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HOME RANGE ATTRIBUTES AND HABITAT SELECTION OF BARRED OWLS AND SPOTTED OWLS IN AN AREA OF SYMPATRY

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Abstract. We compared home range areas and habitat selection of radio-marked Spotted Owls (*Strix occidentalis*) and Barred Owls (*Strix varia*) in an area of sympatry in the northern Cascade Range of Washington in 1986–1989. On average, home ranges of Spotted Owls were 3–4 times larger than ranges of Barred Owls, and there was little overlap of home ranges during the breeding season. Ranges of both species tended to expand during winter. Home range size of both species was negatively correlated with the amount of old forest, but the negative slope of the regression was much steeper for Spotted Owls than for Barred Owls. For both species, home ranges of individual owls typically had high overlap among seasons and years, indicating high site fidelity. Barred Owls generally occupied home ranges at lower elevations than Spotted Owls (mean = 386 ± 27 m vs. 750 ± 68 m). Both species tended to use old forests more than expected, but Spotted Owls tended to use other cover types less than expected, whereas Barred Owls used most other cover types in proportion to their availability. We suggest that Spotted Owls may use larger ranges than Barred Owls because they prey selectively on a few species of nocturnal mammals, whereas Barred Owls forage more evenly across a broad range of prey types, including diurnal and aquatic species. The low overlap of Barred Owl and Spotted Owl home ranges suggests that territorial Barred Owls exclude Spotted Owls from their territories, at least during the breeding season, thus reducing the amount of habitat available to Spotted Owls.

Key words: Barred Owl, habitat selection, home range, Spotted Owl, Strix occidentalis*,* Strix varia*, Washington.*

Atributos del Ámbito de Hogar y Selección de Hábitat de *Strix occidentalis* y *Strix varia* en un Área de Simpatría

Resumen. Comparamos las áreas de los ámbitos de hogar y la selección de hábitat de individuos marcados con radiotransmisores de *Strix occidentalis* y *S. varia* en un área de simpatría en el norte del cordón montañoso Cascade en el estado de Washington, entre los años 1986 y 1989. En promedio, los ámbitos de hogar de *S. occidentalis* fueron 3 a 4 veces más grandes que los ámbitos de *S. varia* y hubo poca superposición de los ámbitos de hogar durante la época reproductiva. Los ámbitos de las dos especies tendieron a expandirse durante el invierno. El tamaño del ámbito de hogar para las dos especies se correlacionó negativamente con la cantidad de bosque antiguo, pero la pendiente de esta regresión fue mucho más pronunciada para *S. occidentalis* que para *S. varia*. Para las dos especies, los ámbitos de hogar a nivel individual tuvieron típicamente una alta superposición entre estaciones y años, indicando una alta fidelidad de sitio. Generalmente *S. varia* ocupó ámbitos de hogar a elevaciones más bajas que *S. occidentalis* (promedio = 386 ± 27 m vs. 750 ± 68 m). Ambas especies tendieron a usar bosques antiguos más de lo esperado, pero *S. occidentalis* tendió a usar otros tipos de vegetación menos de lo esperado, mientras que *S. varia* utilizó la mayoría de los otros tipos de vegetación proporcionalmente a su disponibilidad. Sugerimos que *S. occidentalis* podría utilizar ámbitos de hogar más grandes que *S. varia* debido a que la primera depreda selectivamente sobre algunas especies de mamíferos nocturnos, mientras que *S. varia* se alimenta de un amplio rango de tipos de presas, incluyendo especies diurnas y acuáticas. La baja superposición de los ámbitos de hogar de estas especies sugiere que los individuos territoriales de *S. varia* excluyen a los individuos de *S. occidentalis* de sus territorios, por lo menos durante la época reproductiva, lo que reduciría la cantidad de hábitat disponible para *S. occidentalis*.

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INTRODUCTION

During the 20th century, the Barred Owl (*Strix varia*) expanded its range westward, across the northern U.S. and Canada, then along the Pacific coast of North America, north to southeastern Alaska and south to central California (Grant 1966, Taylor and Forsman 1976, Dark et al. 1998, Houston and McGowan 1999, Kelly et al. 2003, Courtney et al. 2004). As a result of this range expansion, the range of the Barred Owl now completely overlaps the range of the Northern Spotted Owl *(Strix occidentalis caurina*) and partially overlaps the range of the California Spotted Owl (*S. o. occidentalis*; Kelly et al. 2003, Seamans et al. 2004). The number of Barred Owls has increased so rapidly in some areas in British Columbia and Washington that they are now more numerous than Spotted Owls (Dunbar et al. 1991, Pearson and Livezey 2003).

As Barred Owls have expanded their range, they have moved into many areas occupied by Spotted Owls, and there is evidence that they are displacing (Kelly et al. 2003, Pearson and Livezey 2003), killing (Leskiw and Gutiérrez 1998), and, at least occasionally, hybridizing with Spotted Owls (Hamer et al. 1994, Kelly and Forsman 2004, Seamans et al. 2004). A comparison of the diets of the two species in northern Washington suggested that their diets overlap considerably, which suggests that they may also compete for food (Hamer et al. 2001).

Although some studies suggest that forest composition or elevation may differ slightly between areas occupied by Barred Owls and Spotted Owls (Herter and Hicks 2000, Pearson and Livezey 2003), little is known about differences in habitat selection between these two species in areas where they co-occur. In 1986–1989, we conducted a study of Barred Owls and Spotted Owls fitted with radio-transmitters in an area of sympatry in northern Washington. Our objectives were to determine if there were differences in home range attributes or types of forest cover selected by the two species and to examine overlap of home ranges of the two species. Herein, we describe and compare the home ranges and habitat selection of both species and discuss hypotheses regarding fitness of the two species in different forest types. Because this study was located in a region that was near the northern edge of the range of the Spotted Owl, it also allowed us to compare home ranges of Spotted Owls at the edge of their range with home range estimates from other studies of Spotted Owls near the center of their range.

METHODS

STUDY AREA

Our study area was located in the Baker Lake basin on the west slope of the Cascade Mountains in northwestern Washington (Fig. 1). This area was characterized by mountainous terrain with deeply incised valleys. Elevations ranged from 244 m on the valley floor to 1800 m at the upper limits of the forested zone on Mount Baker. The study area was entirely forested except for recent clear-cuts, areas above timberline, and small areas of talus, natural meadows, and marshes. Mean annual precipitation was 254 cm, most of which occurred as rain or snow during winter. The most common vegetation in the study area included mixed forests of western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*) at elevations <400 m, and mixed forests of western hemlock and Pacific silver fir (*Abies amabilis*) at 400–900 m elevation (Franklin and Dyrness 1973). Forests at elevations >900 m were mostly dominated by Pacific silver fir or mountain hemlock (*Tsuga mertensiana*). Red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*) were common associates in lowland conifer forests, especially in riparian zones. Forest age varied from young stands in recent clear-cuts to forests that were >200 years old.

