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HOME RANGE AND HABITAT SELECTION BY NORTHERN SPOTTED OWLS ON THE EASTERN SLOPE OF THE CASCADE MOUNTAINS, WASHINGTON

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ABSTRACT.—We used radiotelemetry to study space use and habitat selection of 16 Northern Spotted Owls (*Strix occidentalis caurina*) on the eastern slope of the Cascade Mountains, Washington, U.S.A., in 1989–1990. We used a geographical information system (GIS) and aerial photo interpretation of digital orthophotos to assign owl locations a value for vegetation type, topographic position, amount of edge, and distance to water. We compared owl relocations and random locations within 95% fixed kernel (FK) home ranges to determine each owl's selection of cover types, using logistic regression and generalized estimating equations (GEE) to estimate an exponential resource selection function likelihood. Minimum convex polygon (MCP) home ranges (SE) averaged 2858 ha (712 ha) for males and 1883 ha (249 ha) for females. Individual 95% FK home ranges averaged 1980 ha (229 ha) for males and 1649 ha (163 ha) for females. Pair home ranges averaged 3419 ha (826 ha) for MCP and 2427 ha (243 ha) for 95% FK. Nonbreeding season home ranges averaged approximately 3.5 times larger than breeding season home ranges for both males and females. Our best habitat model indicated that owls selected closed-canopy forests with a component of large (≥ 50 cm dbh) trees for roosting and foraging. In a given cover type, owls foraged lower on the slope. Management circles centered on nest areas—commonly used as a surrogate for home ranges—can be relatively poor representations of actual ranges used by pairs. However, an alternative for managing Spotted Owl home ranges is not readily available. Maintaining sufficient closed-canopy forest to provide habitat for Spotted Owls in the dry, fire-prone forests on the eastern slope of the Washington Cascades will be a challenge because forestry methods used to reduce the risk or severity of fire generally reduce the prevalence of structural features that characterize good Spotted Owl habitat.

KEY WORDS: *Northern Spotted Owl; Strix occidentalis caurina; habitat selection; home range; fixed kernel; minimum convex polygon; radiotelemetry; Washington.*

ÁREA DE CAMPEO Y SELECCIÓN DE HÁBITAT DE *STRIX OCCIDENTALIS CAURINA* EN LA VERTIENTE ORIENTAL DE LA CORDILLERA CASCADE, WASHINGTON

RESUMEN.—Utilizamos radiometría para estudiar el uso del espacio y la selección de hábitat de 16 individuos de *Strix occidentalis caurina* en la ladera Este de Cascade Mountains, Washington, EEUU, durante el periodo 1989–1990. Utilizamos un sistema de información geográfica (SIG) y foto-interpretación de ortofotografías digitales para asignar a las ubicaciones de los búhos valores según tipo de vegetación, posición

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topográfica, cantidad de borde y distancia al agua. Comparamos las localizaciones y las ubicaciones al azar de los búhos dentro de las áreas de campeo según el Kernel fijo (KF) al 95% para determinar la selección individual de cada búho entre los tipos de cobertura vegetal, utilizando regresión logística y ecuaciones estimativas generalizadas (EEG) para establecer la probabilidad de una función exponencial de selección de recursos. Los mínimos polígonos convexos (MPC) del área de campeo fueron en promedio de (EE) 2858 ha (712 ha) para los machos y 1883 ha (249 ha) para las hembras. El tamaño del área de campeo individual de acuerdo dado según el KF al 95% fue en promedio de 1980 ha (229 ha) para los machos y 1649 ha (163 ha) para las hembras. El tamaño del área de campeo de las parejas fue en promedio de 3419 ha (826 ha) de acuerdo con los MPC y de 2427 ha (243 ha) según el KF al 95%. El tamaño del área de campeo de los machos y las hembras durante la estación no reproductiva fue, en promedio, aproximadamente 3.5 veces más grandes que el tamaño del área de campeo durante la estación reproductiva. Nuestro mejor modelo de hábitat indicó que los búhos seleccionaron bosques de dosel cerrado con un componente de árboles grandes (≥ 50 cm dap) para ser usados como dormitorio y para alimentación. En un tipo de cobertura vegetal dado, los búhos se alimentaban en las partes más bajas de la ladera. El establecimiento de un área de gestión en base a una circunferencia centrada en el área del nido—comúnmente utilizados como una aproximación del área de campeo—puede ser una representación relativamente pobre del área de campeo real utilizada por las parejas. Sin embargo, no se encuentra disponible un método de gestión alternativo para las áreas de campeo de *S. o. caurina*. El mantenimiento de una superficie suficiente de bosques con dosel cerrado que proporcione hábitat a *S. o. caurina* en los bosques secos y propensos a incendios en la ladera este de las Cascadas de Washington constituye un desafío, dado que los métodos utilizados por la industria forestal para disminuir el riesgo o severidad de incendios generalmente reducen el predominio de rasgos estructurales que caracterizan el hábitat adecuado para *S. o. caurina*.

[Traducción del equipo editorial]

The Northern Spotted Owl (*Strix occidentalis caurina*, hereafter Spotted Owl) is often portrayed as a species that is largely restricted to old-growth forests. Although it is true that the majority of Spotted Owls located to date have been found in older forests, it is also true that in some regions, many pairs have been found in forests that are not classical old-growth forests (Forsman et al. 1984, Thomas et al. 1993). For example, over 170 pairs of Spotted Owls were located in one study area in northern California where most forests were 50–80 yr old (Diller and Thome 1999, Thome et al. 2000). Stands in the latter area typically developed multilayered canopies at an early age, with evergreen hardwoods making up much of the understory layers, and sometimes included remnant old trees that were not cut when logging occurred in the early 1900s. Another region where Spotted Owls often occur in conditions that are not typical old-growth is on the eastern slope of the Cascades Range in Washington. In the latter region, many pairs occur in “mixed-age” forests dominated by trees of intermediate age and size, intermixed with variable numbers of larger remnant trees that survived earlier fires or selective logging (Forsman et al. 1996). Other important components of Spotted Owl habitat on the eastern slope of the Cascades are dwarf mistletoe (*Arceuthobium* spp.) brooms, an abundance of truffles (mostly subphylum Basidiomycotina), large snags, and downed

woody debris (Lehmkuhl et al. 2006a, 2006b, Sovern et al. 2011).

In the study described herein our primary objectives were to characterize home ranges and habitat selected by Spotted Owls on the eastern slope of the Cascades Range in Washington, at the scale of the individual home range, and to extrapolate our resource selection function to the population. The study was originally conducted in 1989–1990, and results of preliminary analyses of the data were used in early management recommendations for Spotted Owls in the eastern Cascades (Hanson et al. 1993, U.S.D.A. and U.S.D.I. 1994b). However, a complete analysis of the data was never conducted, and the results were never fully described or published. Since the data were collected, new approaches to estimating home ranges and advances in habitat modeling have been developed. Finally, since many years had elapsed between collecting the telemetry data and this report, we were able to relate the results to current relationships between efforts to protect habitat for Spotted Owls on the eastern slope of the Cascades, while at the same time managing forests to reduce the risk or severity of wildfire.

METHODS

The study was conducted in the Swauk Creek and Taneum Creek drainages in the Cle Elum Ranger District on the eastern slope of the Cascades Mountains

