Joseph B. Buchanan, Jeffrey C. Lewis, D. John Pierce, Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, Washington 98501

Eric D. Forsman, USDA Forest Service, Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis, Oregon 97331

and

Brian L. Biswell, USDA Forest Service, Pacific Northwest Research Station, 3625 93rd Avenue SW, Olympia, Washington 98512

Characteristics of Young Forests Used by Spotted Owls on the Western Olympic Peninsula, Washington

Abstract

Although the dependence of spotted owls (*Strix occidentalis*) on older forests has been well documented, the specific attributes of comparatively younger forests used by owls have not been described in some regions. We collected habitat data at locations used by spotted owls tracked in an intensive radio-telemetry study to develop descriptions of these forests on the western Olympic Peninsula, Washington. After addressing the effects of triangulation error on the placement of our vegetation sampling plots, we collected data at all 16 telemetry locations that could be clearly associated with non-old-growth habitat, as well as 16 random locations. Owl locations were divided into 2 groups to reflect single-use (only one radio location within the error polygon) and multiple-use sites (≥2 radio locations within the error polygon) within home ranges. Vegetation data collected in three arrays of variably-sized plots included measures of stem and snag density (by diameter class), canopy cover, and cover of downed wood and shrubs. Our analyses indicated that single-visit and random locations did not differ with respect to the variables we recorded. However, both differed from multiple-use locations in abundance of larger snags, and amount of canopy closure. A logistic regression model indicated that multiple-use sites could be reliably distinguished from single-use and random locations based on the greater number of snags ≥51 cm diameter at breast height (dbh) and ≥70% canopy closure. Younger forests managed for spotted owl foraging habitat in this region should be in the understory reinitiation stage of stand development, have ≥70% canopy closure, and contain ≥4 snags/0.4-ha that are ≥51 cm dbh. The habitat definitions we propose may not be applicable to other areas characterized by different forest types and prey assemblages.

Introduction

Recent management and conservation strategies for the spotted owl (*Strix occidentalis*) on non-federal lands in Washington include passage of a state habitat protection rule (WAC 222-10-041; see WSFPB 1996), a proposed federal 4(d) rule (USDI 1995), and development of Habitat Conservation Plan (HCP) agreements between landowners and the U.S. Fish and Wildlife Service. Each of these strategies contains provisions for management of suitable habitats on non-federal lands. Specifically, the state rule provides regional descriptions of suitable habitats for spotted owls in Washington. In addition, the state rule and the HCP process allow for modification of habitat definitions based on new research information.

The definitions of habitats used for these management initiatives were derived from descriptions summarized by Hanson et al. (1993). Those descriptions were limited to submature forest types because it was felt that there was general agreement on the definition of old-forest habitat (Hanson et al. 1993). The information used by Hanson et al. (1993) to develop definitions of suitable habitat for the Olympic Peninsula was, in some cases, extrapolated from other parts of western Washington. Data from the western Olympic Peninsula were not readily available at that time although telemetry data had been collected in the home ranges of a number of owl pairs in that region (Forsman unpubl. data). That particular research was designed to estimate home range size and to investigate use of different forest types.

Although Forsman's research was not designed to describe specific habitat attributes within stands used by owls, we felt that it was important to describe the use of submature forest habitat(s) in the region based on conditions at sites known to have been used by spotted owls. The most reliable means to accomplish this was to examine habitat conditions at documented telemetry points (e.g. North and Reynolds 1996). Consequently, we collected habitat data at telemetry-based locations in submature habitats to address two objectives: 1) to provide a better description of non-old-forest habitat used by spotted owls on the western Olympic Peninsula, and 2) to test the null hypothesis that within-stand structural attributes of younger forests did not differ significantly among documented sites with single, multiple, or no documented records of use.

Study Area

We collected habitat data in two general areas on the western Olympic Peninsula in Washington where telemetry research had been conducted by Forsman: the vicinity of Forks in western Clallam County and the vicinity of Neilton in western Jefferson County. Both areas occur at the interface of the coastal lowlands and the foothills of the interior of the peninsula. The lowland region, dominated by state-managed and private lands, is of generally low relief whereas the foothills exhibit greater relief and are managed by the U.S. Forest Service and National Park Service.