CAPTURE AND RADIO-TELEMETRY

When we started our study, the locations of many owl territories in the study area were already known, because biologists from the USDA Forest Service, Washington Department of Wildlife, and Puget Power and Light Company had conducted surveys of Spotted Owls in the area every year from 1981 to 1986. Forest Service personnel continued to monitor the historic owl territories in 1986–1987 while we were radio-tracking owls. During March–June 1986–1987, we also resurveyed much of the study area to confirm presence of owls in historic territories and document the location of pairs at sites not previously surveyed. All

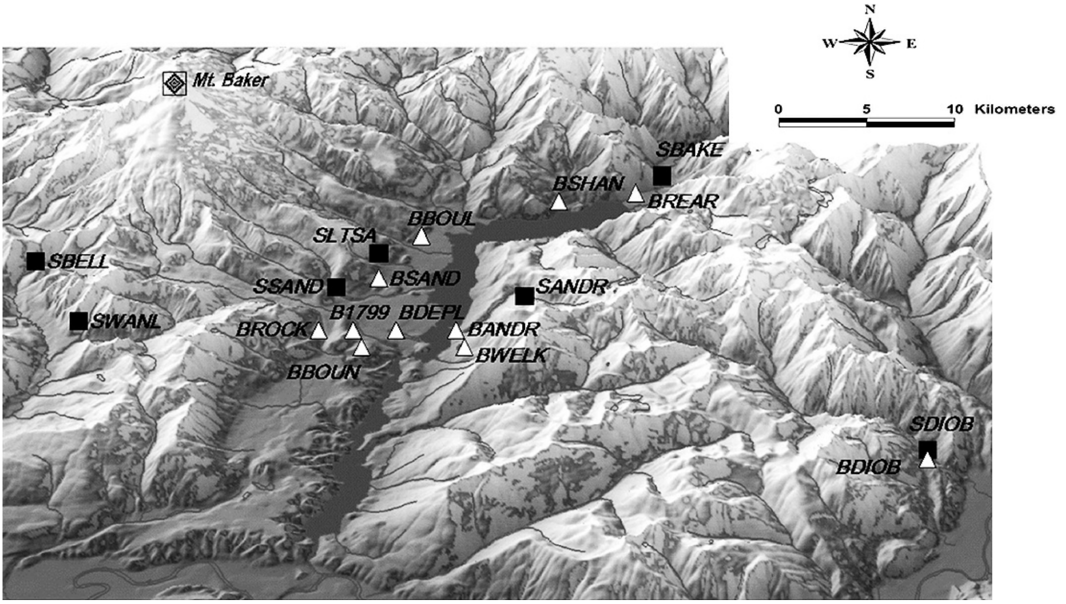

FIGURE 1. Baker Lake study area, Washington, illustrating territory centers of resident pairs of Barred Owls (triangles) and Spotted Owls (squares) that were radio-marked in 1986–1989.

surveyors used vocal lure surveys to locate owls, as described by Forsman (1983) and Reid et al. (1999). We used playback recordings of both species when searching for owls, although we found that Barred Owls were usually responsive to both Barred Owl and Spotted Owl calls (Hamer 1988).

To capture Barred Owls, we used a live Barred Owl decoy and tape recordings of Barred Owl calls to lure the owls into mist nets (Elody 1983, Elody and Sloan 1984). We captured Spotted Owls with noose poles (Forsman 1983), dip nets, or mist nets baited with a tethered gerbil (*Meriones unguiculatus*). Sex of owls was determined based on their vocalizations, measurements, behavior, or presence of a brood patch on nesting females (Forsman 1983, Blakesley et al. 1990, Carpenter 1992).

We captured and radio-marked 23 Barred Owls and 14 Spotted Owls between 11 March 1986 and 30 June 1988 (Fig. 2). Each owl was marked with a backpack transmitter (Model P2, AVM Instrument Company, Livermore, California), as described by Forsman et al. (1984). Total mass of the transmitter and harness was 18–20 g, and transmitter life was 9–15 months. We tried to obtain a minimum of 12 months of data from each owl, although there were cases in which data collection was limited by transmitter failure (Fig. 2). In 10 cases (six Barred Owls, four Spotted Owls), we replaced transmitters so that we could track individuals for more than a year.

We estimated owl locations by triangulating from the ground with a Telonics, Inc. (Mesa, Arizona) handheld H-antenna and TR2 receiver. We used headphones (model H7050, David Clark Company, Inc., Worcester, Massachusetts) to reduce ambient noise while triangulating. We obtained triangulations by driving along roads until we were as close as possible to the focal owl and then using the antenna and a handheld compass to estimate bearings from ≥ 3 locations along the road (Guetterman et al. 1991). Bearings were plotted on 1:15 840 scale orthophotographs. The location of the owl was assumed to be the geometric center of the polygon formed by the intersection of the bearings (Nams and Boutin 1991). If weak signals or inconsistencies in the direction of bearings caused us to suspect signal deflection or movement of an owl during triangulation, we discarded the location. If owls could not be relocated from the ground, we searched for them from a fixed-wing aircraft with two side-looking directional antennas.

We attempted to locate each owl four times per week, with no more than one location per

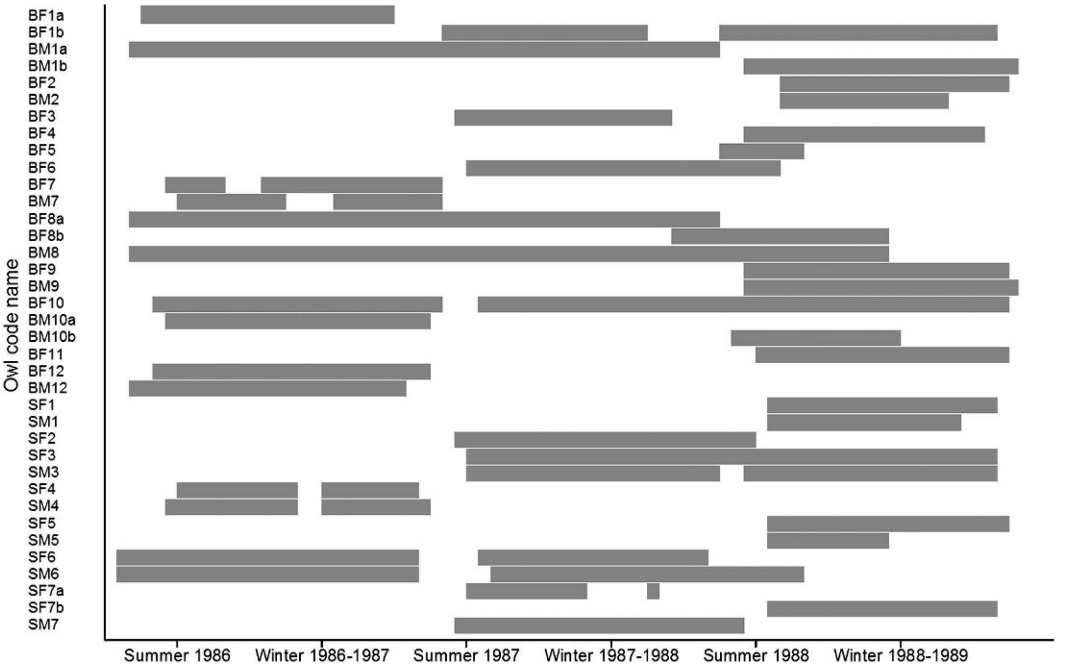

FIGURE 2. Observation periods of 23 Barred Owls and 14 Spotted Owls in the Baker Lake study area, Washington, 1986–1989. Seasonal periods on the *x*-axis are: summer = March-August, winter = September-February. Owl code names that start with "B" or "S" indicate Barred Owls and Spotted Owls, respectively.

day. However, this schedule was occasionally disrupted during spring when we were trapping owls or during winter when some owls expanded their home ranges into areas with poor access. In the latter cases, we sometimes lost track of owls for several days or weeks before we could relocate them. On average, we obtained one location per owl every 2.2 days. Each time we located an owl in one territory, we tried to locate the owls in adjacent territories within the shortest possible time, usually within 1–2 hr.

