
Forest Stand Structure of the Northern Spotted Owl's Foraging Habitat

Malcolm P. North, Jerry F. Franklin, Andrew B. Carey, Eric D. Forsman, and Tom Hamer

ABSTRACT. Although the spotted owl's close association with old growth has been extensively studied, it has been more difficult to identify and quantify the abundance of particular stand structures associated with preferred owl foraging sites. Old-growth forests have a suite of characteristics that distinguish them from younger forests but which also make it difficult to isolate individual structural features important to the spotted owl. This study used an analysis of use-only sites in areas where natural disturbance had created a gradient of old-growth structural characteristics. We used radio telemetry data collected from reproducing owl pairs to locate sample stands and compute a relative measure of owl-use intensity in each stand. Snag volume and tree height class diversity (a measure of canopy layering) were the stand structures significantly associated with owl foraging intensity. Stands with 142 m³/ha of intact snags and a high diversity of tree heights had medium or high foraging use by spotted owls. In these old-growth stands, biological legacies (e.g., large trees and snags) produced by past disturbance provide important forest structures associated with spotted owl foraging use. *For. Sci.* 45(4):520–527.

Additional Key Words: Old growth, stand structure, radio telemetry, canopy structure, biological legacies.

HABITAT PROTECTION FOR THE SPOTTED OWL (*Strix occidentalis*) has become an important goal of forest management in many public forests of the western United States. For the northern spotted owl, research has provided information on the owl's life history and macrohabitat selection (i.e., preferred forest seral stage) (Forsman et al. 1984, Carey et al. 1992); demographics (Forsman et al. 1996); diet (Forsman et al. 1984, Forsman et al. 1991); home range size (Carey et al. 1990, 1992, Solis and Gutiérrez 1990, Carey and Peeler 1995), and the effects of forest fragmentation on owl home range size (Carey et al. 1992, Gutiérrez 1994, Carey and Peeler 1995). While the northern spotted owl's close association

with old growth has been documented extensively (Forsman et al. 1984, Gutiérrez and Carey 1985, Carey et al. 1990, 1992, Thomas et al. 1990), it has been more difficult for managers to evaluate the relative habitat potential of different stands. Mid- to late-seral forests, including old growth, can be highly variable in structure and composition (Spies and Franklin 1991) producing stands that differ in their habitat suitability for different species (Carey 1989). These differences can provide insights for developing prescriptions (e.g., retaining forest structures) to enhance the habitat potential of developing stands. Quantitative measures of specific structures associated with owl use, particularly for foraging areas because of their exten-

Malcolm P. North, Postdoctoral Research Associate, College of Forest Resources, AR-10, University of Washington, Seattle, Washington 98195 Presently Research Plant Ecologist, USDA Forest Service, Pacific Southwest Research Station, Forestry Sciences Lab, Fresno, CA 93710—Phone: (559) 487-5196; Fax: (559) 487-5978; E-mail: mnorth/psw_fresno@fs.fed.us. Jerry F. Franklin, Professor of Forest Ecosystems, College of Forest Resources, AR-10, University of Washington, Seattle, Washington 98195—E-mail: jerry@lternet.edu. Andrew B. Carey, Research Wildlife Biologist, USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington 98502—E-mail: efb@olywa.net. Eric D. Forsman, Research Wildlife Biologist, USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon 97331—E-mail: eforfman/r6pnw_corvallis@fs.fed.us. Tom Hamer, Hamer Environmental, 19997 Hwy 9, Mt. Vernon, WA 98274—E-mail: hamert@aol.com.

Acknowledgments: We thank Kevin Peeler, PNW Research, Olympia, WA, for help with the radio telemetry data sets, and Joel Reynolds, Dept. of Statistics, Univ. of Washington, Seattle, WA, for statistical consulting. Our thanks to three anonymous reviewers for their helpful comments on an earlier version of this manuscript. Funding for this project was provided by the Ecosystem Research Group, College of Forest Resources, Univ. of Washington.

sive size, could help foresters evaluate present and improve potential future spotted owl habitat under their stewardship.

Foraging habitat studies of the California, Mexican, and northern spotted owl (*Strix occidentalis occidentalis*, s.o. *lucida*, and s.o. *caurina*, respectively) have found an association between owl-use areas and several stand characteristics that typify old-growth forests, including high canopy closure, multiple vegetative strata, large tree size classes, and a high volume of woody debris (Laymon 1988, Solis and Gutiérrez 1990, Call et al. 1992, Ganey and Balda 1994). These studies compared site characteristics at owl use to random sites to assess how conditions at foraging sites differed from the surrounding forest. It is difficult, however, to isolate particular structural attributes associated with foraging because conditions at owl use and random sites may be markedly different (e.g., old-growth and young-managed forests). Furthermore, it is hard to quantify forest structures that influence foraging behavior because the use and potential habitat value of the random sites is unknown. To improve our understanding of the habitat potential of different sites requires a quantitative model comparing changes in stand structure with different levels of foraging use at known spotted owl sites.

This study examined how owl-use intensity varied across a range of old-growth forest stand structures. Our objectives were to identify individual forest structures associated with foraging site use and to quantify levels at which changes in structure were associated with changes in owl use-intensity. Our purpose is to provide better information on specific stand structural features associated with northern spotted owl foraging to assist in assessing use intensity of existing habitat and improving silvicultural treatments which might create future owl habitat. Forest structure, however, is probably only one influence on forage site selection as local prey abundance will be influenced by many factors, including a site's foraging history (Carey and Peeler 1995).

