703-59

J. Raptor Res. 34(3):175–186

STAND STRUCTURES USED BY NORTHERN SPOTTED OWLS IN MANAGED FORESTS

Larry L. Irwin[1] and Dennis F. Rock
National Council of the Paper Industry for Air and Stream Improvement (NCASI), P.O. Box 458, Corvallis, OR 97339 U.S.A.

Gregory P. Miller[2]
U.S. Department of Interior, Bureau of Land Management (BLM), Eugene, OR 97408 U.S.A.

Abstract.—We compared vegetative structures in 4–16-ha patches in forest stands used by 12 pairs of Northern Spotted Owls (*Strix occidentalis caurina*) for nesting ($N = 44$) and foraging ($N = 38$) with habitat structures in 50 stands located randomly throughout annual home ranges in a young and mid-successional forest landscape (25–79 yr-old stands) in the foothills of the western Cascades in Oregon. Forest stand structures influenced selection for stands used for foraging and nesting by Spotted Owls, and abundance of these structures varied with successional development as represented by five age classes. Conifer saplings (10–19 cm in diameter at breast height [dbh]) and trees 50–79 cm dbh were more abundant in foraging areas than nest sites or random sites. Large snags (>40 cm dbh) tended to be more abundant, down woody debris was more abundant, and cover of herbs and low-growing shrubs (<0.5 m) was lower in stands in which owls hunted frequently than in randomly located stands of the same age classes. Owls nested in trees as young as 41 yr old, although 65% of nest trees were older than 120 yr of age. We found 22 (50%) nests in forest stands 46–79 yr of age, whereas owls repeatedly foraged in stands as young as 27 yr of age. Silviculturists should be able to create foraging habitat for Northern Spotted Owls in managed forests by emphasizing control of tree densities and form, woody debris, and understory vegetation. Suitable nesting habitat might best be facilitated via retaining legacy trees. Future research should determine the relative contribution of managed forests to owl conservation.

Key Words: *Northern Spotted Owl;* Strix occidentalis caurina; *foraging habitat; managed forests; nesting habitat; Oregon.*

Estructuras de árboles utilizadas por *Strix occidentalis caurina* en bosques manejados

Resumen.—Comparamos las estructuras vegetales de 4–16 parches de bosques utilizados por 12 parejas de *Strix occidentalis caurina* en hábitats de anidación ($N = 44$) y forrajeo ($N = 38$), en estructura de hábitats de 50 parcelas de árboles ubicados al azar a lo largo de los rangos de hogar anuales en paisajes de sucesiones de bosques jóvenes (25–79 años), los cuales estaban ubicados en el piedemonte al oeste de Cascadas en Oregon. Las estructuras de árboles influenciaron la selección de árboles utilizados para el forrajeo y anidación de los búhos. La abundancia de estas estructuras varió con el desarrollo sucesional representado por 5 clases de edad. Las muestras de coniferas (10–19 cm) de diámetro a la altura del pecho (dap) y de árboles 50–79 cm dap fueron más abundantes en áreas de forrajeo que en los sitios de anidación o los sitios escogidos al azar. Los troncos grandes (>40 cm dap) tendían a ser más abundantes, la cobertura de hierbas y arbustos del sotobosque (<0.5 m) fue menor en los fragmentos de árboles en los que los búhos cazaban con frecuencia que en las estructuras de la misma clase de edad ubicadas al azar. Los búhos anidaron en árboles jóvenes de 41 años de edad, aunque el 65% de los árboles con nidos fueron de más de 120 años de edad, mientras que los búhos forrajearon repetidamente en árboles de 27 años de edad. Los silviculturistas podrían crear hábitat de forrajeo para los búhos en bosques manejados enfatizando el control de las densidades de árboles, su forma, y de la vegetación del sotobosque. El hábitat de anidación apropiado puede ser implementado protegiendo los árboles valiosos. Las investigaciones futuras deben determinar la relativa contribución de los bosques manejados a la conservación de los búhos.

[Traducción de César Márquez]

Field studies have repeatedly demonstrated that Northern Spotted Owls (*Strix occidentalis caurina*) selectively use late-successional and old-growth (LS/OG) forest stands (Forsman et al. 1984, Carey et al. 1990, Hunter et al. 1995), and that vegetative structures within such stands likely influence selection of foraging habitats (Solis and Gutiérrez 1990, Call et al. 1992) and nest sites (Forsman et al. 1984,

---

[1] Present address: P.O. Box 68, Stevensville, MT 59870 U.S.A.

[2] Present address: 3165 10th Street, Baker City, OR 97814 U.S.A.

703-59

Buchanan et al. 1993, Buchanan and Irwin 1995, LaHaye and Gutiérrez 1999). North et al. (1999) documented that forest stand structures influenced selection of foraging sites used by Northern Spotted Owls in unharvested forests in Washington. Forest stand structures, including large trees and snags, multiple canopy layers, downed woody debris and shrubs, have been hypothesized to provide favorable microclimates, nest sites, cover from predators, and/or habitat for the owl's prey (Carey 1985, Carey and Johnson 1995, Carey and Peeler 1995). Forest stand structures influence small mammal diversity and abundance (Carey 1995), and many aspects of Spotted Owl biology are influenced by prey abundance, diversity and biomass (Carey et al. 1992, Carey and Peeler 1995, Ward et al. 1998, Carey et al. 1999).

There are no detailed measures of forest stand structures and other habitat attributes in young or managed forests occupied by Northern Spotted Owls. Investigators who have documented Northern Spotted Owl presence in young and mid-successional (Y/MS) forests (defined herein as those 25–79 yr of age) have speculated that such occupancy probably is related to structural legacies from previous, older forests (e.g., Forsman et al. 1977, Irwin et al. 1989). Information on density or abundance of vegetative structures associated with use of Y/MS forests by Northern Spotted Owls could be used for crafting silvicultural prescriptions for producing or enhancing habitat in managed forests, if a breeding population of owls could be found occupying a Y/MS forest landscape. We located such a Y/MS landscape occupied by Northern Spotted Owls at the foot of the Cascade Range in western Oregon, where surveys identified 57 territories occupied by 42 owl pairs and 15 single owls (with annual variation) near Springfield, Oregon in a managed landscape that contained <10% LS/OG forests. Owl pairs at 29 of the 42 sites successfully fledged young 1 yr from 1992–99, providing an opportunity to examine forest stand structure at foraging and nest sites.