Cumulative tracking periods of individual owls ranged from 94 to 1064 days for Barred Owls (mean = 407 ± 52) and 127 to 775 days for Spotted Owls (mean = 413 ± 62). The total number of locations per owl ranged from 39 to 635 for Barred Owls (mean = 194 ± 29) and 46 to 302 for Spotted Owls (mean = 175 ± 32). Although we attempted to obtain equal numbers of nocturnal and diurnal locations from each owl, we ultimately obtained more diurnal than nocturnal locations. This happened primarily because it was difficult to travel at night in some areas in winter, when many roads were covered with snow. Because of the small number of locations for some individuals, we combined all nocturnal and diurnal locations for each owl for analyses of home range areas and habitat selection.

We did not directly estimate telemetry error in this study, but in two other studies that we conducted on Spotted Owls, the median distance between estimated and actual owl locations was 100 m (mean = 140 ± 17 m; Forsman et al. 2005). This estimate is comparable to means reported in three other studies of Spotted Owls in which observers used methods similar to ours (Carey et al. 1992 = 68 ± 4 m; Zabel et al. 1995 = 111 ± 6 m; Glenn et al. 2004 =164 ± 31 m). Errors of this magnitude undoubtedly resulted in some locations in our study falling in the wrong cover types, but we made the assumption that classification errors due to telemetry error were similar in all cover types and that our overall assessment of habitat use was correct.

We used the 95% isopleth of the adaptive kernel estimator to estimate home range areas with program CALHOME (Kie et al. 1996). For six Barred Owls and four Spotted Owls that were tracked for more than a year, we estimated

TABLE 1. Vegetation cover types used to map landscapes for analyses of habitat use by Barred Owls and Spotted Owls in the Baker Lake study area, Washington, 1986–1989.

Forest type	Description
Old forest (OLD)	Forests of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), or Pacific silver fir (*Abies amabilis*) with quadratic mean diameter >50 cm diameter at breast height (dbh).
Mid-age forest (MID)	Forests of Douglas-fir, western hemlock, western redcedar, or Pacific silver fir with quadratic mean diameter 26–50 cm dbh.
Young forest (YNG)	Forests of Douglas-fir, western hemlock, western redcedar, or Pacific silver fir with quadratic mean diameter 0–25 cm dbh.
Hardwoods (HDW)	Hardwood trees or shrubs growing in recent clear-cuts or lowland riparian areas. Hardwood trees were mostly red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*).
Unforested (UNF)	Open areas covered by rocks, snowfields, or water.

two or more annual home ranges as well as a cumulative home range. We defined the cumulative home range as the sum of the annual ranges minus any areas of overlap. For estimates of seasonal home ranges, we divided each year into two phenological periods: ‘‘summer’’ (March–August), when Spotted Owls and Barred Owls nest and feed young, and ‘‘winter’’ (September–February), when they are largely solitary.

We examined second-order habitat selection by owls (i.e., use of different forest cover types within the cumulative home range area of each owl). For this analysis, we used the cumulative 100% minimum convex polygon (MCP) home range area to assess the available habitat for each owl, because we believe that methods like the MCP or 100% adaptive kernel are better for assessing what is available to an animal than methods that more tightly constrain the frame of reference to the observed locations within the home range (e.g., fixed kernel or 95% isopleth of the adaptive kernel). We used program CALHOME (Kie et al. 1996) to calculate MCP ranges. To estimate the amount and distribution of cover types within owl home ranges, we used the Interagency Vegetation Mapping Project map for the western Cascades Washington Province (version 2.0; O'Neil et al. 2002). This vegetation map was a digital raster map developed using geometrically corrected 1996 Landsat 5 Thematic Mapper (TM) images with 25 m resolution. It included themes for vegetation cover, conifer cover, broadleaf cover, quadratic mean tree diameter, and a mask for unforested areas. We used these themes to produce a cover map that included five cover types (Table 1).

Because the cover map was based on a 1996 image that was taken 7–10 years after owls were radio-tracked, we used harvest data from a USDA Forest Service database to correct the cover map so that cover types reflected vegetation that was present at the time of the study. To reduce the ‘‘graininess’’ in the unsmoothed satellite map, we used a 1 ha smoothing algorithm to simplify the cover map. This had the effect of grouping isolated pixels of unique cover types with the predominant cover type in surrounding pixels. Overall accuracy of the final cover map based on visits to a randomly selected sample of 172 UTM coordinates in the study area was 81%.

STATISTICAL ANALYSES

We used mixed-models analysis of variance to evaluate the effects of different variables on size of adaptive kernel home ranges, where owl territory was a random effect and species, year, season, sex, number of days in the sampling period, and percent cover of old forest in the cumulative MCP range were fixed effects. These analyses were conducted with a set of 20 a priori models for seasonal home ranges and 17 a priori models for annual home ranges (Table 2). We used Akaike's information criterion corrected for small sample sizes (AIC_c) to rank models and Akaike weights to evaluate model likelihood (Akaike 1973, Burnham and Anderson 2002). We estimated the amount of variance explained by the best model as the difference in

TABLE 2. A priori models examined in analysis of factors influencing size of seasonal and annual home range areas of Spotted Owls and Barred Owls in the Baker Lake study area, Washington. Variables used in models indicate structure for species (spp), sex, year, season of year (sea), number of days in tracking period (days), and proportion of area covered by old forest (old).

Model structure	Description
Seasonal ranges	
No effects	No effects model
Spp	Species effect only
Sea	Seasonal effect only
Sex	Sex effect only
Year	Year effect only
Days	Sample size effect only (days in tracking period)
Spp + days	Additive effects of species and days
Spp + sea	Additive effects of species and season
Spp + sea + days	Additive effects of species, season, and days
Spp + year + sea	Additive effects of species, year, and season
Spp + sex + old	Additive effects of species, sex, and amount of old forest
Spp + old + spp*old	Additive effects of species and old forest, with interaction between species and old forest
Spp + sex + sea + old	Additive effects of species, sex, season, and old forest
Spp + sea + old	Additive effects of species, season, and old forest
Spp + sea + old + days	Additive effects of species, season, old forest, and days
Spp + sea + days + old + old*spp	Additive effects of species, season, days, and old forest, with interaction between species and old forest
Spp + sea + old + old*spp	Additive effects of species, season, and old forest, with interaction between species and old forest
Spp + sea + old + old*spp + spp*sea	Additive effects of species, season, and old forest, with interactions between species and old forest and species and season
Spp + sea + days + old + spp*old + spp*sea	Additive effects of species, season, days, and old forest, with interactions between species and old forest and species and season
Spp + sex + sea + old + spp*old	Additive effects of species, sex, season, and old forest, with interaction between species and old forest
Annual ranges	
No effects	No effects model
Sex	Sex effect only
Spp	Species effect only
Year	Year effect only
Old	Effect of old forest only
Days	Effect of number of days in sampling period
Spp + sex	Additive effects of species and sex
Sex + year	Additive effects of sex and year
Sex + old	Additive effects of sex and old forest
Sex + year + old	Additive effects of sex, year, and old forest
Spp + old	Additive effects of species and old forest
Spp + year	Additive effects of species and year
Spp + sex + old	Additive effects of species, sex, and old forest
Spp + year + old	Additive effects of species, year, and old forest
Spp + sex + year + old	Additive effects of species, sex, year, and old forest
Spp + sex + year + days + old	Additive effects of species, sex, year, days, and old forest
Spp + old + old*spp	Additive effects of species and old forest, with interaction between species and old forest

residual variance between the intercept-only model and the best model using the estimates of residual variance provided by PROC MIXED in SAS (SAS Institute 1997). We used fixed-effects analysis of variance to compare home range sizes of males and females.

