

Within-Stand Nest Site Selection by Spotted Owls in the Eastern Washington Cascades

Author(s): Joseph B. Buchanan, Larry L. Irwin, Edwin L. McCutchen

Source: *The Journal of Wildlife Management*, Vol. 59, No. 2 (Apr., 1995), pp. 301-310

Published by: Allen Press

Stable URL: <http://www.jstor.org/stable/3808943>

Accessed: 30/12/2009 17:27

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=acg>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Allen Press is collaborating with JSTOR to digitize, preserve and extend access to *The Journal of Wildlife Management*.

WITHIN-STAND NEST SITE SELECTION BY SPOTTED OWLS IN THE EASTERN WASHINGTON CASCADES

JOSEPH B. BUCHANAN,¹ National Council of the Paper Industry for Air and Stream Improvement, 720 S.W. Fourth Street, Corvallis, OR 97339, USA

LARRY L. IRWIN, National Council of the Paper Industry for Air and Stream Improvement, 720 S.W. Fourth Street, Corvallis, OR 97339, USA

EDWIN L. McCUTCHEM,² U.S. Forest Service, Wenatchee National Forest, P.O. Box 811, Wenatchee, WA 98801, USA

Abstract: We describe 83 nest sites (0.2-ha areas) of northern spotted owls (*Strix occidentalis caurina*) in mixed conifer forests on the eastern slope of the Cascade Mountains, Washington. Approximately 74% of the nest sites were in forests in intermediate stages of succession, and 27% were in old-growth forests (median = 122 yr, range 54–700 yr). Most sites were naturally regenerated after fire, but 23% of the nest sites had been partially harvested ≥ 40 years ago. We tested the hypothesis that habitat structure does not influence nest site selection within forested stands, because such knowledge would aid conservation strategies that may include silvicultural prescriptions for creating future habitat. We compared habitat characteristics at 62 nest sites with those at 62 random sites within the same forest stands. Compared with random sites, spotted owl nest sites had canopies of dominant and/or codominant and intermediate trees that were farther aboveground ($P = 0.02$ and 0.07 , respectively), more 35–60-cm-dbh (diam at breast height) Douglas-fir (*Pseudotsuga menziesii*) trees ($P = 0.03$), greater basal area of Douglas-fir trees ($P = 0.02$), more 61–84-cm-dbh ponderosa pine (*Pinus ponderosa*) trees ($P = 0.03$), greater live tree basal area ($P = 0.09$), greater basal area of Class IV snags (broken snags with no branches and little bark; $P < 0.001$), less basal area of a group of relatively uncommon conifer species ($P = 0.02$), fewer 10–34-cm-dbh uncommon conifer species ($P = 0.08$), and less basal area of Class I and II snags (intact or nearly intact snags with branches and most bark remaining; $P = 0.08$ and 0.095 , respectively). Volume of coarse woody debris ($P > 0.13$ in all decay classes) and percent canopy closure ($P = 0.45$) did not differ between nest and random sites. Data support the hypothesis that nest sites are selected as part of an antipredator strategy.

J. WILDL. MANAGE. 59(2):301–310

Key words: Cascade Mountains, fire, habitat, mixed conifer forest, nest sites, northern spotted owl, *Strix occidentalis*, Washington.

Wildlife biologists and forest managers must understand and predict how forestry practices influence wildlife populations. Forest management planning for northern spotted owls requires detailed information on habitat structure at nesting and roosting sites. Information on nest sites from Douglas-fir/western hemlock (*Tsuga heterophylla*) forests in western Oregon (Forsman et al. 1984) and northwestern California (LaHaye 1988) indicates that spotted owls generally select sites within mature and old-growth forests for nesting.

Despite considerable interest in spotted owl ecology (Thomas et al. 1990, U.S. Dep. Inter.

1992), published descriptions of nest site characteristics in mixed-conifer forests are limited to about 10 nests on the eastern slope of the Cascade Mountains in Oregon (Forsman et al. 1984; E. D. Forsman, U.S. For. Serv., Corvallis, Ore., pers. commun.). More information is needed on nest site characteristics from this region because approximately 30% of known spotted owl sites in Washington occur in the eastern Cascade Mountains Province (Washington Dep. Fish and Wildl., Olympia, unpubl. data).

Our objectives were to quantify habitat structure at spotted owl nest sites in mixed-conifer forests and to test the null hypothesis that habitat structure at nest sites was the same as that at random sites within stands used for nesting. Such comparisons may reveal structural details that will support silvicultural prescriptions designed to create future habitat. Further, comparisons may help identify ultimate factors that influence nest placement, such as nest predation (Martin and Roper 1988).