The scale for comparing used and available habitats determines the range of inferences from habitat selection studies (Johnson 1980, Porter and Church 1987). Previous investigators (Laymon and Reid 1986, Carey and Peeler 1995) found that Northern Spotted Owls often concentrated their searches for prey repeatedly in small "pockets" (<16 ha) of forests, and Bingham and Noon (1997) recommended sampling habitat conditions within core areas (Samuel et al. 1985), or those areas within home ranges that receive disproportionate use. Quantifying habitat components in frequently-used stands, which are most likely to occur within core areas, may help identify consistent aspects of the environment that trigger the owl's habitat selection response and influence its survival and reproduction (Bingham and Noon 1997). Thus, our primary goal was to evaluate stand structural factors associated with forests used for nesting and foraging in frequently-used areas within owl home ranges. We wanted to learn if densities of forest stand-structures and other habitat descriptors differed across a successional gradient and among nest sites, foraging areas, and random locations within owl home ranges.

STUDY AREA

The study area was bordered by the Willamette National Forest on the east and forests adjacent to Interstate Highway-5 on the west, and extended south from Brownsville in Linn County to Dorena Reservoir in Lane County, Oregon. About 10% of the land was administered by the USDI Bureau of Land Management (BLM). The remainder was owned by private timber companies or occurred as rural residential areas and farmlands. Forests in the northern and western portions of the study area regenerated following timber harvests that often left scattered nonmerchantable trees or seed trees, many of which were >80 cm in diameter. Forests in the eastern parts of the study area regenerated following extensive wildfires about the turn of the century (Teensma 1987).

The 57 owl territories that we identified lay below 915 m in elevation in the foothills of the McKenzie River drainage. The area was in the Western Hemlock Zone (Franklin and Dyrness 1981), and the forests were predominantly coniferous trees such as Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). Common hardwoods included Pacific dogwood (*Cornus nuttallii*), big leaf maple (*Acer macrophyllum*), and red alder (*Alnus rubra*). Less common species included golden chinquapin (*Castanopsis chrysophylla*) and Pacific yew (*Taxus brevifolia*). Common understory species included swordfern (*Polystichum munitum*), salal (*Gaultheria shallon*), vine maple (*Acer circinatum*), and Oregon grape (*Berberis nervosa*).

METHODS

Radiotracking of 26 owls in the Springfield population provided an opportunity to examine habitat structures at areas of concentrated use for foraging. We also examined forest stand structures at nest sites. Capturing and radiotracking Spotted Owls followed procedures described by Carey et al. (1989, 1990) and Guetterman et al. (1991) To ensure statistical independence, only telemetry locations separated by 72 hr were used in the analysis (Guetterman et al. 1991). This criterion was met by field crews locating radio-tagged owls 2–3 times per week. We used only owls for which telemetry data were gathered continuously according to that schedule for >1 yr (13–27 mo), to provide estimates of year-round use patterns within home ranges. Nocturnal telemetry locations (when owls foraged most frequently) were initially mapped in the field on 7.5-min U.S. Geological Survey quadrangle maps and on aerial photographs. We subsequently mapped owl home ranges and identified core areas using the adaptive kernel (ADK) method (Worton 1989, 1995). Although core areas of Northern Spotted Owls may include up to 75% of the telemetry locations of an individual or pair (Bingham and Noon 1997), we used the 60% ADK isopleth to estimate core area.

Using aerial photographs, we identified forest stands for sampling stand-structural measurements using three criteria: the radio-tagged owls involved were members of pairs of territorial Spotted Owls, at least one of which was monitored for 1 yr; the pairs nested successfully ≥ 1 time during the study; and the stands received repeated or disproportionate use by radio-tagged owls for foraging, which we arbitrarily defined as 4% of the total telemetry locations in areas that comprised 1% of the annual ADK home range. Due to the concentration of use near the center of the home ranges (Rosenberg and McKelvey 1999), such repeatedly-used foraging areas were located within core areas. Sizes of foraging areas sampled varied with the number of telemetry locations and size of error polygons from telemetry, and ranged from 5–15 ha, usually 10 ha. We specified the maximum sampling area at 15 ha based upon similar observations by Laymon and Reid (1986) and Carey and Peeler (1995), as well as our own observations. Also, we specified the minimum foraging area to be at least twice the size of average telemetry-error polygons (1.5–2.0 ha), which we estimated by comparing triangulations with actual (walk-in) observations ($N = 75$) of radio-tagged birds. Although our choice of 4% of telemetry points in 1% of home ranges was arbitrary, the design was similar to that of North et al. (1999), who used 3–9% of telemetry locations to designate "moderately-used" stands and 10% for very highly-used stands. However, they sampled stands 40–80 ha in size, whereas we sampled within much smaller areas that contained a comparatively high density of telemetry points.

We sampled 2–4 frequently-used foraging areas within each core area; few home ranges contained >4 repeatedly-used foraging areas. Thus, the foraging area (or nest site) was the sampling unit, not each owl. North et al. (1999) found that variance in stand structure estimates stabilized at 3–4 plots per stand in homogeneous stands. Thus, we sampled 2 plots in each foraging area or random site, but opted for five plots when we encountered additional variation, as was found in the largest stands sampled (15 ha) and also in those with large-tree legacies from previous stands. Data presented are averages from 104 plots sampled in 38 frequently-used foraging areas within home ranges of 12 pairs of Northern Spotted Owls, either from combined home ranges of both pair members or from one member of a pair. In addition, we collected data from 44 nest stands, using the nest tree as the center of a single plot. Several owl pairs used more than one nest tree; alternate nest trees were sampled only if they were found in different stands.

Specific locations of plots to be sampled within foraging areas and in comparison areas that contained zero or low densities of telemetry locations were established using random coordinates on grid maps (100-m grid intervals) and found in the field using a global positioning system. Statistical comparisons of data from nests and foraging areas were made with data gathered from 50 stands (averaged from three plots/stand) that were selected randomly. The 2–4 foraging stands sampled within individual home ranges were >200 m apart to ensure a broad distribution and sampling of the range of types within home ranges, and we also assumed that the random sites within the 12 home ranges represented the range of variation in habitat conditions used by Spotted Owls in the study area. Examples of home ranges, core areas, and sampling design for estimating habitat structures at frequently-used foraging sites and random sites are shown in Fig. 1.

We sampled several variables associated with four major stand-structural features that are believed to be important to Spotted Owls and/or their prey: densities and sizes of live trees; coarse woody debris, including fallen logs and snags; understory vegetation; and forest canopy structure. Our sampling design employed nested circular plots, following procedures used in Spies (1989) and North et al. (1999), in which the minimum vegetation structure size sampled increased with plot size. These procedures provided tallies of large, infrequently occurring items such as snags and old-growth trees without over-sampling small, less variable structures. Each plot included three nested circular sub-plots: 0.05-, 0.10-, and 0.20-ha in size.