We estimated overlap of seasonal or annual adaptive kernel home ranges as the mean of all

TABLE 3. Estimates of mean and median home range size (ha) of Barred Owls and Spotted Owls in the Baker Lake study area, Washington, 1986–1989, based on the 95% isopleth of the adaptive kernel estimator.

		Female		Male		All owls		ANOVA[b]	
Category	n[a]	Mean ± SE	Median	Mean ± SE	Median	Mean ± SE	Median	F-value	P-value
Annual range									
Barred Owl	19, 12	527 ± 51	498	1184 ± 545	591	781 ± 216	532	2.3	0.14
Spotted Owl	10, 9	3517 ± 1091	2593	1706 ± 392	1259	2659 ± 626	1484	2.2	0.15
Summer range									
Barred Owl	18, 12	299 ± 33	289	300 ± 58	270	299 ± 30	277	0.0	0.99
Spotted Owl	11, 10	1783 ± 464	1653	1199 ± 321	1103	1505 ± 288	1215	1.0	0.32
Winter range									
Barred Owl	16, 11	579 ± 75	552	1488 ± 631	567	950 ± 268	554	3.0	0.10
Spotted Owl	10, 8	2954 ± 857	2415	2875 ± 1714	1301	2920 ± 868	1632	0.0	0.97

[a] Sample size (n) = number of annual or seasonal range estimates for females and males, respectively.
[b] Comparison of means of males and females. Degrees of freedom for F-ratio = 1 and n – 2, where n = sum of the samples for males and females in column two.

possible combinations of overlap in each sample. For example, if an owl was followed in three different winters, we estimated the average overlap of its winter ranges as the mean of all possible combinations of the three winter ranges (winter 1 on winter 2, winter 2 on winter 1, winter 1 on winter 3, winter 3 on winter1, winter 2 on winter 3, and winter 3 on winter 2).

We evaluated habitat selection with the Bonferroni z statistic (Neu et al. 1974, Byers et al. 1984) and with compositional analysis (Aebischer, Marcström et al. 1993, Aebischer, Robertson, and Kenward 1993, Leban 1999). Results of the compositional analysis included a numeric ranking of the different cover types according to their relative "preference," as well as a table of pairwise comparisons (two-tailed t-tests) indicating the degree to which preference differed between types. We were aware that other methods were available for analyses of habitat use (e.g., Rosenberg and McKelvey 1999, Bingham and Brennan 2004), but we chose the above methods because of their statistical simplicity and their long history of use in ecological studies, and because we were uncomfortable with sampling assumptions or statistical issues in some of the other methods (Keating and Cherry 2004).

We used paired t-tests to evaluate the hypotheses that mean elevation, distance to the nearest stream, and distance to the nearest edge with an opening (cover types UNF, HDW, and YNG in Table 1) did not differ between owl locations and a sample of 300 randomly selected locations within the cumulative MCP range of each owl. All elevations and distances were calculated with digital GIS layers. Throughout this paper, we report means ± SE and we use $\alpha \leq 0.05$ as the criterion for statistical significance.

RESULTS

HOME RANGE SIZE

Although differences varied slightly depending on whether we compared means or medians, home ranges of Spotted Owls were typically 2–5 times larger than those of Barred Owls (Table 3). The direction of the difference was the same in all seasonal, annual, and sexual comparisons, but the greatest difference was between females; female Spotted Owls had annual home ranges that were on average 6.7 times larger than female Barred Owls (Table 3). Although not significant, the trend in Spotted Owls was for males to have smaller home ranges than females, whereas the trend in Barred Owls was for males to have larger ranges than females (Table 3).

In the model-based analysis of annual home range size, the model that was best supported by the data included species, amount of old forest, and an interaction between species and the amount of old forest within the home range (Table 4). All other models had ΔAIC values >6, indicating that sex, year, and number of days in the tracking period added little to model fit. Examination of the regression slopes of the interaction between species and amount of old forest indicated that the amount of old forest

TABLE 4. Model selection results from analysis of factors related to home range size of Barred Owls and Spotted Owls in the Baker Lake study area, Washington, 1986–1989. Models are ranked from most to least supported based on differences in Akaike's information criterion corrected for small sample size (ΔAIC_c). K is the number of parameters in the model, $-2\log(\mathcal{L})$ is twice the negative value of the maximized log-likelihood function, and Akaike weight is the relative support for each model. In the analysis of seasonal ranges, only models within 2 AIC units of the best model are shown. For the analysis of annual ranges, there were no models within 2 AIC units of the top model, so only the two best models are shown.

Sampling period and model[a]	$-2\log(\mathcal{L})$	K	ΔAIC_c[b]	Akaike weight
Annual range				
Spp + old + spp*old	884.4	7	0.00	0.94
Spp + old	893.3	6	6.21	0.04
Seasonal range				
Spp + sea + days + old + spp*old	1698.4	8	0.00	0.20
Spp + sea + old + spp*old	1699.8	7	0.13	0.19
Spp + sea + old + spp*sea + spp*old	1698.8	8	0.40	0.17
Spp + sea + days + old + spp*sea + spp*old	1697.6	9	0.49	0.16
Spp + sea + sex + old + spp*old	1699.2	8	0.80	0.14

[a] Model terminology indicates structure for species (spp), season (sea), number of days in the sample period (days), and percent cover of old forest within the home range (old). Plus signs indicate additive effects, and asterisks indicate interactions.

[b] The AIC_c values for the top models in analyses of annual and seasonal home ranges were 901.00 and 1707.78, respectively.

had only a slight negative influence on home range size of Barred Owls, whereas the home range size of Spotted Owls was strongly negatively correlated with the amount of old forest (Fig. 3).

In the analysis of seasonal home range size, the model that best fit the data included species, season, number of days in the tracking period, amount of old forest, and an interaction between species and the amount of old forest (Table 4). The 95% confidence intervals of the beta estimates for species ($\beta = -3596$, 95% CI $= -6174$ to -1019) and amount of old forest ($\beta = -6539$, 95% CI $= -10\,071$ to -3008) did not overlap 0, suggesting that these two variables contributed significantly to model fit. The 95% CI of the beta estimates for days in the sampling period ($\beta = 5.7$, 95% CI $= -3.4$ to 14.8) and season ($\beta = -718$, 95% CI $= -1498$ to 62) overlapped 0, suggesting that these two variables contributed less to model fit. Four competing models ($\Delta AIC_c < 2$) in the analysis of seasonal home range size also included the effects of species, season, and the amount of old forest (Table 4). Akaike weights were fairly evenly distributed among all five top models, indicating that no one model was clearly the best (Table 4).

