HOME RANGE AND HABITAT USE OF NORTHERN SPOTTED OWLS ON THE OLYMPIC PENINSULA, WASHINGTON

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ABSTRACT.—We studied movements and habitat selection of 20 adult northern Spotted Owls (*Strix occidentalis caurina*) on the Olympic Peninsula, Washington in 1987–89. Median annual home range size of individual owls was 1147 ha based on the 75% isopleth of the Fixed Kernel (FK), 2406 ha based on the 95% FK, and 2290 ha based on the 100% Minimum Convex Polygon (MCP). Annual ranges of individual owls tracked >1 yr overlapped by a mean of 70–73%, depending on which estimator was used. Size of annual and cumulative ranges was negatively correlated with the amount of old forest within the cumulative MCP home range and within a 4.3 km radius of the center of activity. Overlap of annual ranges of owls that were paired averaged 64 ± 5% based on the MCP and 69 ± 5% based on the 95% FK. On average, ranges used during the nonbreeding season overlapped breeding season ranges by 65.0 ± 4.5%, and breeding season ranges overlapped nonbreeding season ranges by 62.6 ± 4.9%. Compositional analysis of habitat selection indicated that old forests were the most preferred cover type for foraging and roosting and that clear-cuts and non-forest cover types were rarely used. There was little evidence that owls selected riparian areas or forest edges for foraging or roosting. Our observations are consistent with the hypotheses that northern Spotted Owls use larger foraging areas in regions where northern flying squirrels (*Glaucomys sabrinus*) are their primary source of food, that they prefer old forests for foraging and roosting, and that their home ranges become larger as the amount of old forest declines. The large size of annual ranges on the Olympic Peninsula may be a response to low prey biomass.

KEY WORDS: *Northern Spotted Owl; Strix occidentalis caurina; home range; habitat use; radiotelemetry; Olympic Peninsula; Washington.*

RANGO DE HOGAR Y USO DE HÁBITAT DE *STRIX OCCIDENTALIS CAURINA* EN OLYMPIC PENINSULA, WASHINGTON

RESUMEN.—Estudiamos los movimientos y la selección de hábitat de 20 individuos adultos de *Strix occidentalis caurina* en Olympic Peninsula, Washington, entre 1987 y 1989. La mediana del tamaño del área de hogar de un individuo fue de 1147 ha basada en la isolínea de 75% del kernel fijo (KF), 2406 ha basada en el 95% KF y 2290 ha basada en el 100% del polígono convexo mínimo (PCM). Los rangos anuales de los individuos seguidos por menos de un año se superpusieron en promedio entre un 70% y un 73%, dependiendo del estimador que usamos. Los tamaños de los rangos anuales y acumulativos se correlacionaron negativamente con la cantidad de bosque maduro presente dentro del PCM acumulativo del rango de hogar y a menos de 4.3 km del centro de actividad. La superposición promedio de los rangos de hogar anuales de individuos que conformaban parejas fue de 64 ± 5% basado en el PCM y 69 ± 5% basado en el 95% del KF. En promedio, los rangos usados durante el período no reproductivo se superpusieron con los rangos del período reproductivo en 65.0 ± 4.5%, y los rangos del período reproductivo se superpusieron con los rangos del período no reproductivo en 62.6 ± 4.9%.

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Los análisis de composición de los ambientes seleccionados indicaron que los bosques maduros fueron el tipo de cobertura preferida para alimentarse y reposar, mientras que las áreas completamente taladas y no boscosas fueron usadas en muy pocas ocasiones. Encontramos muy poca evidencia de que las lechuzas seleccionan las áreas riparias o los bordes de bosque para alimentarse o reposar. Nuestras observaciones son consistentes con la hipótesis de que *S. o. caurina* usa grandes áreas de forrajeo en las regiones donde las ardillas voladoras (*Glaucomys sabrinus*) son su fuente principal de alimento, que prefieren bosques maduros para alimentarse y reposar y que sus áreas de hogar aumentan a medida que disminuye la cantidad de bosque maduro. El gran tamaño de los rangos anuales en Olympic Peninsula podría responder a una baja biomasa de presas.

[Traducción del equipo editorial]

Spotted Owls (*Strix occidentalis*) exhibit considerable variation in home range size and patterns of seasonal movements, both within and among regions. For example, in some parts of their range, Spotted Owls may migrate during winter, moving 16–58 km from their breeding season ranges into lowland forests (Laymon 1989, Zabel et al. 1992). In other regions, they are largely resident in the same areas throughout the year (Forsman et al. 1984, Carey et al. 1990, 1992).

Home ranges and habitat selection of Spotted Owls have been studied extensively in Oregon and California, but with the exception of a study by Hamer (1988), little information is available from Washington. We examined home ranges and habitat selection of northern Spotted Owls on the Olympic Peninsula, Washington to determine if patterns of habitat use differed near the northern edge of the range of the owl compared to earlier studies conducted in Oregon (e.g., Forsman et al. 1984, Carey et al. 1990, 1992, Carey and Peeler 1995) and northern California (Solis and Gutiérrez 1990, Zabel et al. 1992, 1995).

STUDY AREA

We conducted our study on two areas on the west side of the Olympic Peninsula, one located 3 km SE of the town of Forks, Clallam County, and the other located 10 km SE of the town of Quinault, Jefferson County (Fig. 1). Both areas were located on the Olympic National Forest, had similar climate, topography and vegetation, and will hereafter be referred to collectively as the "study area."

The study area was characterized by mountainous terrain covered by forests of western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*). Sitka spruce (*Picea sitchensis*) was common on mesic, low elevation areas, and Douglas-fir (*Pseudotsuga menziesii*) and Pacific silver fir (*Abies amabilis*) were often intermixed with western hemlock on upland sites (Henderson et al. 1986). Elevations ranged from 150–1500 m. Precipitation ranged from 280–460 cm/yr, mostly falling as rain during October–May.

The area included a mosaic of seral stages, ranging from clearings in which all trees had been recently har-

vested (clear-cuts) to old-growth forests in which overstory trees were over 500 yr old (Henderson et al. 1986). Approximately half of the area had been clear-cut within the previous 30 yr, but harvested areas were not uniformly distributed within the study area. Some areas were heavily fragmented by recent clear-cuts, whereas other areas had extensive blocks of mature and old-growth forest. Much of the study area was hit by hurricane-force winds in 1921 which severely damaged many stands (Pierce 1921). As a result, many stands included a mixture of 60–80-yr-old trees that regenerated after the wind event, interspersed with old trees (80–500+ yr) that survived the windstorm. All types of natural (unlogged) forest typically had high canopy closure (65–80%), high variation in tree size and age, and high volumes of logs and snags (Henderson et al. 1986). Regenerating stands of young trees in clear-cut areas were usually even-aged, with high canopy closure.