Beginning 2 m from the site center, we made ocular estimates of cover (to the nearest percent) for shrubs and herbs in three height classes (<0.5, 0.5–2.0, and >2.0 m) in four 4-m^2 quadrats placed in the cardinal directions We counted all living trees and all snags (>10 cm dbh) and estimated abundance and length of downed woody debris (pieces >10 cm diameter) within the 0.05-ha subplot. In the 0.1-ha plot, we tallied living trees 51–80 cm dbh and all downed logs (large and small diameter and length). Finally, in the 0.2-ha plot, we recorded the number of large snags (50 cm dbh) and large living trees (80 cm dbh). We also estimated stand age (from annual growth rings), average crown depth (using a clinometer), and average crown volume ($\frac{1}{3}\pi r^2 \times$ height) based upon six living dominant or codominant trees that we judged to typify the dominant canopy trees in each stand sampled. We estimated canopy cover using a concave densitometer (after this study was well underway, we learned that this tool inflates estimates in high closure classes, see Cook et al. 1995). Distance from the ground level to the lower canopy provided an index to flying space under the primary canopy. We sampled only those stand-age classes that owls used for nesting or that radio-tagged owls used repeatedly for foraging. Thus, we discarded random points that fell on non-forested areas or forest age-classes that were not used. For statistical comparisons, we grouped stands into five age classes that approximated a successional gradient: 25–39, 40–59, 60–79, 80–119, and >120 yr. We designated the first three age classes as Y/MS or managed forests and the older two as LS/OG forests.

After evaluating stand structure variables to assess nor-

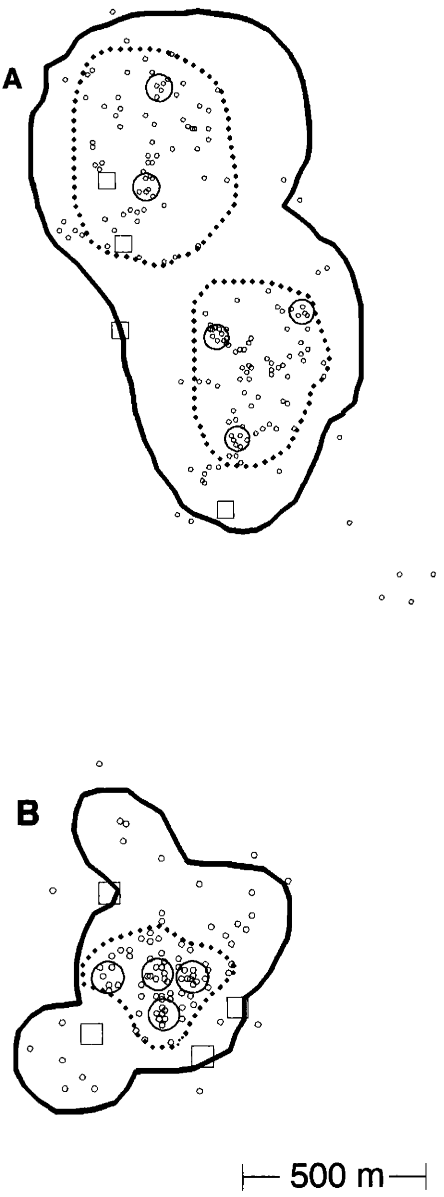

Figure 1. Examples of sampling design for comparing habitat structure at frequently-used foraging areas (large circles) within core areas (dotted lines) of a pair of Northern Spotted Owls (A) and an individual Spotted Owl (B) with that at randomly-located areas (squares). Radiotelemetry points are denoted by small circles and 95% adaptive kernel home ranges are enclosed by solid lines. Both members of the pair in A used two core areas that were separated by unusable habitat.

Table 1. Number of forest stand samples by age class for repeatedly-used foraging sites and nesting sites of Northern Spotted Owls and random sites within Spotted Owl home ranges, western Oregon. Age classes 25–39, 40–59, and 60–79 yr were classified as young or mid-successional (Y/MS) stands and classes 80–119 yr and >120 yr were late-successional and old-growth (LS/OG) stands.

	FOREST STAND AGE CLASS (yr)					
	25–39	40–59	60–79	80–119	>120	TOTAL
Foraging	5	16	5	8	4	38
Nesting	0	11	11	18	4	44
Random	19	10	7	9	5	50

mality of distributions and possible correlations, we tested for effects of succession with a two-way, fixed effects analysis of variance (ANOVA). For comparisons that were statistically significant, Fisher's least significant difference test was used to determine which levels differed. Comparisons among random, foraging, and nesting sites were made using fixed effects ANOVA. In general, we considered comparisons statistically significant if Type-I error levels were <0.05.

RESULTS

Descriptive Data. Core areas of Northern Spotted Owls for which we obtained sufficient telemetry data averaged 372 ha (SE = 67.6 ha) in size for 18 individuals and 417 ha (SE = 128.9 ha) in size for 6 pairs, and occupied <25% of annual ADK home ranges among individuals and pairs. The 44 nests were in stands that ranged in age from 46–168 yr, half (22) of which were in LS/OG forests and half of which were in Y/MS forests (Table 1). These included 11 nests in stands 46–60 yr old. Trees with owl nests were mostly Douglas-firs (86%) of large size (73% >80 cm dbh) and relatively old age (65% >120 yr). Such trees clearly were legacies from previous stands. All but four nests were in living trees. Four nest trees were <60 yr old and <50 cm dbh, with the youngest being 41 yr. The nest structures that we could identify were either cavities (*N* = 17) or debris platforms (*N* = 22) on large limbs or in tree crotches.

Owls foraged in stands with a wider age range than was found at nest sites. Repeatedly-used foraging areas ranged from 27–>200 yr in age. Twenty-six Y/MS stands and 12 LS/OG stands were used repeatedly for hunting (Table 1). Five stands 25–40 yr of age were used repeatedly for foraging. Radio-tagged owls made very little use of stands <25 yr of age. Stand composition was similar to that of