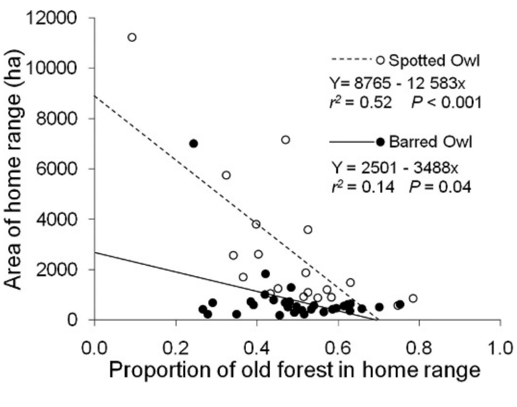

FIGURE 3. Annual home range size of Barred Owls and Spotted Owls in the Baker Lake study area, 1986–1989, was negatively correlated with the percentage of the landscape covered by old forest. This relationship was stronger for Spotted Owls.

For both species, winter ranges tended to be larger than summer ranges (Table 3). For most Barred Owls (22 of 23 birds), this involved a simple expansion of the home range during winter, with the winter range largely overlapping the summer range (mean overlap = 90% ± 3%). The only exception was male BM1b, who moved between a relatively small (741 ha) summer range and a winter range that was 27 km to the west. His movements between his summer and winter home ranges were completed in five days and took place in November and March, respectively. The previous Barred Owl male in the same territory (BM1a) had smaller annual ranges in the two

TABLE 5. Estimates of percent overlap (mean ± SE) of seasonal and annual home range areas of individual owls tracked in more than one season or year in the Baker Lake study area, Washington, 1986–1989. Codes for periods of overlap are: S/S = overlap of summer ranges used in different years, S/W = overlap of summer range on following winter range, W/S = overlap of winter range on previous summer range, W/W = overlap of winter ranges used in different years, and A/A = overlap of annual ranges used in different years.

Species	Period of overlap[a]				
	S/S	S/W	W/S	W/W	A/A
Barred Owl	73 ± 1	41 ± 6	90 ± 3	71 ± 2	76 ± 4
Spotted Owl	66 ± 4	49 ± 7	77 ± 6	59 ± 7	58 ± 10

[a] Sample sizes for the five periods of overlap were 5, 20, 20, 5, and 20 for Barred Owls and 6, 14, 14, 4, and 10 for Spotted Owls (number of comparisons among seasons or years).

years that he was observed at the site (532 and 505 ha). One other Barred Owl (BM10a) had a particularly large winter home range (3077 ha), but this case involved a general expansion of the summer home range, as opposed to a dispersal movement away from the summer range.

Spotted Owls exhibited two types of seasonal home range behavior that we refer to as "winter expansion" and "winter migration." Of the 13 individuals tracked in winter and summer, 10 exhibited winter expansion behavior in which they expanded their home ranges during winter but still used areas that overlapped or were adjacent to the summer range. Two females (SF1 and SF3) and one male (SM4) exhibited winter migration behavior in which they spent part of the winter in areas 7–15 km away from their summer ranges before eventually returning to their previous summer ranges in February or March. We could not detect a consistent pattern to these winter migration events, as individuals that migrated one winter did not always migrate the next winter. Movements associated with winter migration did not consistently involve movements to lower elevations. For example, mean elevations of winter and summer locations of the three Spotted Owls that migrated did not differ (all $P > 0.05$). The three owls that migrated during winter were all paired individuals, so there was no indication that migration was related to pair status.

HOME RANGE OVERLAP

Individual owls. Both species had high average overlap of home ranges used in different seasons and years, reflecting the fact that home ranges tended to be centered on historic nest areas, regardless of whether owls nested in a given year (Table 5). However, home ranges used by individual Barred Owls generally had higher overlap among seasons and years than did those of Spotted Owls (Table 5). This suggests that foraging areas used by Barred Owls were less variable among seasons and years than those used by Spotted Owls. The only exception was that mean overlap of summer ranges on winter ranges was fairly similar for both species, typically averaging between 40% and 50% (Table 5).

Pair members. For Barred Owls, the average overlap of seasonal and annual home ranges of the male and female in each territory was >50%, regardless of whether the frame of reference was overlap of females on males (F/M) or males on females (M/F; Table 6). For Spotted Owls, overlap of ranges of paired individuals also averaged >50% during summer, but overlap of males on females declined to <50% during winter, when the extensive movements of two females resulted in reduced overlap (Table 6). This also resulted in comparatively low average estimates of overlap of annual home ranges of male Spotted Owls on those of their mates (Table 6).

Owls in adjacent territories. On average, home ranges of Barred Owls in adjacent territories overlapped by 4% ± 1% in summer and 9% ± 2% in winter. The home ranges of Spotted Owls in adjacent territories had higher intraspecific overlap than those of Barred Owls, averaging 13% ± 4% in summer and 32% ± 10% in winter. Interspecific overlap of home ranges of Barred Owls on home ranges of Spotted Owls in adjacent territories averaged 6% ± 2% in summer and 7% ± 2% in winter.

TABLE 6. Percent overlap (mean ± SE) of seasonal and annual home ranges of the male and female in each territory (paired owls) in the Baker Lake study area, Washington, 1986–1989. Estimates were based on the 95% isopleth of adaptive kernel home ranges.

Species	Summer[a]		Winter[a]		Annual[a]	
	F/M	M/F	F/M	M/F	F/M	M/F
Barred Owl	70 ± 7	66 ± 6	52 ± 12	66 ± 10	59 ± 8	72 ± 7
Spotted Owl	77 ± 8	57 ± 9	69 ± 12	48 ± 12	75 ± 9	43 ± 10

[a] F/M = overlap of female range on male range; M/F = overlap of male range on female range. Sample sizes for estimates were 11, 11, 10, 10, 12, and 12 for Barred Owls and 10, 10, 6, 6, 8, and 8 for Spotted Owls (number of comparisons among seasons or years).

Overlap of Spotted Owl ranges on ranges of adjacent Barred Owls averaged 17% ± 4% in summer and 30% ± 6% in winter.

HABITAT SELECTION RELATIVE TO ELEVATION, STREAMS, AND EDGES

The Barred Owls in our sample all occupied territories at relatively low elevations adjacent to Baker Lake or along tributaries of the Skagit River (Fig. 1). In contrast, the Spotted Owls that we marked were about equally divided between areas at relatively low elevations (<600 m) and high elevations (>900 m). As a result, the mean elevation of random locations in Barred Owl territories (386 ± 27 m) was much lower than that in Spotted Owl territories (750 ± 68 m). Mean elevations of Barred Owl locations were similar between seasons, averaging 325 ± 14 m in summer and 358 ± 24 m in winter (paired $t_{21} = -1.7$, $P = 0.10$). Elevation of winter locations of Spotted Owls averaged 55 m lower than summer locations (mean = 670 ± 62 m vs. 725 ± 73 m). This difference was statistically significant (paired $t_{13} = 3.5$, $P = 0.004$), but we question whether it was large enough to be biologically significant.