¹ Present address: Washington Department of Fish and Wildlife, 600 Capitol Way N., Olympia, WA 98501, USA.

² Present address: Regional Office, Southwestern Region, U.S. Forest Service, 517 Gold Avenue S.W., Albuquerque, NM 87102, USA.

We thank H. L. Allen, E. L. Bull, E. D. Forsman, M. Hoover, K. A. O'Halloran, and C. Sisco for contributing to project development. For advice and assistance we thank S. S. Chan, T. A. Spies, J. Stepp, B. Wagner, and members of the Interagency Spotted Owl Scientific Committee. D. A. Manuwal and S. D. West provided advice and support. We are grateful to L. A. Brennan, J. Calambokidis, W. S. LaHaye, K. Seidel, and K. Sorensen for consultation on sampling procedures and computer manipulations. Many people assisted in the field by directing us to nest sites or providing other logistical support; these people are acknowledged in Buchanan et al. (1993). W. M. Block, L. A. Brennan, R. J. Gutiérrez, D. W. Hays, B. G. Marcot, G. Miller, and an anonymous reviewer commented on the manuscript.

STUDY AREA

We conducted this study primarily in the Wenatchee National Forest (WNF) on the eastern slope of the Cascade Mountains, Washington. However, we also sampled 13 nests in forests adjacent to WNF, including 9 on private lands, 2 on Yakama Nation tribal lands, 1 in Okanogan National Forest, and 1 in North Cascades National Park. The WNF contained a variety of coniferous species in several vegetation associations that graded with elevation and moisture from ponderosa pine associations at lower elevations to grand fir (*Abies grandis*) and Douglas-fir associations at mid-elevations (Franklin and Dyrness 1973). Vegetation associations varied with aspect, slope, elevation, disturbance history, and soil type (Cobb 1988).

Fires and silvicultural practices have influenced the landscape in the eastern Cascades. Prior to the onset of fire suppression after 1900, relatively frequent (2–6/100 yr) ground fires limited establishment of shade-tolerant species such as Douglas- and grand fir (Agee and Edmonds 1992). Stands of these species became established during lengthy fire intervals, but were prone to destruction by catastrophic fire. Since 1900, these species have invaded ponderosa pine stands (Antos and Habeck 1981, Agee and Edmonds 1992); grand fir has assumed codominance in many areas (Arno 1976, Antos and Habeck 1981). The presuppression tendency for destruction of grand fir forests by catastrophic fire may partly explain the rather limited distribution of old-forest spotted owl habitat in the region (Agee and Edmonds 1992).

Until about 1950, most timber harvests in the region were characterized by entries designed to remove dominant ponderosa pines (Wellner 1984). Douglas-fir also was taken in these partial harvests, and in most cases dominant trees were removed in preference to smaller and/or mistletoe-infected trees (Wellner 1984).

METHODS

Data Collection

We collected vegetational and topographic data at 85 of 102 known spotted owl nests from 1988 to 1990. Data were incomplete for 2 sites. Fledgling spotted owls were observed at 81 (95%) of the nest sites. We defined a nest stand as contiguous forest habitat that contained a spotted owl nest site. We did not consider stands younger than the stem exclusion stage (see below) or open stands within the ponderosa pine association to be part of the nest stand.

Using data from the first 2 years, we calculated minimum sample sizes that would provide reliable estimates of 15 vegetational variables (probability of 0.90 that the 95% CI would be within 20% of the observed sample mean, following Mosher et al. 1987; Zar 1984:108). Eleven of 15 variables were estimated reliably with 9–23 samples, although 3 required 55–66 samples. Required sample size for reliable estimates of snag density exceeded the total number of nest sites we examined.

For each nest site we recorded elevation, slope (using a clinometer), aspect, and topographic position relative to ridges or valleys. We described previous disturbances such as disease, logging, or wildfire.

We described stand development at each site on the basis of 4 physiognomic stages following Oliver (1981). The stand initiation stage is the establishment of the regenerating stand by an even-aged cohort of trees and may last >40 years. During stem exclusion, the second stage, the initial cohort occupies all available growing space and prevents other trees from invading the stand. This is followed by the understory reinitiation stage, where shade-tolerant (or moisture-limited) tree species begin to develop ≥ 1 strata in the understory. Forests of the old-growth stage are characterized by uneven-aged cohorts that result from perturbations of various scale and intensity.