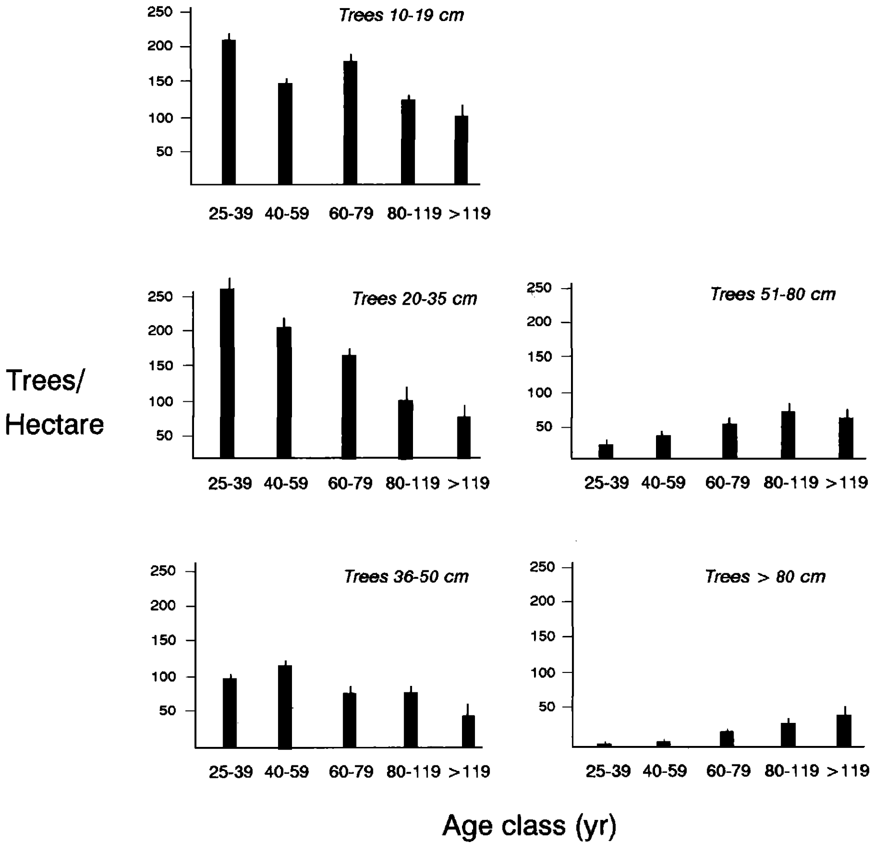

Figure 2. Successional patterns of tree densities by size- and age-class in stands frequently used for foraging or nesting or at random locations within home ranges of Northern Spotted Owls. Vertical lines above bars indicate standard errors.

Douglas-fir forests of western Oregon in that stands typically consisted of abundant, small-diameter western hemlock seedlings and trees (<20 cm dbh) with Douglas-fir tending to be the large-diameter trees.

Density of Live Trees. Average densities of trees seemed to differ among the five classes that we used to express successional gradients. Stands 25–39 yr of age contained highest densities of trees <35 cm dbh. Stands 40–79 yr of age contained moderate densities (>40/ha) of trees >50 cm dbh and mature and older stands (80 yr old) contained relatively high densities of large trees with >19 trees/ha >80 cm dbh (Fig. 2). In general, densities of trees in the three diameter classes <50 cm declined with advancing age and densities of trees >50 cm dbh increased. Nearly all stands sampled contained more than one large (>80 cm dbh) tree/ha.

We found relatively few differences in densities of trees of five diameter classes among nesting, foraging, or random sites within owl home ranges (Table 2). Foraging sites contained more sapling trees (10–19 cm dbh) and more 51–80 cm dbh trees than either nesting or random sites. In turn, nest sites contained the most trees in the 20–35 cm dbh class and fewest in the 51–80 cm dbh class. Foraging sites tended to contain a few more large trees (>80 cm dbh) than random or nesting sites.

Snags and Downed Wood Debris. We found successionally-related gradients in densities of large snags in comparisons that included all stands that we sampled (Table 3). Large snags increased and small snags tended to decrease with advancing

Table 2. Comparisons of tree densities by size class among nesting, foraging, and random locations within Northern Spotted Owl home ranges, western Oregon. Row values with different superscripts are statistically different at the indicated level of probability, based on ANOVA.

TREE SIZE CLASS (dbh in cm)	TREE DENSITY (No./ha ± SE)			
	RANDOM	FORAGING	NESTING	P^{a}
10–19	120^{a} ± 16	186^{b} ± 19	162^{c} ± 17	0.041
20–35	164^{a} ± 13	142^{b} ± 16	188^{c} ± 14	0.109
36–50	87 ± 7	84 ± 8	79 ± 8	0.814
51–80	56^{a} ± 4	62^{a} ± 5	43^{b} ± 4	0.018
>80	15 ± 2	19 ± 2	15 ± 2	0.201

stand age and large snags generally were more abundant at foraging and nesting sites than at random, although the differences were not consistent among all age classes. There were no differences in densities of small-diameter snags among foraging, nesting, and random locations.

There were no clear successional gradients in the densities or volumes of downed woody debris (Table 4), although the youngest stands usually contained the least amount of woody debris. Foraging areas contained greater densities and volumes of both large and small woody debris than random sites. Foraging areas also contained as much as 50% more downed trees than nest sites or random locations within home ranges. The volume of large woody debris was greater at nest sites than random sites and several significant comparisons occurred within age classes at foraging and nesting sites and random locations. Although estimates of the volume of woody debris were more variable than density estimates, foraging sites in managed stands contained from 150–200% more debris volume than random sites of the same age classes.

Canopy Structure. Canopies of all stands were dense, averaging >80% closure. Average crown volume increased with advancing stand age, but did not differ among foraging, random or nesting locations within home ranges, except that trees in the five foraging stands sampled that were 60–79 yr of age contained smaller crown volumes than those at random sites (Table 5). Tree crown volume was significantly lower at foraging sites than at random sites in stands <40-yr old. Average crown depth of trees at foraging sites was less than that in nest sites or random locations for stands <80 yr of age (i.e., Y/MS stands).

The index of flying space beneath the forest canopy increased with advancing stand age and was significantly less at foraging sites than at random sites within home ranges over all age classes com-

Table 3. Snag densities at Northern Spotted Owl foraging, nesting, and random locations, western Oregon.

AGE CLASS (yrs)	SNAG DENSITIES (No./ha ± SE)				
	FORAGING	NESTING	RANDOM	P^{a}	OVERALL
Large Snags (≥50 cm dbh)					
25–39	4.4 ± 1.4	n.d.[b]	2.1 ± 0.6	0.1461	3.0 ± 1.3
40–59	2.5 ± 1.5	5.5 ± 1.9	6.1 ± 1.8	0.271	4.1 ± 1.1
60–79	7.0 ± 3.4	7.7 ± 2.3	2.6 ± 2.9	0.378	6.1 ± 1.3
80–119	12.0 ± 2.1	6.1 ± 1.3	9.6 ± 1.9	0.0575	8.3 ± 1.1
≥120	17.6 ± 4.1	12.5 ± 4.1	5.3 ± 3.7	0.1277	11.4 ± 1.7
Overall	7.0 ± 1.1	7.0 ± 1.0	4.7 ± 0.9	0.0165	
Small Snags (<50 cm dbh)					
25–39	129 ± 39	n.d.[b]	125 ± 18	0.9377	133 ± 16
40–59	112 ± 24	124 ± 29	171 ± 31	0.5442	130 ± 13
60–79	91 ± 13	91 ± 13	53 ± 16	0.5076	79 ± 16
80–119	111 ± 25	92 ± 17	77 ± 24	0.4722	88 ± 13
120	79 ± 30	70 ± 26	52 ± 23	0.5099	66 ± 21
Overall	108 ± 14	100 ± 12	126 ± 13	0.5012	

[a] Probability values in same row do not differ, as determined from ANOVA.