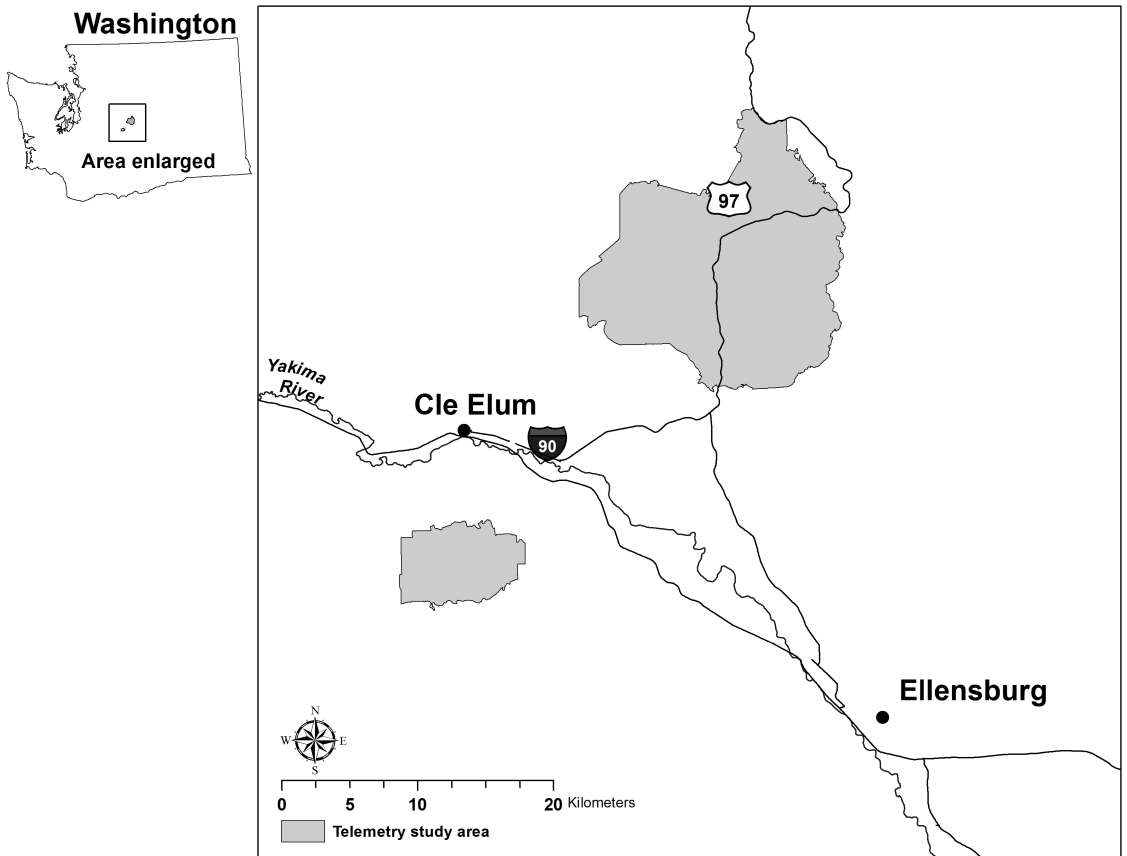


Figure 1. Cle Elum radiotelemetry study area, Washington, U.S.A., 1989–1990.

in Washington, U.S.A. (Fig. 1). Most lands in the study area were administered by the U.S. Forest Service or were owned by private timber companies (Plum Creek Timber Company, Boise Cascade Timber Company). The terrain was mountainous, except for a broad flat valley along the Yakima River bisecting the northern and southern halves of the study area (Fig. 1). Elevations ranged from 732–1646 masl. The climate was characterized by cool, dry winters and warm, dry summers. Annual precipitation averaged 54 cm, most of which occurred from January–April as snow.

Forest cover was a complex mosaic of mixed-conifer stands on northern slopes and relatively open stands of ponderosa pine (*Pinus ponderosa*) on southern slopes. Mixed-conifer stands typically had moderate to high canopy cover (>50%) and were dominated by Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*), with variable amounts of ponderosa pine, western larch (*Larix occidentalis*),

lodgepole pine (*P. contorta*), and western white pine (*P. monticola*). Western hemlock (*Tsuga heterophylla*) was present in some mixed-conifer stands at higher elevations near the crest of the Cascades. Douglas-fir trees in the study area were commonly infected with dwarf mistletoe (*Arceuthobium douglasii*), a plant parasite that causes the limbs of the host to grow in dense, deformed clumps (Hawksworth and Wiens 1972). These deformities tended to be most severe in older trees.

The study area was characterized by an extensive network of roads and harvest units, including clearcuts and selectively logged (thinned) areas. Many stands within the home ranges of the owls that we studied had been selectively logged one or more times in the previous 50 yr. Richards (1989) estimated that >75% of the Swauk Creek drainage in the northern portion of our study area had undergone some level of commercial harvest since 1910. Most historical harvest involved the selective removal of

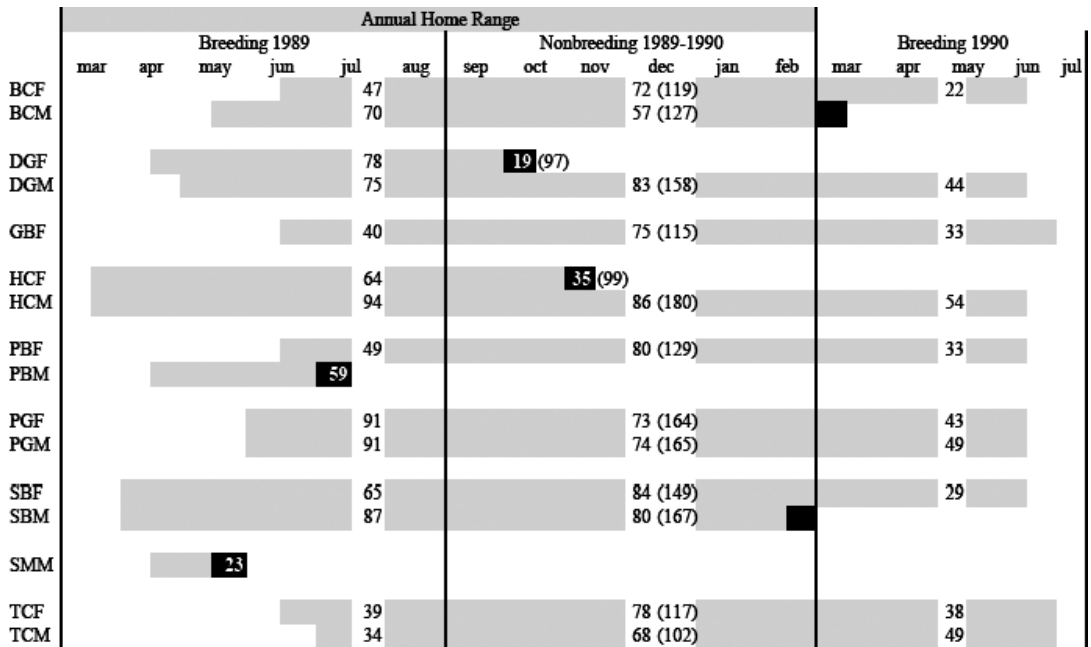


Figure 2. Tracking periods and number of relocations for 16 radio-marked Northern Spotted Owls (*Strix occidentalis caurina*) on the Cle Elum Study Area, Washington, U.S.A., 1989–1990. Bars indicate the tracking period for each owl. Numbers indicate the number of relocations in each period (breeding, nonbreeding) used in home-range calculations. Numbers in parentheses are the number of locations used to estimate an owl’s annual home-range area. Bars ending in black boxes indicate the owl died. Owls in adjacent rows were paired in 1989.

individual trees. Selectively logged stands typically were dominated by trees with a diameter at breast height (dbh) of 10–50 cm, but also included scattered larger trees (≥ 50 cm dbh) that were not cut during logging.

We radio-marked most owls in April–May 1989, midway through the breeding season (Fig. 2). We used AVM model P2 transmitters (AVM Instrument Co. Ltd., Colfax, California, U.S.A.) installed in a backpack configuration with a harness of 5-mm-wide tubular Teflon ribbon (Dunstan 1972, Forsman 1983, Guetterman et al. 1991). Transmitter frequency was 165–166 MHz, and transmitter mass with harness was 18–20 g. All transmitters were removed after the study was complete. All of the owls marked were territorial adults that were initially located by conducting calling surveys to find their roost sites (Reid et al. 1999).

We attempted to obtain one location per owl at least three nights per wk and at least one diurnal location per owl each wk. This schedule was occasionally disrupted when snowstorms or road closures made access to some areas difficult. The order

in which owls were located was varied on different nights to ensure that sampling for each individual did not occur at the same time each night. The sampling schedule in which we obtained only one location per night was adopted to reduce autocorrelation between locations (Swihart and Slade 1985a, 1985b). However, this was probably not necessary, as Otis and White (1999) found that autocorrelation is generally not important in studies of home range and habitat use when the individual animal is used as the sample unit (see also Aebischer et al. 1993a, 1993b).

Locations were classified as nocturnal if they occurred from 0.5 hr after sunset to 0.5 hr before sunrise (Pacific Standard Time). Except in the case of incubating or brooding females, we classified all diurnal locations as “roosting” locations. All nocturnal relocations were estimated by triangulating from roads or trails with a portable radio receiver (Telonics Model TR-2, Mesa, Arizona, U.S.A.), a handheld “H” antenna (Telonics Model RA-2A), and a magnetic compass. At least three azimuths were recorded to establish each location, us-

ing the methods described by Forsman et al. (1984) and Guetterman et al. (1991). Azimuths were plotted on 1:12 000 scale United States Geological Survey orthophotos or topographic maps. The position of the owl was considered to be the geometric center of the polygon formed by the intersection of the azimuths. During the day, relocations of roosting owls were obtained by triangulation or by homing in on owls and visually locating them in their roost trees.