Study Areas

Sample stands were concentrated in three locales of Washington State, two areas on the west side of the Olympic Peninsula near the town of Forks and near Lake Quinault, and one in the North Cascade Range near Mt. Baker (Figure 1). Stands in all three areas were predominantly old growth with dominant trees ≥ 100 cm dbh and ≥ 300 yr old, or wind or fire disturbed stands with old-growth legacy structures.

The Olympic Peninsula sites were located in the Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) zones (Franklin and Dyrness 1988) at 200 to 700 m elevation. The sites were in a band of coastal rainforest with year-round moderate temperatures and mean annual precipitation of 280 cm. The most common plant association was Sitka spruce/swordfern-oxalis (*P. sitchensis*/*Polystichum munitum*-*Oxalis oregana*), although study sites were dominated by western hemlock and western red cedar (*Thuja plicata*) (Henderson et al. 1990).

On the Olympic Peninsula, many overstory trees in west-aspect stands within 50 km of the Pacific Coast were signifi-

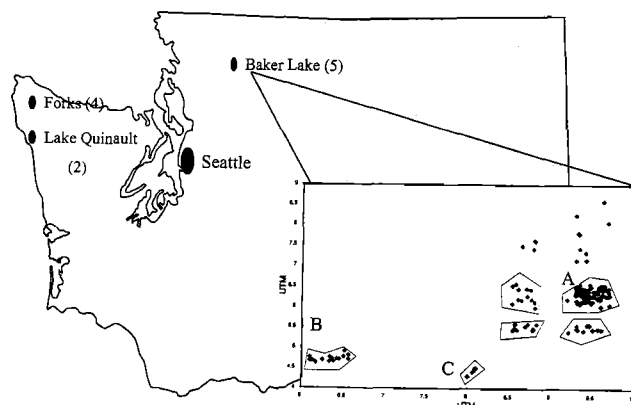


Figure 1. Study site locations and the number of owl-pair telemetry data sets used at Forks, Lake Quinault, and Baker Lake, Washington. Radio telemetry locations and stand boundaries are shown for one pair near Baker Lake. Stand A is a high use stand (36% of the total selected telemetry locations), stand B is a medium use stand (7%), and stand C is a low use stand (2%).

cantly affected by a 1921 storm with winds in excess of 250 km/hr (Henderson et al. 1990). Storm damage varied between owl-use sites depending on distance from the coast, aspect, slope, and soils. Some inland, leeward stands were unaffected by the storm. This event left a legacy of large-diameter, tall snags, abundant coarse woody debris, and scattered large trees with irregular crowns. In most stands it also released the advanced regeneration of shade-tolerant species, such as western hemlock, western redcedar, and silver fir (*Abies amabilis*), which currently dominate the overstory.

The North Cascade sites were at 250 to 800 m elevation in the *Tsuga heterophylla* zone (Franklin and Dyrness 1988) in the western foothills of the Cascade Range. The dominant plant association was western hemlock/sword fern-foam flower (*T. heterophylla*/*P. munitum*-*Tiarella trifoliata*). The vegetation in all stands was a mixture of Douglas-fir, western hemlock, and western red cedar. Annual precipitation is approximately 220 cm (Henderson and Peters 1985).

In the North Cascades, severe localized windstorms in 1911 and 1917 blew over some trees in owl-use stands near Baker Lake. These stands had a few scattered large western redcedar and Douglas-fir, but 50 to 70% of the overstory trees were western hemlock and silver fir that were released following the windstorm. In another area, east of Baker Lake, a wildfire in 1865 killed approximately 65% of the trees in what are presently owl-use stands (Henderson and Peters 1985). Remnant large Douglas-fir and western redcedar were mixed with a few large, decayed snags and a younger cohort of Douglas-fir and western hemlock. None of these stands has been harvested, and all have multilayered canopies and high levels of coarse woody debris.

Methods

Identifying particular structural attributes associated with spotted owl foraging is difficult because old growth in the Pacific Northwest has a suite of associated vegetative characteristics that distinguish it from younger seral stages (i.e., large diameter trees, snags and logs, multilayered canopies, diverse understory, etc.). An effective analysis must identify

this array of old-growth attributes and distinguish how owl foraging intensity changes with different levels of particular stand structures. To increase the discriminant power of our analysis, we imposed two conditions on our study design. First, we identified a gradient of foraging use intensity from radio telemetry data and avoided using absence or random sites of unknown forage value. Second, to separate the covariance of forest structures in old growth, owl telemetry data sets were screened to select pairs using areas that included a past disturbance (e.g., fire or windstorm) so as to provide foraging sites with a gradient of old-growth attributes. For example, a windstorm that blows down much of a stand's overstory reduces the number and size of dominant trees and changes canopy structure while increasing snag and coarse woody debris abundance. This variation provided a range of stand structures to analyze against changes in owl-use patterns.

In this microhabitat study, the forest stand, not the owl pair, was the unit of analysis. Differences in stand structure were compared against levels of owl use-intensity during foraging. We assumed that different owl pairs would have similar stand structure preferences although forest species composition may vary (Carey et al. 1992, Carey and Peeler 1995). Studies using multiple owl pairs have found a consistent macrohabitat association between different owl pairs and old-growth forests (Forsman et al. 1984, Carey et al. 1990), but differences in microhabitat structure use between pairs was not tested explicitly.