[b] No data.

Table 4. Average density and volume of large (>50 cm diameter) woody debris and volume of small (10–50 cm diameter) woody debris in Northern Spotted Owl foraging, nesting, and random sites, western Oregon.

AGE CLASS (yr)	FORAGING	NESTING	RANDOM	P^{a}	OVERALL
Density of Large Woody Debris (No./ha ± SE)					
25–39	86 ± 27	n.d.^{b}	65 ± 12	0.4816	77 ± 12
40–59	113 ± 16	73 ± 18	62 ± 19	0.1022	82 ± 10
60–79	147 ± 29	79 ± 19	66 ± 24	0.0987	95 ± 12
80–119	111 ± 21	76 ± 13	82 ± 19	0.3893	91 ± 10
120	139^{a} ± 22	55 ± 22	65 ± 20	0.0435	86 ± 16
Overall	117^{a} ± 10	74 ± 9	68 ± 8	0.0003	
Volume of Large Woody Debris (m^3/ha ± SE)					
25–39	184 ± 55	n.d.^{b}	125 ± 25	0.3377	186 ± 35
40–59	278 ± 41	143 ± 41	159 ± 50	0.0757	193 ± 28
60–79	368^{a} ± 73	197^{b} ± 49	115^{c} ± 62	0.0476	216 ± 35
80–119	243 ± 65	218 ± 40	103 ± 57	0.1932	197 ± 29
120	345 ± 132	344 ± 132	88 ± 114	0.2821	252 ± 47
Overall	281^{a} ± 28	206^{b} ± 25	123^{c} ± 23	0.0002	
Volume of Small Woody Debris (m^3/ha ± SE)					
25–39	28^{a} ± 4	n.d.^{b}	17 ± 2	0.0336	20 ± 3
40–59	19 ± 4	23 ± 4	16 ± 4	0.4706	19 ± 2
60–79	31 ± 6	19 ± 4	21 ± 5	0.2884	24 ± 3
80–119	39^{a} ± 6	17^{b} ± 4	23^{b} ± 5	0.0163	25 ± 92
120	39 ± 9	12 ± 9	16 ± 8	0.1357	22 ± 4
Overall	28^{a} ± 2	19^{b} ± 2	19^{b} ± 2	0.0031	

[a] Probability values in same row do not differ, as determined by ANOVA. Row values with different superscripts are significant at the level of probability indicated.

[b] No data.

Table 5. Comparison of canopy structure in stands used for foraging and nesting with random locations within Northern Spotted Owl home ranges, western Oregon.

AGE CLASS (yr)	FORAGING	NESTING	RANDOM	P^{a}	OVERALL
Average Crown Volume (m^3 ± SE)					
25–39	197^{a} ± 61	n.d.^{b}	303 ± 31	0.0337	226 ± 47
40–59	253 ± 30	228 ± 98	352 ± 49	0.1309	282 ± 38
60–79	292^{a} ± 89	373^{b} ± 88	571^{a} ± 75	0.0369	424 ± 47
80–119	489 ± 84	477 ± 69	491 ± 79	0.9857	487 ± 39
120	716 ± 112	246 ± 147	641 ± 101	0.6344	536 ± 63
Overall	349 ± 36	376 ± 38	418 ± 32	0.1564	
Average Crown Depth (m ± SE)					
25–39	12.7^{a} ± 1.4	n.d.^{b}	17.0 ± 0.7	0.0113	15.4 ± 1.0
40–59	14.0^{a} ± 0.5	17.1^{b} ± 1.1	17.2^{b} ± 0.7	0.0012	16.0 ± 1.1
60–79	14.4^{a} ± 1.2	18.6^{b} ± 2.5	21.3^{b} ± 1.0	0.0013	18.0 ± 1.0
80–119	18.6 ± 1.1	20.2 ± 2.0	19.0 ± 1.5	0.843	19.0 ± 1.1
120	20.4 ± 1.6	14.5 ± 4.0	20.2 ± 1.5	0.9161	18.1 ± 1.5
Overall	15.5^{a} ± 0.6	18.3^{b} ± 1.3	18.3^{b} ± 0.5	0.0006	

[a] Probability values do not differ, as determined from ANOVA.

[b] No data.

Table 6. Average distance from ground to lowermost whorls of branches on trees at Northern Spotted Owl foraging, nesting, and random locations, western Oregon.

AGE CLASS (yr)	AVERAGE DISTANCE (m ± SE) FORAGING	NESTING	RANDOM	P^{a}	OVERALL
25–39	13.0 ± 2.0	n.d.^{b}	16.2 ± 1.0	0.165	12.3 ± 1.1
40–59	13.8^{a} ± 0.9	16.4^{b} ± 1.3	20.2^{c} ± 1.2	0.0003	16.6 ± 0.8
60–79	18.3 ± 2.7	15.7 ± 1.5	19.9 ± 2.3	0.657	17.9 ± 1.1
80–119	22.2^{a} ± 1.8	17.4^{b} ± 1.1	29.0^{c} ± 1.7	0.0148	22.1 ± 0.9
>120	21.2 ± 3.5	22.9 ± 2.4	31.4 ± 3.1	0.0681	25.3 ± 1.4
Overall	16.8^{a} ± 1.1	17.4^{a} ± 1.2	21.3^{b} ± 1.0	0.0026	

[a] Probability foraging, nesting, and random values do not differ, as determined by ANOVA.

[b] No data.

bined and for stands in the 40–59 and 80–119 year categories (Table 6). The same was true for nest sites in overall comparisons with flying space tending to be less at nest sites.