METHODS

Capture and Radio-marking. We captured owls with noose poles (Forsman 1983) and marked them with back-pack transmitters (Model P2, AVM Instrument Company, Livermore, CA U.S.A.), as described by Forsman et al. (1984). Total mass of transmitter and harness was 18–20 g, and transmitter life was 9–15 mo. We tried to obtain a minimum of 12 mo of data from each owl. We replaced transmitters on six individuals after 9–12 mo, and tracked them for nearly 2 yr.

Sampling Schedule. We attempted to obtain one nocturnal foraging location per night on each owl at least 3 nights per wk, and one diurnal roost location per owl at least 3 d per wk. Our sampling schedule was intended to reduce autocorrelation between sequential locations (Swihart and Slade 1985a, 1985b). However, Aebischer et al. (1993) and Otis and White (1999) have suggested that autocorrelation is generally irrelevant when individual animals are used as the sample unit in home-range studies, so we used all of our data, including a few cases (129 of 7346 locations) when we obtained 2–3 locations on the same owl in one night. We classified all locations as foraging locations if they occurred from 0.5 hr after sunset to 0.5 hr before sunrise. We excluded locations of incubating or brooding females from analyses of habitat selection, until females began to forage when the young were about 2 wk old.

Radio Triangulation. We estimated owl locations by triangulating with a Telonics hand-held H-antenna and TR2 receiver (Telonics, Mesa, AZ U.S.A.). We used a hand-held compass to estimate azimuths from ≥3 locations
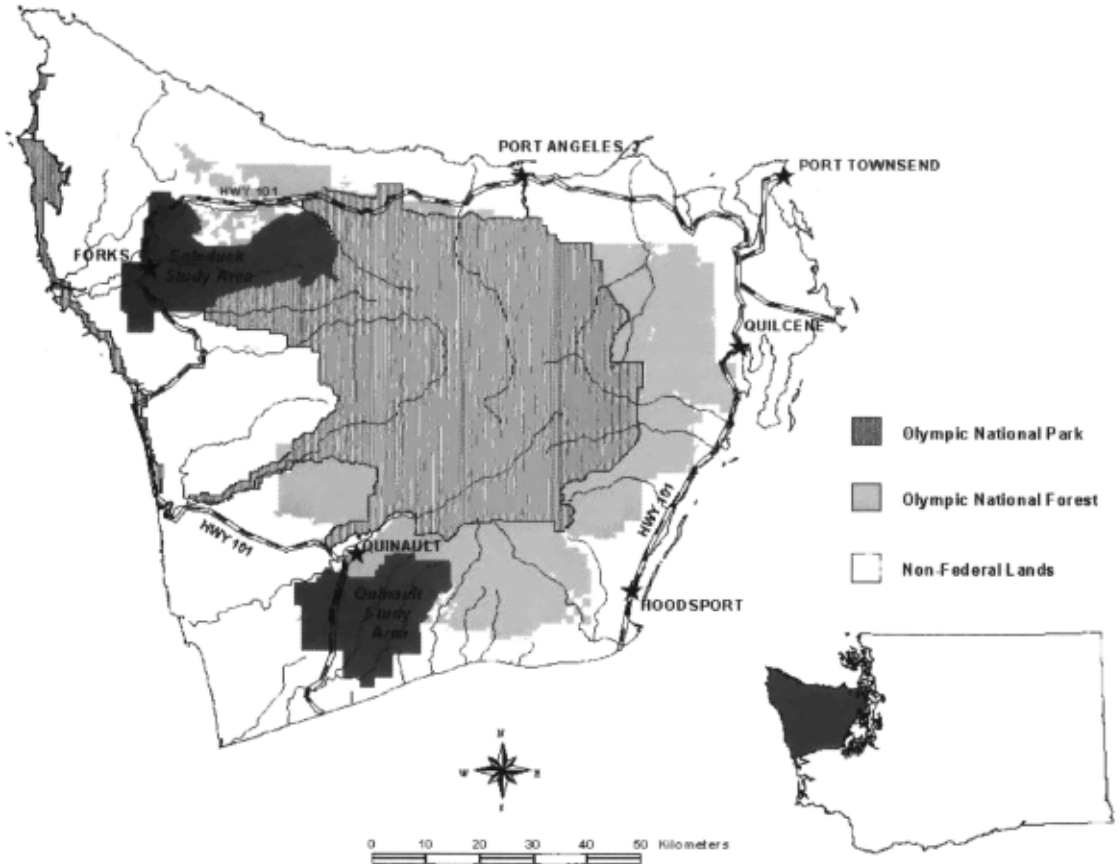
Figure 1.   Location of radiotelemetry study areas on the Olympic Peninsula, Washington, 1987–89.

along roads (Guetterman et al. 1991). Azimuths were plotted on 1:12 000 or 1:24 000 scale U.S. Geological Survey orthophotos or topographic maps. We considered the position of the owl to be the geometric center of the polygon formed by the intersection of ≥3 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. We used all locations to estimate home ranges, but only locations with error polygons ≤8 ha were used for analyses of habitat use.

Telemetry Error. We estimated telemetry error with 63 blind trials in which one observer placed transmitters in trees in owl home ranges and another observer then triangulated on the transmitters at night. The median distance between estimated and actual transmitter locations was 100 m ($\bar{x} = 140 \pm 17$ m). This estimate was similar to or less than error estimates in previous telemetry studies of Spotted Owls (Carey et al. 1990, Glenn et al. 2004). Errors of this magnitude undoubtedly resulted in some locations 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 should reflect actual habitat use.

Home-range Estimation. We estimated cumulative and annual ranges with the Minimum Convex Polygon (MCP) and Fixed-Kernel (FK) methods (Hayne 1949, Seaman and Powell 1996). For estimates of MCP ranges, we used 100% MCP polygons. For FK estimates, we used 95% and 75% isopleths, which we interpreted as the "home range," and "area of concentrated use," respectively. We used Program CALHOME (Kie et al. 1996) to estimate MCP ranges and Version 4.28 of Program KERNELHR (Seaman et al. 1998) to estimate FK ranges. Contrary to the recommendation of Seaman and Powell (1996), we used the FK method without least-squares-cross-validation (LSCV). We did so because we believe that kernel estimates based on locations where owls stop long enough for the observer to obtain a location tend to underestimate home range areas of owls (because movements across intervening non-forest areas usually happen so quickly that they cannot be documented with a point on the map). Thus, we feel that the LSCV option, which tends to fit the home range isopleth more tightly to the observed points, is likely to cause an even greater underestimate of home ranges. We used all locations for MCP estimates, but we only used foraging locations for FK estimates (because FK estimates that include large

Table 1. Vegetation cover types used to map landscapes for analyses of habitat use by northern Spotted Owls on the Olympic Peninsula, Washington, 1987–89.

Old Forest: Multilayered stands of western hemlock and western redcedar in which the dominant overstory trees were typically ≥100 cm DBH. Pacific silver fir was often subdominant or codominant with hemlock or redcedar. Douglas-fir was codominant on a few areas. Also included mixed-age stands of mature and old forest in which both age classes were common. Many of the latter stands were the result of a hurricane force windstorm in January 1921 (Pierce 1921).