Using Radio Telemetry Locations

Models of animal microhabitat are often developed by comparing vegetation between sites where an animal has been located ("presence") and either random locations or sites where the animal was not found ("absence") (Noon 1986). This type of analysis is limited because the actual habitat value of the absence or random sites is unknown (Johnson 1981). An alternative method is only to analyze presence sites and derive a measure of use-intensity based on radio telemetry locations on reproducing animals (North and Reynolds 1996).

To provide information on use patterns, we used three guidelines to screen owl telemetry data sets. First, only owl pairs with telemetry data of >1 yr (16–44 months) were selected to provide a better estimate of general use patterns within a home range. Second, we selected owl pairs that had a history of reproductive success to ensure selected sites were capable of supporting reproduction. Third, owl-pair home ranges were selected in which past fire and wind disturbance had affected some of the owl-use sites providing a range of stand structure. These disturbances produced a gradient of old-growth characteristics by varying the abundance of different stand structures.

Using these criteria, we selected telemetry data for 11 owl pairs in western Washington. Locations were screened to select for foraging behavior, telemetry error, decrease autocorrelation, and for stands of similar size. To select probable foraging locations, night telemetry locations for males and nonnesting season females were used. To reduce telemetry error, only locations with a triangulation polygon

of ≤ 2 ha were selected. To reduce autocorrelation between telemetry locations (Swihart and Slade 1985), only locations separated by ≥ 72 hr were included in the analysis (Carey et al. 1989). To standardize size of use-sites, telemetry locations were plotted, and use stands were identified by boundaries on aerial photos defined by clearcuts or distinct changes in stand age and structure (i.e., adjacent young, managed forests). Only stands between 40 and 80 ha (the dominant grain in these managed landscapes) were included in the analysis (Figure 1). Stands of this size in the study areas had a relatively homogeneous structure. Telemetry data for each owl pair were screened to meet these criteria and a subset of locations was selected for use in the subsequent analysis.

We calculated owl use-intensity by using the number of telemetry points in a stand as a percentage of the total number of locations for each pair. This identified each stand with a percentage of total telemetry locations ranging from 1 to 36%. A histogram of the number of stands for each percentage value was made indicating three general cluster patterns in use-intensity: 1–2%, 3–9%, and $\geq 10\%$. These values corresponded to the general pattern noted in telemetry locations within each owl home range. Owl use was very high (stands with $\geq 10\%$) in a few selected stands with many visits, whereas other sites had a moderate number of repeat visits (3–9%) and a few stands had only 1–4 visits (1–2%). There was no difference between mean distances from the core activity area or nest site to foraging areas between low, medium, and high use stands (ANOVA, $P > 0.26$). Using the histogram groupings and this home-range use pattern, stands with 1–2% of total telemetry points were assigned a low-use intensity. Stands with 3–9% of total telemetry points were given a medium-use intensity value and stands with $\geq 10\%$ of the telemetry locations were assigned a high-use intensity value. This selection process identified 43 stands with low, medium, and high use values that were distributed widely across the 11 owl home ranges.

Stand Structure Sampling

We sampled 172 randomly located plots in 43 stands: 13 low use, 12 medium use, and 18 high use. We used a nested circular plot design where the minimum vegetation structure size sampled increased with plot size. This system provided an effective means of sampling large, less common trees and snags without oversampling small diameter structures. In a pilot study of stand-level means for tree, snag, and log variables, we found that variance stabilized at 3–4 plots per stand. Although old growth is highly variable across its geographic range, within the study area sample stands were relatively homogeneous within their 40–80 ha area.

At each plot, we recorded aspect, slope, slope position, elevation, canopy cover, distance to the nearest large opening (i.e., clearcut, field, or urban area), and distance to the nearest perennial water. In four 0.0004 ha plots, a string grid overlay was used for ocular estimates of herb and shrub cover to the nearest percent. In a 0.05 ha plot, all trees (species, dbh, height, canopy class, crown form, cavities, and mistletoe rating) and snags (species, dbh, height, decay class, and number of cavities) ≥ 5 cm dbh were measured with diameter tape and clinometer and classified by trained field techni-

cians. In a 0.1 ha plot, we measured all trees and snags ≥ 50 cm dbh, all logs (large and small diameter, length, and decay class), and crown dimensions of all trees (total height, height to full crown, height to partial crown, arc of the partial crown [degrees/360°], crown shape, and two crown diameters) to calculate foliage volume. In a 0.2 ha plot, all snags ≥ 50 cm dbh and all trees ≥ 80 cm dbh were measured. Measurement variables of forest structure were calculated from the plot data, standardized to per ha values, and averaged for the four sample plots collected in each owl-use stand.

Variable Selection

Although there were many potential site variables given the number of measurement categories describing each structure, only measurements of stand structure that previous research suggests may be important to the owl were included in the analysis. Results from habitat analyses for the northern, California, and Mexican spotted owl were reviewed (Forsman et al. 1984, Carey et al. 1990, Solis and Gutiérrez 1990, Call et al. 1992, Ganey and Balda 1994) and six categories of stand characteristics were developed: live trees, snags, logs, topographic characteristics, understory vegetation, and canopy structure. For each of the 6 categories, measures of structure for each of the 43 stands were calculated from plot data.

