Table 1. Abbreviations and descriptions of variables used to characterize habitat selection by northern spotted owls and barred owls in the redwood region of northwestern California, USA, 2007-2011.

Variable	Description	Abbreviation
Basal area	Cross-sectional area of all stems ≥ 10 cm dbh at breast height (m^2/ha)	BA
Hardwood basal area	Basal area of all live hardwoods ≥ 10 cm dbh (m^2/ha)	BAHARD
Quadratic mean diameter	Diameter of tree corresponding to average basal area of stand of trees (cm)	QMD
Percent hardwood	Ratio of hardwood BA to BA of all stems ≥ 10 cm dbh	PERHARD
Large snag	Presence of a snag ≥ 66 cm dbh within 16.1 m plot	SNAG
Understory vegetation	Total percent understory vegetation (≤ 0.5 m tall)	VEG
Aspect	Cardinal direction at plot center (N, NE, E, SE, S, SW, W, NW)	ASPECT
Slope	Angle of slope at plot center (degrees)	SLOPE
Elevation	Elevation above mean sea level at plot center (m)	ELEV
Distance to nest	Distance of plot center to nest or center of activity (m)	NEST
Distance to stream	Distance of plot center to perennial streams (m)	STREAM
Young forest	Distance of plot center to young forest stands (10-25 cm dbh)	YOUNG
Heatload ^a	$\tan(\text{SLOPE}) \times \sin(\text{ASPECT}) - \tan(\text{SLOPE}) \times \cos(\text{ASPECT})$	HEATLOAD

^afollowing Stage (1976)

Habitat Analysis and Model Development

I examined habitat selection of spotted and barred owls at the home range spatial scale, corresponding to Johnson's (1980) third order of selection. I developed a RSF of nocturnal foraging habitat selection for both species using coefficients estimated by the discrete-choice model (Manly et al. 2002, McDonald et al. 2006, Irwin et al. 2007, 2012). The discrete-choice model is similar to the logistic regression model, but differs by allowing the composition of choice sets to vary among choices. It also estimates the probability of a single resource variable to be used during a single choice rather than multiple choices (McDonald et al. 2006, Irwin et al. 2007, 2012). Using a discrete-choice model was particularly applicable to my study, because I was able to account for habitat changes, such as timber harvesting or thinning that occurred during the study (Irwin et al. 2007, 2012) as well as seasonal changes and thereby develop a set of new habitat choices for each owl's seasonal (6 month) home range.

I used an *a priori* approach to model habitat selection of spotted and barred owls (Burnham and Anderson 2002). I began the modeling process by developing a biological background on habitat variables and combinations of variables that were most likely to influence foraging selection as indicated from previous habitat studies on northern spotted owls (e.g., Franklin et al. 2000, Irwin et al. 2007, 2012, Wiens et al. 2014). I attempted to incorporate findings from barred owl studies on habitat selection conducted in the Pacific Northwest, however data were limited and confounded by differences in study design. I created a set of verbal hypotheses used to assemble a set of biologically

relevant models that could be used to assess the habitat use and partitioning between spotted and barred owls, keeping in mind that little empirical data exists on barred owls. I examined the habitat variables for co-linearity using a Pearson's correlation matrix calculated in R, but did not find evidence of any significant correlations between variables ($r < 0.6$ for all pairwise comparisons). I then developed a choice set for each individual owl based on habitat variables measured in each vegetation plot within individual 95% fixed-kernel seasonal home ranges.

I limited the number of models by including no more than two habitat variables in a single model. I did this, because little information exists on barred owl habitat selection and resource competition with spotted owls. Thereby limiting the number of variables and number of models would allow for ready interpretation of my results by land managers. I also used this approach to avoid over-fitting my data to the models. I developed 27 models that included different combinations of map-based variables and vegetation variables predicted to influence owl foraging behavior. I then considered each of these models with OWL (0=spotted owl, 1=barred owl) as an interaction variable to identify differences in resource use by each species. If models with the interactive effects of OWL ranked higher than models without interactive effects, then it is likely that some degree of resource partitioning exists between the species. I also included spotted and barred owls in the same models rather than developing independent models for each species, because my objective was to compare variation in habitat use between the two species rather than at the individual level.

Even though there is home range overlap between mated pairs, I modeled the two sexes separately, because males and females hunt independently for nocturnal prey (Irwin et al. 2012). I used a stratified Cox proportional hazards model in R (v 3.0.2) with Package ‘survival’ (v 1.35) to estimate log-likelihood values and parameter coefficients for variables to include in my RSF models. I stratified my models by season and year to account for differences in sampling periods between owls. Selection ratios were determined from the exponent of the model coefficient, where (selection ratio = $\exp[\text{coefficient}]$), to estimate the probability of selection as selection ratios, where a value >1 with a confidence interval >1 indicated positive selection and a value <1 with a confidence intervals <1 indicated a negative selection for a particular resource variable (Manly et al. 2002, McDonald et al. 2006, Irwin et al. 2012). These values represent the change in relative probability of selection for every one unit of change in the covariate, with the assumption that all other variables remained constant (Manly et al. 2002, McDonald et al. 2006, Irwin et al. 2012). I used second order Akaike’s Information Criterion, adjusted for small sample sizes (AIC_c), to rank models from the candidate set. The best model in the set has the lowest AIC_c value and largest AIC_c weight (Burnham and Anderson 2002). Models with a ΔAIC_c value within 2.0 from the best plausible model were considered to be competitive (Burnham and Anderson 2002).

RESULTS

Radio Telemetry and Home Range

A total of 10 spotted owls and 18 barred owls were captured, radio-marked, and monitored from 2007-2011 resulting in 1417 owl telemetry locations (Table 2). These included 13 barred owls and 2 spotted owls in RNSP and 5 barred owls and 8 spotted owls on timberland (Table 2). All radio-marked spotted owls were pair members, resulting in 5 territories, and radio-marked barred owls included 4 mated pairs and 3 individuals, resulting in 7 territories.

Average home range size for spotted and barred owls during the breeding season was 391 ha ($n = 9$, $SE = 79$, $Range = 53-643$) and 303 ha ($n = 21$, $SE = 37$, $Range = 90-639$), respectively, and 560 ha ($n = 11$, $SE = 159$, $Range = 90-1563$) and 442 ha ($n = 13$, $SE = 97$, $Range = 148-1401$) during the nonbreeding season, respectively (Figure 4). I did not find a significant difference between the average breeding home range size of spotted and barred owls or average home range size during the nonbreeding season (P -value = 0.26 and P -value = 0.42, respectively; see example Figures 2 and 3).

Due to premature radio failure, emigration, or mortality and adhering to a minimum of 28 locations, I was only able to obtain home range estimates for 11 barred owls and 10 spotted owls, totaling 54 seasonal home range estimates in 12 territories. Of these, 30 were during the breeding season and 24 were during the nonbreeding season (Table 3). I was unable to calculate home ranges of 8 barred owls, all located in the

Redwood National and State Parks due to insufficient telemetry locations: five were due to mortality or radio battery failure and two were due to owls leaving the study area.

Table 2. Summary by land ownership of northern spotted owl and barred owl sites monitored using radio telemetry in coastal northwestern California, USA, 2007-2011.