The managed forests of the area are dominated by western hemlock (*Tsuga heterophylla*) although Sitka spruce (*Picea sitchensis*) and Douglas-fir (*Pseudotsuga menziesii*) are dominant in some areas. Other species, such as western redcedar (*Thuja plicata*) and Pacific silver fir (*Abies amabilis*), also occur in the area. Most suitable habitat on federal lands is typical old-growth forest (Mills et al. 1993, Forsman and Giese 1997) whereas suitable habitat on state and private lands occurs in a variety of conditions including: 1) young stands containing residual forest elements from stands largely destroyed by a catastrophic wind storm in 1921, 2) young stands which lack residual forest elements, and 3) remnant patches of old forest. Much of the nonfederal land area has been fragmented by timber harvests conducted in the last few decades.

Methods

Selection of Sampling Sites

The telemetry data were collected in 1987-1989 (Forsman unpubl. data). Most of the telemetry points represented nocturnal foraging locations of owls (n=10); a smaller number (n=6) were diurnal roost locations. The nocturnal points were determined by triangulation whereas the diurnal points were based on either triangulation or visual contacts of roosting owls. All independent telemetry points were subsequently placed on a map, digitized and entered into a database. Estimates of home range size and shape, used to identify the area within which random sampling would occur (see below), were made using the minimum convex polygon procedure (Hayne 1949).

To determine the stand location of mapped telemetry sites, we imported the digital data to a Geographic Information System (GIS) where they were overlaid on a series of orthophotos of the areas within the owl home ranges. We used these orthophotos and other maps of the study area to locate sites for sampling.

The inherent error associated with triangulation (White and Garrott 1986) made it necessary to develop a sampling scheme that addressed this potential source of bias. Forsman assessed the degree of triangulation error in the eastern Cascade Mountains in Washington and found a mean distance of 158 m between the estimated and actual locations of radio signals (E. Forsman, unpubl. data). We believe this error estimate was appropriate (and conservative) for the current study because the areas where we sampled habitat were characterized by less rugged terrain than the assessment study area; this may have resulted in a lower incidence of signal bounce. In addition, our study area was highly accessible due to a well developed road system, which made it possible to travel quickly to multiple points from which to receive radio signals required for triangulation.

Our goal was to sample habitat features in the vicinity (i.e., within the error polygon) of the telemetry locations and to compare with features at sites not known to be used by foraging owls within home ranges. We assumed that the area in the immediate vicinity of the mapped telemetry point was representative of the habitat being used by the owl at the time the radio signals were received. For this reason, we used a 316x316 m (10 ha) polygon (referred to below as a "cell") centered on the mapped telemetry point, to define the area within which we collected vegetation data. For consistency with our use of a grid of 10-ha squares to identify sites for random sampling, we used a square rather than a circular plot to represent the error polygon.

Our primary objective was to describe submature habitats used by spotted owls, so we rejected all telemetry points recorded in stands of old-forest habitat and those that we felt could reasonably be associated with nearby old-growth habitats. Given the possible magnitude of triangulation error that occurred in the collection of the telemetry data, we also rejected points that would result in erroneous sampling of unused non-suitable habitats. Therefore, we discarded all telemetry points that contained any of the following within the 316x316 error cell: 1) a stand or patch of more than 2 ha of old forest, 2) any amount of old forest that was contiguous with a stand or patch of old forest more than 2 ha in size outside the error cell, and 3) a stand or patch of less than 2 ha of suitable non-old-forest habitat in a cell otherwise comprised of non-suitable habitat.

Many of the stands were readily identified as old forest or non-suitable habitat and excluded based on our inspection of ortho-photos. However, habitat assessments of other stands required site visits. We defined any stand with an average of ≥ eight trees/0.4 ha of > 76 cm diameter at breast height (dbh) to be old forest, based in part on the definition used by the USFS in this region (Fierst et al. 1992a, 1992b). For this sampling strategy we considered any forest condition less than dispersal habitat to be unsuitable. Dispersal habitat was defined in part on the Washington State Forest Practices rules (WAC 222-10-041): stands with ≥70% conifer composition, ≥70% canopy closure, and ≥6.1 m open space between the top of the understory vegetation and the bottom of the live canopy.