We used all relocations for estimates of home-range area but we only used relocations for analysis of habitat selection if the area of the polygon formed by the intersection of the azimuths was ≤ 1 ha. This filter excluded approximately 6% of our original locations from habitat-selection analyses. Because of concerns that error polygons might not accurately reflect actual owl locations (Nams and Boutin 1991), we evaluated the accuracy of nocturnal telemetry locations with two different blind trials ($n = 23$ and $n = 40$) on two different study areas where one observer placed transmitters in owl home ranges and another observer triangulated on the transmitters at night. Estimated locations from the triangulations were then compared to the actual locations of the transmitters, which were located to the nearest m with a Global Positioning System (GPS) unit. Median triangulation error in the two trials was 142 and 89 m, respectively. These error estimates were similar to several other studies of Spotted Owls in which observers used similar methods (Glenn et al. 2004 mean = 164 m, Forsman et al. 2005 mean = 140 m, Clark 2007 mean = 136 m). The relatively large errors associated with triangulations were of concern; however, we assumed that misclassifications due to telemetry error were similar in all cover types, and that the overall assessment of habitat selection was correct. In addition, the estimated triangulation errors in our field tests were small compared to the home-range areas of the owls, so, at least for estimates of home-range area, triangulation error was not a concern.

Estimation of Home-range Area. We used the Minimum Convex Polygon (MCP) and Fixed Kernel (FK) methods to estimate annual home-range areas (Hayne 1949, Worton 1989, Horne and Garton 2006). Estimates of MCP ranges were based on 100% MCP polygons. We evaluated the 95% and 50% isopleths of Fixed Kernel home ranges with the adehabitat module (Calenge 2006) in Program R (version 2.12.1, R Development Core Team 2010). We used a composite method to incorporate the

smoothing parameter (h) for kernel home-range estimation. We calculated the likelihood cross validation (CVh) estimation of h with program Animal Space Use 1.3 (Horne 2009). We used CVh for the smoothing parameter when CVh was $>$ the reference level for h . If CVh was \leq the reference level of h , then we used h as the smoothing parameter (Wiens et al. 2014). We used this two-pronged approach so that kernel estimates of home-range areas based on relatively small numbers of relocations of owls that had relatively large movements would not be “overly smoothed” (Wiens 2012). We used 50% FK home ranges to estimate the core area in each owl’s home range. The justification for using the 50% FK isopleth to estimate core areas came from modeling done by Wiens (2012), who found that, for Spotted Owls and Barred Owls (*Strix varia*), the 50% FK isopleth closely approximated core area estimates produced by the Bingham and Noon (1997) method, which estimated core use areas based on a comparison of telemetry locations within a 95% adaptive kernel home range and a uniform distribution of points in the same area. For seasonal analyses, we divided the year into two phenological periods, the “breeding season” (March–August), which corresponded to the period when Spotted Owls nested and fed young, and “winter” (September–February), when Spotted Owls were largely solitary (Fig. 2). Estimates of seasonal home-range areas were limited to owls tracked ≥ 120 d during the season of interest. We estimated the combined home-range area of each pair of owls by calculating the union of the individual ranges of the male and female (sum of both ranges minus the area of overlap).

Because roost locations and incubation or brooding locations of central-place foragers like Spotted Owls are concentrated near the nest area during the nesting season, we were concerned that a statistical estimator like the FK might underestimate foraging areas if roosts and incubation or brooding locations were included in the sample used to estimate home ranges. For this reason, we excluded incubation, brooding, and roost locations during the breeding season from FK estimates of home-range area. Thus, our FK home ranges are more appropriately “foraging home ranges.” However, these foraging home ranges typically contained all of the roosts and nests used by the owls in our sample.

Estimates of overlap of ranges of pair members or owls on adjacent territories were limited to owls tracked during approximately the same time

Table 1. Variables used for modeling habitat selection of Northern Spotted Owls (*Strix occidentalis caurina*) on the Cle Elum Study Area, Washington, 1989–1990.

VARIABLE (CODE)	VARIABLE (CODE)	DESCRIPTION
Cover type (COVTYPE)	Closed-canopy, large tree (CCL)	Conifer forests in which the overstory trees included a mixture of large (>50 cm DBH) trees and smaller, generally younger trees. Canopy cover $\geq 80\%$.
	Closed-canopy, small tree (CCS)	Conifer forests dominated by 10–50 cm DBH trees with few large (>50 cm dbh) trees. Canopy cover $\geq 80\%$.
	Moderate canopy (MOD)	Forests with canopy cover 50–79%. Variable tree size.
	South aspect moderate canopy (SAM)	A special case of the moderate canopy type with aspects 158–248° and slopes >1%. Variable tree size and canopy cover 50–79%.
	Open canopy (OC)	Conifer forests with canopy cover <50%. Size of trees highly variable.
	Non-forest (NON)	Non-forested areas, including clear-cuts, talus slopes, rocky outcroppings, natural meadows, gravel pits, agricultural areas, and residential areas.
Total edge (TE)		Total edge of all polygons within 140 m of telemetry location (m).
Topographic position (TOPO)		The percentile of maximum elevation within 1000 m of the focal pixel, with 0 being the base of the slope and 100 being a hilltop.
Solar insolation (SOLAR)		Measured in annual mean daily watt-hours as calculated by the ArcGIS Solar Analysis extension.
Distance to water (WATER)		Distance to nearest perennial stream.
Proportion of COVTYPE (Px)		Proportion of COVTYPE _x in the 140-m-radius circle centered on telemetry location.
Edge (EDGE)		Y if the 140-m-radius circle centered on the telemetry location contained >10% of another cover type; N otherwise.
Slope (SLOPE)		% slope.

periods. For each comparison we calculated two estimates (% overlap of owl *i* on owl *j* and % overlap of owl *j* on owl *i*) with the adehabitat module (Calenge 2006) of Program R (version 2.12.1, R Development Core Team 2010), and with ArcGIS. We also calculated the overlap among adjacent males and adjacent females. We considered two owls to have adjacent home ranges if the minimum distance between the edges of their annual MCP home ranges was <2 km. We used the 2-km distance because we reasoned that owls with home ranges separated by >2 km were unlikely to frequently encounter each other. We also calculated the probability of finding one owl in the FK home range of an adjacent owl (PHR) based on the method described by Fieberg and Kochanny (2005) in program R. This PHR parameter is an easily interpretable, nonspatial metric that is suitable for assessing home-range overlap between utilization-distribution estimates of home-range area (Fieberg and Kochanny 2005). We used logistic regression to test for differences between

males and females for home-range area and overlap, and between breeding and nonbreeding pairs during the breeding season.

Habitat Mapping and Assessment of Habitat Selection. We used the 95% FK range as the frame of reference for third-order habitat selection (use of different forest types within the area available to each owl, Johnson 1980). For the habitat selection analyses, we subdivided stands into five broad forest types based primarily on the dbh and canopy cover of overstory and understory trees, and one non-forest type, collectively “cover types” (Table 1). Cover-type polygons were first delineated with canopy cover data from the Interagency Vegetation Mapping Project (U.S.D.I. BLM 2003). We further divided “moderate canopy” cover-type polygons into a “south aspect moderate” type for those portions of the “moderate canopy” polygons with aspect = 158–248° and slopes >1% in ArcGIS 9 (Esri Inc. Redlands, California, U.S.A.). We split out the south aspect portions of the moderate

canopy polygons because stands on south aspects were more likely to be naturally open stands compared to stands with similar canopy cover on other aspects (Lillybridge et al. 1995). Tree size in cover-type polygons with $\geq 80\%$ canopy cover was classified using 1-m resolution digital orthophotos in GIS. We included a covariate for topographic position (TOPO), which was the percentile of maximum elevation within 1000 m of the focal pixel, with 0 being the base of the slope and 100 being a hilltop. We used a measure of solar insolation (SOLAR), measured in annual mean daily watt-hours as calculated by the ArcGIS Solar Analysis extension (Esri Inc., Redlands, California, U.S.A.).