Variable	RNSP	GDRC	City of Arcata
Years of study	2007-2011	2008-2011	2008-2011
Spotted owls radio-tracked	2	6	2
Barred owls radio-tracked	12	2	5
Used locations	476	681	260
Available locations	3311	2924	1500

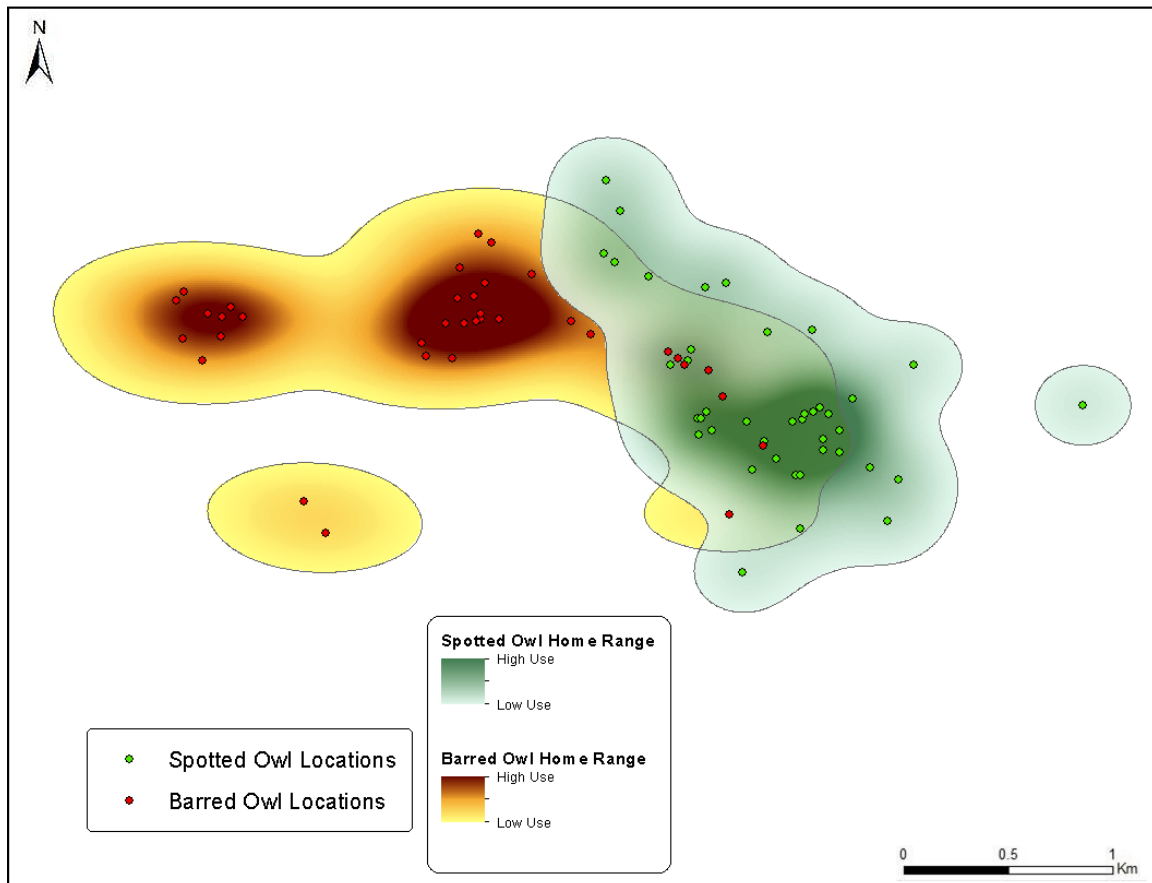


Figure 2. Home range example of a male northern spotted owl and a female barred owl located in adjacent territories on Green Diamond Resource Company land. Pictured home ranges are 95% fixed-kernel estimates calculated during the breeding season in 2011.

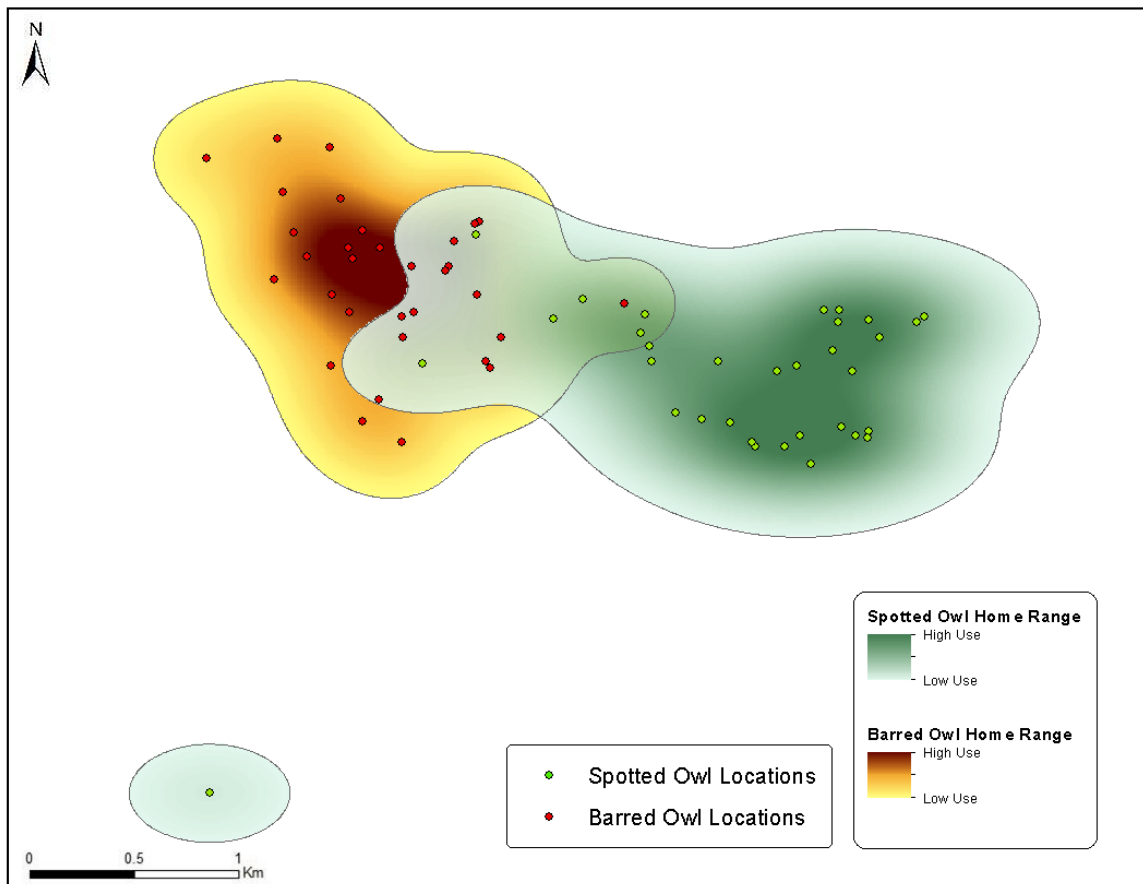


Figure 3. Home range example of a female northern spotted owl and a male barred owl located in adjacent territories on Green Diamond Resource Company land. Pictured home ranges are 95% fixed-kernel estimates calculated during the nonbreeding season in 2010-2011.

Table 3. Home range size (ha) of male and female spotted owls and barred owls in coastal northwestern California, USA, 2007-2011 using a 95% fixed-kernel estimator.