Mature Forest: Conifer-dominated stands in which the overstory trees were typically 50–99 cm DBH.

Young Forest: Relatively even-aged stands in which most trees were 31–60 cm DBH. Regenerated on burned areas and old clear-cuts.

Mixed-young Forest: Same as Young Forest except with inclusions of mature trees, usually remnants left during previous fires or harvest.

Pole-sapling: Single-layered conifer stands in which most trees were 10–30 cm DBH. Mostly young stands regenerating on old clear-cuts.

Hardwood/Riparian: Riparian areas dominated by red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*), and variable amounts of western redcedar.

Clear-cut/Non-forest: Recent clear-cuts dominated by bare soil, grasses, shrubs or small seedling conifers. Also included small areas of meadows, gravel pits, and agricultural, or residential areas.

numbers of roosting locations clustered at the nest site or central place will underestimate foraging areas during the breeding season).

Estimation of Annual, Cumulative, and Seasonal Ranges. Although we marked some owls in June or July of 1987, we did not begin regular sampling of most individuals until late July or August 1987. For these owls, we estimated the first annual range through the end of July 1988. If they were monitored after July 1988, we computed a second annual range for the second year. A few individuals were not marked until fall 1987 or summer 1988, in which case the annual range was estimated for one year only. There was only a weak positive correlation between the number of days in the tracking period and estimates of annual home-range size, regardless of which home range estimator was used (95% FK $r_{32} = 0.221$, $P = 0.223$; MCP $r_{32} = 0.208$, $P = 0.253$). Therefore, we used all annual ranges for comparisons among owls, regardless of the monitoring period.

For six owls tracked in both years, we estimated the cumulative range from the union of the annual ranges (range A + range B minus the area of overlap). Estimates of home range overlap between years, seasons, pair members, or owls on adjacent territories were based on the percent of range A overlaid by range B or the percent of range B overlaid by range A. In most cases, we computed overlap of ranges based on three different frames of reference (75% FK, 95% FK, and 100% MCP). For estimates of overlap of seasonal ranges, we only used the 95% FK.

For seasonal analysis of home ranges, we divided each year into two phenological periods, the "breeding season" (March–August), when Spotted Owls nest and feed young, and the "nonbreeding season" (September–February), when Spotted Owls are largely solitary. Estimates of seasonal ranges were limited to owls tracked ≥120 d during the season of interest.

Habitat Mapping and Assessment of Habitat Use. We examined second-order habitat selection (i.e., use of different forest cover types within the home range of each

owl). We developed a cover-type map of the study area that included seven cover types based on structural differences in vegetation as determined from on-the-ground examination of stands and aerial photo interpretation (Table 1). We visited virtually all stands within the study area on one or more occasions to determine the size and species composition of trees. We did not use canopy closure to differentiate among cover types because nearly all forests on the study area had relatively high (≥70%) canopy closure, regardless of stand age or tree size. Cover types were mapped on 1:12 000 scale orthophotos and digitized into an ARC/INFO (ESRI Inc., Redlands, CA U.S.A.) GIS layer. For convenience, we use the term cover type, even though we recognize that our designation of cover type was based on only one component of habitat (i.e., vegetation structure). Site visits to 403 randomly selected grid coordinates indicated that map accuracy was 83%.

We used compositional analysis (Aebischer et al. 1993) to evaluate relative preference of cover types for foraging and roosting. This method treats the individual as the sample unit, accounts for lack of independence among proportions, is not sensitive to serial correlation between locations, and is based on a unique set of observed and expected values for each cover type in the home range of each individual. Expected use was equal to the proportion of the cumulative MCP home range covered by each cover type, and the observed use was the proportion of locations in each cover type. We used Program RSW (Leban 1999) to conduct the analysis. Results of this analysis included a numeric ranking of the different cover types according to their relative "preference," as well as a table of pair-wise comparisons (*t*-tests) indicating the degree to which preference differed between types.

We used paired *t*-tests to determine if the distribution of foraging or roosting locations differed from random locations relative to elevation, distance to the nearest stream, or distance to the nearest open area (clear-cuts/non-forest in Table 1). For these analyses, we computed
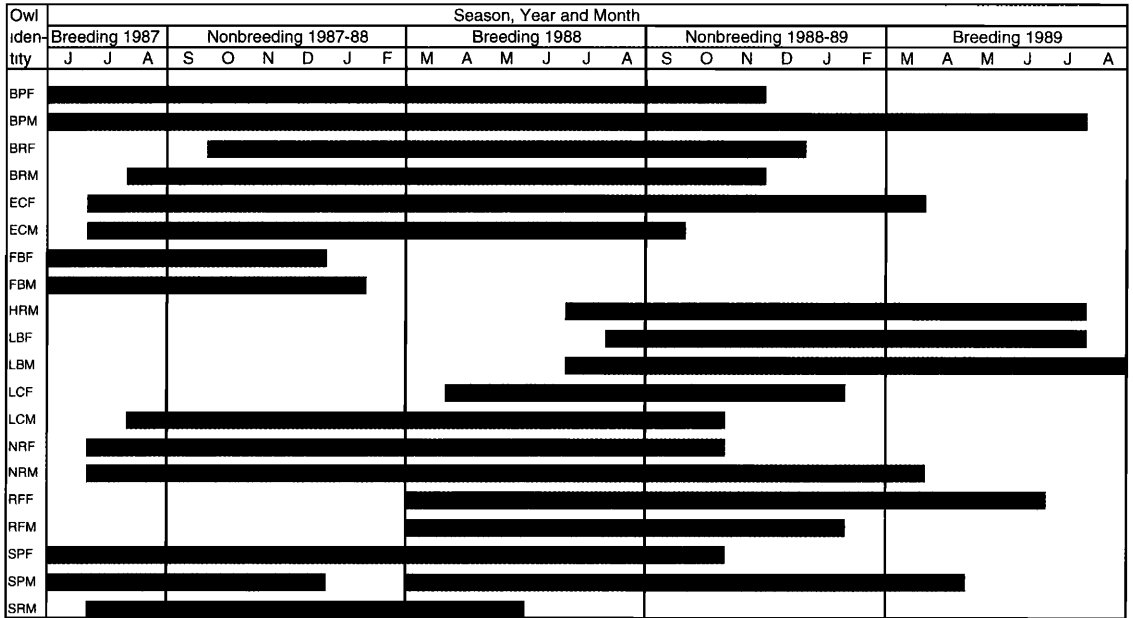
Figure 2. Observation periods of 20 radio-marked northern Spotted Owls observed on the Olympic Peninsula, Washington, 1987–89. Vertical lines indicate intervals used for calculation of seasonal ranges.

mean expected values from a random sample of 200 locations in forest areas in the 100% MCP home range of each owl. We used digital stream layers and elevation layers in GIS to compute elevation and distance to the nearest stream for each owl location and each random location.