Environmental conditions associated with forest edges are known to influence the composition and structure of forest stands in a zone associated with the edge area (Chen et al. 1992). Because a number of years had elapsed between the collection of telemetry data and our habitat assessments, we believed there was some potential for changes in edge conditions since the date of documented owl use. To minimize the effects of forest edge in our vegetation sampling, we did not sample vegetation within an interior stand buffer of 20 meters adjacent to gravel roads and 50 meters adjacent to clearcuts or stands of saplings.

We also collected data at random plots. We selected these sites by establishing a fixed grid of 316x316 m cells over the study area and randomly selecting cells from within the MCP home ranges. We collected data only at those random cells that met the conditions described above for sampling at the telemetry-based points. We collected data at a number of random cells equal to the number of telemetry-based points (i.e. $n = 16$).

Collection of Habitat Data

We collected data in three pairs of nested 0.1-ha and 0.8-ha plots at each telemetry-based point or randomly selected cell. One set of nested plots was centered on the point we identified as our best estimate of the actual telemetry location. We selected the plot center for the other two pairs of plots by randomly selecting two octants (i.e., northwest, northeast, southeast, or southwest) from the central point and placing the plots immediately adjacent to the central one in each of the two octants. At one site we repeated the random draw when one of the plots was too close to a forest edge. The data from the three plots at a point or in a cell were pooled in our analyses. Because one of our goals was to compare our data with the new Washington State Forest Practices rules (WAC 222-10-041) for spotted owls, we collected data using parameter categories based on values in those rules.

We used the larger 0.8-ha plot size to provide a greater area for measuring the abundance of certain uncommon features and measured more common features within the smaller plots (Spies and Franklin 1991, Buchanan et al. 1995). In the smaller (0.1-ha), more intensively sampled plot we tallied all trees in each of two dbh classes: 10-51 cm and 51-76 cm. We also tallied the number of snags 25-51 cm dbh and categorized them in one of three height classes (<5 m, 5-12 m, >12 m).

We measured canopy opening (the inverse of canopy closure) at the central point and at the plot edge in each octant in the smaller plots using a concave spherical densiometer (Lemmon 1956). To address concerns about the precision of single densiometer readings within a stand (Cook et al. 1995, but see Nuttle 1997) we recorded multiple estimates within each plot and then used the mean value of all plot measurements to represent the stand value. At each of these five points we recorded canopy opening in each of the four cardinal directions. Thus, we recorded a total of 20 estimates for each of the three sampling plots in each stand.

We believed that estimation of total tree height would be difficult and potentially inaccurate due to the height of trees and the fact that limited visibility of the uppermost portion of the canopy would produce error in our estimates. For this reason, we measured the height to the base of the overstory canopy, using a clinometer, to provide an indication of the height of trees in the stand. The height to the base of the overstory canopy (hereafter referred to as "canopy base height") was defined as the height above ground to the lowest living branches that occur on at least three sides of the bole of a tree. We measured canopy base height on five dominant and/or co-dominant trees: the tree nearest to the plot center and the trees nearest to the perimeter of the 0.1-ha plot in each octant.

Small mammal prey populations of the spotted owl are believed to derive important resource benefits from downed wood and shrub cover components within the forest (Carey and Johnson 1995). We estimated the proportion of the ground covered by downed wood ≥2.4 m long and ≥10 cm diameter at the small end. Because of the difficulty in accurately estimating ground cover types over a 0.1-ha area, we estimated cover as either absent, <5%, or by increments to the nearest 10%. In some stands we noted that the coverage of downed wood in contact with the ground was lower than the cover of all downed wood which included those pieces not in contact with the ground. For this reason, we differentiated between the cover of downed wood in contact with the ground and the overall coverage. We included only the downed wood in decay classes I-IV (Sollins 1982) because they are distinctly identifiable as logs and could be measured. The proportion of ground covered by woody shrubs and conifer seedlings was estimated as none, <5%, or in increments of 10%.

In the 0.8-ha plots we tallied all trees ≥76 cm dbh and all snags ≥51 cm dbh. We used the same height categories for these large snags that we used above for the smaller snags.