Home range^a	<i>n</i> (F, M)^b	Mean	SE	Range
Breeding				
Spotted owl	9 (4, 5)	391	79	53-643
Barred owl	21 (13, 9)	303	37	90-639
Nonbreeding				
Spotted owl	11 (6, 5)	560	159	90-1563
Barred owl	13 (5, 8)	442	97	148-1401

^a Breeding = 1 March – 31 August; Nonbreeding = 1 September – 28 February

^b Number of owls included in estimates, where; F = female, M = Male

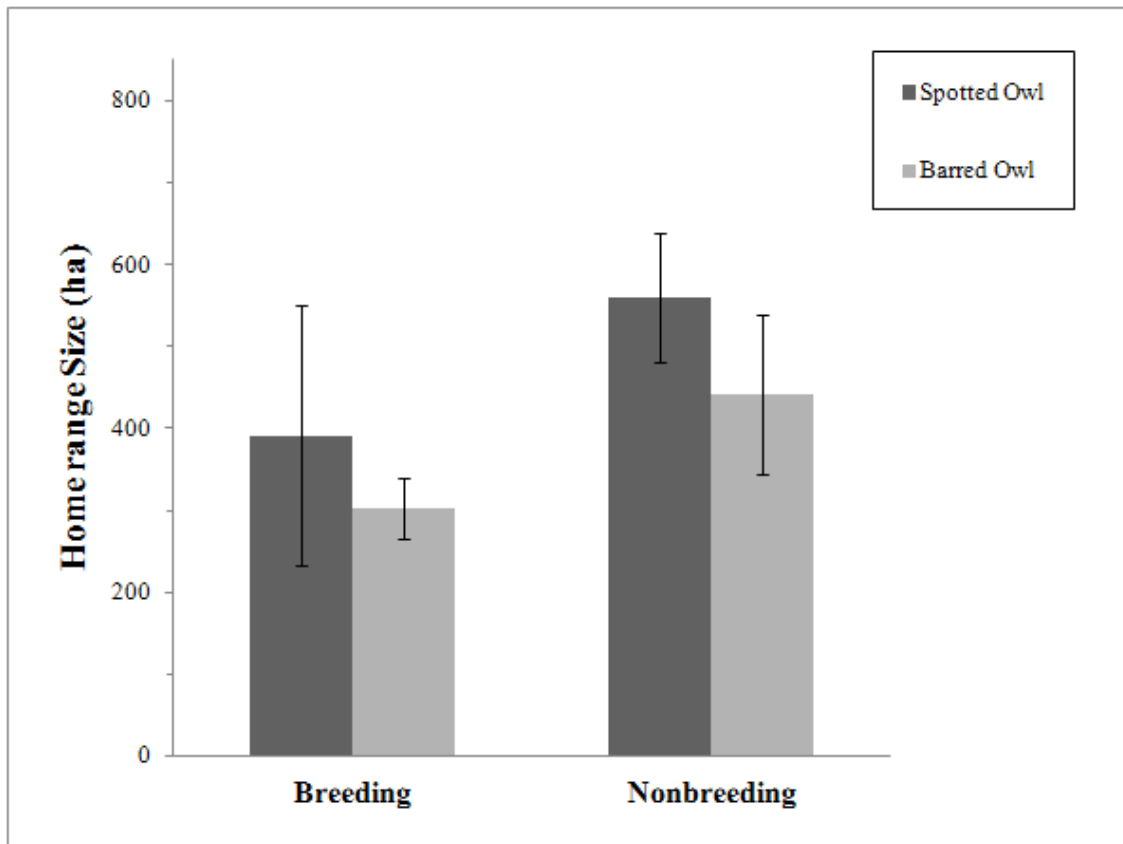


Figure 4. Mean home range size comparison of northern spotted owls and barred owls during the breeding (391 ± 79 , 303 ± 37 , respectively) and nonbreeding (560 ± 159 , 442 ± 97 , respectively) seasons in coastal northwestern CA, USA from 2007-2011.

Habitat Use Analysis

In addition to the owls that died or exited the study area prior to obtaining a sufficient number of telemetry locations, I excluded four owls (two mated spotted owls and two mated barred owls) from the habitat selection analysis due to logistical difficulties associated with vegetation collection. In total, I was able to estimate a discrete-choice RSF for 17 owls (8 spotted owls and 9 barred owls) over 41 seasonal (bi-annual) home ranges. This resulted in 969 used locations and 4361 random locations for 9 barred owls and 448 used locations and 1957 random locations for 8 spotted owls. Altogether, I had 1417 used locations out of 6318 (7735 available + used) vegetation plots, equaling a ratio of approximately 1:4.5, which reduced the probability of introducing “contamination” into the parameter estimates (Johnson et al. 2006).

I created a 95% confidence set of models by including models with AIC_c weights that summed to 0.95. The confidence set contained 9 models (Table 4) and all included the variable NEST, indicating that proximity to the nest or center of activity was the strongest predictor of foraging habitat selection for both spotted owls and barred owls. Other important predictor habitat variables included various combinations of understory vegetation, basal area of hardwoods, percent hardwoods, and basal area of all trees. My results also indicated that the quadratic form of hardwood basal area was an important predictor of owl habitat selection, even though the linear form ranked slightly higher with a lower AIC_c value. Models that held no or little AIC_c weight included various combinations of the variables QMD, HEATLOAD, SNAG, YOUNG, STREAM, ELEV,

SLOPE, and ASPECT (Table 5). The null model with no variables was ranked 47th out of 55 total models and held zero AIC_c weight.

Table 4. Ranking of top 9 discrete-choice models within the 95% confidence set that examined foraging habitat selection of northern spotted owls and barred owls in the coastal northwestern California, USA.

Model^a	K^b	AIC_c^c	ΔAIC^d	AIC_c wt^e	Log likelihood
VEG x OWL + NEST x OWL	6	19031.39	0	0.3	-9510.69
PERHARD x OWL + NEST x OWL	6	19032.88	1.49	0.14	-9511.44
BAHARD x OWL + NEST x OWL	6	19032.9	1.52	0.14	-9511.45
BAHARD x OWL + BAHARD² x OWL + NEST x OWL	7	19033.1	1.75	0.12	-9510.57
NEST + VEG	3	19033.5	2.11	0.1	-9514.75
NEST + BAHARD ²	4	19034.81	3.43	0.05	-9514.41
NEST x OWL	4	19036.23	4.84	0.03	-9515.11
BA x OWL + NEST x OWL	6	19036.36	4.97	0.02	-9513.18
BA + NEST	3	19036.53	5.15	0.02	-9516.27

Models in bold within 2ΔAIC_c from top model.

^aSee Table 1 for variable abbreviations

^bNumber of parameters

^cAkaike's Information Criterion adjusted for small sample sizes

^dDifference in the AIC_c score between the model and top model in the model set

^eAkaike weight

Table 5. Continuous habitat variables that held little or no AIC_c weight in discrete-choice models.

Variable	Range		Mean	SE
	Low	High		
ASPECT (deg.)	0.00	337.5	154.58	1.76
STREAM (m)	0.00	3943.12	306.28	68.17
ELEV (m)	18.00	1914.00	495.06	2.76
HEATLOAD	-0.42	1.10	0.26	0.01
QMD (m ²)	0.00	414.06	62.63	0.59
SLOPE (deg.)	0.00	70.00	22.55	0.13

The models that presented a ΔAIC_c value of <2 from the top model were considered competitive (Table 6). These included four models and accounted for 70% of the total AIC_c weight. All top models contained both the variable NEST and included OWL as an interaction term. The top model, which accounted for 30% of the AIC_c weight, included the variables NEST and VEG with OWL as an interaction term. The following top 3 competing models, which accounted for an additional 40% of the AIC_c weight, included the habitat variables PERHARD, BAHARD, and BAHARD², respectively, in combination with the variable NEST and the interactive effects of OWL. The presence of OWL in all my top ranked models provided evidence that the species influenced the use of the aforementioned habitat variables.

Since the primary objective of my study was to examine habitat use and resource partitioning between spotted owls and barred owls, I will proceed by focusing on variables modeled with the interactive effects of OWL. The coefficients for a habitat variable interacted with OWL can be interpreted as their relevance to barred owls (e.g., a positive coefficient indicated that barred owls are more likely to select a particular habitat variable in comparison to spotted owls). Collectively, my models examined if the species itself influenced the relative probability of use of habitat variables. The positive coefficient in the top model for the interaction between OWL and VEG (0.107×10^{-1}) indicated that barred owls were more likely to select foraging habitat that contained a greater percentage of understory vegetation than spotted owls (Table 6, Figure 5a). The selection ratio for the interaction between OWL and VEG was >1 with confidence

intervals also >1 , indicating that both species were positively influenced by the percent of understory vegetation (Table 7).