Understory Vegetation. We found no clear successional trends in understory vegetation cover. Cover of understory vegetation <0.5-m tall was significantly less at foraging locations than at random locations for most age classes (46.0 vs. 65.3%, $P = 0.001$), but understory vegetation cover at nest sites generally did not differ from that at random locations (Fig. 3, 66.2 vs. 65.3%, $P = 0.894$). Understory cover in the other two height classes was more variable. In separate ANOVA comparisons that pooled stands in the two broader classes of Y/MS and LS/OG forests, foraging locations contained

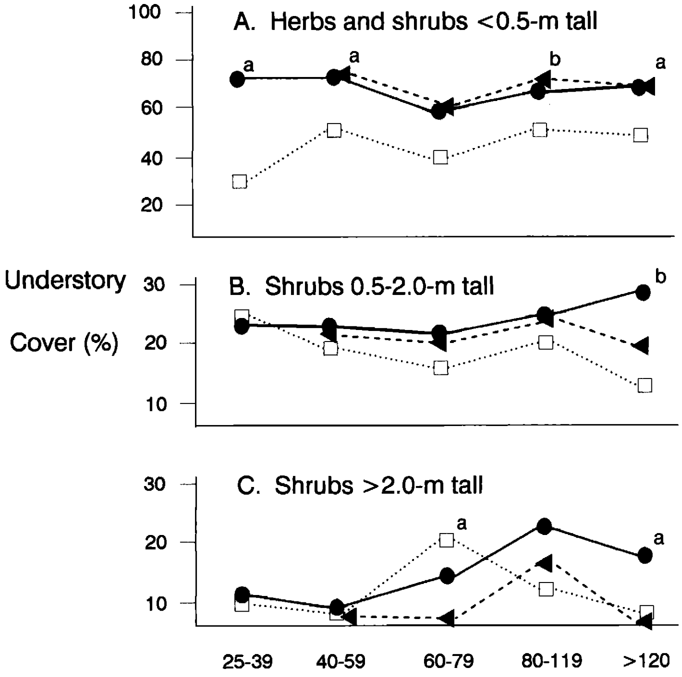

Figure 3. Comparisons by ANOVA of successional trends among foraging areas (squares), nest sites (triangles), and random locations (dots) for three understory cover classes within Northern Spotted Owl home ranges. Superscripts indicate within-age class comparisons that were statistically different at Type-I error probabilities of <0.05 (a) and 0.05–0.10 (b).

less understory vegetation cover 2.0 m in height than did nest sites and random locations in Y/MS forests (64.3% vs. 89.2% and 89.6%, $P < 0.040$). Understory cover at nest sites did not differ from random locations within Y/MS and LS/OG classes.

DISCUSSION

Most forest stand structures increased in abundance with advancing forest succession and probably influenced the choice of Y/MS forests by Northern Spotted Owls for nesting and foraging habitats. The most important stand structures in influencing habitat use were the amount of woody debris and, less consistently, the number of large snags at foraging sites and large-diameter trees at nest sites. The direct connection of standing and downed dead trees to owl biology probably occurs through the relationship between dead wood and the owl's prey. This appears particularly likely for northern flying squirrels (*Glaucomys sabrinus*), which are associated with snags (Carey 1995) and are the primary prey for owls in forests similar to those we studied (Forsman et al. 1984). Northern flying squirrel abundance in Y/MS forests may equal that of LS/OG forests if old-forest legacies (i.e., large trees and snags and downed wood debris) are present and understory vegetation is relatively well-developed (Carey 1995). Many other small forest mammal prey of Spotted Owls also are associated with coarse woody debris on the forest floor (Maser and Trappe 1984, Carey 1995, Carey and Johnson 1995), such as woodrats (*Neotoma* spp.), deer mouse (*Peromyscus maniculatus*), Townsend's chipmunk (*Tamias townsendii*), and western red-backed vole (*Clethrionomys occidentalis*).

Although owl foraging occurred in a broad array of structural conditions across all successional spectra, conditions of nesting sites were more specific. For example, foraging occurred in stands as young as 27 yr, whereas nesting occurred in stands >45 yr. Further, 50% of the nests were in LS/OG stands, which comprised <10% of the study area, and trees containing nests in Y/MS stands were often much older than trees that typified the nest stands. Finally, understory vegetation <2.0-m tall did not influence nest-site choice but did influence use of foraging sites.

Densities of live trees and small and large snags varied with advancing succession at sites used frequently for foraging, which was expected due to competition among trees during the course of forest development (Oliver and Larson 1990). Therefore, most of the stands we sampled were classified as within the stem-exclusion or understory reinitiation phases (Oliver and Larson 1990) of forest succession. However, most of the repeatedly-used foraging stands also contained structural legacies from previous forests, including large trees, large snags and large woody debris, and many nesting sites classified as being in 60-, 80-, or 120-yr old stands met several of the structural components defining old-growth forests in the Western Hemlock Zone (Franklin et al. 1981, Old-Growth Definition Task Group 1986). Similarly, densities of trees 80 cm dbh in most of the stands >80 yr of age met the large-tree criterion of the definition of old-growth forests, or 20 such large trees/ha (Franklin et al. 1981, Old-Growth Definition Task Group 1986). In fact, some of the stands that were 60–79-yr old also contained enough trees 80 cm dbh to meet the large-tree criterion used to define old-growth forest. This was particularly true for 60–79-yr old, repeatedly-used foraging stands which averaged 19 large trees/ha. Such large-diameter trees were not necessarily old, although some were old-growth residuals from previous stands, and others were broken-topped, old-growth western hemlock trees that did not protrude through the overstory canopy.

Because sites that we measured were used frequently for foraging or for nesting and were within core areas (i.e., areas disproportionately used within home ranges), structural features of stands might be important determinants of habitat selection of Northern Spotted Owls. Indeed, several variables exhibited little variation across all age classes of stands within core areas. All stands that were repeatedly used contained dense forest canopies (>80% cover, as estimated by a spherical densitometer) and had well-developed understory vegetation. All but the youngest sites contained large volumes of coarse woody debris, 1 large snag/ha, and at least a few live trees >80 cm in diameter. "Flying space," which varied as expected with advancing succession, was consistently lower at foraging and nesting sites than at random locations.

We were not certain why "flying space" was lower at foraging sites, even though tree diameters and crown volumes were the same as at random locations. It was possible that the lower-slope positions and east and northern aspects of foraging sites may have influenced the development of tree crowns there because of the limited amount of sunlight they receive. In such topographic conditions,

703-59

trees do not self-prune as rapidly as in other topographic settings (Oliver and Larson 1990), so flying space would be lower. In this case, the reduced flying space in foraging sites was simply a consequence of their use of lower topographic locations in the habitat.

We are also unsure what can be inferred from the information on understory vegetation cover, the total of which generally was less at foraging sites than at random and nesting locations. The differences did not appear to be caused by variation in sampling nest sites. Our results were contrary to those of Carey (1995) who suggested use of silvicultural manipulations to increase ericaceous shrubs which would accelerate growth of Northern Spotted Owl habitat in areas where LS/OG is lacking, but they were similar to those of Solis and Gutiérrez (1990) who found less shrub and herb cover at frequently-used Northern Spotted Owl foraging sites in northern California and those of Call et al. (1992) who found less herbaceous cover at owl sites than random locations for California Spotted Owls (*S. o. occidentalis*). We presume that Spotted Owl response to understory vegetation may be unimodal or asymptotic with gradients of understory vegetation cover and with variation in abundance or access to small mammal communities. There is evidence of such nonlinear responses by small mammals to gradients of understory vegetation density and composition (Carey 1995). If so, it seems possible that understory vegetation can be either too sparse, resulting in low prey densities, or too dense, thereby impeding access by owls to prey. The management application of this is to maintain patchy understories providing prey that are both abundant and accessible to owls.