To test the accuracy of the tree-size attribute feature of the closed-canopy polygons in the cover-type map, we randomly generated 142 points in 53 closed-canopy polygons, located these points on the ground with a GPS, counted the number of large (>50 cm dbh) conifers present, and averaged the counts from each polygon. This test indicated that we were able to differentiate the “large-tree” and “small-tree” stand types using aerial photo interpretation 79% of the time based on a cutoff of >20 large stems/ha.

We conducted separate analyses for foraging and roosting because we suspected that owls might select differently for foraging and roosting habitat (Forsman et al. 1984). Previous studies of Spotted Owls showed owls used similar habitat regardless of season (Forsman et al. 1984), thus we did not analyze habitat selection by season. Locations of incubating or brooding females were excluded from all analyses of habitat selection. For analysis of roosting habitat, we used the 95% FK home range estimated from foraging locations.

We estimated the area of different cover types available to each owl by generating random points within the 95% FK home range in ArcGIS (Esri Inc., Redlands, California, U.S.A.). Random points were spaced ≥ 140 m apart so we could evaluate the amount of edge and habitat heterogeneity within the home range at a scale approximating our estimated telemetry error. This process resulted in 98–244 random points in each home range. We used logistic regression to estimate the β coefficients of an exponential resource selection function likelihood (RSF; Johnson et al. 2006, Lele et al. 2013, McDonald 2013). We considered owl locations as samples of used resource units, and estimated the resource units available to each owl with random points in each owl’s home range (Design III study;

Manly et al. 2010). We included seven covariates for habitat modeling (Table 1). For analyses of habitat selection, we used generalized estimating equations (GEE) with PROC GENMOD in SAS (SAS Institute, Cary, North Carolina, U.S.A.) using the option REPEATED = subject, where subject was defined as an individual owl. Using GEE was necessary to account for violating the assumption of independence of observations, which could result in unduly small variance estimates and increased potential for TYPE I errors (Koper and Manseau 2009, Fieberg et al. 2010). We ranked models with the quasi-likelihood under the independence model criterion (QIC, Pan 2001). We used QIC in a similar manner to Akaike’s Information Criterion (AIC) in an Information Theoretic approach (Burnham and Anderson 2002). We used the non-habitat cover type (non-forest areas) as the reference level for parameterizing logistic regression models that included the cover type covariate.

In the absence of home-range data for a particular area, habitat management recommendations for pairs of Spotted Owls are often based on circles of varying radii, within which various amounts of habitat are protected around nest sites. For example, in eastern Washington, current Washington Department of Natural Resource guidelines for Spotted Owl management on private lands are to maintain at least 40% cover of old forest habitat within a 2.9-km-radius circle centered on the nest or center of activity (Washington State Environmental Policy Act 2001, Washington Administrative Code 222-10-041). Likewise, the United States Fish and Wildlife Service (U.S.F.W.S.) developed guidelines for consultation under section 7 of the Endangered Species Act, which included a 2.9-km-radius circle around Spotted Owl nest sites for evaluating “incidental take” for projects affecting Spotted Owl habitat (U.S.D.A. and U.S.D.I. 1994a). The rationale for this circle size was developed based on preliminary analysis of the median MCP home ranges of owl pairs from our sample of marked individuals (Hanson et al. 1993, U.S.D.A. and U.S.D.I. 1994b). To investigate the extent to which regulatory circles approximated areas actually used by pairs of owls, we computed overlap of the annual home ranges of pairs with 2.9-km-radius circles centered on nest sites or centers of activity.

To test the predictive power of the RSF, we performed a *k-fold* cross-validation analysis following Johnson et al. (2006). We first generated a surface in GIS based on the RSF estimated without the

Table 2. Estimated area of annual home ranges of 13 radio-marked Northern Spotted Owls (*Strix occidentalis caurina*) on the Cle Elum Study Area, Washington, U.S.A., 1989–1990.

OWL	SEX	HOME-RANGE ESTIMATES (HA) ^a								
		NO. OF RELOCATIONS			INDIVIDUAL OWLS			PAIRS		
		FORAGING	ROOSTING	TOTAL	MCP	95% FK	50% FK	MCP	95% FK	50% FK
BCF	♀	87	32	119	1445	1256	216			
BCM	♂	95	32	127	5925	2634	330	6308	2800	330
DGM	♂	116	42	158	2244	2030	221			
GBF	♀	87	28	115	1461	1388	274			
HCF	♀	65	33	98	1577	1456	202			
HCM	♂	123	57	180	3851	2354	268	3943	2694	286
PBF	♀	93	36	129	2844	2211	234			
PGF	♀	118	46	164	2835	2314	430			
PGM	♂	117	48	165	1772	1635	287	2883	2453	456
SBF	♀	103	46	149	1380	1347	226			
SBM	♂	125	42	167	1199	1059	208	1495	1483	282
TCF	♀	88	29	117	1640	1575	262			
TCM	♂	78	24	102	2157	2168	311	2469	2707	347

^a MCP = 100% minimum convex polygon, 95% FK = 95% fixed kernel, 50% FK = 50% fixed kernel. Fixed kernel home-range area based on foraging locations only.

locations from one owl, then divided the RSF surface into 10 bins by geometrical interval (1 = low RSF, 10 = high RSF). We then compared the observed proportion of owl locations in each RSF bin from the withheld owl to the proportion in each bin predicted by the model. We repeated this process for 12 owls that had >80 foraging locations.

RESULTS

We radio-marked 16 owls (eight males, eight females), all of which were resident, paired individuals in the breeding season of 1989. Nine owls (four males, five females) were nesting when they were radio-marked. Of the 16 owls, six died during the study, four from avian predation, one from starvation, and one from unknown causes. Of the six owls that died, five were tracked ≥ 90 d and used to estimate seasonal or annual home ranges. Thus, we obtained usable data on 15 owls (Fig. 2). Total relocations of radio-marked owls included 654 roost locations, 1639 foraging locations, and 152 incubating/brooding locations. The mean number of relocations per owl was 166 (range 58–234) and the mean sampling period per owl was 322 d. Of the 654 roost relocations, 120 (18%) were determined solely by triangulation, and 534 (82%) were determined by homing in on owls to locate them in their roost trees. The latter cases included 497 cases where owls were actually observed in their roosts

and 37 cases where the roost location was narrowed down to one or two trees, but where the owl was roosting in such dense foliage that it could not be seen.

Home-range Characteristics. *Movements.* Although all owls that we tracked were paired residents that we regularly found in the same areas, three of them changed territories between 1989 and 1990. In two cases these movements occurred after a mate died. In the other case, a radio-marked male left its previous mate and joined a new mate at a territory where the previous male had died.

Annual ranges. Annual home-range area of individual males averaged 2858 ± 712 ha (\pm SE) for the MCP and 1980 ± 229 ha for the 95% FK (Table 2). Comparable estimates for females were 1883 ± 249 ha for the MCP and 1649 ± 163 ha for the 95% FK (Table 2). These averages did not include data from three owls that were tracked for <180 d. The male with the largest annual MCP range (5925 ha) greatly expanded his range during the fall and winter. Annual estimates of home-range areas were similar for males and females, regardless of which home-range estimator we used (all 95% Wald CIs for beta estimates overlapped 0). Median estimates of annual ranges of pairs of owls were 2883 ha for the MCP (range = 1495–6308 ha), 2694 ha for the 95% FK (range = 1483–2800 ha), and 330 ha for the 50% FK (range = 282–456 ha).

Table 3. Estimated area (ha) of seasonal home ranges of radio-marked Northern Spotted Owls (*Strix occidentalis caurina*) on the Cle Elum Study Area, Washington, U.S.A., 1989–1990.