Table 6. Coefficients and standard errors for the habitat covariates of the 4 top discrete-choice models for northern spotted owls and barred owls in the coastal northwestern California, USA.

Covariate	Model 1		Model 2		Model 3		Model 4	
	Coefficient	SE	Coefficient	SE	Coefficient	SE	Coefficient	SE
VEG	0.047x10 ⁻²	0.477x10 ⁻²						
NEST	-0.124x10 ⁻²	0.957x10 ⁻⁴	-0.124x10 ⁻²	0.955x10 ⁻⁴	-0.124x10 ⁻²	0.955x10 ⁻⁴	-0.123x10 ⁻²	0.955x10 ⁻⁴
OWL	-0.360	0.185	-0.222	0.119	-0.002	0.114	-0.132	0.108
PERHARD			-0.003	0.899x10 ⁻¹				
BAHARD							0.172x10 ⁻²	0.688x10 ⁻³
BAHARD ²							-0.507x10 ⁻⁵	0.225x10 ⁻⁵
VEG x OWL	0.107x10 ⁻¹	0.689x10 ⁻²						
NEST x OWL	0.347x10 ⁻³	0.146x10 ⁻³	0.313x10 ⁻³	0.145x10 ⁻³	0.302x10 ⁻³	0.145x10 ⁻³	0.300x10 ⁻²	0.144x10 ⁻³
PERHARD x OWL			0.313	0.015				
BAHARD x OWL					0.129x10 ⁻²	0.588x10 ⁻³		
BAHARD ² x OWL							0.264x10 ⁻⁵	0.196x10 ⁻⁵
AIC_c	19031.39		19032.88		19032.90		19033.14	
ΔAIC	0		1.49		1.52		1.75	
Model rank	1		2		3		4	

^aAkaike's Information Criterion adjusted for small sample sizes

^bDifference in the AIC_c value relative to the model with the lowest AIC_c

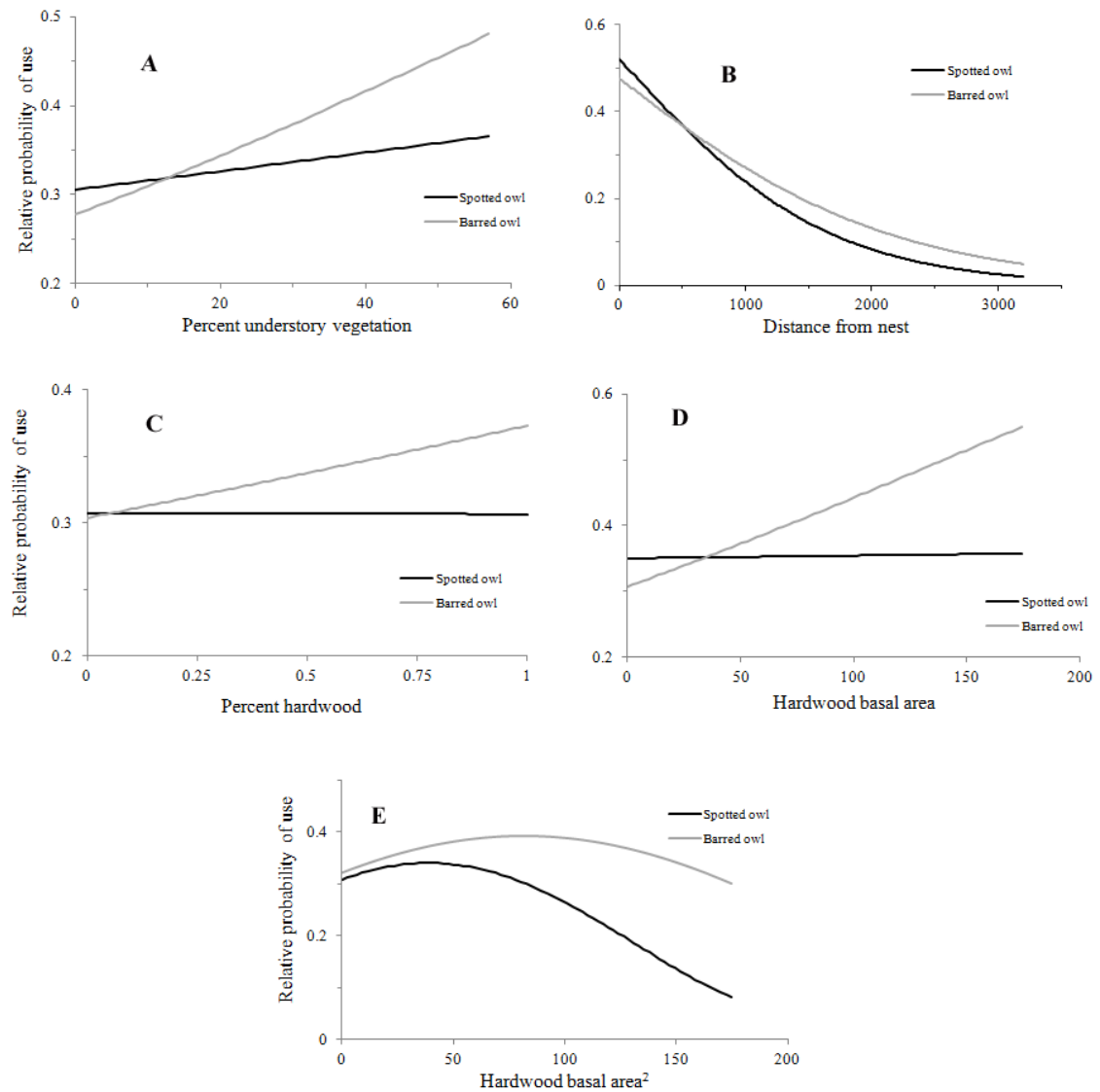


Figure 5. Results from the top 4 models showing relative probability of use as a function of (a) percent understory vegetation (b) distance from nest (c) percent hardwood (d) hardwood basal area (e) hardwood basal area². Variables not listed on the x-axis were held constant at their median values.

Table 7. Selection ratios for the top discrete-choice resource selection model estimated for foraging habitat selection for northern spotted owls and barred owls with confidence intervals calculated as $\exp(\text{coefficient} \pm 1.96(\text{coefficient standard error}))$.

Covariate	Selection Ratio	SE	Approximate 95% CI	
			Lower	Upper
VEG	1.005	.00477	0.995	1.014
NEST	0.999	.0000957	0.997	0.999
OWL	0.698	.185	0.485	1.061
OWL x VEG	1.011	.00689	1.008	1.014
OWL x NEST	1.000	.000146	0.100	1.001

Distance from the nest or the NEST variable was important for both species, whereas spotted owls and barred owls showed very similar negative response patterns between distance from the nest and foraging habitat use (Figure 5b).

Hardwoods were an important predictor of barred owl foraging behavior in comparison to spotted owls. The second and third top models indicated that barred owls were more likely to select areas for foraging that contained a higher percentage of hardwoods and a greater basal area of hardwoods, respectively, than spotted owls (Table 6). In the second top model, barred owls showed a steady positive relationship as the percentage of hardwoods increased from 0-100 (Figure 5c). In comparison, spotted owls did not appear to respond to percent of hardwoods, but rather had a steady and slightly negative relationship with the variable when modeled with barred owls. The basal area of hardwoods and probability of spotted owl habitat use showed similar results, but the relationship was slightly positive (Figure 5d). However, the 4th top model, which included the quadratic term for hardwood basal area, revealed that both species have a non-linear relationship between probability of foraging use and hardwood basal area (Figure 5e). This model indicated that both species respond positively to hardwood basal area, but are limited at higher hardwood densities (Figure 5e). Barred owls appeared to be less sensitive and have a higher tolerance to the amount of hardwood basal area than spotted owls (Table 6, Figure 5e). Basal area of hardwoods for barred owls appears to be maximized at 80 m²/ha, whereas spotted owls their peak probability of selection at approximately 39 m²/ha hardwood basal area.