Although there was considerable variation among individuals, the mean distance to the nearest perennial stream was almost identical between Barred Owl locations and random locations (319 ± 26 m vs. 327 ± 18 m; paired $t_{22} = -0.4$, $P = 0.71$). In contrast, Spotted Owl locations tended to be closer to the nearest perennial stream than random locations (mean = 367 ± 34 m vs. 460 ± 13 m; paired $t_{13} = -2.8$, $P = 0.02$). Mean distance to the nearest opening was nearly identical between owl and random locations for Barred Owls (173 ± 18 m vs. 174 ± 18 m; paired $t_{22} = -0.1$, $P = 0.92$) and for Spotted Owls (184 ± 11 m vs. 173 ± 18 m; paired $t_{13} = 1.0$, $P = 0.32$).

HABITAT SELECTION RELATIVE TO FOREST COVER TYPES

Neu et al. (1974) method. Forest cover types that were comprised of trees >25 cm in diameter at breast height (dbh) were used in proportion to availability or more than expected by the majority of Spotted Owls (Table 7). Old forests appeared to be the most preferred cover type, with 57% of Spotted Owls using such stands more than expected and no Spotted Owls using such stands less than expected (Table 7). Unforested areas, young forest (0–25 cm dbh), and hardwoods were used less than expected by the majority of Spotted Owls (Table 7).

Fifty-seven percent of Barred Owls used old forest more than expected, but, in contrast to Spotted Owls, 26% of Barred Owls used old forest less than expected (Table 7). Most other cover types were used in proportion to availability by the majority of Barred Owls, except the unforested cover type, which was used less than expected by 82% of individuals (Table 7).

Compositional analysis. Rank scores of the five cover types indicated that old forest was the most preferred cover type for Spotted Owls, followed in declining order of preference by mid-age forest, unforested areas, hardwoods, and young forest (Table 8). Confidence in the ranking of old forest as the most preferred type was high, as indicated by the low *P*-values in comparisons with all other cover types except for unforested. The comparatively high ranking of the unforested cover type was surprising, because this type was rare (<1% cover) in most home ranges, and 11 of 14 Spotted Owls did not use this cover type at all. However, the small

TABLE 7. Percentage of Spotted Owls and Barred Owls using different cover types less than expected, more than expected, or in proportion to availability in the Baker Lake study area, Washington, 1987–1989. Results are based on the method of Neu et al. (1974).

Species and category of use	Cover type				
	Unforested	Hardwoods or shrubs	Young forest	Mid-age forest	Old forest
Barred Owls[a]					
Use < expected	82	35	39	26	26
Use = expected	18	61	52	57	17
Use > expected	0	4	9	17	57
Spotted Owls[a]					
Use < expected	67	79	79	22	0
Use = expected	33	21	21	64	43
Use > expected	0	0	0	14	57

[a] All estimates were based on a sample of 23 Barred Owls and 14 Spotted Owls, except for the unforested type, which were based on 17 Barred Owls and six Spotted Owls that had this cover type in their home ranges.

areas of rock talus that were present in some home ranges were often occupied by pikas (*Ochotona princeps*) and bushy-tailed woodrats (*Neotoma cinerea*), which could explain why some owls were occasionally found in or adjacent to these unforested areas.

For Barred Owls, old forest was ranked as the most preferred cover type, followed in descending order by mid-age forest, hardwoods, young forest, and unforested areas (Table 9). *P*-values in comparisons between old forest and other cover types were mostly small, indicating that the ranking of old forest as the most preferred type was strong (Table 9). Large *P*-values for most comparisons among other cover types indicated little difference in their relative preference. The most notable exception was the unforested cover type, which had significant *P*-values in all comparisons with other cover types (Table 9).

DISCUSSION

HOME RANGE SIZE

Our estimates of seasonal and annual home ranges of Spotted Owls are considerably larger than have been reported in other studies in Oregon and northwestern California, but are similar to or smaller than estimates from the Olympic Peninsula in Washington and from some high elevation study areas in the Sierra Nevada, California (Table 10). Carey et al. (1992) and Zabel et al. (1992) suggested that large home ranges of Spotted Owls on the

TABLE 8. Pairwise comparisons and rank scores from compositional analysis of habitat use by Spotted Owls in the Baker Lake study area, Washington, 1986–1989. Cover types are defined in Table 1. Rank scores indicate relative preference for cover types from lowest (0) to highest (4). A positive t-value indicates that the row cover type ranked higher than the column cover type, and a negative t-value indicates that the row cover type ranked lower than the column cover type. A significant P-value suggests that confidence in the direction of the relationship is high.

Cover type		OLD	MID	UNF	HDW	YNG	Rank
OLD	t		2.6	1.5	5.7	5.1	4
	P		0.02	0.16	<0.001	<0.001	
MID	t	−2.6		1.1	3.4	3.5	3
	P	0.02		0.31	0.005	0.004	
UNF	t	−1.5	−1.1		0.2	0.6	2
	P	0.16	0.31		0.85	0.54	
HDW	t	−5.7	−3.4	−0.2		1.0	1
	P	<0.001	0.005	0.85		0.33	
YNG	t	−5.1	−3.5	−0.6	−1.0		0
	P	<0.001	0.004	0.54	0.33		

TABLE 9. Pairwise comparisons and rank scores from compositional analysis of habitat use by Barred Owls in the Baker Lake study area, Washington, 1986–1989. Cover types are defined in Table 1. Rank scores indicate relative preference for cover types from lowest (0) to highest (4). A positive *t*-value indicates that the row cover type ranked higher than the column cover type, and a negative *t*-value indicates that the row cover type ranked lower than the column cover type. A significant *P*-value suggests that confidence in the direction of the relationship is high.

Cover type		OLD	MID	HDW	YNG	UNF	Rank
OLD	*t*		1.6	2.2	2.3	4.1	4
	P		0.14	0.04	0.03	<0.001	
MID	*t*	−1.6		0.6	2.0	3.4	3
	P	0.14		0.56	0.06	0.002	
HDW	*t*	−2.2	−0.6		1.3	3.7	2
	P	0.04	0.56		0.22	0.001	
YNG	*t*	−2.3	−2.0	−1.3		2.3	1
	P	0.03	0.06	0.22		0.03	
UNF	*t*	−4.1	−3.4	−3.7	−2.3		0
	P	<0.001	0.002	0.001	0.03		

Olympic Peninsula and in high elevation forests in the Sierra Nevada were a response to low density of preferred prey in those regions, but we could not address this hypothesis because we did not sample prey.

Our estimate of the mean annual home range size of Barred Owls (781 ± 216 ha) was smaller than results reported by Mazur et al. (1998) in Saskatchewan, but was larger than was reported in studies in Minnesota and Michigan (Table 10). However, none of these results are directly comparable, because methods and sampling intervals were not the same among studies.

The few radio-telemetry studies that have been conducted on Barred Owls suggest that, compared to Spotted Owls, they have small home ranges in most areas in which they occur (Table 10). However, most previous studies of Barred Owl home ranges were based on owls that had small numbers of locations, or that were tracked for less than a year, or both (Nicholls and Warner 1972, Fuller 1979, Elody and Sloan 1985, Mazur et al. 1998). Thus, there is a need for additional studies to evaluate home range attributes of Barred Owls, especially in areas where they are sympatric with Spotted Owls.

Reasons for the differences in home range size of Barred Owls and Spotted Owls in our study are unclear. We suspect that Barred Owls may require smaller foraging areas than Spotted Owls because they are more of a generalist predator than the Spotted Owl. In our study area, diets of the two species overlapped by about 76%, but diets of Barred Owls tended to be more evenly distributed across a broader range of prey types, including species that were rare in diets of Spotted Owls, such as fish, amphibians, and diurnal mammals (Hamer et al. 2001). These differences may allow Barred Owls to find enough food in much smaller areas than Spotted Owls.