OWL AND SEX OR OWL PAIR	BREEDING SEASON 1989 ^a			NONBREEDING SEASON ^a			BREEDING SEASON 1990 ^{a,b}		
	MCP	95% FK	50% FK	MCP	95% FK	50% FK	MCP	95% FK	50% FK
BC ♀	614	993	234	1444	1660	316	140	262	54
BC ♂	593	735	132	5925	4767	896			
DG ♀	459	403	56	427	1070	223			
DG ♂	306	276	52	1952	2996	692	454	537	92
GB ♀	623	925	186	1461	2343	573	390	501	70
HC ♀	997	1211	170	1315	1819	301			
HC ♂	861	772	104	2981	3498	914	244	389	55
PB ♀	884	1000	119	2718	4479	1209	206	288	32
PB ♂	728	687	61						
PG ^a ♀	639	721	151	2578	4621	1165			
PG ♂	596	694	140	1621	1985	440	444	621	83
SB ♀	539	686	84	1361	2050	489	152	187	22
SB ♂	655	680	108	1150	1599	345			
TC ♀	299	372	64	1640	3197	733	226	296	40
TC ♂	152	305	71	2157	1986	404	789	1080	166
Mean (SE)	576(59)	688(66)	114(13)	2052(349)	2719(326)	621(86)	338(52)	463(68)	68(11)
BC pair	748	1071	237						
DG pair	487	443	61						
HC pair	1196	1316	172						
PG pair	723	863	176						
SB pair	714	875	113						
TC pair	327	399	83						
Mean (SE)	699(120)	828(145)	140(27)						

^a MCP = 100% minimum convex polygon, 95% FK = 95% fixed kernel, 50% FK = 50% fixed kernel. Fixed kernel home-ranges area based on foraging locations only.

^b 1990 breeding season home-range does not include one location we classified as exploratory behavior.

Seasonal ranges. Winter home-range areas averaged approximately 3.5 times larger than breeding season home ranges (Table 3). Overlap of MCP winter ranges on breeding-season ranges averaged 87% ± 2% (range = 52–100%, n = 14) and overlap of MCP breeding-season ranges on winter ranges averaged 33% ± 2% (range = 7–80%, n = 14). The smaller overlap of breeding ranges on winter ranges resulted because much of the winter activity occurred in areas that were used infrequently during the breeding season. Mean estimates of the area of seasonal ranges did not differ between males and females, regardless of which estimator was compared (all 95% CIs for beta estimates from logistic regression overlapped 0).

Home-range overlap. Overlap of MCP home ranges of owls that were paired averaged 69% during the breeding season, 59% during winter, and 62% during the annual period (Table 4). Overlap of 95% FK home ranges for paired owls were similar to MCP home ranges (Table 4). Estimates of overlap of

ranges of paired males and females during the breeding season were similar for both breeding and nonbreeding pairs (95% CI for beta estimate broadly overlapped 0).

On average, the annual MCP home ranges of individual owls occupying adjacent territories overlapped by 15% for both males and females (Table 4). Annual 95% FK home ranges overlapped 14% for adjacent males and 19% for adjacent females (Table 4). These estimates only included overlap between adjacent individuals that we monitored and did not reflect the total amount of overlap between each owl and its neighbors because there were adjacent pairs that we did not have radio-marked, and because tracking periods for individual owls did not always exactly overlap. The probability of finding an owl in the 95% FK home range of its mate was slightly higher for females than for males during both the breeding season (0.88 vs. 0.83) and nonbreeding season (0.83 vs. 0.77, Table 4). The probability of finding an owl

Table 4. Estimated overlap of home ranges of radio-marked Northern Spotted Owls (*Strix occidentalis caurina*) on the Cle Elum Study Area, Washington, U.S.A., 1989–1990.

OVERLAP	SEASON ^c	n ^d	95% FIXED KERNEL				50% FIXED KERNEL				100% MCP	
			HR ^a		PHR ^b		HR ^a		PHR ^b		HR ^a	
			MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE
Paired male (i) on female (j)	Breed	11	71	5	0.83	0.05	79	8	0.39	0.06	72	6
	Winter	6	73	8	0.77	0.09	72	14	0.38	0.08	67	5
	Annual	7	69	11	0.82	0.07	70	13	0.47	0.10	68	9
Paired female (i) on male (j)	Breed	11	65	7	0.88	0.02	65	9	0.49	0.06	66	7
	Winter	6	65	13	0.83	0.07	55	12	0.50	0.11	51	15
	Annual	7	63	13	0.81	0.07	68	13	0.50	0.11	56	12
Combined pair overlap	Breed	22	68	4	0.86	0.03	72	6	0.44	0.04	69	4
	Winter	12	69	8	0.80	0.05	63	9	0.44	0.06	59	8
	Annual	14	66	8	0.82	0.05	69	9	0.49	0.07	62	8
Adjacent males ^e	Breed	24	4	2	0.03	0.02	0	0	0.00	0.00	2	1
	Winter	18	15	4	0.16	0.05	3	2	0.03	0.02	12	4
	Annual	24	14	4	0.16	0.05	2	1	0.02	0.01	15	4
Adjacent females ^e	Breed	24	5	2	0.07	0.03	0	0	0.00	0.00	6	3
	Winter	20	22	6	0.24	0.07	5	3	0.05	0.02	16	6
	Annual	20	19	6	0.19	0.07	1	0	0.02	0.01	15	5

^a % of the home range of owl *i* overlapped by the home range of owl *j*.

^b The probability of finding owl *i* in the home range of owl *j* (Fieberg and Kochanny 2005).

^c Breed = 1 March–30 Aug, Winter = 1 Sep–28 Feb, Annual = Breed + Winter.

^d For the groups “paired male on female” and “paired female on male,” *n* = the number of comparisons of overlap of owl *i* on owl *j*. For the groups “combined pair overlap,” “adjacent males,” and “adjacent females,” *n* = the number of comparisons of owl *i* on owl *j*, and owl *j* on owl *i*.

^e Adjacent owls were those owls whose MCP home ranges were ≤ 2 km apart.

in the 95% FK home range of its adjacent same-sex neighbor was lower for males than females in all seasons (Table 4). In cases where we had data from multiple pairs in close proximity to each other, MCP home ranges of pairs were sometimes almost completely overlapped by home ranges of other pairs, whereas 95% FK home ranges of adjacent pairs were somewhat more discrete.

Habitat Selection. *Habitat selected for foraging.* The top model for foraging habitat among the single factor models we evaluated was the model that included the topography covariate (Table 5). This model indicated that selection decreased 2% for each 1% increase in topographic position, or in other words, for similar cover types, owls were more likely to forage at lower topographic positions (relative risk ratio = 0.98, 95% CI = 0.96–0.99, Table 6). This model accounted for 94% of the QIC weight of the single-factor models we evaluated. The Δ QIC value for the next closest single factor model (cover type) was 5.6 units greater than the top model. However, several of the 95% CIs for risk ratios for the cover type categories did not include 1, so we com-

bined topography and cover type in several additive and interactive *post-hoc* models (Table 5). We also included quadratic forms of the topography covariate (Table 5). The model including topography plus the additive effect of cover type significantly improved model fit over the topography only model (Δ QIC = 109). There was only weak evidence of a lower limit to the topographic position which owls would use for foraging in a given cover type compared to what was available (95% CIs for relative risk ratios of quadratic form of TOPO overlapped 1). Among the six cover types we mapped, owls selected closed-canopy, large-tree forest for foraging most often. Relative risk ratios were 3.9 times higher (95% CI = 2.9–5.4) for closed-canopy large-tree forest compared to non-habitat given the same topographic position. Selection for small-tree forest was only slightly lower than selection for closed-canopy large-tree forest (risk ratio 3.6 vs. 3.9, respectively). Owls selected moderate canopy forest more than non-habitat (risk ratio = 2.0), but the 95% CIs for the estimated risk ratio were only slightly >1 (95% CI = 1.3–3.2). Thus, the closed-canopy large-tree forest and closed-canopy small-tree

Table 5. Ranking of habitat models used to assess habitat used for foraging by radio-marked Northern Spotted Owls (*Strix occidentalis caurina*) on the Cle Elum Study Area, Washington, U.S.A., 1989–1990. Models in italics were *post-hoc* models evaluated after ranking single-factor models. Variable codes are described in Table 1.

MODEL	QIC	Δ QIC	QIC WT
<i>COVTYPE + TOPO</i>	4287.67	0.00	0.64
<i>COVTYPE * TOPO</i>	4289.70	2.03	0.23
<i>COVTYPE + TOPO</i> ²	4290.92	3.25	0.13
<i>COVTYPE * TOPO</i> ²	4296.55	8.88	0.01
TOPO	4396.74	109.07	0.00
TOPO ²	4396.79	109.12	0.00
COVTYPE	4402.35	114.67	0.00
PCCL	4411.43	123.76	0.00
PSAM	4430.14	142.47	0.00
POC	4444.28	156.61	0.00
SOLAR	4449.49	161.82	0.00
PNON	4454.67	166.99	0.00
PMOD	4482.85	195.18	0.00
WATER	4487.59	199.91	0.00
PCCS	4488.55	200.88	0.00
TE	4519.24	231.57	0.00
EDGE	4522.05	232.34	0.00
SLOPE	4526.84	237.14	0.00
INTERCEPT	4528.05	238.35	0.00

forest types were the only cover types selected consistently by the owls. The model including an interaction between topography and cover type was nearly competitive (Δ QIC = 2.03), but the 95% CIs for the risk ratios for the interaction terms all overlapped 1, suggesting only weak evidence of an interaction between topography and cover type. The Δ QIC values

for models that included distance to water were all >50 QIC units greater than the top models, indicating owls had no tendency to forage near water.