DISCUSSION

Home Range

The redwood region of northwestern California provided a unique opportunity to compare the home range size and habitat use of sympatric northern spotted owls and barred owls in the southern portion of their range, an area where barred owl densities are still relatively low and spotted owl populations remain relatively high. The study area is comprised of distinctive climate characteristics that are heavily influenced by the Pacific Ocean, resulting in little temperature variation throughout the year, high fog conditions, and high annual rainfall. All of which support a highly productive ecosystem that can influence prey availability, nesting and roosting habitat, and ultimately home range size and foraging habitat selection. Therefore, the results of my study differ to some degree from previous spotted and barred owl studies conducted in geographical regions to the north.

I found that the average home range size of spotted owls was slightly greater than barred owls in the breeding (1.29 times greater) and nonbreeding (1.26 times greater) seasons, but not statistically significant (P -value = 0.26 and P -value = 0.42, respectively). These differences were small in comparison to the results of studies conducted in the northwestern Cascades of Washington and in the Coast Range of western Oregon, where spotted owls were observed to have seasonal and annual home ranges that were 2-5 times larger than barred owls (Hamer et al. 2007, Wiens et al. 2014). Owls in my study area

also exhibited little seasonal variation in home range size (303-442 ha, respectively for barred owls and 391-560 ha, respectively for spotted owls), which is contrary to previous studies that indicated a home range expansion during the nonbreeding season (Glenn et al. 2004, Forsman et al. 2007, Hamer et al. 2007, Wiens et al. 2014). I attribute the lack of seasonal variation in home range size to the mild climate and general lack of temperature change between seasons in the redwood region. As a result, prey availability likely remains relatively constant throughout the year.

Average spotted owl home range size in my study area was smaller in comparison to results found in the northern portion of their range (Forsman et al. 1984, Carey et al. 1992, 1995, Glenn et al. 2004, Hamer et al. 2007, Wiens et al. 2014). My results are consistent with the trend for spotted owls to have smaller home ranges in the southern portion of their range (Carey et al. 1990, Zabel et al. 1995, Clark 2007), which is likely a response to higher prey availability in northern California. In my study area, the spotted owl diet predominately consists of dusky-footed woodrats by biomass, which are larger, more abundant, and occur in greater densities than the important prey items (e.g., northern flying squirrels, red tree voles) to the north (Courtney et al. 2004, Zabel et al. 1995). Spotted owls therefore do not need to forage as far from their center of activity or nest site to meet their energetic needs (Zabel et al. 1995). Furthermore, the smaller home range size in my study area could in part be attributed to the lower density of barred owls in northern California. As reported by Wiens et al. (2014), spotted owls tended to shift their movements and increase their home range size to avoid agonistic interactions with barred owls. It is possible that barred owls are just beginning to colonize California and

that spotted owl home ranges will become larger in upcoming years as density and numbers of barred owls increase.

Habitat Use

As expected, the results of my top 4 RSF models suggest that the distance to nest or center of activity is the strongest predictor of spotted owl and barred owl foraging habitat selection at the home range scale in my study area. Surprisingly, both species were influenced nearly identically by the distance to nest variable. As a generalist species, barred owls consume a wider variety of prey items and I would expect that they would be able to forage closer to their nest or center of activity in comparison to spotted owls. Spotted owls have more specialized diets consisting primarily of arboreal and semi-arboreal small mammals (Wiens et al. 2014), which should require them to travel greater distances to find sufficient prey to meet their energetic requirements. However, all spotted owl territories used in my analysis occurred on fragmented timberland, and likely provided ideal habitat conditions for both nesting and foraging in coastal northwestern California (Zabel et al. 1995, Ward et al. 1998, Franklin et al. 2000). These areas contained both patches of older forests with structurally-complex residual trees and patches of nearby younger forests and recent clear-cuts, likely resulting in foraging sites that were close to spotted owl nesting and roosting locations. This result is consistent with my findings that spotted owls have smaller home ranges in my study area as compared with study areas in Washington and Oregon.

Total percent understory vegetation was also as an important predictor of owl foraging habitat selection in my top model. As indicated by the OWL interaction variable, barred owls showed a stronger positive response to understory vegetation than spotted owls. Dusky-footed woodrats, which provide an important food source for spotted owls and potentially for barred owls as well in northern California, require dense vegetation for cover and food sources (Horton and Wright 1944, Hooven 1959, Murray and Barnes 1969). Consistent with my findings, Hamm and Diller (2009) found a positive correlation with shrub layer vegetation and dense understory vegetation and dusky-footed woodrat abundance in the redwood region of northwestern California. Other studies have found that spotted owls forage near edges of young and mature forests (Ward et al. 1998, Zabel et al. 1995), where woodrat abundance and thick brush are likely high. My results show that both barred and spotted owls respond positively to understory vegetation, suggesting that the two species may be focusing on areas where dusky-footed woodrats are abundant. However, dietary analysis studies are needed to confirm this.

I also found that both species are influenced by the relative amount or percent of hardwoods and the density of hardwoods by basal area. However, barred owls had a strong positive relationship with both hardwood variables when modeled with the interactive effects of OWL, indicating that in comparison, spotted owls did not show a selection preference for hardwoods. While I cannot directly compare the results of my models to other studies, my results are somewhat comparable to studies conducted in western Oregon and California that found spotted owl habitat selection associated with the presence or relative diameter of hardwoods (Glenn et al. 2004, Irwin et al. 2007,

2012, Wiens et al. 2014). It is possible that barred owls are competitively excluding spotted owls from foraging in areas that contain a high proportion of hardwoods.

Contrary to my prediction, I did not find evidence that distance to perennial streams influenced foraging habitat selection. This was in contrast to several other studies that found that spotted owls were more likely to forage in riparian areas or closer to streams (Hamer et al. 2007, Herter and Hicks 2000, Pearson and Livezey 2003, Irwin et al. 2012, Wiens et al. 2014). The habitat selection patterns of both spotted and barred owls likely varies throughout their geographic range and is dependent on land use patterns and availability of prey. The redwood region of California is unique in that much of the area lies in a temperate rain forest and is dominated by heavy coastal fog, high rainfall, and relatively mild temperatures that vary little throughout the year. All of these factors create a highly productive ecosystem that supports not only the relatively fast growing redwood and Douglas fir trees that dominate the area, but the dense understory vegetation that is characteristic of the coastal redwood region. Such understory vegetation can support a wide variety of prey items for both owl species outside of riparian areas. In addition, Franklin et al. (2000) and Ward et al. (1998) found that high contrast edges, typically associated with clear-cuts, in northwestern California contain abundant sources of prey. Due to logging restrictions around larger streams in California, such areas with high prey numbers would generally occur outside of the riparian area.

My study area also contained hardwood tree species that are unique to the southern portion of the spotted owl's range. Tanoak, which was the most abundant

deciduous tree species in my study, and California bay laurel, which was the third most abundant deciduous tree species in my area, are not necessarily associated with riparian areas and do not occur in western Washington and much of western Oregon. Both tree species produce fruit that likely provide an important food source to many small mammals, which can positively influence both species to forage outside of the riparian area in coastal northwestern California. However, this is purely speculative, because I did not conduct dietary analysis of either species nor did I model the effects of individual hardwood species in relation to habitat selection.