We used 2 plot arrays to sample habitat features at nest sites because size and frequency of

objects being measured influence plot size (Spies and Franklin 1991). We used a 0.1-ha plot centered at the nest tree (Noon 1981, Mosher et al. 1987) for estimating stand age, tree height, snag abundance, and dwarfmistletoe (*Arceuthobium douglasii*) infestation. We used a clinometer to determine tree and canopy height (height to the lowest primary canopy) of each of 3 dominant and/or codominant and 3 intermediate trees (canopy positions defined by Spurr and Barnes 1980). We determined age of each of the 6 sample trees by counting growth rings from an increment core extracted at breast height. We also measured all snags ≥ 10 cm dbh and ≥ 2.4 m tall. We recorded species, decay class, dbh (using a diam tape), and height (using a clinometer) of each snag. We used definitions developed by Cline et al. (1980) to assign snags to 1 of 4 decay classes: (1) fully intact; (2) bole intact or broken near top, some bark and branches missing; (3) bole intact or broken near top, no bark or branches remaining; and (4) bole broken at or below midpoint, no bark or branches remaining, sapwood soft. The presence of mistletoe in each sample tree was rated as none, moderate, or high infection in the upper, middle, or lower third of the canopy (Hawksworth and Wiens 1972).

We were occasionally unable to obtain an adequate ($n < 3$) sample of dominant trees within the 0.1-ha plot. For this reason we combined dominant and codominant trees into 1 category for sampling and analyses (22 sites) and non-randomly selected trees for measurement. To test whether trees we selected were representative of those at nest sites, we compared canopy height, tree age, and mistletoe infection scores between chosen and randomly selected dominant and/or codominant and intermediate trees at 15 sites and found no differences (t -tests; in all cases $P > 0.13$).

We arranged 5 0.04-ha circular plots around each nest tree: 1 centered at the nest tree, and the adjacent 4 were tangential to the central plot, arranged in each cardinal direction. In each plot we tallied the number of conifer saplings < 10 cm dbh and > 1.2 m tall, and we measured dbh of all trees ≥ 10 cm dbh with a diameter tape. We categorized downed logs according to decay class and calculated volume within plot boundaries from the length of each log and diameter at each end. We modified definitions developed by Sollins (1982) to assign logs to 1 of 4 decay classes: (1) fully intact; (2) bole intact

or broken, some branches and bark missing; (3) most branches and all bark missing; and (4) all branches and bark missing, bole oval to flat and collapsing. We ocularly estimated the number of distinct canopy layers in each plot to provide a general description of stand structure.

We estimated vegetational closure at nest sites from black-and-white photographs taken within 1.2 m of plot center at each 0.04-ha plot (Chan et al. 1986). We took vertical photos ≤ 1 m aboveground with a camera equipped with an 8-mm $f/2.8$ fisheye lens, which provided a 180° hemispherical view of the plot. We analyzed percent vegetational closure from negatives using program FISHOUT (For. Sci. Dep., Oregon State Univ., Corvallis; Chan et al. 1986). We used the average value of the 5 canopy closure estimates for the nest site. Because of a procedural error we were able to compare canopy closure at only 22 pairs of nest and random sites.

We collected habitat data at 62 random sites within nest stands to evaluate habitat features that may have influenced nest site selection at the within-stand level. Thirteen stands contained multiple nests. At these sites we randomly selected 1 nest to pair with a random site. Most (6 of 8) of the remaining nest site stands where random sites were not sampled occurred at the extreme northern and southern edges of our study area, so we believe sampling was representative of the region.

We restricted random sites to locations > 68 m (to avoid duplication of nest site) and < 400 m from the nest tree because we intended to make comparisons at the within-stand level. We determined each random site location by selecting a distance and compass bearing from the nest tree, using a random numbers table. None of the random sites occurred within the nest site sampling location. All random sites were tree-centered. Habitat sampling procedures at random sites were identical to those used at nest sites.

Data Analysis

We compared habitat features between 62 pairs of nest and random sites, using the mean from the 5 plots for all variables measured within 0.04-ha plots. We used Bartlett's test to estimate whether variances were homoscedastic. We then evaluated skewness and kurtosis using the Shapiro-Wilk test (Shapiro and Wilk 1965). We compared variables that met assumptions of homoscedasticity and normality using paired-sam-

ple *t*-tests. Variables that violated the assumptions were natural log-transformed (to meet parametric assumptions) prior to paired-sample parametric analysis or were analyzed untransformed using the Wilcoxon paired-sample test (Zar 1984).