Habitat selected for roosting. The single-factor model including cover type was the most strongly supported model for roosting habitat, receiving almost all of the model weight (Tables 7, 8). The Δ QIC value for the single-factor topography model was 139 units greater than the cover type model, but based on the results from foraging habitat modeling, we evaluated several *post-hoc* models that included various forms of the topography covariate in combination with cover type. The Δ QIC for the best of these *post-hoc* models (cover type*topography) was still 8 units greater than the single-factor cover type model (Table 7), so there was little evidence the owls in this study selected lower slopes for roosting. Owls selected the closed-canopy large-tree cover type most often for roosting (relative risk ratio = 12.8, 95% CI = 6–27), followed by the closed-canopy small-tree cover type (relative risk ratio = 11.0, 95% CI = 5–26). There was little evidence that owls selected any of the other cover types for roosting (relative risk ratios >1 but 95% CIs nearly overlapped 1).

Model validity. Based on the *k-fold* cross validation of our RSF, we found a good fit between the mean observed proportion of use and the mean proportion of use predicted by the model ($R^2 = 0.93$). A χ^2 test of the frequencies of observed vs. predicted locations in each RSF bin did not show a significant lack of fit ($\chi^2_9 = 11.24, P = 0.26$). If owls were not selecting habitat according to our RSF, the slope of the regression line of observed use vs. use predicted

Table 6. Parameter estimates and risk ratios for the top model in the analysis of habitat selected for foraging by radio-marked Northern Spotted Owls (*Strix occidentalis caurina*) on the Cle Elum Study Area, Washington, U.S.A., 1989–1990. Variable codes are described in Table 1.

VARIABLE	MODEL ESTIMATES				RISK RATIOS		
	β	SE	95% CI		ESTIMATE	95% CI	
			LOWER	UPPER		LOWER	UPPER
Intercept	-0.77	0.20	-1.17	-0.37	0.46	0.31	0.69
MOD	0.73	0.23	0.28	1.18	2.07	1.32	3.25
CCL	1.37	0.16	1.05	1.68	3.93	2.86	5.39
CCS	1.27	0.20	0.88	1.65	3.56	2.42	5.23
OC	0.31	0.23	-0.14	0.76	1.36	0.87	2.14
SAM	0.52	0.26	0.00	1.03	1.68	1.00	2.80
NON ^a	0.00	0.00	0.00	0.00	1.00	1.00	1.00
TOPO	-0.02	0.01	-0.04	-0.01	0.98	0.96	0.99

^a Non-forest was used as the reference level for parameterizing models.

Table 7. Model rankings for habitat used for roosting by radio-marked Northern Spotted Owls (*Strix occidentalis caurina*) on the Cle Elum Study Area, Washington, U.S.A., 1989–1990. Models in italics were *post-hoc* models evaluated after single factor models were evaluated. Variable codes are described in Table 1.

MODEL	QIC	Δ QIC	QIC WT
COVTYPE	2455.90	0.00	0.98
<i>COVTYPE * TOPO</i>	2464.24	8.34	0.02
<i>COVTYPE + TOPO</i>	2466.81	10.91	0.00
PCCL	2505.42	49.52	0.00
PNON	2525.25	69.35	0.00
PMOD	2532.64	76.74	0.00
SOLAR	2534.87	78.97	0.00
PSAM	2558.86	102.95	0.00
POC	2560.74	104.84	0.00
PCCS	2571.71	115.80	0.00
WATER	2577.29	121.38	0.00
EDGE	2579.97	124.06	0.00
INTERCEPT	2583.77	127.87	0.00
TE	2586.03	130.13	0.00
SLOPE	2589.86	133.96	0.00
TOPO	2595.21	139.31	0.00

by our RSF would be zero (Johnson et al. 2006). Our regression of observed vs. expected use indicated a nonrandom association between observed and predicted use for RSF bins (β for slope = 0.99, $P < 0.0001$).

Relationships Between Landscape Composition and Home-range Area. The mean amount of the most selected cover types (closed-canopy large tree and closed-canopy small tree) within home ranges of individual owls was 1126 ha (range = 656–1733 ha) for the 95% FK annual range and ac-

counted for 63% of the average home-range area (range = 42–82%, Table 9). Within the 95% FK home range, the amount of selected forest was positively correlated with home-range area ($R^2 = 0.51$, $P = 0.009$ from ANOVA), but the percent cover of selected forest was not ($P = 0.307$). The mean amount of selected forest within the home ranges of pairs of owls was 1509 ha (62%) for the 95% FK annual range.

Difference Between Management Circles and Home Ranges. On average, 2.9-km-radius circles centered on nests included 62% of the annual MCP home range of owl pairs (range = 29–99%, $n = 5$) and 73% of the annual 95% FK home range of owl pairs (range = 59–97%, $n = 5$). On average, the 2.9-km circles included 903 ha that was outside the annual MCP range of each pair (range = 663–1157 ha) and 918 ha that was outside the annual 95% FK home range of each pair (range = 551–1210 ha). Circles contained 40–160% of the area and 88–95% of the proportion of selected forest contained in pair MCP home ranges. To test the overlap of regulatory circles at a landscape level, we joined the 2.9-km-radius circles located in the northern portion of our study, where we had four adjacent overlapping pair home ranges. We then joined together the MCP home ranges of the four pairs and overlaid the combined management circles on the joined polygon. The area within the joined circles overlapped 54% of the area of the joined MCP home-range polygons. The area within the joined circles, but outside the joined home-range polygons, was 2400 ha. Most of the area within the joined MCP polygons that was outside the circles was due to the area used by one male that

Table 8. Parameter estimates and risk ratios for the top model in the analysis of habitat used for roosting by radio-marked Northern Spotted Owls (*Strix occidentalis caurina*) on the Cle Elum Study Area, Washington, U.S.A., 1989–1990. Variable codes are described in Table 1.

VARIABLE	MODEL ESTIMATES				RISK RATIOS		
	β	SE	95% CI		ESTIMATE	95% CI	
			LOWER	UPPER		LOWER	UPPER
Intercept	-3.66	0.38	-4.42	-2.91	0.03	0.01	0.05
MOD	1.15	0.50	0.17	2.13	3.16	1.18	8.44
CCL	2.55	0.38	1.81	3.30	12.85	6.09	27.10
CCS	2.40	0.44	1.53	3.27	11.04	4.63	26.36
OC	1.38	0.57	0.26	2.49	3.96	1.29	12.09
SAM	1.32	0.61	0.14	2.51	3.76	1.15	12.33
NON ^a	0.00	0.00	0.00	0.00	1.00	1.00	1.00

^a Non-forest was used as the reference level for parameterizing models.

Table 9. Percent coverage of different forest types within annual 95% fixed kernel home ranges of radio-marked Northern Spotted Owl (*Strix occidentalis caurina*) individuals and pairs on the Cle Elum Study Area, Washington, U.S.A., 1989–1990.

OWL AND SEX OR OWL PAIR	HOME RANGE (ha)	FOREST TYPES							
		MIXED OLD FOREST	MIXED YOUNG FOREST	MODERATE CANOPY	NON- FOREST	OPEN CANOPY	SOUTH ASPECT MOD	MIXED OLD + MIXED YOUNG	
BC	♀	1256	56	11	14	7	6	8	66
BC	♂	2634	55	11	11	6	6	11	66
DG*	♀	598	36	24	13	13	6	9	59
DG	♂	2030	35	16	17	14	8	11	51
GB	♀	1388	54	26	8	7	1	4	80
HC*	♀	1456	20	22	28	5	11	14	43
HC	♂	2354	21	26	24	8	10	12	47
PB	♀	2211	27	16	17	14	13	14	42
PG	♀	2314	48	10	14	12	6	10	59
PG	♂	1635	46	13	15	9	6	10	59
SB	♀	1347	47	12	14	12	8	8	58
SB	♂	1059	53	8	12	12	6	8	62
TC	♀	1575	58	23	8	5	1	5	82
TC	♂	2168	63	17	6	6	2	6	80
Mean (SE)^a		1831(148)	47(4)	16(2)	13(1)	9(1)	6(1)	9(1)	63(4)
BC pair		2800	54	12	12	6	6	11	65
HC pair		2694	22	25	24	8	10	12	47
PG pair		2453	48	11	14	12	6	10	59
SB pair		1483	49	11	14	11	7	7	60
TC pair		2707	62	17	7	7	2	6	79
Mean (SE)		2427(217)	47(6)	15(2)	14(3)	9(1)	6(1)	9(1)	62(5)

had the largest home range of all the owls in our sample. A repeat analysis of the same pairs based on the 95% FK pair ranges indicated that the combined circles overlapped the combined home ranges of the four pairs of owls by 75%, with an area of 2968 ha within the circles that was outside the combined home-range polygon (Fig. 3).