For live trees, basal area of all trees and large trees only (dbh ≥ 80 cm) were calculated because large diameter trees are a distinguishing characteristic of old growth (Franklin et al. 1981), and some studies have found higher basal area of large trees in foraging sites compared to random sites (Laymon 1988, Solis and Gutiérrez 1990, Call et al. 1992). The standard deviation of tree diameter is usually higher in structurally complex stands, and in one study (Spies and Franklin 1991) was one of the best discriminants of old growth from younger age stands. Stem density for all trees, large trees (≥ 80 cm), and subcanopy trees, classified as intermediate or suppressed, was calculated because stands with fewer but larger trees may provide better prey capture opportunities than stands with a high density of understory trees (Forsman et al. 1984).

For snags, we calculated basal area, volume, and volume of intact snags (decay classes I–III). Snag volume was calculated using diameter, height, and an estimated top diameter assuming a taper function of 1.2 cm per meter of height (Spies and Franklin 1991). The volume of intact snags was analyzed because decay class IV and V snags (Cline et al. 1980) are usually unstable and may not provide secure cavity sites. The volume of all logs, volume of big logs (small diameter ≥ 50 cm and length ≥ 8 m) and density of big logs (no./ha) was calculated. Foraging studies for the California (Laymon 1988, Call et al. 1992) and Mexican (Ganey and Balda 1994) spotted owl have suggested owl-use stands have higher log volumes than random comparison sites.

Two understory vegetation variables were included in the analysis: total understory cover and the coefficient of variation of cover. High understory cover may limit the owl's ability to capture prey on the forest floor (Carey 1991). The variability of shrub cover between the 0.0004 ha plots was calculated because foraging success may increase in stands with a mix of openings and cover (Carey 1995).

Canopy structure may play an important role in forage site selection because of its potential to provide protection from predators (Forsman et al. 1984), modify microclimate conditions (Carey 1985), influence prey abundance, or facilitate prey capture (Carey 1995). Canopy cover was measured using the average of 10 moosehorn readings (a modified funnel topped with a clear sighting grid with 100 points) systematically collected at each plot. Total crown volume per ha was estimated by summing the volume of canopy space occupied by each tree in the 0.1 ha plot. Crown volume was modeled as the sum of two solids for each tree (Van Pelt and North 1996, in press), a sectioned cylinder for the partial crown and one of four conic shapes (cone, cylinder, truncated ellipse, or umbrella) for the full crown. The sum of the partial and full crown volumes approximates the amount of canopy space each tree crown occupies by treating each crown as a simple solid. The model does not account for crown irregularities or the lack of foliage inside the crown shell near the tree bole.

Multilayer canopies are considered a distinguishing characteristic of old-growth forests (Franklin et al. 1981), and structural diversity may increase foraging success by providing low perches and sufficient openings for prey capture. Canopy layering was measured by applying the Berger-Parker index (d), a measure of evenness (Magurran 1988), to seven height classes (2–4, 4–8, 8–16, 16–32, 32–48, 48–64, > 64 m) and five canopy classes assigned to each live tree (North 1993). The index is calculated as

$$d = N_{total}/N_{max}$$

where N_{total} is the total number of trees and N_{max} is the number of trees in the height or canopy class with the most trees. High Berger-Parker index values indicate a greater diversity (i.e., more evenness and less dominance) in tree heights or canopy classes and provide a rough measure of multilayering (see Carey et al. 1992 for a similar application with four vegetation strata).

The number of cavities large enough for a squirrel den (diameter ≥ 8 cm) observed from the ground was also tallied. Although large, intact snags may be present in a stand, they may not have excavated cavities. While this measure was an effort to tally available cavities directly, it was prone to some error when the surveyed snag or possible cavity could not be observed clearly.

Analysis

The first step of the analysis evaluated the distribution of each of the 25 variables for all stands using the Shapiro-Wilk test. Nonnormal variables ($P \leq 0.05$, Zar 1984) were log- or sine-transformed. Differences in structure variables between use-intensity class were evaluated with ANOVA and Tukey's post-hoc analysis (SPSS 1996). Because the methods used to screen telemetry and identify suitable stands reduced sample size, the power of the ANOVA test was calculated to determine the precision of the analysis (Borenstein et al. 1997).

Following the ANOVA analysis, significant structure variables were evaluated with multivariate analysis to examine interaction effects and determine the best predictors of owl use-intensity. Before multivariate analysis, variables

were checked for multicollinearity, which is often a problem in microhabitat analysis because different measures of structure are often highly correlated within the same macrohabitat (e.g., old-growth stands with large diameter trees usually have large snags and logs). However, using old growth in which disturbance had produced variable stand conditions helped reduce possible collinearity problems among structure variables. To test for collinearity, variables were assessed against a threshold variance inflation factor (VIF) of 15 (Belsley et al. 1980, SPSS 1996).

Classifications of owl-use intensity were modeled against selected structure variables using a classification and regression tree (CART) analysis. CART produces tree-based classifiers using binary recursive partitioning. Data are successively split along coordinate axes of the predictor variables so as to maximize the difference between the response variable in the left and right branches of the node (SYSTAT 1997). Splitting stops when all the nodes are either pure in their responses or contain too few observations to warrant further splitting. CART uses maximum likelihood algorithms that do not require an equal covariance structure between the independent variables or multivariate normality, two conditions required by discriminant and regression analyses rarely met by ecological data (North and Reynolds 1996). CART models produce a dichotomous tree output, which shows a hierarchical relation between the independent variables and indicates threshold values at which classification of the dependent variable (i.e., owl-use intensity) changes. A comparative study found CART had equal or lower misclassification rates than discriminant analysis and produced a more heuristic model (LeMay et al. 1994).