Northern Spotted Owls used Y/MS forests substantially more frequently than reported by Forsman et al. (1984) and Carey et al. (1990) for Spotted Owl home ranges elsewhere in western Oregon. Such differential use of habitats by raptors may be due to local and structural differences in preferred habitats (Mosher et al. 1986). In the managed-forest landscape that we studied, stand structural differences were the most important habitat features determining use by Northern Spotted Owls. For example, turn-of-the-century wildfires left large legacy trees and timber harvesting about 60 yr prior to our study left cull or seed trees across the landscape. Both types of disturbance provided numerous snags and downed structural legacies. Also, the area contained frequent pockets of root-rot (*Armillaria* spp.) that resulted in large piles of downfall.

We believe our information merits judicious application in forest management strategies, which increasingly strive to protect wildlife by applying information from stand- to landscape-levels. Recent examples include the conservation strategy for federal timberlands in the range of the Northern Spotted Owl (Thomas et al. 1993) and that described by Hicks et al. (1999) for managed, private timberlands. Doing so requires an understanding of both the diversity of forest stand structures used by owls and silvicultural procedures than can create them within the context of natural disturbance and timber management. Northern Spotted Owls apparently discriminate and select among Y/MS stands on the basis of stand-structural differences; therefore, providing these structures should be important parts of prescriptions for enhancing the value of young stands. Our information could help forest managers assess the value of future habitat, allowing them to schedule management activities across landscapes. We believe that extensively-managed Y/MS landscapes could contribute significantly to the long-term persistence of Northern Spotted Owls. Until such contributions are demonstrated to support viability, we strongly caution against drawing the inference that Y/MS forests with structural legacies might be an equivalent substitute for LS/OG forests.

Solis and Gutiérrez (1990) predicted that studies of Northern Spotted Owls in managed landscapes would show use of habitats that structurally resemble old-growth forests. Indeed, we found that Spotted Owls selected large, old trees for nests and that they selected foraging areas on the basis of coarse woody debris and understory vegetation in a managed landscape dominated by Y/MS stands. This information provides additional support for habitat restoration as part of a strategy for recovery of the Northern Spotted Owl (Carey 1995) and for blending goals of a forest-based economy with those of a healthy biotic community.

Silvicultural prescriptions could accelerate development of habitat for owls and perhaps other species that frequent LS/OG forests. We suggest that foraging habitat should contain seven large (40 cm dbh) snags/ha and 280 m^3/ha of coarse woody debris, based on averages for 26 repeatedly-used sites in Y/MS forests in forest patches 16 ha in size. These values are similar to those of North et al. (1999), who worked with Northern Spotted Owls in unmanaged forests and those of Buchanan et al. (1999), who recommended some 10 large snags/ha based upon 16 telemetry points in young forests in western Washington. Noting that both small- and large-diameter woody debris apparently influenced use for foraging, we wonder if equivalent amounts of small-diameter logging residue might be piled to create woody debris. Doing so would constitute a topic for experimental research. Foraging success by Northern Spotted Owls may be optimal in stands with a mix of canopy gaps and patchy ground cover (Carey 1995). Thus, precommercial thinnings in patches might support foraging in such areas by maintaining understory vegetation (Omule 1988, Carey and Curtis 1996), as long as total understory cover does not exceed about 75–80%. Skillful applications are required in our area because salal (*Gaultheria shallon*) may quickly form dense patches that exclude both herbaceous and tree-seedling establishment (Huffman et al. 1994). Nesting habitat involves more advanced successional development. Silvicultural prescriptions for providing suitable nest sites in managed forests could be facilitated by thinning to low densities (Tappeiner et al. 1997) and retaining small patches (perhaps 4 ha) that include large legacy trees. We recommend prescriptions that can ensure presence of 4 such trees/ha after a stand age of 40 yr, based upon the observation that only a few nesting stands contained <3 trees/ha >80 cm dbh. Because physical features such as topography and elevation influence use of foraging sites by Spotted Owls (Haufler and Irwin 1993), silvicultural manipulations should vary with topoedaphic conditions. For example, we found that Spotted Owls used areas on the lower half of slopes and near riparian areas most often for foraging (Irwin 1994). Carey and Peeler (1995) also found significant use of lower-slope positions by Northern Spotted Owls in western Oregon. Therefore, management of these areas should be site-specific to ensure their integrity.

ACKNOWLEDGMENTS

This study was funded by Northwest Forest Resource Council, Association of O & C Counties, Bureau of Land Management, and NCASI. We expressly thank R. Doerner, L. Lauritzen, and D. Robertson for helping to secure financial support. R.J. Anderson and D. Woodworth facilitated home range analyses. L. Diller, E. Forsman, and two anonymous reviewers provided helpful criticisms of previous drafts.

LITERATURE CITED

BINGHAM, B.B. AND B.R. NOON. 1997. Mitigation for habitat "take": application to habitat conservation planning. *Conserv. Biol.* 11:127–139.

BUCHANAN, J.B. AND L.L. IRWIN. 1995. Within-stand nest site selection by Spotted Owls in the eastern Washington Cascades. *J. Wildl. Manage.* 59:301–310.

———, ———, AND E.L. MCCUTCHEN. 1993. Characteristics of Spotted Owl nest trees on the Wenatchee National Forest. *J. Raptor Res.* 27:1–7.

———, J.C. LEWIS, D.J. PIERCE, E.D. FORSMAN, AND B.L. BISWELL. 1999. Characteristics of young forests used by Spotted Owls on the western Olympic Peninsula, Washington. *Northwest Sci.* 73:255–263.

CALL, D.R., R.J. GUTIÉRREZ, AND J. VERNER. 1992. Foraging habitat and home-range characteristics of California Spotted Owls in the Sierra Nevada. *Condor* 94:880–888.

CAREY, A.B. 1985. A summary of the scientific basis for Spotted Owl management. USDA For. Serv. Gen. Tech. Rep. PNW-185, Portland, OR U.S.A.

———. 1995. Sciurids in Pacific Northwest managed and old-growth forests. *Ecol. Applic.* 5:648–661.

——— AND R.O. CURTIS. 1996. Conservation of biodiversity: a useful paradigm for forest ecosystem management. *Wildl. Soc. Bull.* 24:610–620.

——— AND M.L. JOHNSON. 1995. Small mammals in managed, naturally young, and old-growth forests. *Ecol Applic.* 5:336–352.

——— AND K. PEELER. 1995. Spotted Owls: resource and space use in mosaic landscapes. *J. Raptor Res.* 29:223–239.