Based on a preliminary analysis of our data, the Washington State Forest Practices Board (1996) adopted land management guidelines in which they stipulated that land managers should maintain a minimum of 5863 acres (2372 ha) of "suitable habitat" within a 4.3-km radius around Spotted Owl site centers (known or suspected nest areas) on the Olympic Peninsula. To evaluate the amount of protection afforded by these guidelines, we examined the proportion of each cumulative owl home range that fell within a 4.3-km radius of the nest area or main roost area of each owl, and we compared median and mean areas of "suitable habitat" in cumulative owl ranges with the target in the Forest Practices Rules. All means are expressed as $\bar{x} \pm 1$ SE.

RESULTS

Sample Size and Tracking Periods. We monitored 22 owls in 12 territories, including 10 resident pairs, one territory where we marked one member of a resident pair, and one territory where we marked an adult female that did not appear to have a mate. We did not use the data from the unpaired adult female because she did not exhibit site fidelity. We also did not use data from one female that died shortly after she was radio-marked.

Of the 11 pairs in which one or both members were radio-marked, three nested during the study, including one pair in 1987 and two pairs in 1988.

On average, we tracked individual owls for 438 $\pm$ 34 d (range = 166–711 d; Fig. 2). Total relocations per owl, not counting incubation locations, averaged 366 $\pm$ 35 (range = 126–685). Of 3262 roost locations, we estimated 2360 (72%) by triangulation and located 902 (28%) by homing in on transmitters to locate owls visually in their roost trees.

Annual Ranges. Median estimates of annual ranges of individual owls were 1147 ha (75% FK), 2406 ha (95% FK), and 2290 ha (100% MCP; Table 2). Most mean estimates of ranges were larger than medians because means were skewed by a few individuals with large ranges (Table 2). All owls with annual MCP or FK ranges >5000 ha were individuals that expanded their ranges substantially during fall and winter. Annual ranges were smaller for females than for males, with the exception of the 75% FK estimate (Table 2). In six cases in which we monitored owls for two yr, the sequential annual ranges overlapped by 70 $\pm$ 6% based on the 75% FK (range = 18–100%), 73 $\pm$ 5% based on the 95% FK (range = 27–100%), and 73 $\pm$ 4% based on the MCP (range = 38–100%).

Table 2. Estimates of annual home-range areas of individual northern Spotted Owls on the Olympic Peninsula, Washington, 1987–89. Estimates include the 100% minimum convex polygon (MCP) and the 75% and 95% isopleths of the Fixed Kernel (FK).

OWL, SEX, AND YEAR[a]	NUMBER OF DAYS AND NUMBER OF LOCATIONS IN SAMPLE PERIOD[b]			HOME RANGE ESTIMATES (ha)		
	DAYS	ROOST LOCATIONS	FORAGE LOCATIONS	75% FK	95% FK	100% MCP
BPF87	410	160	191	771	1696	1779
BPF88	116	66	70	2209	4196	3295
BPM87	386	147	180	1935	4865	6122
BPM88	325	144	145	3106	8469	8351
BRF87	302	51	136	415	1189	1402
BRF88	142	39	58	804	1720	1151
BRM87	373	52	172	532	1172	1367
BRM88	123	26	37	530	1045	683
ECF87	354	72	129	7927	15212	10704
ECF88	276	100	128	1404	4207	6668
ECM87	370	68	159	1108	2104	1917
ECM88	65	55	62	982	1876	1294
FBF87	166	73	79	1586	3483	3086
FBM87	206	99	106	1202	2411	2230
HRM88	366	201	186	2465	6924	7954
LBF88	345	137	143	2195	4931	4950
LBM88	391	168	184	1513	3232	3288
LCF88	246	65	109	967	2235	1915
LCM87	354	45	140	678	1504	2000
LCM88	94	23	42	509	1074	894
NRF87	387	133	174	734	1786	2350
NRF88	95	58	58	2597	5795	4537
NRF88	95	58	58	2597	5795	4537
NRM87	387	165	210	1186	3084	4284
NRM88	274	153	157	5003	11558	11252
RFF88	348	208	190	980	2092	2235
RFF89	114	50	44	554	1294	975
RFM88	309	152	144	2516	7059	6704
SPF87	396	154	169	468	1115	1323
SPF88	86	48	55	1228	2402	1406
SPM87	396	154	167	568	1583	1861
SPM88	247	151	142	1072	2533	3593
SRM87	314	34	92	2817	5693	3879
Mean				1642	3736	3608
Median				1147	2406	2290
Mean ♀[c]				1656	3557	3185
Mean ♂[d]				1631	3893	3981
Median ♀[c]				967	2235	1915
Median ♂[d]				1186	2533	3288

[a] First two letters indicate owl name, third letter indicates sex of owl, and numbers indicate year of estimate.
[b] Total locations for NRF87 and SPF87 also included 63 and 76 incubation locations, respectively.
[c] $N = 16$ owl years.
[d] $N = 17$ owl years.

Table 3. Estimates of the cumulative home-range areas of northern Spotted Owls on the Olympic Peninsula, Washington, 1987–89. Estimates include the 100% minimum convex polygon (MCP) and the 75% and 95% isopleths of the Fixed Kernal (FK) estimator.

OWL CODE NAME, SEX	NUMBER OF DAYS AND NUMBER OF LOCATIONS IN SAMPLE PERIOD			HOME RANGE ESTIMATES (ha)		
	DAYS	ROOST LOCATIONS	FORAGE LOCATIONS	75% FK	95% FK	100% MCP
BPF	526	226	261	2216	4303	3527
BPM	711	291	325	3235	8521	8715
BRF	444	90	194	804	1746	1562
BRM	496	78	209	645	1281	1372
ECF	630	172	257	7927	15212	10916
ECM	435	134	221	1215	2166	1932
LCM	449	68	182	845	1636	2026
NRF[a]	482	191	232	2580	5995	4852
NRM	661	318	367	5003	11561	11252
RFF	462	258	234	985	2164	2298
SPF[a]	482	202	224	1230	2436	1831
SPM	643	305	309	1090	2643	3716
Mean[b]				2315	4972	4500
Median[b]				1222	2539	2912
Mean ♀[c]				2624	5309	4164
Mean ♂[c]				2006	4635	4836
Median ♀[c]				1173	3384	2912
Median ♂[c]				1152	2404	2870

[a] Total locations for NRF and SPF also included 62 and 76 incubation locations, respectively.
[b] $N = 12$.
[c] $N = 6$.