Owl foraging use intensity was analyzed using the "twoing" model of CART (Breiman et al. 1984). The pruning level for the classification tree was set to stop splitting response nodes at either a minimum proportion of 0.05, or five responses. CART models are algorithm-based, making reliability difficult to assess without further testing. Without collecting a new data set, model reliability was evaluated using a jackknifing procedure. Each stand was separated, one at a time, from the other stands, and independently classified using equations calculated from the 42 stands remaining in the model.

Results

Of the 25 variables, 4 (overstory cover, distance to an opening, distance to water, and total crown volume) were not normally distributed and were log-transformed. Aspect was transformed and compared using the Watson-Williams test (Zar 1984). Because of the sample size, an explicit calculation of the trade-off between Type I and II errors was made. To detect a "large" effect (0.4, cf. Cohen 1988) in foraging use-intensity with a sample size of 12 (the number of stands in the medium use or smallest category), an alpha of 0.1 produced a power of 0.7 (Borenstein et al. 1997).

Six stand attributes were significantly different by owl use-intensity level (Table 1), the density of trees ≥ 80 cm dbh, snag basal area, snag volume, intact snag volume (decay classes I–III), foliage volume, and diversity of tree height

classes. The three snag variables were collinear (VIF 35–46) Morrison et al. (1987, 1992) suggest keeping the variable that is the most biologically meaningful or easiest to measure, and discarding the other collinear variables before a multivariate analysis. We selected snag volume because it is a more direct measure of biomass than basal area and does not depend on assumptions about use depending on decay condition.

The CART analysis selected two variables for classifying different levels of owl-use intensity, snag volume, and tree height class diversity (Figure 2). The first classification division between low use and medium and high foraging use sites was a snag volume of 142.1 m³/ha. A tree height class diversity value of < 3.1 distinguished most medium-use from high-use foraging stands. The jackknife test of the CART analysis misclassified 6 of the 43 stands (14%), 4 medium and 2 high foraging use stands.

Discussion

Our study focused on differences in foraging use in response to variation in old-growth stand structure. To assess long-term owl viability, forest managers need to know how habitat differs among available old-growth stands, and the future habitat potential of mature and managed stands. The precision of our analysis ($\alpha = 0.1$, $\beta = 0.7$) was limited by a sample size restricted to meeting criteria for identifying old-growth stand structure. Starting with 11 owl pairs, each with 80–300 telemetry locations, telemetry and sample stands were screened to meet conditions which provided a standardized measure of owl-use intensity against a gradient of old-growth conditions within the study areas. A study without restrictions on stand disturbance history and which used randomly selected "absence" sites would have a much larger sample size and much "noisier" data. This study's selection criteria traded a large sample size for a highly specified data set designed to separate the covariance of structural attributes in old growth used by owls. Selecting sample areas where disturbance has affected some of the stands could bias the identification and quantification of stand structures because fire and wind disturbance increase snag and coarse woody debris volume, and reduce the number of large live trees. However, comparing values in this study with a large regional assessment of old-growth Douglas-fir (Table 2 in Spies and Franklin 1991) found few significant differences.

Of the 25 stand structures examined, all of the snag variables were significantly different between owl use-intensity levels. In the CART analysis a snag volume greater than 142.1 m³/ha was correlated with an increase in foraging use from low to medium and high. In the study areas, $\geq 70\%$ of the snag volume was derived from large snags (dbh ≥ 50 cm) rather than the small but numerous suppressed and intermediate dead trees. The size of large snags on medium and high foraging use areas averaged 86 cm dbh (SD = 15.4) and 24 m tall (SD = 14.3), with a mean density of 15/ha (SD = 4.6). Snag sizes were variable on sample plots, but medium and high use areas often had large rot-resistant snags (western redcedar or Douglas-fir) resulting from the site's past disturbance.

Table 1. Mean values and standard deviation (in parentheses) of structural attributes in foraging stands with low, medium, and high owl-use intensity. Variables are grouped by six general site characteristics. Values with different letter superscripts are significantly different at $P \leq 0.1$. (Tukey post-hoc ANOVA analysis).