We compared scores for categorical variables using Chi-square analysis with Yates correction for continuity when $df = 1$ (Zar 1984:48). For comparisons of site aspect, we used Rayleigh's test (Batschelet 1981) to examine differences in angular distribution, and we used the Watson-Williams test to compare paired angular distributions (Batschelet 1981). We used these tests rather than Rao's spacing test (Bergin 1991) because they are similarly robust and the distributions were not polymodal. We arcsine-transformed variables expressed as percentages (e.g., slope) to attain normal distribution prior to analysis. We used linear regression to evaluate relationships between elevation and latitude and between slope and elevation. We used SYSTAT for regression and paired-sample analyses (Wilkinson 1988). We used $\alpha < 0.1$ to denote statistical significance (Hinds 1984).

RESULTS

General Site Characteristics

The 83 nest sites were in mixed conifer stands within grand fir, Douglas-fir, or western hemlock forest associations. The majority (57%) of nest sites were in the understory reinitiation phase of stand development, 27% were in old growth, and 17% were in the stem exclusion phase. Nest sites were 2.4–56.0 km east of the Cascade Mountains' crest at 381–1,463 m elevation. Northern sites were lower in elevation than southern ones, and there was an inverse correlation between elevation at nest sites and latitude ($F = 24.8$; 1, 81 df; $P < 0.001$).

Of the 83 nest sites, 78 (94%) were on slopes (22 on top third, 22 on middle third, and 34 on bottom third), 4 (5%) were on bottomland, and 1 (1%) was on a broad butte. Slope at nest sites (41%) did not differ from that at random sites (37%) ($t = 1.62$, $P = 0.11$) and was not correlated with elevation ($F = 1.6$; 1, 60 df; $P > 0.50$). The mean direction of slope exposure for all nest sites was 20° (angular deviation = 75.2°), and the distribution of site aspects was random ($z = 1.58$, $P > 0.2$). However, nest and random sites differed in aspect angle (35 vs. 48° , respectively; $F = 7.54$; 1, 120 df; $P = 0.015$) even though nest and random sites were < 400 m apart.

Evidence of past fire was visible at 92% of 83 nest sites. We did not examine ages of fire scars and were unable to determine how many nest sites burned subsequent to fires that initiated the current stands. However, fire scars at nearly all sites were on older or residual trees, larger snags, or logs.

Thirteen nest sites had been partially logged, primarily by overstory removal about 1940–50. Commercial firewood removal was evident at 2 nest sites, and residual downed logs at another nest site suggested that trees may have been felled as a firebreak. The proportions of nest and random sites with a history of logging activity (21 vs. 34%, respectively) did not differ ($\chi^2 = 1.36$, 1 df, $P = 0.5$). Various levels of logging had occurred at 46% of the nest stands in the paired sample (i.e., evidence of logging activity was noted at either nests or random sites).

We observed root rot (primarily laminated root rot caused by the fungus *Phellinus wierii*), ranging from minor to extensive infestation, at 17 of 52 (33%) nest sites visited in 1988–89. Dwarfmistletoe was present at equal proportions of nest and random sites (78 and 77%, respectively; $\chi^2 = 0.01$, 1 df, $P = 0.9$), and occurred at 84% of 83 nests.

Site Age

Ages of dominant and/or codominant and intermediate trees did not differ between paired nest and random sites ($t = 0.09$, 61 df, $P = 0.9$, and $t = 1.32$, 61 df, $P = 0.19$, respectively; Fig. 1). Median ages of dominant and/or codominant trees were 131 and 132 years at nest and random sites, respectively. Median age of dominant and/or codominant trees at all nest sites ($n = 83$) was 122 years (range 54–700). Median ages of intermediate trees were 94 and 83 years at nest and random sites, respectively. Of nest sites < 122 years, ages of dominant and/or codominant trees (first quartile = 94 yr) and intermediate trees (first quartile = 81 yr) were similar.

Vegetational Structure

Dominant and/or codominant trees at nest sites were the same height as those at random sites in nest stands, although height of intermediate trees was greater at nest sites (Table 1). Canopy heights of both dominant and/or codominant and intermediate trees were greater

at nest sites than at random sites. In paired comparisons between nest and random sites, there were no differences in the rating of mistletoe infestation at any canopy position (upper, middle, lower) in dominant and/or codominant (Wilcoxon test, $P > 0.30$ in all cases) and intermediate ($P > 0.45$ in all cases) Douglas-fir trees.

There were no differences in snag densities between nest and random sites except that small snags (10–34 cm dbh) were more abundant at nest sites than at random sites (Table 2). We found no differences in basal area of all snags between nest sites and random sites. However, basal area of class IV snags was greater at nest sites, and basal area of hard snags (decay classes I and II) was greater at random sites (Table 2).

Total basal area of all live trees at nest sites was greater than at random sites (Table 3). Comparisons for each tree species revealed that only Douglas-fir had a greater basal area at nest sites than at random sites. Douglas-fir composed over half of the basal area of live trees at nest (54%) and random sites (51%) and ranged among sites from a low to nearly exclusive proportion of live tree basal area. Random sites had a greater basal area of a combined group of less common conifer species.