Overlap of annual ranges of nine owls of the same sex that occupied adjacent territories averaged 5 ± 2% for the 75% FK (range = 0–25%), 21 ± 3% for the 95% FK (range = 3–58%), and 26 ± 4% for the MCP (range = 0–58%). These estimates probably did not reflect total overlap with adjacent residents because there were adjacent pairs that we did not have radio-marked and because tracking periods for individual owls were not always exactly the same. However, even with incomplete data on some individuals and no data on the pairs that were not radio-marked, it was clear that home ranges of neighbors overlapped considerably, particularly during winter. In one case, a male from one territory (BPM) was found on several occasions during winter, roosting in the traditional nest area of an adjacent male (HRM).

Cumulative Ranges. Median estimates of cumulative ranges of individual owls monitored in two sequential years were 1222 ha (75% FK), 2539 ha (95% FK), and 2912 ha (MCP; Table 3). Cumulative ranges of females averaged larger than cumu-

lative ranges of males for all comparisons except the mean MCP (Table 3).

Seasonal Ranges. Ranges of individual owls based on the 95% FK averaged 3360 ± 572 ha during the breeding season (range = 883–10 205 ha, median = 2052 ha, $N = 21$) and 3175 ± 572 ha during the nonbreeding season (range = 611–12 352 ha, median = 2168 ha, $N = 29$). There was no consistent pattern of larger ranges in one season or the other. Median estimates of seasonal ranges were smaller than means because means were positively skewed by a few individuals with large ranges. Overlap of nonbreeding season ranges on breeding season ranges averaged 65 ± 4.5% (range = 8–98%, $N = 36$), and overlap of breeding season ranges on nonbreeding ranges averaged 63 ± 4.9% (range = 1–100%, $N = 36$). Overlap of breeding season ranges of two owls tracked in two different breeding seasons averaged 74 ± 8.9% (range = 58–91%). Overlap of nonbreeding ranges of nine owls tracked in two different nonbreed-

Table 4. Results of compositional analysis of habitat use for foraging by northern Spotted Owls on the Olympic Peninsula, Washington, 1987–89. Rank scores indicate relative preference of cover types from highest (6) to lowest (0). Results of pairwise t-tests indicate the relative preference of cover types. 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 was high.

Cover Type[a]		Old Forest	Mature Forest	Mixed-Young Forest	Young Forest	Pole-Sapling	Hard-Wood/Riparian	Clear-Cut/Non-Forest	Rank
Old Forest	t		3.127	4.459	4.637	8.427	4.443	8.103	6
	P		0.006	<0.001	<0.001	<0.001	<0.001	<0.001	
Mature Forest	t	−3.127		−1.454	0.774	2.429	0.391	4.183	4
	P	0.006		0.162	0.448	0.025	0.700	0.001	
Mixed-young Forest	t	−4.459	1.454		2.756	6.676	2.743	6.528	5
	P	<0.001	0.162		0.013	<0.001	0.013	<0.001	
Young Forest	t	−4.637	−0.774	−2.756		1.561	−0.471	2.631	2
	P	<0.001	0.448	0.013		0.135	0.643	0.017	
Pole-sapling	t	−8.427	−2.429	−6.676	−1.561		−2.826	2.370	1
	P	<0.001	0.025	<0.001	0.135		0.011	0.029	
Hardwood/Riparian	t	−4.443	−0.391	−2.743	0.471	2.826		3.860	3
	P	<0.001	0.700	0.013	0.643	0.011		0.001	
Clear-cut/Non-forest	t	−8.102	−4.183	−6.528	−2.631	−2.370	−3.860		0
	P	<0.001	0.001	<0.001	0.017	0.029	0.001		

ing seasons averaged 59 ± 6.3% (range = 10–100%).

During the breeding season, movements of owls were typically centered on the nest tree or, in the case of nonnesting pairs, a regularly-used roost area. Winter ranges typically included part of the breeding-season range plus areas peripheral to the breeding-season range. However, a few individuals spent little time in their breeding-season ranges during the winter season. The most dramatic example was the Elk Creek Female (ECF). After nesting and producing a juvenile in 1987, she left the nest area in August and spent most of the fall and winter in an area 5–15 km away from the nest area before eventually returning to the nest area in June of 1988. The Neilton Ridge Male (NRM) also had a very large nonbreeding range in 1988–89, but in his case, the nonbreeding range overlapped most of the breeding season range.

Ranges of Pairs. There were 14 cases where we monitored annual ranges of paired owls in the same year. The annual ranges of these pairs (union of annual ranges of male and female) averaged 2397 ± 558 ha for the 75% FK (median = 1570 ha), 5449 ± 1111 ha for the 95% FK (median = 4081 ha), and 5414 ± 895 ha for the MCP (median = 5032 ha). Overlap of annual ranges of paired

owls averaged 70 ± 5% based on the 75% FK (range = 14–100%), 69 ± 5% based on the 95%FK (range = 14–100%), and 64 ± 5% based on the MCP (range = 14–100%). Estimates of mean overlap of annual ranges were similar, regardless of which sex was used as the frame of reference, so we based the above averages on all possible combinations of overlap.

Cumulative ranges of five pairs that were monitored in both years averaged 3945 ± 1282 ha for the 75% FK (median = 4053 ha), 8278 ± 2550 ha for the 95% FK (median = 9329 ha), and 7488 ± 1951 ha for the MCP (median = 9195 ha). Overlap of cumulative 95% FK ranges of paired individuals averaged 68 ± 14% for males on females and 72 ± 12% for females on males.

Habitat Selection. Use of cover types for foraging and roosting was nonrandom. Old Forest was the most preferred type for foraging, followed by Mixed-young Forest, Mature Forest, Hardwood/Riparian Forest, Young Forest, Pole-sapling, and Clear-cut/Non-forest (Table 4). Pairwise comparisons of rank indicated that Old Forests were consistently preferred over all other cover types (Table 4). Although Mixed-young Forest ranked higher than Mature Forest, pairwise comparisons of rank indicated little difference between the two types

Table 5. Results of compositional analysis of habitat use for roosting by northern Spotted Owls on the Olympic Peninsula, Washington, 1987–89. Rank scores indicate relative preference of cover types from highest (6) to lowest (0). Results of pairwise t-tests comparisons indicate the relative preference of cover types. 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 was high.