Data Analysis

We analyzed the data set to determine whether there were differences in habitats among 3 categories of sites. The first category consisted of randomly-selected sites from which we had no documented use by spotted owls. The other two categories were sites consisting of single or multiple telemetry locations. We classified the latter sites by placing a 316x316 m error cell over the mapped location of the telemetry point and determining whether other telemetry locations occurred in the cell (multiple sites) or whether the cell was characterized by the single point. We collected vegetation data at only the first point location randomly selected within the cells with multiple locations (i.e., we did not double-sample within the 316x316 m cells).

Power analysis was conducted on preliminary data to determine the probability of failing to reject a null hypothesis that was false (a Type-II error), as suggested by Steidl et al. (1997). We collected data at 9 telemetry-based sites (5 single- and 4 multiple-location sites) to estimate sample size requirements necessary to achieve a desired level of statistical power ($\beta \leq 0.2$), following Hintze (1996). We used two variables well documented as important or potentially indicative habitat features for spotted owls: the number of large-diameter snags and the number of large-diameter trees. The analysis indicated $\beta < 0.1$ when $n = 5$ and $\alpha < 0.10$ in comparing the number of large trees at the single and multiple-point telemetry-based sites. Similarly, when comparing the number of large snags, we found that $\beta < 0.2$ when $n = 5$, and $\beta < 0.1$ when $n = 10$ (with $\alpha = 0.10$ for both). We concluded that our projected sample sizes were adequate for testing the hypothesis that these features are important to owls in younger/marginal habitats.

We assessed data distributions prior to statistical analysis. As expected in a sample of forest habitat data, many of the variables exhibited right-skewed distributions. In subsequent multiple-comparison analyses using generalized linear models (GLIM; Crawley 1993) a Poisson error distribution was incorporated in the ANOVA model. In situations where the data were over-dispersed (i.e., the data were not Poisson distributed), we used a scale parameter to approximate a negative binomial distribution (Crawley 1993). In GLIM, ANOVA models can be designed to compare all mean values against a specific mean, or reference value. We used this procedure for all three possible comparisons with each of two reference values (i.e., single- and multiple-point data versus data from random sites, and multiple-point data versus single-point data).

We identified correlations among variables that were significant in the univariate analyses, and that might confound subsequent logistic regression (LR) analyses, by conducting Pearson correlation analyses for the three categories of site data. We excluded variables from the final analysis that were highly correlated ($P < 0.10$) with other variables. Finally, we used LR (Hosmer and Lemeshow 1989) to identify the combination of variables that best distinguished among sites used multiple times and those sites used once or not at all. A forward stepwise procedure was used to incorporate only those variables which significantly ($P < 0.10$) improved the model (Crawley 1993).

Results

We collected vegetation data at 16 independent telemetry locations, 11 in the Forks area and five near Neilton. Our sample included 8 sites with single relocation points and 8 sites with multiple relocation points. Overall, we sampled from the home ranges of four female and three male spotted owls.

Although we did not collect data on tree species composition, all stands we visited were dominated (e.g., ≥95% of stem count or basal area) by conifers, primarily western hemlock and Sitka spruce. The only variables that differed among multiple owl location sites, single owl location sites, and random cells were canopy opening (Table 1) and three measures of the abundance of large-diameter snags (Table 2). There was slight variability among other habitat features, but none of the differences were significant (Tables 1, 2).

Because there were no differences in vegetation features at single-location points and random cells, we combined those data and used LR to compare vegetation characteristics of those sites with the multiple-location sites. Due to significant correlations among some large snag variables, we chose a single variable, the abundance of large-diameter snags, that we felt was most biologically meaningful to include in the LR analysis. Only 2 variables were retained in the final LR model: 1) percent of canopy opening, and 2) abundance of large-diameter snags. The probability that a particular site was used multiple times by a spotted owl increased with an increase in the number of large-diameter snags and amount of canopy opening. The final LR model and associated parameter estimates of the probability of multiple use (PM) was:

$$PM = \frac{1}{1 + e^{5.283 - 0.110\,(\%\ \text{canopy opening}) - 1.280\,(\text{number of lage snags})}}$$

with coefficient standard errors of 1.911, 0.062, and 0.527, respectively. The equation appeared to fit the data well, as indicated by a lack-of-fit analysis ($\chi^2 = 19.63$) and the Kappa statistic (0.667). Additionally, the model chi-square statistics (Afifi and Clark 1990) indicated that both variables were useful in sample classification (large-diameter snags: Wald $\chi^2 = 5.44$, $P = 0.020$; canopy opening: Wald $\chi^2 = 3.10$, $P = 0.078$). The probability that a site was used multiple times by a spotted owl was most strongly associated with the abundance of large-diameter snags (Figure 1).