While hardwood species were important predictors of habitat use, both species exhibited a quadratic relationship between foraging habitat use and hardwood basal area. Basal area is a method of sampling that measures the amount of wood volume, or density, of trees within an area. This implies that foraging use was positively associated with the number or size of hardwood trees up to a certain volume or threshold until the stand became too dense to support successful foraging. Foraging use by spotted owls peaked at a lower hardwood basal area (approximately 39m²/ha) than barred owls (approximately 80m²/ha). Hardwoods are typically considered an understory or secondary canopy component in the Pacific Northwest and are more likely to be found within stands of larger, more dominant trees such as Douglas fir and coast redwoods in my study area. However, when hardwoods reach a certain density within an area, they become the dominant overstory component, which may provide less than optimal canopy cover for spotted owl foraging activities. In addition, a dominant coniferous overstory and a hardwood understory, or a multi-story canopy, can provide more perches for hunting as

well as offer greater protection from inclement weather and predators. Even though my results are not directly comparable to other studies, they are similar to those of Irwin et al. (2012), who found a quadratic relationship between spotted owl foraging habitat selection and basal area of Douglas fir trees in Oregon and California. Both species should tend to select habitat features that provide a balance between the ability to catch prey and sufficient canopy cover to provide protection from predators and inclement weather (Irwin et al. 2012).

Comparing my results with previous studies on spotted owls is confounded by a number of factors that are primarily influenced by differences in the geographic location of the study area and the scale at which habitat variables were measured. Most habitat selection studies on spotted owls used coarse-scale variables that were generated at the landscape level using satellite imagery. The finer-scale measures of habitat associations of spotted and barred owls at the home range scale can yield different results than at the landscape level, as demonstrated by Wiens et al. (2014) and my study, which indicated the importance of an understory vegetation component. Furthermore, comparisons between the spotted owls in my study area to spotted owls in other areas of the subspecies' range are confounded by differences in management practices and habitat types; all of which affect prey availability and thus foraging habitat selection. For example, timber harvest operations in California are in general more restrictive in comparison to the timber harvesting that occurs in both Oregon and Washington. In addition, the northern California redwood ecosystem differs from other parts of the subspecies' range. Although my study suggests that there is some degree of resource

partitioning between the two species by the high ranking of models with the interactive effects of OWL, I recommend caution in extrapolating the results of my study area to other areas where spotted and barred owls co-exist.

MANAGEMENT RECOMMENDATIONS

I found that the foraging habitat selection of both species was largely influenced by the same habitat variables, suggesting that there is potentially a high degree of competitive overlap between spotted and barred owls in coastal northwestern California. However, my top 4 models ($AIC_c < 2$) all contained the interactive effects of OWL, providing evidence that some degree of resource partitioning exists between the two species with percent understory vegetation, percent hardwoods, and basal area of hardwoods. Exploitative competition by sympatric barred owls may lead to a reduction of available habitat resources such as prey items and nesting substrate that are necessary for spotted owl survival and reproduction. Barred owl populations have expanded rapidly in recent decades, and are likely to continue to increase creating even more competition and strain for resources on an already declining species. Conserving older and second growth forests with high structural complexity is necessary to maintain favorable nesting and roosting substrate and reduce pressure on already limited resources for spotted owls. However, my results suggest that the ecological similarity of the two species may limit the ability of foresters and other resource managers to implement habitat modifications that favor foraging conditions specifically for spotted owls. I recommend further research be directed at studying the diets of both species and studying the habitat characteristics around spotted and barred owl nest sites. I also recommend studying how spotted owls react, both behaviorally and spatially, to the wide-spread removal of barred owls. I believe that my results indicate that recovering or even

maintaining spotted owl populations throughout their range will require a dual effort of preserving habitat conditions and managing barred owl populations.

LITERATURE CITED

- Anthony, R.G., E.D. Forsman, A.B. Franklin, D.R. Anderson, K.P. Burnham, G.C. White, C.J. Schwarz, J.D. Nichols, J.E. Hines, G.S. Olson, S.H. Ackers, L.S. Andrews, B.L. Biswell, P.C. Carlson, L.V. Diller, K.M. Dugger, K.E. Fehring, T.L. Fleming, R.P. Gerhardt, S.A. Gremel, R.J. Gutiérrez, P.J. Happe, D.R. Herter, J.M. Higley, R.B. Horn, L.L. Irwin, P.J. Loschl, J.A. Reid, S.G. Sovern. 2006. Status and trends in demography of Northern Spotted Owls, 1985 - 2003 Wildlife Monographs 163:1–48.
- Anthony, R. J., M. A. O’Connell, M. M. Pollock, and J. G. Hallett. 2003. Associations of mammals with riparian ecosystems in Pacific Northwest forests. Pages 510–563. *in* C. J. Zabel and R. G. Anthony, editors. Mammal community dynamics: management and conservation in the coniferous forests of western North America. Cambridge University Press, United Kingdom.
- Atsatt, P. R., and T. Ingram. 1983. Adaptation to oak and other fibrous, phenolic-rich foliage by a small mammal, *Neotoma fuscipes*. *Oecologia* 60:135–142.
- Bailey, L. L., J. A. Reid, E. D. Forsman, and J. D. Nichols. 2009. Modeling co-occurrence of northern spotted owls and barred owls: accounting for detection probability differences. *Biological Conservation* 142:2983–2989.
- Bell, J. F., and J. R. Dilworth. 1990. Log scaling and timber cruising. Oregon State University Press, Corvallis, USA.
- Blackburn, I.R. 1992. The distribution, status and habitat selection of the northern spotted owl in southwestern British Columbia: a summary of the 1991 field season. British Columbia Ministry of Environment, Lands and Parks, Fish and Wildlife Branch, Surrey, BC, Canada.
- Buchanan, J. B., T. L. Fleming, and L. L. Irwin. 2004. A comparison of barred and spotted owl nest-site characteristics in the Eastern Cascade Mountains, Washington. *Journal of Raptor Research* 38:231–237.
- Buchanan, J.B., R.J. Gutiérrez, R.G. Anthony, T. Cullinan, L.V. Diller, E.D. Forsman, and A.B. Franklin. 2007. A synopsis of suggested approaches to address potential competitive interactions between Barred Owls (*Strix varia*) and Spotted Owls (*S. occidentalis*). *Biological Invasion* 9:679–691.

- Burnham K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, second edition. Springer, New York, New York, USA.
- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346-352.
- Carey, A. B., S. P. Horton, and J. A. Reid. 1989. Optimal sampling techniques for radiotelemetry studies of spotted owl habitat and home range. U.S. Forest Service Report PNW-416, Portland, Oregon, USA.
- Carey, A.B., S.P. Horton, and B.L. Biswell. 1992. Northern spotted owls: influence of prey base and landscape character. *Ecological Monographs* 62:223–250.
- Carey, A.B. and K.C. Peeler. 1995. Spotted owls: resource and space use in mosaic landscapes. *Journal of Raptor Research* 29:223-239.
- Carey, A.B., C.C. Maguire, B.L. Biswell, and T.M. Wilson. 1999. Distribution and abundance of *Neotoma* in western Oregon and Washington. *Northwest Science* 73:65–81.
- City of Arcata. 1994. Arcata Community Forest and Jacoby Creek Forest Management Plan 1994.
- Cooper, A.B., and J.J. Millspaugh. 1999. The application of discrete choice models to wildlife resource selection studies. *Ecology* 80:566-575.
- Courtney, S.P., J.A. Blakesley, R.E. Bigley, M.L. Cody, J.P. Dumbacher, R.C. Fleischer, A.B. Franklin, J.F. Franklin, R.J. Gutierrez, J.M. Marzluff, and L. Sztukowski. 2004. Scientific evaluation of the status of the Northern Spotted Owl. Sustainable Ecosystems Institute, Portland, Oregon.
- Crozier, M. L., M.E. Seamans, R.J. Gutiérrez, P.J. Loschl, R.B. Horn, S.G. Sovern, and E.D. Forsman. 2006. Does the presence of Barred Owls suppress the calling behavior of Spotted Owls? *Condor* 108:760–769.
- Dark, S.J., R.J. Gutierrez, and G.I. Gould Jr. 1998. The Barred Owl (*Strix varia*) invasion in California. *Auk* 115:50–56.
- Devereux, J. G. and J. A. Mosher. 1984. Breeding ecology of Barred Owls in the central Appalachians. *Journal of Raptor Research* 18:49–58.
- Diller, L.V., and D.M. Thome. 1999. Population density of Northern Spotted Owls in managed young-growth forests in coastal Northern California. *Journal of Raptor Research* 33:275-286.