Cover Type[a]		Old Forest	Mature Forest	Mixed-Young Forest	Young Forest	Pole-Sapling	Hardwood/Riparian	Clear-cut/Non-Forest	Rank
Old Forest	t		2.605	3.326	4.823	8.079	4.752	16.554	6
	P		0.017	0.004	<0.001	<0.001	<0.001	<0.001	
Mature Forest	t	−2.605		0.121	1.141	5.124	1.361	10.527	5
	P	0.017		0.905	0.268	<0.001	0.189	<0.001	
Mixed-young Forest	t	−3.326	−0.121		1.163	5.195	1.711	9.010	4
	P	0.004	0.905		0.259	<0.001	0.103	<0.001	
Young Forest	t	−4.823	−1.141	−1.163		3.541	0.447	7.540	3
	P	<0.001	0.268	0.259		0.002	0.660	<0.001	
Pole-sapling	t	−8.079	−5.124	−5.195	−3.541		−3.271	2.543	1
	P	<0.001	<0.001	<0.001	0.002		0.004	0.020	
Hardwood/Riparian	t	−4.752	−1.361	−1.711	−0.447	3.271		6.477	2
	P	<0.001	0.189	0.103	0.660	0.004		<0.001	
Clear-cut/Non-forest	t	−16.554	−10.527	−9.010	−7.540	−2.543	−6.477		0
	P	<0.001	<0.001	<0.001	<0.001	0.020	<0.001		

(Table 4). Similarly, Young Forest ranked lower than Mature and Hardwood Forest, but pairwise comparisons indicated that these differences were weak (Table 4). Pole-sapling stands ranked lower than all other types except Clear-cuts, but the pairwise comparisons with other types indicated that preference for Pole-sapling was not greatly different from Young Forest (Table 4). Large P-values for all pairwise comparisons of Clear-cuts relative to other cover types indicated that Clear-cuts were the least preferred cover type for foraging. In fact, out of 3822 foraging locations where cover type could be determined, only 57 (1.5%) occurred in Clear-cuts or Non-forest areas, and we suspected that some of these cases were due to telemetry or mapping error.

Use of cover types for roosting indicated that Old Forests were preferred over all other cover types (Table 5). Mature Forest ranked higher than Mixed-young, Young Forest, and Hardwood/Riparian Forest, but pairwise comparisons of these types indicated that differences among them were weak (Table 5). Pole-sapling, Clear-cuts, and Non-forest areas were rarely used for roosting. Of 902 roosts located visually, none were located in Clear-cuts or Non-forest. Of 2275 roosts located by triangulation alone, and for which cover type was determined, eight were in Clear-cuts or Non-forest types; we suspected these were due to triangulation or mapping error.

Habitat Use Relative to Forest Edges, Streams, and Elevation. On average, foraging locations and roost locations were closer to openings (233 ± 24 m, and 271.9 ± 33.0 m, respectively) than were random locations (304 ± 34 m; t_{forage} = −4.10, P = 0.001, t_{roost} = −2.04, P = 0.055; N = 20 owls). However, the number of locations within 100 m of an edge was similar between random locations and foraging locations (28.4% vs. 33.5%) and random locations and roost locations (28.4% vs. 29.9%), so we concluded that there was little evidence that owls either preferred or avoided forest edges for roosting or foraging.

Mean elevations at foraging locations (315 ± 29 m) and roosting locations (322 ± 31 m) were slightly lower than elevations at random locations (354 ± 36 m; t_{forage} = −3.63, P = 0.002, t_{roost} = −3.09, P = 0.006, N = 20 owls). Mean distance to the nearest stream was similar for foraging (98 ± 14 m), roosting (112 ± 19 m), and random locations (94 ± 10 m; t_{forage} = 0.73, P = 0.475, t_{roost} = 1.75, P = 0.097, N = 20 owls).

Landscape Composition and Home Range Size. Size of annual ranges was negatively correlated

with the percent cover of older forest (cover types: Old and Mature forest) in the cumulative MCP range, regardless of whether the estimator was the 75% FK ($r_{31} = -0.53$, $P = 0.002$), 95% FK ($r_{31} = -0.59$, $P < 0.001$), or MCP ($r_{31} = -0.67$, $P < 0.001$). Size of annual ranges was also negatively correlated with the amount of older forest in a 4.3 km circle centered on the central place (75% FK $r_{31} = -0.34$, $P = 0.058$; 95% FK $r_{31} = -0.40$, $P = 0.028$; MCP $r_{31} = -0.46$, $P = 0.009$).

Overlap of Management Circles with Home Ranges. On average, a 4.3-km radius circle centered on the nest site or center of activity included 94 ± 2% of the annual 75% FK home range, 86 ± 4% of the annual 95% FK home range, and 83 ± 4% of the annual MCP range. For 12 owls tracked in both years, average overlap of the 4.3-km radius circle on the cumulative range was 99 ± 13% for the 75% FK range, 79 ± 7% for the 95% FK range, and 76 ± 7% for the MCP range. The counterintuitive result in which overlap of the 4.3-km circle was lower on the 75% FK annual range than on the 75% FK cumulative range occurred because the estimates were based on different individuals. If we defined "suitable habitat" as the cover types that had the top three preference rankings based on compositional analysis (cover types = Old, Mature, and Mixed-young Forest), then the mean amount of suitable habitat within a 4.3-km radius circle was 3105 ± 236 ha.

DISCUSSION

Home Range Attributes. The large ranges observed in our study suggest that biomass of suitable prey for Spotted Owls is lower on the Olympic Peninsula than in western Oregon and northwestern California, where home ranges tend to be smaller (Forsman et al. 1984, Carey et al. 1990, 1992, Zabel et al. 1995, Bingham and Noon 1997, Glenn et al. 2004). We did not have data on total prey biomass in our study area, but Carey et al. (1992) found that flying squirrels, which are the primary prey of Spotted Owls on the Olympic Peninsula, were relatively uncommon on the peninsula compared to western Oregon.

As in our study, Carey et al. (1990) and Glenn et al. (2004) found that home range size of northern Spotted Owls was inversely related to the amount of old forest in the home range. This suggests that Spotted Owls respond to decreasing amounts of their preferred habitat by increasing the size of their ranges to encompass more old for-

est. However, Zabel et al. (1995) found no correlation between home-range size of Spotted Owls and the proportion of the range covered by large trees. Instead, they found that home-range size was positively correlated with the proportion of flying squirrels in the diet and negatively correlated with the proportion of woodrats (*Neotoma* spp.) in the diet. In our study area, the diet was dominated by flying squirrels (Forsman et al. 2001), which tend to be most abundant in old forests (Carey et al. 1992, Waters and Zabel 1995). This could explain why home ranges in our study area became larger as the amount of old forest declined. However, for a central-place forager like the Spotted Owl, the ability to increase the size of the home range and still function as a part of the resident breeding population is probably limited by energetic and social constraints (Carey et al. 1992).

In our study, annual home ranges of paired owls typically overlapped by 50–80%. Similar estimates were obtained in a number of other studies (Forsman et al. 1984, Carey et al. 1990, Glenn et al. 2004). Our estimates of mean overlap of annual ranges of owls on adjacent territories were higher than values reported by Forsman et al. (1984:23; MCP overlap = 12%) and Glenn et al. (2004:41; 95% FK overlap = 14.9 ± 4.3% and 6.7 ± 2.2% on two different study areas).