The logistic regression model correctly classified six of eight (75%) multiple-location sites and 22 of 24 (92%) single-point and random sites. The overall correct classification rate was 88%. The two incorrectly classified multiple-location

TABLE 1. Mean (±SE) values of habitat characteristics recorded at random sites (i.e., no documented use; $n = 16$ cells) and those sites used by spotted owls as determined by radio-telemetry (both single and multiple telemetry locations; $n = 8$ sites for each) on the western Olympic Peninsula, Washington. Habitat variables are reported on a per 0.4-ha basis.

	Use Category				
Variable	Random Location	Single Location	Multiple Location	F Statistic	*P*
No. 10.2-50.7 cm trees	238.6 (23.00)	257.0 (47.60)	197.3 (30.41)	0.726	0.493
No. 50.8-76.1 cm trees	23.1 (4.95)	21.2 (6.41)	38.2 (7.52)	1.632	0.213
No. trees (all dia. classes)	263.4 (20.00)	279.4 (42.40)	238.9 (27.40)	0.409	0.668
Canopy base height (m)	16.9 (1.07)	16.4 (1.49)	19.6 (1.02)	1.594	0.220
Canopy opening (%)[1]	6.2 (1.04)a	10.9 (2.17)a	14.4 (4.47)b	3.982	0.030

[1] Variables with different letters were significantly different.

TABLE 2. Median (with 25% and 75% quartiles) values of habitat characteristics recorded at random sites (i.e., no documented use: $n = 16$ cells) and those sites used by spotted owls as determined by radio-telemetry (both single and multiple telemetry locations: $n = 8$ sites for each) on the western Olympic Peninsula, Washington. We report median values in this table because these data were not normally distributed. Habitat variables are reported on a per 0.4-ha basis.

Variable	Use Category			F Statistic	*P*
	Random Location	Single Location	Multiple Location		
No. ≥76 cm trees	0.9 (0.04, 2.5)	0.6 (0.04, 2.7)	3.9 (1.2, 4.8)	2.235	0.125
No. 25-51 cm snags, 2-5 m tall	0.0 (0.0, 1.0)	0.0 (0.0, 2.3)	0.0 (0.0, 1.0)	0.538	0.590
No. 25-51 cm snags, 5-12 m tall	0.0 (0.0, 1.3)	0.0 (0.0, 2.3)	0.7 (0.0, 2.3)	0.385	0.684
No. 25-51 cm snags, ≥12 m tall	0.7 (0.0, 1.3)	2.0 (0.0, 4.0)	0.7 (0.0, 2.7)	0.841	0.442
No. 25-51 cm snags, all heights	1.3 (0.0, 3.7)	4.0 (0.7, 6.0)	2.0 (0.3, 6.0)	0.490	0.618
No. ≥51 cm snags, 2-5 m tall	0.2 (0.0, 0.3)a	0.3 (0.04, 0.3)a	1.6 (0.8, 2.7)b	18.050	0.00001
No. ≥51 cm snags, 5-12 m tall	0.0 (0.0, 0.1)a	0.1 (0.0, 0.3)a	0.7 (0.3, 2.1)b	9.838	0.0006
No. ≥51 cm snags, ≥12 m tall	0.6 (0.3, 1.1)	1.1 (0.4, 1.6)	1.4 (1.0, 2.5)	1.215	0.311
No. ≥51 cm snags, all heights	0.8 (0.3, 1.9)a	1.3 (0.9, 2.3)a	3.8 (2.5, 6.9)b	9.445	0.0007
Downed wood in contact with ground (%)	7.5 (5.0, 12.1)	3.8 (2.5, 9.4)	5.0 (3.1, 6.9)	1.190	0.319
Total downed wood (%)	7.5 (5.0, 16.0)	6.3 (2.5, 10.6)	5.0 (5.0, 9.4)	0.477	0.625
Shrub cover (%)	8.3 (2.5, 31.5)	10.0 (3.8, 32.5)	5.8 (2.9, 25.8)	0.327	0.723

[1] Variables (within a row) with different letters were significantly different.