Stand Attributes	Owl-use intensity		
	Low ($n = 13$)	Medium ($n = 12$)	High ($n = 18$)
Live Trees:			
Basal area (m^2/ha)	65.5 (15.3)	75.5 (25.7)	75.9 (22.5)
Big tree basal area*	25.2 (14.1)	42.9 (29.8)	42.8 (28.2)
Standard deviation of dbh	25.2	29.2	30.2
Tree density (no./ha)	411.8 (83.5)	446.3 (140.2)	425.3 (128.1)
Big tree density	26.5 ^a (11.4)	33.8 ^{ab} (11.1)	38.9 ^b (13.7)
Sub-canopy tree density [†]	223.4 (59.1)	280.9 (129)	267.7 (128.1)
Snags:			
Basal area	8.9 ^a (2.2)	17.9 ^b (4.4)	21.9 ^c (5.1)
Volume (m^3/ha)	75.8 ^a (45.2)	167 ^b (45.2)	254.1 ^c (94)
Volume of "intact" ^{††} snags	69.6 ^a (25.6)	120.7 ^a (59.5)	215.2 ^b (102.2)
Logs:			
Volume	315.3 (136.6)	400.5 (194.5)	440.9 (142.6)
Volume of big logs [§]	142.7 (101)	217.2 (208.1)	228.6 (136.2)
Density of big logs	23.4 (16.4)	28.6 (10.7)	33.3 (14.6)
Site Characteristics:			
Distance to opening (m)	221.2 (173.8)	308.6 (244.2)	222.2 (119.6)
Distance to water (m)	127.89 (109.08)	118.48 (140.15)	151.81 (90.7)
Aspect	142° (47°)	125° (32°)	153° (28°)
Elevation (m)	342 (53)	311 (67)	324 (62)
Understory Vegetation:			
Total cover (%)	83.9 (61.5)	57.2 (34.5)	60.6 (36.9)
Coefficient of variation of cover	72.7	79.5	82.4
Canopy:			
Overstory cover (%)	92.6 (2.4)	93.6 (2)	92.8 (3.4)
Foliage volume (m^3/ha)	77,262 ^a (14,198)	92,532 ^a (23,931)	106,699 ^b (19,867)
Diversity of canopy classes [#]	2.4 (0.6)	2.44 (0.5)	2.3 (0.3)
Diversity of height classes	2.4 ^a (0.3)	2.8 ^b (0.4)	3.4 ^c (0.5)
Coefficient of variation of tree heights	43.5	50.2	51.7
Mistletoe rating ^{§§}	2.0 (1.4)	1.46 (0.9)	2.2 (1.2)
Number of cavities	19.3 (9.8)	25.5 (10.2)	27.7 (14.6)

* Big trees were defined as trees with dbh ≥ 80 cm

† Subcanopy trees were trees classed as intermediate or suppressed.

†† Intact snags were those assigned a decay class of I, II, or III (Cline et al. 1980).

§ Big logs were defined as having a diameter ≥ 50 cm. and a length ≥ 8 m.

|| Understory cover included total herb and shrub cover up to 4 m high.

Trees were visually assessed and categorized as one of five canopy classes: emergent, dominant, codominant, intermediate, or suppressed.

§§ Values are the average Hawksworth rating on a scale of 0–6 (Hawksworth 1977).

The other feature of stand structure associated with foraging use intensity was height class diversity. High use stands had values greater than 3.1, which is a measure of how much diversity there is between height classes for all trees within a stand. For example, in high-use stands where height class diversity averaged 3.4 (d) and mean density was 425.3 trees/ha (n_{total}), the maximum number of trees (n_{max}) in any one of the six height categories would be 125/ha. As height class diversity increases, the canopy is less dominated by trees of similar height and heterogeneity increases. Stands with a wide range of tree heights usually have a greater number of foliage layers. In southwestern Oregon, Carey et al. (1992) also identified foliage height diversity as an important feature of owl roost and foraging sites.

Snag volume could be important to owl foraging sites because it influences local prey abundance (Carey 1995). Snags, particularly large intact snags, are likely to have excavated cavities used by the northern flying squirrel (*Glaucomys sabrinus*) (Carey 1991), a staple of the owl's diet

in mesic forests (Forsman et al. 1984, Forsman et al. 1991). Study results from experiments with cavity nesting boxes (Witt 1991) suggest that the density of flying squirrels may be influenced by cavity availability. Consequently, stands with high snag volumes could provide the structures needed to support higher prey populations for the owl. Although a direct measure of cavity density was not significant in the analysis, this may result from the limitations of a ground-based census. Many cavities are probably obscured from ground view, while some tallied observations probably include shallow holes started by woodpeckers which are not cavities.

Spotted owl foraging success in mono-layer and multi-layer stands has not been tested, so the potential role of a diverse canopy structure is unknown. Hunting success should be improved by stands with a canopy structure that facilitates location and capture of prey. Generally, owls fly to a perch and wait for prey (Forsman et al. 1984, Carey et al. 1989, Guetterman et al. 1991). Good foraging conditions therefore

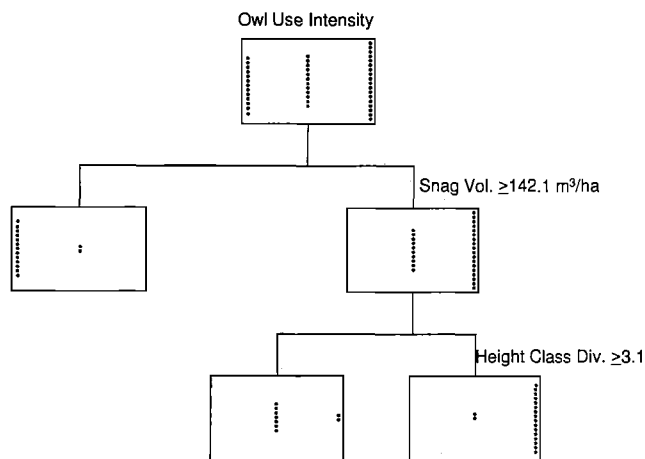


Figure 2. The classification tree of owl-use intensity predicted from snag volume and height class diversity. The dots represent each of the 43 stands and are arranged in 3 vertical columns: low, medium, and high use from left to right. The model was run through 43 jackknife iterations, and final nodes indicate the number of correct and incorrect model classifications for each use level (e.g., 2 medium use stands were misclassified as low use in the node on the left). Owl foraging use is higher in stands with a snag volume $> 142 \text{ m}^3/\text{ha}$ and a more diverse canopy structure.

might be found in stands that are open enough for unobstructed flight and yet provide spotted owls with perches at all levels in the canopy. Stands with high tree height diversity would have low perches available for hunting and yet enough open space to facilitate sub-canopy flight and prey capture.