Habitat Selection. Our study, and most other studies in which telemetry methods have been used to examine habitat selection by northern Spotted Owls, indicated that, given a choice, most individuals selectively used older forests for foraging and roosting and that younger stands generally provided lower quality habitat (e.g., Forsman et al. 1984, Call 1989, Carey et al. 1990, 1992, Solis and Gutiérrez 1990, Gutiérrez et al. 1995). However, there have been two radiotelemetry studies of northern Spotted Owls in landscapes dominated by young forest, where patterns of habitat selection were less clear. Glenn et al. (2004) examined habitat selection by Spotted Owls in young forests in northwest Oregon and did not find strong selection for any cover type. In a landscape where old forest comprised less than 10% of the available cover, Irwin et al. (2000) found that northern Spotted Owls infrequently used stands <25 yr of age and foraged primarily in mid-age stands (25–79 yr old) or in remnant patches of old forest. However, Irwin et al. (2000) did not conduct a landscape-level analysis of use-versus-availability with their data, so

we could not determine if use of different cover types differed from availability.

California Spotted Owls (*S. o. occidentalis*) in the Sierra Nevada Mountains tended to forage in forests with ≥40% canopy cover, but did not show a strong preference relative to tree age or tree size (Zabel et al. 1992). However, at two of the three study areas described by Zabel et al. (1992), the majority of foraging and roosting locations were in stands dominated by large (>53 cm DBH) trees.

Of the 5–6 species of small mammals that comprise the primary diet of Spotted Owls, several appear to be most abundant in older forests. For example, there are a number of studies that suggest that red tree voles (*Arborimus longicaudus*) and red-backed voles (*Clethrionomys californicus*) are most abundant in older forests (Corn and Bury 1986, Aubry et al. 1991, Rosenberg et al. 1994). While not all studies of northern flying squirrels have found significantly higher numbers in old forests, the trend in most studies was toward higher numbers in old forests (Carey et al. 1992, Rosenberg and Anthony 1992, Waters and Zabel 1995, Lehmkuhl et al. (in press). Therefore, an obvious hypothesis is that differences in abundance of preferred prey cause northern Spotted Owls to select for older forests (Forsman et al. 1984, Carey et al. 1992). Ward et al. (1998) posed a similar hypothesis to explain high use of forest edges by Spotted Owls in northwestern California, where the diet was dominated by dusky-footed woodrats (*N. fuscipes*), which were most abundant in brushy openings adjacent to forests. In contrast, in areas where they feed mainly on flying squirrels, Spotted Owls either avoid non-forest edges or use them in proportion to availability (Zabel et al. 1995, Glenn et al. 2004, this study).

Streams and Elevation. Although Glenn et al. (2004) found evidence that Spotted Owls foraged selectively in riparian vegetation, we found no evidence that foraging or roosting locations were closer to streams than were random locations. We concluded that there was no evidence from our data that owls were either selecting or avoiding riparian areas. Although Spotted Owls in our study foraged at lower elevations than expected, the mean difference between observed and expected foraging locations was only 39 m. We were not convinced that this relatively small difference was biologically meaningful.

Management Implications. Based on the results of our study, we agree with Forsman et al. (1984),

Thomas et al. (1990), and Carey et al. (1992) that management for northern Spotted Owls in western Washington and Oregon should focus on the retention of old forests. Although Franklin et al. (2000) and Olson et al. (2004) found that northern Spotted Owls may have higher reproductive output in landscapes that include a mixture of old forest and edges with other forest types, those studies were conducted in areas where woodrats were a primary prey, and the results may not apply to areas like the Olympic Peninsula, where flying squirrels are the primary prey.

Bingham and Noon (1997, 1998) suggested that the U.S. Fish and Wildlife Service should focus on the most heavily-used portion of the home range, or "core area," as the frame of reference for assessment of "take" of Spotted Owls. If this approach is used on the Olympic Peninsula, then we believe it would be reasonable to use our estimates of the 75% isopleth of the FK annual range as the criteria for estimates of core areas, although other methods have been proposed (Bingham and Noon 1997). We agree with Bingham and Noon (1997) that it makes sense to use repeatable measures of home range areas as the frame of reference for assessments of "take," but this should not be misconstrued as a recommendation to manage Spotted Owls based only on core areas. If the objective is to provide Spotted Owls with enough habitat to survive and reproduce on a site, then we agree with Buchanan et al. (1998) that management should be based on amounts of habitat within the entire home-range areas of radio-marked owls, not just core areas.

Our estimates of the median and mean amounts of "suitable habitat" within cumulative MCP ranges of Spotted Owls (1824 ha and 2253 ± 286 ha) are similar to or slightly lower than the management target adopted by the Washington State Forest Practices Board (1996) for management around Spotted Owl nest sites (2373 ha of suitable habitat within a 4.3-km radius). We found that a 4.3-km radius circle centered on the nest site encompassed about 83–87% of the mean cumulative home range used by individual Spotted Owls on the peninsula. Based on these results, we see no reason to suggest changes to the 1996 Forest Practices Rules (Washington State Forest Practices Board 1996). However, it remains to be seen if Spotted Owls will persist in areas where old and mature forests are gradually replaced with less-preferred types that are also classified as "suitable."

LITERATURE CITED

AEBISCHER, N.J., V. MARCSTRÖM, R.E. KENWARD, AND M. KARLBOM. 1993. Survival and habitat utilization: a case for compositional analysis. Pages 343–353 in J.D. Le-breton and P.M. North [EDS.], Marked individuals in the study of bird population. Birkhäuser Verlag, Basel, Switzerland.

AUBRY, K.B, M.J. CRITES, AND S.D. WEST. 1991. Regional patterns of small mammal abundance and community composition in Oregon and Washington. Pages 285–294 in L.F. Ruggerio, K.B. Aubry, A.B. Carey, and M.H. Huff [TECH. COORDS.], Wildlife and vegetation of unmanaged Douglas-fir forests. Gen. Tech. Rep. PNW-GTR-285. USDA, Forest Service, Pacific North-west Research Station, Portland, OR U.S.A.

BINGHAM, B.B. AND B.R. NOON. 1997. Mitigation of hab-itat "take": application to habitat conservation plan-ning. Conserv. Biol. 11:127–139.

———— AND ————. 1998. The use of core areas in com-prehensive mitigation strategies. Conserv. Biol. 12:241–243.

BUCHANAN, J.B., F.J. FREDERICKSON, AND D.E. SEAMAN. 1998. Mitigation of habitat "take" and the core area concept. Conserv. Biol. 12:238–240.

CALL, D.R. 1989. Home range and habitat use by Cali-fornia Spotted Owls in the central Sierra Nevada. M.S. thesis, Humboldt State University, Arcata, CA U.S.A.

CAREY, A.B., S.P. HORTON, AND B.L. BISWELL. 1992. North-ern Spotted Owls: influence of prey base and land-scape character. Ecol. Monogr. 62:223–250.

———— AND K.C. PEELER. 1995. Spotted Owls: resource and space use in mosaic landscapes. J. Raptor Res. 29:223–229.

————, J.A. REID, AND S.P. HORTON. 1990. Spotted Owl home range and habitat use in southern Oregon Coast Ranges. J. Wildl. Manage. 54:11–17.