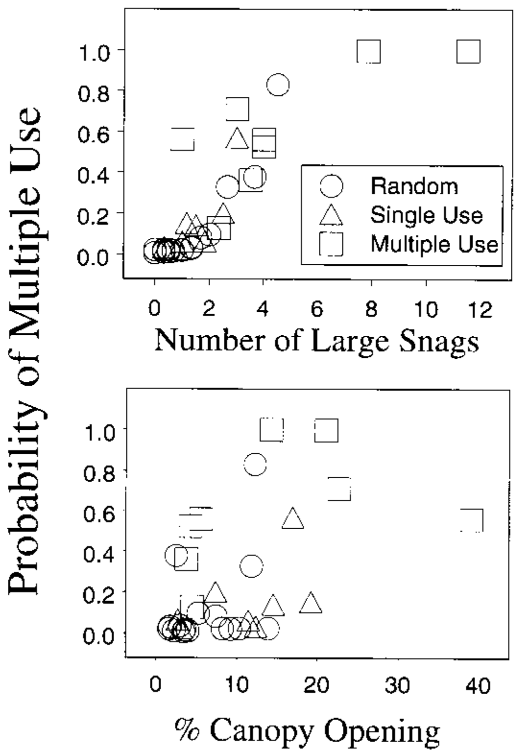

Figure 1. Relationship between probability that a site was used multiple times by a spotted owl and the abundance of large-diameter snags/0.4-ha (top); although a significant component of the final model, the relationship between owl use and amount of canopy opening was not as strong (bottom).

sites appeared to have been misclassified because of low measures of canopy opening (4% canopy opening in both cases). Conversely, the incorrectly classified single-point and random locations had greater canopy opening (12% and 17%). All four misclassified sites had between 2.3 and 4.5 large-diameter snags per 0.4 ha.

Discussion

Our results suggested that the abundance of large-diameter snags and the amount of canopy closure are important habitat components that distinguish among submature (SM) and young forest marginal (YFM) habitats used by spotted owls in the western Olympic Peninsula. The snag and canopy opening values at multiple-location and single-point/random sites were similar to SM and YFM habitats, respectively, as defined in the rules. For this reason, we compared the data from this study to those definitions, and make recommendations as to how local definitions might be modified in accord with local information.

The current Washington State Forest Practices Rules define SM habitat as a conifer-dominated stand (≥30% conifer) with ≥70% canopy closure, 115-280 trees (≥10 cm dbh) per 0.4 ha, ≥3 snags per 0.4 ha of ≥51 cm dbh and at least 5 m in height, and optional provisions for using other correlated attributes (WAC 222-16-085-1[b]). The definition for YFM habitat differs in that the snag requirement is ≥2 snags per 0.4 ha and the cover of downed wood and shrubs is ≥10% and 25-60%, respectively (WAC 222-16-085-1[b]). According to our model, a stand of SM habitat (on our study area) with 3 large snags (≥51 cm dbh) and 30% canopy opening (70% canopy closure) would have a 0.85 probability of being used multiple times by spotted owls. Reducing the amount of canopy opening to 10% or 0% results in lower probabilities of multiple use (0.61 and 0.20, respectively). This suggests that efforts to open dense stands through silvicultural manipulations (i.e., commercial thinning) may improve habitat quality and benefit spotted owls.

The biological significance to spotted owls of large-diameter snags has long been recognized in the Pacific Northwest (Forsman et al. 1984). These snags are used as nest sites by spotted owls (Forsman et al. 1984, Forsman and Giese 1997) and are an important habitat element, particularly in terms of denning and resting sites for their primary prey, the northern flying squirrel (*Glaucomys sabrinus*; Carey et al. 1997). Our results suggest that SM habitat is typified by, among other things, the presence of ≥4 large-diameter (i.e., ≥51 cm dbh) snags/0.4 ha ≥5 m in height. Nearly one-half of these large-diameter snags were ≥12 m in height. Relatively short snags (2.4-4.9 m) were more abundant on multiple-use sites compared to single-use sites, suggesting a possible value of these structures to spotted owls. The abundance of the shorter snags may, however, be correlated with other attributes that more strongly influence owl use of these stands (e.g. possibly the number of large snags ≥12 m in height); additional work is needed to investigate the biological importance of these structures.