Although the differences were not all significant, trends in most studies have indicated that ranges of Spotted Owls and Barred Owls tend to be larger in winter than in summer. This was true in most of the study areas examined by Forsman et al. (1984), Carey et al. (1992), Zabel et al. (1992), Mazur et al. (1998), and Glenn et al. (2004). Patterns of home range expansion during winter reflect a variety of behaviors, including a general expansion of the area of use, a slight shift to a winter range that does not overlap the summer range, or a migration to a winter range that is some distance from the summer range (Forsman et al. 1984, 2005, Laymon 1989, Carey et al. 1992, Zabel et al. 1992, Mazur et al. 1998). One obvious explanation for the increase in size of home ranges in winter is that, during winter, owls cease to be central-place foragers and are not energetically constrained by the need to return to a central place multiple times each night. Thus, the energetic cost of searching for prey in areas far from a central locality should be lower than in summer, and owls can probably increase their fitness by seeking out areas with higher prey biomass or prey availability and by reducing predation pressure on prey popula-

TABLE 10. Published estimates of home range size of radio-marked Spotted Owls and Barred Owls.

Species and location	Mean ± SE (ha)[a]	n[b]	Source
Spotted Owl			
Washington			
Olympic Peninsula	3608 ± 505	32 (20)	Forsman et al. (2005:370)
Northern Cascades	2659 ± 626	19 (14)	This study
Oregon			
Northern Coast Range	1108 ± 137	15	Glenn et al. (2004:40)
Central Coast Range[c]	1913 ± 510	6	Forsman et al. (1984:18)
Central Coast Range	2214 ± 360	9	Glenn et al. (2004:40)
Central Cascades	1177 ± 79	6	Forsman et al. (1984:18)
Douglas County	1580 ± 285	9	Carey et al. (1990:14)
Southwest Oregon	817 ± 151	2	Zabel et al. (1995:436)
California: northwest coast			
Klamath	591 ± 78	9	Zabel et al. (1995:436)
Mad River	422 ± 57	10	Zabel et al. (1995:436)
NW California	901 ± 182	12	Sisco (1990:10–11)
California: Sierra Nevada			
Northern Sierra Nevada	5231 ± 1674	6	Zabel et al. (1992:152)
Central Sierra Nevada	1654 ± 89	5	Call (1989:17)
Southern Sierra Nevada (conifer forest)	2416 ± 469	16	Zabel et al. (1992:152)
Southern Sierra Nevada (oak woodland)	422 ± 157	5	Zabel et al. (1992:152)
Barred Owl			
Minnesota: Cedar Creek[d]	572 ± 143	6	Fuller (1979:25)
Minnesota: Cedar Creek	229 ± ?[e]	10	Nicholls and Warner (1972:218)
Saskatchewan	971 ± 154	8	Mazur et al. (1998:748)
Michigan	282 ± ?[e]	7	Elody and Sloan (1985:5)
North Cascades, Washington	781 ± 216	31 (22)	This study

[a] We converted all estimates to mean ± SE, regardless of how they were presented in the original study. All estimates were based on the 100% minimum convex polygon method except in our study (95% adaptive kernel) and the Saskatchewan Barred Owl study (95% minimum convex polygon).
[b] If multiple annual ranges were estimated for some individuals, the first number indicates number of ranges estimated, and the number in parentheses indicates number of owls tracked.
[c] Owls were tracked for only five months (April–August).
[d] Most owls in this study were tracked for only 2–3 months.
[e] We could not calculate SE because authors did not provide data except for a mean.

tions near their nest areas outside the nesting season (Carey and Peeler 1995). Because Spotted Owls and Barred Owls that migrate or expand their home ranges in winter usually return to the same breeding territory in the next breeding season, we do not think that winter migration or home range expansion is a prospecting expedition in which owls seek out better territories or mates, although this could certainly be a secondary benefit. The fact that some Spotted Owls simply expand their ranges during winter, whereas others leave the breeding area altogether, indicates a high degree of behavioral plasticity, both within and among individuals and local populations (Laymon 1989, Zabel et al. 1992). Thus, we believe that all Spotted Owls, regardless of subspecies, can be expected to migrate or greatly expand their winter ranges at least occasionally in response to local variation in prey biomass or availability. This type of activity appears to be most common among Spotted Owls that live at high elevations or high latitudes, where winters are more severe (Laymon 1989, Zabel et al. 1992, this study).

Compared to Spotted Owls, winter migration was uncommon in the Barred Owls that we studied, possibly because Barred Owls tended to be found at lower elevations where the depth and duration of snow cover in winter was less than at sites occupied by Spotted Owls. Nevertheless, occasional examples of winter migration by Barred Owls (Mazur et al. 1998, this study) indicate that Barred Owls also have considerable behavioral plasticity regarding seasonal responses to changing prey or weather conditions.

HOME RANGE OVERLAP

Intraspecific home range overlap. The small average overlap between seasonal home ranges of Barred Owls in adjacent territories indicated that Barred Owls had relatively well-defined territories that they were able to defend against conspecifics. This observation is in agreement with a number of studies in the eastern U.S., in which researchers found that Barred Owls defended their home range areas throughout the year (McGarigal and Fraser 1985, Nicholls and Fuller 1987, Mosher et al. 1990). In contrast, we found that home ranges of Spotted Owls in adjacent territories overlapped by an average of 13% during the breeding season and 31% in winter. This suggests that home ranges of Spotted Owls are not synonymous with a well-defended territory, but are broadly overlapping foraging areas that are too large to defend consistently, especially during winter (Forsman et al. 1984).

Interspecific home range overlap. Evidence suggests that, before the range expansion of the Barred Owl, Spotted Owls occurred in forests throughout most of the Pacific Northwest (Gabrielson and Jewett 1940, Jewett et al. 1953, Forsman et al. 1984, Gutiérrez et al. 1995). By the time our study started, Barred Owls occupied the majority of lowland forest areas around Baker Lake. It was unclear if Barred Owls had displaced Spotted Owls from these lowland areas, but it was clear that most of the Spotted Owls in the area were restricted to moderate to high elevation areas in the headwaters of the tributaries of the Baker River. Nesting areas of the remaining Spotted Owls were typically located so far from nest areas of adjacent pairs of Barred Owls that the ranges of the two species had little overlap, except during winter, when the extensive movements of some Spotted Owls overlapped multiple Barred Owl territories. This suggests that, once they move into a new area and establish territories, Barred Owls are interspecifically territorial and largely exclude Spotted Owls from their territories, especially during the breeding season. It is unclear if the persistence of Spotted Owls in the higher elevation areas around Baker Lake indicates that Spotted Owls are able to outcompete Barred Owls in these areas, or if Spotted Owls will eventually be displaced there as well.