At least 2 cautions should be noted when interpreting these results. First, stand structures other than snag volume and tree height class diversity should not be discounted, because components of old growth are dynamically linked. Large-diameter trees are needed first in a stand before high volume snags are produced and these in turn become big coarse woody debris pieces. A high diversity in tree heights is usually found in stands with a range of tree diameter sizes and a mix of shade tolerant and intolerant species. Singular focus on 1 or 2 stand characteristics could skew management from considering the dynamics of a complex old-growth ecosystem in their entirety. While there is variation in owl habitat quality between different stands of late seral stage forest, old growth is the defining forest condition consistently used by spotted owls in western Washington (Thomas et al. 1990).

A second concern is that foraging microhabitat probably differs in other regions. Diets and home range size vary across the spotted owl's range, indicating that microhabitat structure may vary among regions. We do not know if stand structures that are useful for differentiating forage use-intensity in western Washington will be useful for similar investigations in other areas of the northern spotted owl's range. Certainly the changes in forest composition, structure, and preybase found within the owl's geographic distribution suggest foraging stand structures will vary.

Although our results may be particular to these study sites, this technique might help quantify foraging structures in other areas where telemetry data on spotted owls have been collected. In place of a presence/absence comparison, the power to identify and quantify particular forest structures

associated with owl foraging will be improved by restricting the analysis to sites with established, repeated use. A gradient of use intensity can then be calculated to compare across a sample of stands with different forest structure. This approach does require telemetry datasets large enough to identify stands with repeated owl use even after reducing the dataset to select for foraging locations in similar size stands. Within the spotted owl's range, however, an extensive research effort has produced several large, multi-year telemetry datasets in areas with variable forest structure.

In our study area, stands with high use by owls typically included many "legacies" (large trees and snags) that survived a fire or windstorm that destroyed much of the previous stand. The survival of just a few dominant and co-dominant trees from the original old-growth stand increased structural heterogeneity and produced more height class diversity in the regenerating stands. Large snags were created when tree tops were snapped in early-century windstorms or rot-resistant tree species were killed by fire. The carry-over of these large structures into the regenerating stands may have produced sufficient foraging habitat for the owl even though other attributes of the stand were typical of younger forests. Old-growth legacy structures in younger stands may improve wildlife habitat quality for many late-seral associated species. A series of studies in Pacific Northwest Douglas-fir forests found few differences in wildlife density or diversity between old-growth stands and mature stands that had post-disturbance, old-growth legacies (Ruggiero et al. 1991). Legacy structures, such as large trees and snags, may diversify habitat conditions in young, regenerating stands and eventually improve foraging conditions for future spotted owl use.

Literature Cited

- BELSLEY, D.A., E. KUH, AND R.E. WELSCH. 1980. Regression diagnostics Identifying influential data and sources of collinearity. Wiley, New York 292 p.
- BORENSTEIN, M., H. ROTHSTEIN, AND J. COHEN. 1997. SamplePower 1.0. SPSS Inc., Chicago, IL. 217 p.
- BREIMAN, L., J.H. FRIEDMAN, R.A. OLSEN, AND C.J. STONE. 1984. Classification and regression trees. Wadsworth and Brooks, Monterey, CA.
- 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-GTR-185.
- CAREY, A.B. 1989. Wildlife associated with old-growth forests of the Pacific Northwest. Natur. Areas J. 9:151-162.
- CAREY, A.B. 1991. The biology of arboreal rodents in Douglas-fir forests USDA For. Serv. Gen. Tech. Rep. PNW-GTR-276.
- CAREY, A.B. 1995. Sciurids in Pacific Northwest managed and old-growth forests. Ecol. Applic. 5:648-661.
- CAREY, A.B., S.P. HORTON, AND J.A. REID. 1989. Optimal sampling for radiotelemetry studies of spotted owl habitat and home range. USDA For. Serv. Res. Rep. PNW-GTR-416.
- CAREY, A.B., S.P. HORTON, AND B.L. BISWELL. 1992. Northern spotted owls Influence of prey base and landscape character. Ecol. Monogr. 62:223-250.