Our data on forest community composition and percent canopy opening were consistent with existing habitat definitions (e.g. Hanson et al. 1993). With only one exception, the stands we visited had <30% canopy opening (≥70% canopy closure). The greater canopy opening in the multiple-location sites appeared to be related to greater structural complexity of the stands. Specifically, the multiple location stands had greater canopy opening, more large-diameter snags, and tended to have fewer stems, all indications of the understory reinitiation stage of stand development (Oliver 1981).

The range of stem densities we noted in stands used by owls (Table 1) was greater than previously recommended for this region (115-280 stems/0.4 ha; Hanson et al. 1993). Specifically, 2 of the 8 (25%) multiple-use locations had more than 280 stems/0.4 ha, but only 4 (13%) of the 32 telemetry-based or random sites had stem counts >380/0.4 ha. For this reason, we suggest that the upper limit of acceptable stem density is about 380 stems/0.4 ha ≥ 10 cm dbh for the western Olympic Peninsula. A component of the total stem count was the abundance of 51-76 cm trees; the differences among site categories for this diameter class (and the relatively low P value), although not significant, suggest potential selection by owls. A retrospective power analysis suggests that additional investigation is warranted to evaluate the possible importance of this habitat attribute (e.g. data from 80 sample plots would be required, with power of 0.80 and $\alpha = 0.10$, to detect a 50% change in the density of 51-76 cm trees found at random plots).

Downed wood and shrub cover are believed to be important components of spotted owl habitat by providing cover and other resources for small mammal prey (Carey and Johnson 1995). We found that the amounts of downed wood and shrub cover in the stands were variable, and that overall the mean amount of cover did not differ among the categories of sites. Furthermore, the mean amounts of downed wood and shrub cover we recorded were lower than the lower limit required in the Forest Practices rules (WSFPB 1996). Our data suggest that 5% cover of downed wood might be appropriate for defining the lower threshold of this component of spotted owl habitat. Similarly, a lower range in shrub cover (e.g. ≥10%) may be warranted. We recognize, however, that these values represent only what the owls in our study used on average, and may not reflect optimal conditions for prey species in SM habitats (Carey and Johnson 1995).

Certain limitations apply when using telemetry data to make inferences about habitat quality. One of the primary concerns in this type of analysis is that the recorded occurrence(s) in an area may not reflect the actual ecological value of the site (North and Reynolds 1996; see Van Horne 1983). In the context of our study, this means that there may be situations where owls use a site to a greater or lesser degree than is indicated by telemetry data. There are many possible reasons for this, including sampling problems related to the number of telemetry locations or the timing or frequency in which they were collected, and ecological factors such as occupancy of the study area by unknown conspecifics, other competitors, or predators. In this study we used telemetry data collected from resident, reproductive owls that were intensively monitored (302-462 locations/owl) during all seasons of the year (13-23 months/owl; Forsman in prep.). We have no way to evaluate whether the ecological factors above influenced the habitat use we observed, although such influences likely occur in all natural populations. Therefore, we believe that the telemetry sampling results represented variations in intensity of use and were adequate for our purposes.

Although we believe the data reported above confirm and refine our understanding of habitat attributes used by spotted owls in this region, caution is warranted. Our primary objective was to compare the attributes at telemetry relocation sites in lower-quality habitats with those at random locations. We defined the lowest-quality habitats used by the spotted owls in this study, but further research in an area, which includes a wider successional range of habitats, may better define the lower limit of habitat suitability for spotted owls. Moreover, we believe it is important to distinguish between regulatory definitions of habitat and those used for conservation purposes. Regulatory definitions represent thresholds to facilitate identification of sites or stands where an assessment, typically to evaluate potential impacts, may be required. For conservation planning purposes, however, we believe that the higher values of attributes found in our study (e.g. ≥4 large snags/0.40 ha) are more appropriate because they reflect habitats that the owls appear to use to a greater extent than YFM. Habitats that are used to a greater proportion than their availability (e.g. mature and old forest seral stages; Forsman, unpubl. data) are generally thought to have greater value than habitats used less than or equal to their proportional availability.

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