CORN, P.S. AND R.B. BURY. 1986. Habitat use and terres-trial activity by red tree voles (Arborimus longicaudus) in Oregon. J. Mammalogy 67:404–406.

FORSMAN, E.D. 1983. Methods and materials for locating and studying Spotted Owls. Gen. Tech. Rep. PNW-162. USDA, Forest Service, Pacific Northwest Re-search Station, Portland, OR U.S.A.

————, E.C. MESLOW, AND H.M. WIGHT. 1984. Distribu-tion and biology of the Spotted Owl in Oregon. Wildl. Monogr. 87:1–64.

————, I.A. OTTO, S.G. SOVERN, M. TAYLOR, D.W. HAYS, H. ALLEN, S.L. ROBERTS, AND D.E. SEAMAN. 2001. Spa-tial and temporal variation in diets of Spotted Owls in Washington. J. Raptor Res. 35:141–150.

FRANKLIN, A.B., D.R. ANDERSON, R.J. GUTIÉRREZ, AND K.P. BURNHAM. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwest-ern California. Ecol. Monogr. 70:539–590.

GLENN, E.M., M.C. HANSEN, AND R.G. ANTHONY. 2004. Spotted Owl home range and habitat use in young forests of western Oregon. J. Wildl. Manage. 68:33–50.

GUETTERMAN, J.H., J.A. BURNS, J.A. REID, R.B. HORN, AND C.C. FOSTER. 1991. Radiotelemetry methods for study-ing Spotted Owls in the Pacific Northwest. Gen. Tech. Rep. PNW-272. USDA, Forest Service, Pacific North-west Research Station, Portland, OR U.S.A.

GUTIÉRREZ, R.J., A.B. FRANKLIN, AND W.S. LAHAYE. 1995 Spotted Owl. The Birds of North America No. 179. The Birds of North America, Inc. Philadelphia, PA U.S.A.

HAMER, T.E. 1988. Home range size of the Northern Barred Owl and Northern Spotted Owl in western Washington. M.S. thesis, Western Washington Univer-sity. Seattle, WA U.S.A.

HAYNE, D.W. 1949. Calculation of size of home range. J. Mammalogy 30:1–18.

HENDERSON, J.A., D.H. PETER, R.D. LESHER, AND D.C SHAW. 1986. Forested plant associations of the Olym-pic National Forest. Ecological Technical Paper R6-ECOL-TP 001-88. USDA, Forest Service, Portland, OR U.S.A.

IRWIN, L.L., D.F. ROCK, AND G.P. MILLER. 2000. Stand structures used by northern Spotted Owls in managed forests. J. Raptor Res. 34:175–186.

KIE, J.G., J.A. BALDWIN, AND C.J. EVANS. 1996. CALHOME· A program for estimating animal home ranges. Wildl Soc. Bull. 24:342–344.

LAYMON, S.A. 1989. Altitudinal migration movements of Spotted Owls in the Sierra Nevada, California. Condor 91:837–841.

LEBAN, F. 1999. Program RSW—Resource selection for Windows, Version 1.00 Beta 8.4. University of Idaho, Moscow, ID U.S.A.

LEHMKUHL, J.F., K.D. KISTLER, J.S. Begley, AND J. BOULAN-GER. (in press). Demography of northern flying squir-rels informs ecosystem management of western inte-rior forests. Ecol. Appl.

NAMS, V.O. AND S. BOUTIN. 1991. What is wrong with er-ror polygons? J. Wildl. Manage. 55:172–176.

OLSON, G.S., E.M. GLENN, R.G. ANTHONY, E.D. FORSMAN, J.A. REID, P.J. LOSCHL, AND W.J. RIPPLE. 2004. Model-ing demographic performance of northern Spotted Owls relative to forest habitat in Oregon. J. Wildl Manage. 68:1039–1053.

OTIS, D.L., AND G.C. WHITE. 1999. Autocorrelation of lo-cation estimates and the analysis of radiotracking data. J. Wildl. Manage. 63:1039–1044.

PIERCE, F.R. 1921. Tornado destroys great forest. *Pop. Mech.* 35:659–662.

ROSENBERG, D.K. AND R.G. ANTHONY. 1992. Characteristics of northern flying squirrel populations in young second- and old-growth forests of western Oregon. *Can. J. Zool.* 70:161–166.

——, K.A. SWINDLE, AND R.G. ANTHONY. 1994. Habitat associations of California red-backed voles in young and old-growth forests in western Oregon. *Northwest Sci.* 68:266–272.

SEAMAN, D.E., B. GRIFFITH, AND R.A. POWELL. 1998. KERNELHR: a program for estimating animal home-ranges. *Wildl. Soc. Bull.* 26:95–100.

—— AND R.A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for home-range analysis. *Ecology* 77:2075–2085.

SOLIS, D.M., JR. AND R.J. GUTIÉRREZ. 1990. Summer habitat ecology of northern Spotted Owls in northwestern California. *Condor* 92:739–748.

SWIHART, R.K. AND N.A. SLADE. 1985a. Influence of sampling interval on estimates of home-range size. *J. Wildl. Manage.* 49:1009–1025.

—— AND N.A. SLADE. 1985b. Testing for independence of observations in animal movements. *Ecology* 66:1176–1184.

THOMAS, J.W., E.D. FORSMAN, J.B. LINT, E.C. MESLOW, B.R. NOON, AND J. VERNER. 1990. A conservation strategy for the northern Spotted Owl: report of the Interagency Scientific Committee to address the conservation of the northern Spotted Owl. USDA, Forest Service and USDI, Bureau of Land Management, Portland, OR U.S.A.

WARD, J.P., JR., R.J. GUTIÉRREZ, AND B.R. NOON. 1998. Habitat selection by Northern Spotted Owls: the consequences of prey selection and distribution. *Condor* 100:79–92.

WASHINGTON STATE FOREST PRACTICES BOARD. 1996. Final environmental impact statement on forest practices rule proposals for northern Spotted Owl, Marbled Murrelet, and western gray squirrel. Washington State Forest Practices Board, Olympia, WA U.S.A.

WATERS, J.R. AND C.J. ZABEL. 1995. Northern flying squirrel densities in fir forests of northeastern California. *J. Wildl. Manage.* 59:858–866.

ZABEL, C.J., K. MCKELVEY, AND J.P. WARD, JR. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern Spotted Owls (*Strix occidentalis caurina*). *Can. J. Zool.* 73:433–439.

——, G.N. STEGER, K.S. MCKELVEY, G.P. EBERLEIN, B.R. NOON, AND J. VERNER. 1992. Home-range size and habitat-use patterns of California Spotted Owls in the Sierra Nevada. Pages 149–163 *in* J. Verner, K.S. McKelvey, B.R. Noon, R.J. Gutiérrez, G.I. Gould, Jr., and T.W. Beck [EDS.], The California Spotted Owl: a technical assessment of it current status. USDA, Forest Service, Pacific Southwest Research Station, Albany, CA U.S.A.