- Diller, L. V., Dumbacher, J. P., Bosch, R. P., Bown, R. R. and Gutiérrez, R. J. 2014. Removing barred owls from local areas: Techniques and feasibility. *Wildlife Society Bulletin* 38: 211–216.
- Dugger, K. M., F. Wagner, R. G. Anthony, and G. S. Olson. 2005. The relationship between habitat characteristics and demographic performance of northern spotted owls in southern Oregon. *Condor* 107:863–878.
- Dugger, K. M., R. G. Anthony, and L. S. Lawrence. 2011. Transient dynamics of invasive competition: barred owls, spotted owls, habitat, and the demons of competition present. *Ecological Applications* 27:2459–2468.
- Dunbar, D.L., B.P. Booth, E.D. Forsman, A.E. Hetherington, and D.J. Wilson. 1991. Status of the Spotted Owl, *Strix occidentalis*, and Barred Owl, *Strix varia*, in southwestern British Columbia. *Canadian Field-Naturalist* 105:464–468.
- Dunstan, T. C., and S. D. Sample. 1972. Biology of Barred Owls in Minnesota. *Loon* 44:111–115.
- Elody, B. I., and N. F. Sloan. 1985. Movements and habitat use of Barred Owls in the Huron Mountains of Marquette County, Michigan, as determined by radiotelemetry. *Jack-Pine Warbler* 63:3–8.
- Evans, J., and R. LeValley. 1982. The Spring migration, Middle Pacific Coast Region. *American Birds* 36:889–892.
- Fitts, K.M., and P.T. Northen. 1991. Small mammal populations in clearcut areas of the Jackson Demonstration State Forest, Mendicino, County, California. Technical report of the CA Department of Fish and Game, Yountville, CA.
- Forsman, E. D. 1983. Methods and materials for locating and studying spotted owls. USDA Forest Service Technical Report PNW-162, Portland, Oregon.
- Forsman, E. D., C. E. Meslow, and H. M. Wight. 1984. Distribution and biology of the Spotted Owl in Oregon. *Wildlife Monographs* 87:1–64.
- Forsman, E. D., R. G. Anthony, E. C. Meslow, and C. J. Zabel. 2004. Diets and foraging behavior of northern spotted owls in Oregon. *Journal of Raptor Research* 38:214–230.
- Forsman, E. D., T. J. Kaminski, J. C. Lewis, K. J. Maurice, S. G. Sovern, C. Ferland, and E. M. Glenn. 2005. Home range and habitat use of northern spotted owls on the Olympic Peninsula, Washington. *Journal of Raptor Research* 39:365–377.

- Forsman, E.D., R.G. Anthony, K.M. Dugger, E.M. Glenn, A. B. Franklin, G.C. White, C.J. Schwarz, K.P. Burnham, D.R. Anderson, J.D. Nichols, J.E. Hines, J.B. Lint, R.J. Davis, S.H. Ackers, S. Andrews, B.L. Biswell, P.C. Carlson, L.V. Diller, S.A. Gremel, D.R. Herter, J.M. Higley, R.B. Horn, J.A. Reid, J. Rockweit, J.P. Schaberl, T.J. Snetisinger, and S.S. Sovern. 2011. Population demography of northern spotted owls. *Studies in Avian Biology* No. 40. University of California Press, California, U.S.A.
- Franklin, A. B., D. R. Anderson, R. J. Gutierrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. *Ecological Monographs* 70:539–590.
- Franklin, A. B., R. J. Gutiérrez, J. D. Nichols, M. E. Seamans, G. C. White, G. S. Zimmerman, J. E. Hines, T. E. Munton, W. S. LaHaye, J. A. Blakesley, G. N. Steger, B. R. Noon, D. W. Shaw, J. J. Keane, T. L. McDonald, and S. Britting. 2004. Population dynamics of the California spotted owl (*Strix occidentalis occidentalis*): a meta-analysis. *Ornithological Monographs* 54:1–54.
- Franklin, J.F., T.A. Spies, R. Van Pelt, A.B. Carey, D.A. Thornburgh, D.R. Berg, D.B. Lindenmayer, M.E. Harmon, W.S. Keeton, D.C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155:399-423.
- Glenn, E. M., M. C. Hansen, and R. J. Anthony. 2004. Spotted owl home range and habitat use in young forests of western Oregon. *Journal of Wildlife Management* 68:33–50.
- Gremel, S.A. 2005. Factors controlling distribution and demography of northern spotted owls in a reserved landscape. M.S. Thesis, University of Washington, Seattle, Washington.
- Green Diamond Resource Company. 2009. Status of northern spotted owls in young growth timberlands in northern California 1990-2009. Annual submitted report to the Office of Management and Authority and the U.S. Fish and Wildlife Service in fulfillment of the requirements of Endangered Species Permit, TE057043-3, issued to Green Diamond Resource Company, Korbelt, CA, 95550.
- Green Diamond Resource Company. 2013. Green Diamond Resource Company HCP Annual Report. Spotted owl studies V11: 47-75.

- Guetterman, J. H., J. A. Burns, J. A. Reid, R. B. Horn, and C. C. Foster. 1991. Radio telemetry methods for studying spotted owls in the Pacific Northwest. USDA Forest Service General Technical Report PNW-GTR-272. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon.
- Gutiérrez, R.J., M. Cody, S. Courtney, and D. Kennedy. 2004. Assessment of the potential threat of the northern barred owl. *In*: Final report: scientific evaluation of the status of the northern spotted owl. Sustainable Ecosystems Institute, Portland, OR.
- Gutiérrez, R.J., M. Cody, S. Courtney, and A.B. Franklin. 2007. The invasion of barred owls and its potential effect on the Spotted Owl: a conservation conundrum. *Biological Invasions* 9:181–196.
- Hamer, T.E., D.L. Hays, C.M. Senger, and E.D. Forsman. 2001. Diets of northern barred owls and northern spotted owls in an area of sympatry. *Journal of Raptor Research* 35:221-227.
- Hamer, T.E., E.D. Forsman, and E.M. Glenn. 2007. Home range attributes and habitat selection of barred owls and spotted owls in an area of sympatry. *Condor* 109:750–768.
- Hamm, K.A. 1995. Abundance of dusky-footed woodrats in managed forests of north coastal California. MS Thesis, Humboldt State University, Arcata, CA.
- Hamm, K.A., and L.V. Diller. 2009. Forest management effects on abundance of woodrats in northern California. *Northwestern Naturalist* 90:97-106.
- Haney, J. C. 1997. Spatial incidence of barred owl (*Strix varia*) reproduction in old-growth forest of the Appalachian Plateau. *Journal of Raptor Research* 31:241–252.
- Herter, D. R., and L. L. Hicks. 2000. Barred owl and spotted owl populations and habitat in the central Cascade Range of Washington. *Journal of Raptor Research* 34:279–286.
- Hooven, E.F. 1959. Dusky-footed woodrat in young Douglas-fir. Corvallis, OR: Oregon Forest Lands Research Center, Research Note 41. 23 p.
- Horne, J. S., and E. O. Garton. 2006. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel homerange analysis. *Journal of Wildlife Management* 70:641–648.