———, 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.

———, S.P. HORTON, AND B.L. BISWELL. 1992. Northern Spotted Owls: influence of prey base and landscape character. *Ecol. Monogr.* 62:223–250.

———, ———, AND J.A. REID. 1989. Optimal sampling for radiotelemetry studies of Spotted Owl habitat and home-range. USDA For. Serv. Res. Pap. PNW-RP-416, Portland, OR U.S.A.

———, J. KERSHNER, B. BISWELL, AND L. DOMINGUES DE TOLEDO. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. *Wildl. Monogr.* No. 142.

COOK, J.G., T.W. STUTZMAN, C.W. BOWERS, K.A. BRENNER, AND L.L. IRWIN. 1995. Spherical densitometers produce biased estimates of forest canopy cover. *Wildl Soc. Bull.* 23:711–717.

FORSMAN, E.D., E.C. MESLOW, AND M.J. STRUB. 1977. Spotted Owl abundance in young versus old-growth forests. *Wildl. Soc. Bull.* 5:43–47.

———, ———, AND H.M. WIGHT. 1984. Distribution and

703-59

biology of the Spotted Owl in Oregon. *Wildl. Monogr.* No. 87.

FRANKLIN, J.F. AND C.T. DYRNESS. 1981. Natural vegetation of Oregon and Washington. Oregon State Univ. Press, Corvallis, OR U.S.A.

———, K. CROMACK, JR., W. DENISON, A. MCKEE, C. MASER, J. SEDELL, F. SWANSON, AND G. JUDAY. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PNW-118, Portland, OR U.S.A.

GUETTERMAN, J.H., J.A. BURNS, J.A. REID, R.B. HORN, AND C.C. FOSTER. 1991. Radio telemetry methods for studying Spotted Owls in the Pacific Northwest. USDA For. Serv. Gen. Tech. Rep. PNW-272, Portland, OR U.S.A.

HAUFLER, J.B. AND L.L. IRWIN. 1993. An ecological basis for forest planning for biodiversity and resource use. *Proc. Int. Union Game Biol.* 21:73–81.

HICKS, L.L., H.C. STABINS, AND D.R. HERTER. 1999. Designing Spotted Owl habitat in a managed forest. *J. Forest.* 97:20–25.

HUFFMAN, D.W., J.C. TAPPIENER, II, AND J.C. ZASADA. 1994. Regeneration of salal (*Gaultheria shallon*) in the central Coast Range of Oregon. *Can. J. Bot.* 72:39–51.

HUNTER, J.E., R.J. GUTIÉRREZ, AND A.B. FRANKLIN. 1995. Habitat configuration around Spotted Owl sites in northwestern California. *Condor* 97:684–693.

IRWIN, L.L. 1994. A process for improving wildlife habitat models for assessing forest ecosystem health. *J. Sustain. Forestry* 2:293–306.

———, S. SELF, AND L. SMITH. 1989. Status of Northern Spotted Owls in managed forestlands in northern California. Timber Assoc. of Calif., Unpubl. Rep. Sacramento, CA U.S.A.

JOHNSON, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.

LAHAYE, W.S. AND R.J. GUTIÉRREZ. 1999. Nest site selection and nesting habitat of the Northern Spotted Owl in northwest California. *Condor* 101:324–330.

LAYMON, S.A. AND J.A. REID. 1986. Effects of grid-cell size on tests of a Spotted Owl HSI model. Pages 93–96 *in* J. Verner, M.L. Morrison, and C.J. Ralph [EDS.], Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison, WI U.S.A.

MASER, C. AND J.M. TRAPPE. 1984. The seen and unseen world of the fallen tree. USDA For. Serv. Gen. Tech. Rep. PNW-285, Portland, OR U.S.A.

MOSHER, J.A., K. TITUS, AND M.R. FULLER. 1986. Developing a practical model to predict nesting habitat of woodland hawks. Pages 31–35 *in* J. Verner, M.L. Morrison, and C.J. Ralph [EDS.], Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison, WI U.S.A.

NORTH, M.P., J.F. FRANKLIN, A.B. CAREY, E.D. FORSMAN, AND T. HAMER. 1999. Forest stand structure of the Northern Spotted Owl's foraging habitat. *For. Sci.* 45: 520–527.

OLD-GROWTH DEFINITION TASK GROUP. 1986. Interim definitions for old-growth Douglas-fir and mixed-conifer forests in the Pacific Northwest and California. USDA For. Serv. Res. Note PNW-447, Portland, OR U.S.A.

OLIVER, C.D. AND B.L. LARSON. 1990. Forest stand dynamics. McGraw-Hill, Inc., New York, NY U.S.A.

OMULE, S.A.Y. 1988. Growth and yield 35 years after commercially thinning 50-year old Douglas-fir. British Columbia Ministry Forests and Lands. For. Resource Develop. Agree. Rep. 021, Victoria, BC Canada.

PORTER, W.F. AND K.E. CHURCH. 1987. Effects of environmental pattern on habitat preference analysis. *J. Wildl. Manage.* 51:681–685.

ROSENBERG, D.K. AND K.S. MCKELVEY. 1999. Estimation of habitat selection for central-place foraging animals. *J. Wildl. Manage.* 63:1028–1038.

SAMUEL, M.D., D.J. PIERCE, AND E.O. GARTON. 1985. Identifying areas of concentrated use within the home range. *J. Anim. Ecol.* 54:711–719.

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

SPIES, T.A. 1989. Characterization of old-growth Douglas-fir forests of western Oregon and Washington. Unpubl. study plan. U.S. Forest Service, Corvallis, OR U.S.A.

TAPPEINER, J.C., D. HUFFMAN, D. MARSHALL, T.A. SPIES, AND J.D. BAILEY. 1997. Density, ages, and growth rates in old-growth and young-growth forests in coastal Oregon. *Can. J. For. Res.* 27:638–648.

TEENSMA, P.D. 1987. Fire history and fire regimes of the central western Cascades of Oregon. Ph.D. dissertation, Univ. Oregon, Eugene, OR U.S.A.

THOMAS, J.W., M.G. RAPHAEL, R.G. ANTHONY, E.D. FORSMAN, A.G. GUNDERSON, R.S. HOLTHAUSEN, B.G. MARCOT, G.H. REEVES, J.R. SEDELL, AND D.M. SOLIS. 1993. Viability assessments and management considerations for species associated with late-successional and old-growth forests of the Pacific Northwest. The report of the Scientific Analysis Team, USDA For. Serv., 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.

WORTON, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.

———. 1995. Using Monte Carlo simulation to evaluate kernel based home range estimators. *J. Wildl. Manage* 59:794–800.

Received 2 September 1999; accepted 18 March 2000