HABITAT USE

Use of edges. In our analysis, there was no indication that Spotted Owls or Barred Owls disproportionately used areas near edges with unforested openings or early seral vegetation. This finding is in contrast to studies in northwestern California, in which there was evidence that Spotted Owls foraged disproportionately near edges with brushy clear-cuts (Ward et al. 1998). Ward et al. (1998) and Franklin et al. (2000) suggested that disproportionate use of forest edges by Spotted Owls in California was a response to high densities and accessibility of dusky-footed woodrats (*Neotoma fuscipes*) along edges, where Spotted Owls could forage with reduced risk of predation, compared to foraging in open areas. In contrast, Spotted Owls in our study area fed primarily on flying squirrels (*Glaucomys sabrinus*), which are not associated with forest edges (Hamer et al. 2001). In the Oregon Coast Ranges, where Spotted Owls feed mainly on flying squirrels, woodrats, and tree voles (*Arborimus longicaudus*), Glenn et al. (2004) found that Spotted Owls avoided edges with openings, but seemed to prefer edges between conifer forests and hardwood forests. Glenn et al. (2004) speculated that the association with hardwood edges could have been a response to high numbers of woodrats in riparian areas (Carey et al. 1999), but did not have data to test this hypothesis. Whether edges between conifer forest and hardwood forest are good habitat for flying squirrels is unknown. The considerable variation in use of edges by Spotted Owls in different regions and forest types suggests that the relative abundance or availability of preferred prey may determine which types of edge are preferred or avoided in different regions.

Distance to streams. We do not know why Spotted Owl locations were closer to streams than random points, whereas Barred Owl locations did not differ from random. This finding is particularly puzzling given the fact that Barred Owl diets in our study area tended to include more fish and amphibians than did the diets of Spotted Owls (Hamer et al. 2001). A possible explanation for the lack of association between Barred Owls and streams is that many areas occupied by Barred Owls were in areas of low relief around Baker Lake, where there were many areas that were seasonally or permanently flooded (ponds, marshes, and alder-dominated floodplains). These areas did not consistently show up as streams on our digital map.

Elevation. In our study, mean differences in elevation between observed and expected locations of Spotted Owls and Barred Owls were so small that we did not consider them biologically significant. Thus, we conclude that: (1) within their home ranges, neither species selected habitat based on elevation, and (2) seasonal differences in weather had a negligible influence on elevation of foraging and roosting locations. However, the dramatic difference in mean elevations of Barred Owl locations (335 ± 15 m) and Spotted Owl locations (691 ± 67 m) suggests that Spotted Owls may have been excluded from areas at lower elevation by Barred Owls. The tendency of Barred Owls to occur at lower elevations and on gentler slopes than Spotted Owls has been noted in several studies (Pearson and Livezey 2003, Buchanan et al. 2004, Gremel 2005). Although Spotted Owls appear to be able to occupy higher elevation areas than Barred Owls, the trade-off for living in high elevation forests could be reduced survival or fecundity in years with severe winters.

Use of cover types. The pattern of use of cover types by Barred Owls and Spotted Owls suggests a classic contrast between a generalist predator (the Barred Owl) and a specialist predator (the Spotted Owl). Barred Owls used most cover types in proportion to availability, but did show a slight preference for old forest. In contrast, the majority of Spotted Owls avoided young forests and unforested areas and spent most of their time foraging in old or mid-age forests. This pattern was difficult to discern based on the rank scores produced by compositional analysis, but was clearly evident based on the method of Neu et al. (1974). These results are not surprising for Spotted Owls, because most previous studies of habitat use by Spotted Owls in the Pacific Northwest and northern California have indicated a preference for foraging and roosting in older forests (Forsman et al. 1984, 2005, Gutiérrez et al. 1984, Call 1989, Carey et al. 1990, 1992, Sisco 1990, Solis and Gutiérrez 1990, Carey and Peeler 1995; but see Zabel et al. 1992, 1995, Glenn et al. 2004 for exceptions). Several recent studies also suggest that survival rates or reproductive rates of Spotted Owls tend to increase with increasing amounts of mature and old forests, although these relationships are often best represented by quadratic or pseudo-threshold models in which survival or fecundity eventually level off or decline once the amount of old forest exceeds about 50%–70% of the landscape (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). Seamans and Gutiérrez (2007) also found that colonization rates of territories occupied by Spotted Owls were positively correlated with the amount of mature and old forest.

Barred Owls occur throughout much of eastern North America, where they commonly occupy landscapes that include a mosaic of forests, farmland, riparian zones, and urban areas (Bent 1938, McGarigal and Fraser 1984, Laidig and Dobkin 1995). Results from a number of studies indicate that they prefer to nest or forage in older forests (Dunstan and Sample 1972, McGarigal and Fraser 1984, Elody and Sloan 1985, Haney 1997, Mazur et al. 1997, 1998), but in most of these studies, old forests were dominated by hardwoods or mixed associations of conifers and hardwoods (but see Laiding and Dobkin 1995). Although our results suggest that old coniferous forests are preferred habitat for Barred Owls, recent surveys in western Oregon and Washington have detected large numbers of Barred Owls in relatively young forests as well (Kelly et al. 2003). This suggests that, although they may prefer older forests, Barred Owls are also able to occupy areas of relatively young forest if suitable nest sites are present.

Given that Barred Owls are so widespread in the eastern U.S. and have persisted in many highly disturbed areas (Laidig and Dobkin 1995), we do not think that our findings should be interpreted to mean that Barred Owls in Washington State need large areas of old forest. However, our findings do suggest that old forests are good habitat for Barred Owls, especially in low elevation areas. Gremel (2005) reached the same conclusion regarding Barred Owls on the Olympic Peninsula of Washington. Considering that their diets overlap by about 75% (Hamer et al. 2001), that they utilize similar cover types for foraging and roosting, and that Barred Owls generally respond aggressively toward Spotted Owls (Dunbar et al. 1991, Dark et al. 1998; TEH, unpubl. data), it is not surprising that Spotted Owls in our study area were found only in areas considerably removed from Barred Owls.

One caution regarding our data is that, because of small sample sizes, we used the combined sample of foraging and roosting locations for each owl in our analyses of habitat selection. This may have obscured important differences in habitat selection for foraging and roosting (Forsman et al. 1984, Carey et al. 1990). Samples dominated by roost locations may also have caused a negative bias in adaptive kernel estimates of home range size, because roosts tend to be concentrated near the traditional nest area, at least during the breeding season. Thus, any bias in our estimates of home range size would tend toward underestimation of the actual areas used for foraging.

BIOLOGY, POLITICS, AND MANAGEMENT OF BARRED OWLS AND SPOTTED OWLS

In the western U.S., where they have rapidly expanded into the traditional range of the Spotted Owl, Barred Owls are considered an invasive pest by many biologists and conservationists (Levy 2004). There is mounting evidence that they are having a negative influence on occupancy rates or colonization rates of Spotted Owl territories (Olson et al. 2005). This has led to considerable discussion in recent years about conducting experiments to determine if the removal of Barred Owls will result in reoccupancy of historic territories by Spotted Owls (Buchanan et al. 2007). In stark contrast, after Barred Owls expanded their range into Saskatchewan, Mazur et al. (1998) suggested that managers should retain old forests to improve habitat for the new species. These divergent views regarding how to respond to the large-scale range expansion of a native North American species represent a real challenge to the conservation community and to land managers. Ultimately, we think there is little that managers can do to change the scope or intensity of the Barred Owl range expansion because it is such a large-scale event that it cannot be controlled. What we can do from this event is to learn from it. Although we may never know what precipitated the range expansion of the Barred Owl, the possibility that it was facilitated by human-caused alteration of vegetation or fire regimes should give us pause, and hopefully will lead to more rational discourse regarding the role of humans in natural systems.

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