DISCUSSION

Median annual MCP home ranges of individual owls in our study were 42% larger than those reported for Oregon, but 33% smaller than those reported for the Olympic Peninsula in Washington, and 42% smaller than on the Yakama Indian Nation in Washington. Although these comparisons are somewhat confounded by differences in tracking periods, it appears that annual home ranges of Spotted Owls are larger in areas where the northern flying squirrel (*Glaucomys sabrinus*) is the primary food source than in areas where woodrats (*Neotoma* spp.) predominate in the diet (Carey et al. 1992, Zabel et al. 1992). This relationship is likely due

to regional differences in densities or biomass of flying squirrels and woodrats in the diet of owls (Carey et al. 1992, Forsman et al. 2001, 2004, Lehmkühl et al. 2006a, 2006b).

As in most other studies of Spotted Owls (and many other raptors) we found that winter ranges were larger than breeding season home ranges, regardless of whether owls were breeding or not (Forsman et al. 1984, 2005, Hamer et al. 2007, Wiens 2012). This likely occurs because selection favors individuals that reduce the depletion of prey within their breeding ranges by expanding their ranges and foraging elsewhere during winter. Carey et al. (1992) suggested that prey became locally depleted near Spotted Owl nest areas and heavily used roost areas, and that owls rested these areas in winter by foraging further from areas that were heavily used during the breeding season. It is also possible that expansion of home ranges during fall and winter is a form of prospecting, whereby territory holders familiarize themselves with adjacent territories and test for opportunities to acquire better territories or

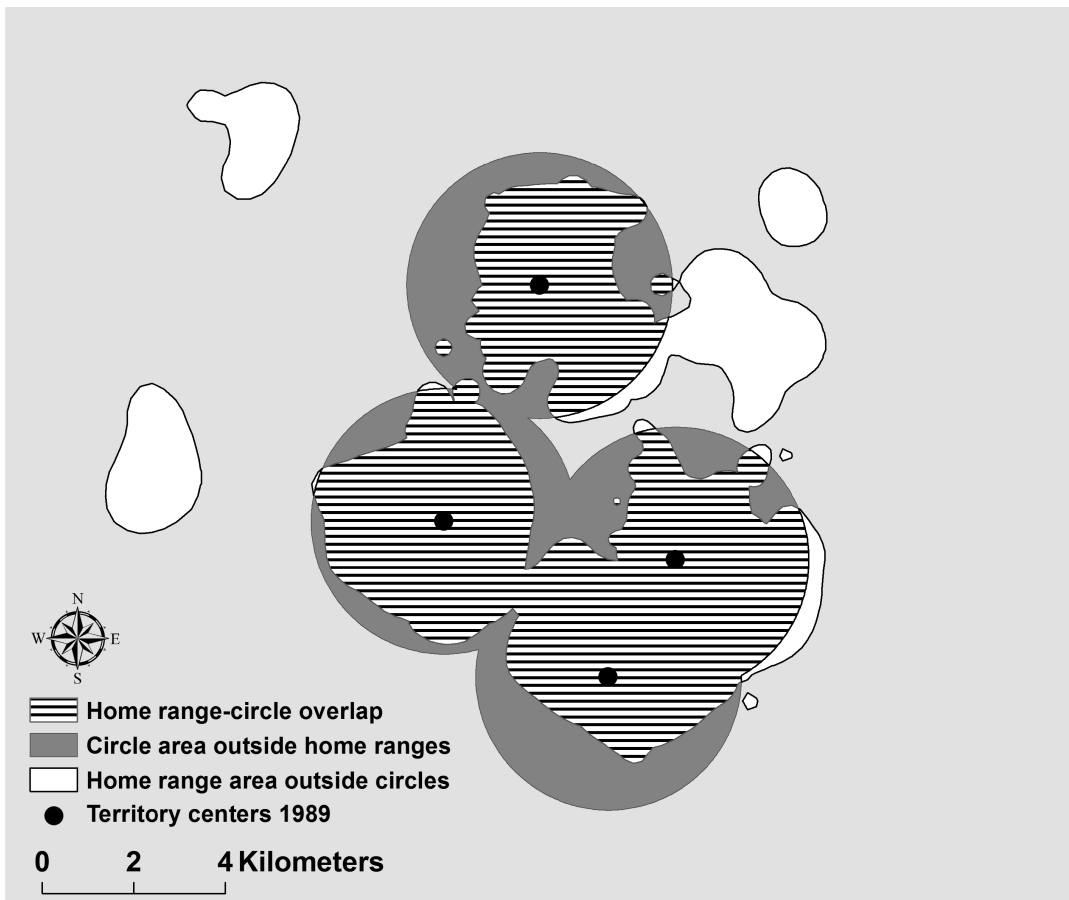


Figure 3. Overlap between 95% fixed kernel home ranges of four pairs of radio-marked Northern Spotted Owls (*Strix occidentalis caurina*), and 2.9-km-radius circles centered on the territory centers, Cle Elum Study Area, Washington, U.S.A., 1989–1990.

mates. The winter portion of an owl's home range may thus be an extremely important component of its life history, and should be carefully considered when developing management recommendations (Buchanan et al. 1998 and see below).

Average overlap of MCP home ranges of pair members was slightly greater in the breeding season than in the winter (69% vs. 59%). This was expected because paired owls were necessarily confined to the nest area during the breeding season at least in years when they nested. Overlap of seasonal MCP home ranges was slightly less for adjacent males than adjacent females during the breeding and winter seasons, but was similar for both sexes based on annual MCP home ranges. Likewise, the probability of finding an adult male within the 95% FK home range of an adjacent male was slightly less than the

probability of finding a female in the range of an adjacent female, especially during winter (male = 0.16, female = 0.24). It was unclear if this was because males were less tolerant of adjacent males or was because males vocalized more often in winter than females and thus were more likely to be detected by adjacent males. Our estimate of the average overlap between MCP home ranges of adjacent owls (approximately 15%) was similar to home-range overlap noted in several other studies of Spotted Owls. For example, the average overlap of home ranges of Spotted Owls on adjacent territories was 12% on one study in Oregon (Forsman et al. 1984), 15% and 7% on two other study areas in Oregon (Glenn et al. 2004), and approximately 24% on the Olympic Peninsula in Washington (Forsman et al. 2005). These overlap estimates were not directly

comparable because of methodological differences, but do support the notion that home ranges of Spotted Owls are too large to be consistently defended. Instead, the owls seem to space themselves far enough apart to ensure a low level of territorial interactions with their neighbors, with territorial boundaries that are poorly defined and inconsistently defended (Forsman 1980). Thus, the classic notion of a consistently defended territory does not apply to Spotted Owls. Instead, they occupy territories with ill-defined boundaries and broad areas of overlap that are "... contested occasionally by all parties, but defended consistently by none" (Forsman 1980:46).

Our estimates of annual ranges are probably smaller than would be obtained by multiple years of tracking, because cumulative ranges based on the union of multiple annual ranges typically grow larger with time (Carey et al. 1992). We do not view this as a problem but we do want to emphasize it so that managers are aware that pairs of owls that are observed over many years are likely to use cumulative ranges that are, in some cases, much larger than the annual ranges described here.