- Horton J.S. and J.T Wright. 1944. The woodrat as an ecological factor in southern California watersheds. *Ecology* 25:341–351.
- Irwin, L.I., L.A., Clark, D.C. Rock, and S.L. Rock. 2007. Modeling foraging habitat of California spotted owls. *Journal of Wildlife Management* 71:1183-1191.
- Irwin, L. L., D. F. Rock, and S. C. Rock. 2011. Habitat selection by northern spotted owls in mixed-conifer forests. *Journal of Wildlife Management* 76:200–213.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, M. S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. *Journal of Wildlife Management* 70:347–357.
- Kelly, E.G., E.D. Forsman, and R.G. Anthony. 2003. Are Barred Owls displacing spotted owls? *Condor* 105:45–53.
- Kelly, E.G. and E.D. Forsman. 2004. Recent records of hybridization between barred owls (*Strix varia*) and northern spotted owls (*S. occidentalis caurina*). *Auk* 121:806-810. 25:523–532.
- Lack, D. 1946. Competition for food by birds of prey. *Journal of Animal Ecology* 15:123–129.
- LaHaye, W.S., and R.J. Gutierrez. 1999. Nest sites and nesting habitat of the northern spotted owl in northwestern California. *Cooper Ornithological Society* 101:324-330.
- Laidig, K. J., and D. S. Dobkin. 1995. Spatial overlap and habitat associations of barred owls and great horned owls in southern New Jersey. *Journal of Raptor Research* 29:151–157.
- Lamberson, R. H., R. McKelvey, B. R. Noon, and C. Voss. 1992. A dynamic analysis of northern spotted owl viability in a fragmented forest landscape. *Conservation Biology* 6:505–512.
- Leskiw, T., and R.J. Gutiérrez. 1998. Possible predation of a spotted owl by a barred owl. *Western Birds* 29:225–226.

- Livezey, K.B., and T.L. Fleming. 2007. Effects of barred owls on spotted owls: the need for more than incidental detections and correlational analyses. *Journal of Raptor Research* 41:319–325.
- Livezey, K. B. 2009. Range expansion of barred owls, part I: chronology and distribution. *American Midland Naturalist* 161:49–56.
- Livezey, K.B. 2010. Killing barred owls to help spotted owls 1: a global perspective. *Northwestern Naturalist* 91:107-133.
- Manly, B.F.J., L.L McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic, Dordrecht, The Netherlands.
- Marcot, B. G., and J. W. Thomas. 1997. Of spotted owls, old growth, and new policies: a history since the Interagency Scientific Committee report. General technical report PNW-GTR-408. U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Portland, Oregon.
- Mazur, K. M., and P. C. James. 2000. Barred owl (*Strix varia*). *In*: Poole A., and F. Gill (eds) *The birds of North America*. No. 508. The Academy of Natural Sciences Philadelphia, PA and the American Ornithologists' Union, Washington, DC.
- McCracken, M.L., B.F.J. Manly, and M. Vander Heyden. 1998. The use of discrete-choice models for evaluating resource selection. *Journal of Agricultural, Biological and Environmental Statistics* 3:268-279.
- McDonald, T. L., B. F. Manly, R. M. Nielson, and L.V. Diller. 2006. Discrete-choice modeling in wildlife studies exemplified by northern spotted owl nighttime habitat selection. *Journal of Wildlife Management* 70:375–383.
- McKelvey, K. S., B. R. Noon, and R. H. Lamberson. 1993. Conservation planning for species occupying fragmented landscapes: the case of the northern spotted owl. Pages. 424–450 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. *Biotic interactions and global change*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Millsbaugh, J. J., and J. M. Marzluff, editors. 2001. *Radio tracking and animal populations*. Academic Press, San Diego, California, USA.
- Newton, I. 1979. *Population ecology of raptors*. T. and A.D. Poyser, London, UK.
- Noon, B.R., and J.A. Blakesley. 2006. Conservation of the northern spotted owl under the Northwest Forest Plan. *Conservation Biology* 20:288-296.

- Olson, G.S., R.G. Anthony, E.D. Forsman, P.J. Loschl, J.A. Reid, K.M. Dugger, E.M. Glenn, and W.J. Ripple. 2005. Modeling of site occupancy dynamics for northern spotted owls, with emphasis on the effects of barred owls. *Journal of Wildlife Management* 69:918–932.
- Pearson, R.R., and K.B. Livezey. 2003. Distribution, numbers, and site characteristics of spotted owls and barred owls in the Cascade Mountains of Washington. *Journal of Raptor Research* 37:265–276.
- Pearson, R.R., and K.B. Livezey. 2007. Spotted owls, barred owls, and late-successional reserves. *Journal of Raptor Research* 41:156–161.
- R Development Core Team. 2010. R: a language for statistical computing. Vienna, Austria: R foundation for statistical computing
- Rosenberg, D.K., and K.S. McKelvey. 1999. Estimation of habitat selection for central-place foraging animals. *Journal of Wildlife Management* 63:1028-1038.
- Sakai, H.F., and B.R. Noon. 1993. Dusky-footed woodrat abundance in different-aged forests in northwestern California. *Journal of Wildlife Management* 57:373–382.
- Schmidt, K. 2003. Northern spotted owl monitoring and inventory, Redwood National and State Parks, 2002 annual report. Orick, California, USA.
- Schmidt, K. 2010. Northern spotted owl monitoring and inventory, Redwood National and State Parks 2009 Annual Report. Orick, California, USA.
- Schmidt, K. 2013. Northern spotted owl monitoring and inventory Redwood National and State Parks 2012 annual report. Orick, California, USA.
- Seaman, D. E., J. J. Millsbaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R.A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739–747.
- Singleton, P.H., J.F. Lehmkuhl, W.L. Gaines, and S.A. Graham. 2010. Barred owl space use and habitat selection in the eastern Cascades, Washington. *Journal of Wildlife Management* 74:285-294.
- Tanner, R.G. 1999. Habitat use by northern spotted owls in coastal redwood forests of northwestern California. M.S. Thesis, Humboldt State University, Arcata, CA.
- Taylor, A.L., and E.D. Forsman. 1976. Recent range extensions of the barred owl in western North America, including the first records for Oregon. *Condor* 78: 560-561.

- Thome, D.M., L.V. Diller, and C.J. Zabel. 1999. Forest stand characteristics and reproduction of northern spotted owls in managed north-coastal California forests. *Journal of Wildlife Management* 63:44-52.
- U.S. Fish and Wildlife Service. 1990. 50 CFR Part 17 Endangered and threatened wildlife and plants; determination of threatened status for the northern spotted owl; final rule. *Federal Register* 55:26114–26194.
- U.S. Department of Agriculture Forest Service (USFS) and Bureau of Land Management (BLM). 1994. Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest within the range of the Northern Spotted Owl. USDA Forest Service, Portland, Oregon, and BLM, Moscow, Idaho.
- U.S. Fish and Wildlife Service. 2011. Revised recovery plan for the northern spotted owl (*Strix occidentalis caurina*). U.S. Department of Interior, Portland, Oregon, USA.
- U.S. Fish and Wildlife Service [USFWS]. 2012. Experimental removal of barred owls to benefit threatened northern spotted owls: draft EIS. U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- Van Lanen, N.J., A.B. Franklin, K.P. Huyvaert, and R.F. Reiser II. 2011. Who hits and who hoots at whom? Potential for interference competition between barred and northern spotted owls. *Biological Conservation* 144:2194-2201.
- Ward, J.R., R.J. Gutiérrez, and B.R. Noon. 1998. Habitat selection by northern spotted owls; the consequences of prey selection and distribution. *Condor* 100:79–92.
- Wiens, J. D., R. G. Anthony, and E. D. Forsman. 2011. Barred owl occupancy surveys within the range of the northern spotted owl. *Journal of Wildlife Management* 75:531–538.
- Wiens, J. D., R. G. Anthony, and E. D. Forsman. 2014. Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon. *Wildlife Monographs* 185:1-50.
- Zabel, C.J., J. K. McKelvey, and J.P. Ward Jr. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (*Strix occidentalis caurina*). *Canadian Journal of Zoology* 73:433-439.