- CAREY, A.B., AND K.C. PEELER. 1995. Spotted owls: Resource and space use in mosaic landscapes. *J. Raptor Res.* 29:223-239.
- CAREY, A.B., 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.
- CLINE, S.P., A.B. BERG, AND H.M. WRIGHT. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *J. Wildl. Manage.* 44:773-786.
- COHEN, J. 1988. Statistical power analysis for the behavioral sciences. Ed. 2. Lawrence Erlbaum Assoc., Hillsdale, NJ. 567 p.
- FORSMAN, E.D., E.C. MESLOW, AND H.M. WRIGHT. 1984. Distribution and biology of the spotted owl in Oregon. *Wildl. Monogr.* 87:1-64.
- FORSMAN, E.D., I. OTTO, AND A.B. CAREY. 1991. Diet of spotted owls on the Olympic Peninsula, Washington and the Roseburg District of the Bureau of Land Management. P. 527 in *Wildlife and vegetation of unmanaged Douglas-fir forests*, Ruggiero, L.F., et al. (tech. coords.). USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285.
- FORSMAN, E.D., S. DESTEFANO, M.G. RAPHAEL, AND R.J. GUTIÉRREZ. 1996. Demography of the northern spotted owl. *Stud. Avian Biol.* 17. P. 1-122.
- FRANKLIN, J.F., et al. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-118.
- FRANKLIN, J.F., AND C.T. DYRNESS. 1988. Natural vegetation of Oregon and Washington. Oregon State Univ. Press, Corvallis, OR. 452 p.
- GANEY, J.L., AND R.P. BALDA. 1994. Habitat selection by Mexican Spotted Owls in northern Arizona. *Auk* 111:162-169.
- GUETTERMAN, J.H., J.A. BURNS, J.A. REID, R.B. HORN, AND C.C. FOSTER. 1991. Radio telemetry methods of studying spotted owls in the Pacific Northwest. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-272.
- GUTIÉRREZ, R.J. 1994. Changes in the distribution and abundance of Spotted Owls during the past century. *Stud. Avian Biol.* 15:293-300.
- GUTIÉRREZ, R.J., AND A.B. CAREY. 1985. Ecology and management of the spotted owl in the Pacific Northwest. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-185.
- HAWKSWORTH, F.C. 1977. The 6-class dwarf mistletoe rating system. USDA For. Serv. Gen. Tech. Rep. RM-GTR-48. 7 p.
- HENDERSON, J.A., AND D.H. PETERS. 1985. Preliminary plant associations and habitat types of the Mt. Baker Ranger District, Mt. Baker-Snoqualmie National Forest. USDA For. Serv. PNW, Olympia, WA. 135 p.
- HENDERSON, J.A., D.H. PETERS, R.D. LESHER, AND D.C. SHAW. 1990. Forested plant associations of the Olympic National Forest. USDA For. Serv. Region 6 Ecol. Tech. Pap. 001-88.
- JOHNSON, D.H. 1981. The use and misuse of statistics in wildlife habitat studies. P. 11-19 in *The use of multivariate statistics in studies of wildlife habitat*, Capen, D.E. (ed.). USDA For. Serv. Gen. Tech. Rep. RM-GTR-87.
- LAYMON, S.A. 1988. Ecology of the spotted owl in the central Sierra Nevada, California. Ph.D. diss., Univ. of California, Berkeley, CA. 284 p.
- LEMAY, V.M., D.E. TAIT, AND B.J. VAN DER KAMP. 1994. Classification of cedar, aspen, and true fir trees as decayed versus sound. *Can. J. For. Res.* 24:2068-2077.
- MAGURRAN, A.E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, NJ. 179 p.
- MORRISON, M.L., I.C. TIMOSI, AND K.A. WITH. 1987. Development and testing of linear regression models predicting bird-habitat relationships. *J. Wildl. Manage.* 51:247-253.
- MORRISON, M.L., B.G. MARCOT, AND R.W. MANNAN. 1992. Wildlife-habitat relationships: Concepts and applications. Univ. of Wisconsin Press, Madison, WI. 343 p.
- NOON, B.R. 1986. Summary: Biometric approaches to modeling—The researcher's viewpoint. P. 197-202 in *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates*, Verner, J., M.L. Morrison, and C.J. Ralph (eds.). The Univ. of Wisconsin Press, Madison, WI.
- NORTH, M.P. 1993. Stand structure and truffle abundance associated with the northern spotted owl. Ph.D. diss., Univ. of Washington, Seattle, WA. 113 p.
- NORTH, M.P., AND J.H. REYNOLDS. 1996. Microhabitat analysis using radiotelemetry locations and polytomous logistic regression. *J. Wildl. Manage.* 60:639-653.
- RUGGIERO, L.F., K.B. AUBRY, A.B. CAREY, AND M. HUFF. 1991. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285.
- 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., AND J.F. FRANKLIN. 1991. The structure of natural, young, mature, and old-growth Douglas-fir forests in Oregon and Washington. P. 91-110 in *Wildlife and vegetation of unmanaged Douglas-fir forests*, Ruggiero, L.F., et al. (tech. eds.). USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285.
- SPSS. 1996. SPSS base 7.0 for Windows: User's guide. SPSS Inc., Chicago, IL. 564 p.
- SWIHART, R.K., AND N.A. SLADE. 1985. Testing for independence of observations in animal movements. *Ecology* 66:1176-1184.
- SYSTAT. 1997. New Statistics: SYSTAT 7.0. SPSS Inc., Chicago, IL.
- THOMAS, J.W., et al. 1990. A conservation strategy for the northern spotted owl. Rep. of the Interagency Comm. to Address the Conserv. Strategy of the Northern Spotted Owl. USDA For. Serv., Portland, OR.
- VAN PELT, B., AND M. NORTH. 1996. Analyzing canopy structure in Pacific Northwest old-growth forests with a stand-scale crown model. *Northwest Sci.* 70 (Special Issue):15-30.
- VAN PELT, B., AND M. NORTH. In press. Testing a ground-based canopy model using the Wind River Canopy Crane. Selbyana.
- WITT, J.W. 1991. Increasing the carrying capacity of second-growth stands for flying squirrels with the use of nest boxes. P. 529 in *Wildlife and vegetation of unmanaged Douglas-fir forests*, Ruggiero, L.F., et al. (tech. eds.). USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285.
- ZAR, J.H. 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ. 718 p.