Subsequent to our radiotelemetry study, we detected three additional Spotted Owl pairs that we believe were present when we conducted our study. The presence of these previously unknown owls probably influenced the area and shape of home ranges and habitat use of the owls in our study. Likewise, we had some data on the distribution of Barred Owls within our study area (Forsman et al. 2011), but we were unable to determine the extent that the Barred Owls influenced the behavior of our radio-marked Spotted Owls. A large amount of quantitative evidence accumulated in recent years suggests that Spotted Owls alter their behavior in the presence of Barred Owls (Kelly et al. 2003, Olson et al. 2005, Crozier et al. 2006, Dugger et al. 2011, Wiens 2012, Wiens et al. 2014). Thus, it is probable that the home ranges and habitat use of the Spotted Owls that we observed could have been influenced by competition with Barred Owls as has been shown in other areas (Wiens et al. 2014). This is likely to be a confounding factor in all future studies of space use by Northern Spotted Owls, because Barred Owls are now present in large numbers in most of the range of the Northern Spotted Owl (Forsman et al. 2011, Wiens et al. 2014).

Habitat Selection. Our best model for foraging habitat suggested that owls selected forests with closed canopies (closed-canopy large-tree and

closed-canopy small-tree categories) at lower topographic positions. The ranking of cover types in our best model for foraging habitat suggested that owls selected stands in a continuum from open-canopy (least selected) to closed-canopy stands (most selected). And among closed-canopy stands, those containing a large-tree component were the most selected. These stands often had components that contributed to structural complexity or prey density that are difficult to represent in remotely sensed data such as aerial photo interpretation. Lehmkuhl et al. (2006a, 2006b) found that understory plant species richness, truffle biomass, lichen biomass, presence of large snags, dwarf mistletoe (*Arceuthobium* spp.) brooms, and decayed downed logs were important habitat attributes for northern flying squirrels and/or bushy-tailed woodrats, which were the primary prey species for the owls we studied (Forsman et al. 2001). We suspect the strength of selection for the closed-canopy large-tree cover type for foraging would have been greater had we been able to integrate the above structural features into our habitat maps and hence into our modeling. Unfortunately, collecting structural vegetation data at this fine scale was beyond the scope of our study. Recent developments in Gradient Nearest Neighbor (GNN) GIS modeling hold some promise for integrating fine-scale vegetation attributes into landscape scale analyses, but GNN data need to be applied at the appropriate scale and for the appropriate management goal (Ohmann and Gregory 2002, Pierce et al. 2009).

Regardless of cover type, owls selected areas lower on the slope for foraging, a finding that was in agreement with a few other studies that reported that Spotted Owls foraged lower on slopes than expected (e.g., McDonald et al. 2006, Wiens 2012). In our study area, we suspect that selection for areas lower on the slope may be partly due to differences in cover types that are the result of topography. Forests that are lower on the slope tend to have larger trees and denser canopies than forests on ridges. This could explain why the model that included both cover type and topography best explained our results in the foraging analysis. Although our distance to water and topography covariates were somewhat correlated, distance to water was not a good predictor of habitat selection for foraging. This was not entirely surprising given that some previous studies of Spotted Owls have found nest or foraging locations were closer to water than expected, (Folliard et al. 2000, Loehle et al. 2011),

whereas other studies have not (Forsman et al. 2005).

Our analysis indicated that closed-canopy forest types (closed-canopy large-tree and closed-canopy small-tree) were selected for roosting over the other cover types (open canopy, moderate canopy, and south-aspect moderate). Risk ratios for the closed-canopy large-tree and closed-canopy small-tree cover type classes were much greater in the analysis of roosting habitat than in the analysis of foraging habitat, indicating that selection for the closed-canopy forests types was even stronger for roosting than for foraging. This result was consistent with Forsman et al. (1984) and Wiens (2012), who found that Spotted Owl selection for old forests or dense stands was stronger for roosting than it was for foraging. Topographic position did not appear in a competing model with cover type for roosting habitat (ΔQIC approximately equal to 8). The fact that owls on our study area selected open-canopy stands or south-facing stands only slightly more strongly than non-habitat suggested that forests with open canopies were poor roosting habitat.

Barrows (1981) and Forsman et al. (1984) suggested that Spotted Owls selected old forests with high canopy closure for roosting because those forest types provided the owls with hiding cover from predators and also provided better protection from rain, snow, and high summer temperatures. We did not evaluate roost attributes relative to weather conditions or escape cover, but our results certainly suggest that owls on our study area may have been selecting roosts based on the same considerations proposed by Barrows (1981) and Forsman et al. (1984).

In our analysis, open-canopy forests on south aspects were not selected much differently than open-canopy mixed-conifer forests. This suggested that canopy cover was more important than species composition. We concluded, therefore, that for landscape scale assessments of habitat quality, open-canopy cover types could be lumped together as poor quality habitat for Spotted Owls on our study area.

Management Implications. The owls that we radio-marked were included in a long-term demography study in which Anthony et al. (2006) and Forsman et al. (2011) estimated survival, reproduction, population growth rate, and recruitment of Spotted Owls in 1992–2008. Results from those studies indicated that the owl population in our study area has declined significantly since our radiotelemetry study was conducted in 1989–1990 (Forsman et al.

2011). This decline is likely due to a combination of habitat loss and the gradual invasion of our study area by Barred Owls, which have become common on the study area in the past 50 yr (Kelly et al. 2003, Livezey 2009, Forsman et al. 2011). In the face of competition with Barred Owls, we think that habitat protection for Spotted Owls continues to be the single most important factor that land managers can control to the benefit of Spotted Owls. Because Barred Owls and Spotted Owls appear to select similar forest types (Singleton et al. 2010, Wiens et al. 2014), protecting Spotted Owl habitat may be even more important now than when our data were collected.

The prevailing management paradigm for forests in the eastern Cascades of Washington and Oregon is to attempt to increase the resilience of forests to insects and fire, primarily with the use of thinning and prescribed fire (e.g., Franklin et al. 2008, U.S.D.A. 2010). In the recently released final recovery plan for the Spotted Owl in the eastern Cascades province (U.S.F.W.S. 2011), the proposed focus for recovery was shifted from the reserve strategy espoused in the Northwest Forest Plan (U.S.D.A. and U.S.D.I. 1994b) to a strategy that would maintain a certain proportion of Spotted Owl habitat in a shifting mosaic across the landscape. This shift in strategy on behalf of the U.S.F.W.S. was due in part to concerns that a reserve system was not sustainable in dry eastern Cascade forests (Agee and Edmonds 1992, Courtney et al. 2004, Spies et al. 2006). In theory, opportunities for management of forests to achieve restoration goals and maintain Spotted Owl habitat do exist (Gaines et al. 2010). However, the recent dramatic population decline of Spotted Owls on the eastern slope of the Cascades in Washington (Forsman et al. 2011) would argue for a conservative approach to managing existing Spotted Owl habitat, as is advocated in the final recovery plan (U.S.F.W.S. 2011). A conservative approach is especially warranted due to the uncertain effects that management strategies such as prescribed fire and thinning will have on Spotted Owls and their prey (Tiedemann et al. 2000), and uncertainty regarding assumptions used to develop the management strategies (Hanson et al. 2009, Spies et al. 2009). Lehmkuhl et al. (2007) presented an approach to modeling Spotted Owl habitat and accomplishing forest restoration goals, but it remains to be seen if this approach will work considering the dramatic decline of the Spotted Owl population in recent years. It is clear that Spotted Owl habitat is at risk

from fire, as was evidenced by recent large fires that burned portions of our study area in 2012 and 2014.

Our analysis of 2.9-km-radius circles as a proxy for Spotted Owl home ranges indicated that home ranges of pairs of Spotted Owls typically contained more selected forest habitat than would be protected if landowners followed the 2006 Washington State Forest Practices Board Rules. Those rules called for protection of 40% cover of suitable habitat within a 2.9-km-radius circle around nest sites (WAC 222-10-041). We suggest, therefore, that managers may want to consider changing the current forest practices rules to increase the amount of habitat protected around sites occupied by Spotted Owls. In our study area, one approach might be to manage for the mean or median amount of selected habitat within a typical 95% FK pair home range (1505 or 1456 ha, respectively). This would increase the amount of habitat retained within the 2.9-km-radius circle from 40% to 55–57%. Another alternative would be to manage for more than the mean or median amount of selected habitat. Although our analysis demonstrated that management circles could be a relatively poor representation of actual home ranges used by Spotted Owls, we see no easily applicable alternative to management circles, because the use of radiotelemetry to determine actual ranges of owls on every site would be counterproductive, both in terms of cost, and the potential negative effects on survival and reproduction of the owls (Paton et al. 1991, Foster et al. 1992).

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