With 3 exceptions there were no differences between nest and random sites in densities of 6 tree species and 2 combined species groupings for each of 6 diameter classes (Table 4). There were no differences in the abundance of small (10–34 cm dbh) Douglas- and grand fir, the 2 most common species at nest sites (Table 4; $t = 1.43$, $P = 0.17$). However, Douglas-fir trees of the 35–60- and 61–84-cm size classes were more abundant than grand firs ($t = 3.63$, $P < 0.001$, and $t = 3.96$, $P < 0.001$, respectively). In addition, Douglas-fir trees ≥ 85 cm dbh occurred at more nest sites (19 sites, 32%) than grand firs of the same size class (1 site, 2%; $\chi^2 = 16.4$, 1 df, $P < 0.001$).

Sapling density of all species did not differ

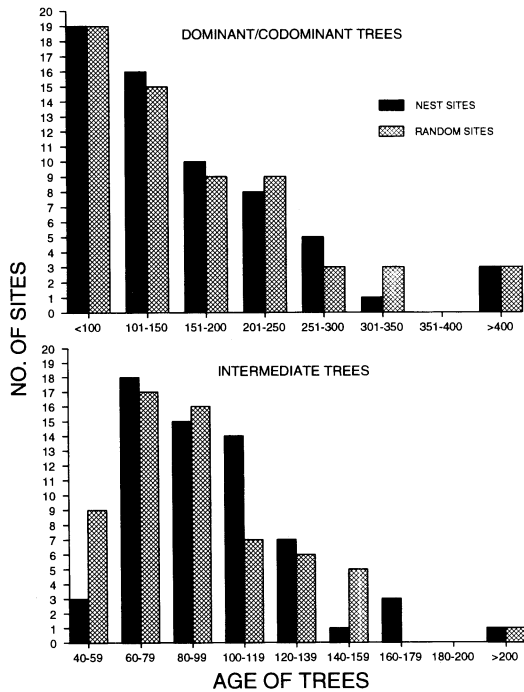


Fig. 1. Mean age of dominant and/or codominant (top) and intermediate trees (bottom) at 62 spotted owl nest and random sites in the eastern Cascades, Washington, 1988–90.

between nest and random sites ($t = -1.51$, $P = 0.14$). Sapling density (n/ha) ranged from 1 to 1,245 ($\bar{x} = 397.5$) and from 25 to 1,865 ($\bar{x} = 457.5$) at nest and random sites, respectively. The coefficient of variation of mean sapling abundance among sites was $>70\%$ at nest and random sites.

Analysis of photographs of vegetational cover at 22 paired sites revealed no difference between nest ($\bar{x} = 75\%$, range 57–95%, SD = 10.61) and random sites ($\bar{x} = 72\%$, SD = 8.55; $t = 0.71$, $P = 0.45$). The mean number of canopy layers in 0.04-ha plots was 1.7 for nest sites ($n = 61$, SD = 0.43) and 1.65 for random sites ($n = 61$, SD = 0.48; $t = 1.1$, $P = 0.4$).

There were no differences between nest and

Table 1. Paired-sample (t -test) comparisons of height (m) of dominant and/or codominant and intermediate trees at spotted owl nest and random sites in the eastern Cascades, Washington, 1988–90 ($n = 62$).

Variable	Nest		Random		P
	\bar{x}	SD	\bar{x}	SD	
Height of dominant/codominant	31.9	4.7	31.8	6.2	0.73
Height of intermediate	19.8	4.0	18.7	4.8	0.08
Canopy height of dominant	15.4	4.3	13.7	5.1	0.02
Canopy height of intermediate	10.0	3.7	8.8	4.1	0.07

Table 2. Paired-sample (*t*-test, Wilcoxon test) comparisons of snag density (no./ha) by diameter class and basal area (m²/ha) by decay class at spotted owl nest and random sites in the eastern Cascade Mountains, Washington, 1988–90 (*n* = 62).

Snag variable	Nest		Random		P
	\bar{x}	SD	\bar{x}	SD	
Size class ^a					
10–34	47.52	48.02	33.00	31.02	0.08
35–60	9.39	11.76	13.73	19.17	0.36
61–84	2.27	4.84	3.56	6.72	0.27
85–110	1.48	3.56	0.79	3.75	0.29
>110	0.30	1.78	0.20	1.28	0.56
All size classes	60.86	51.18	51.38	40.51	0.39
Decay class ^b					
I	0.43	0.24	0.77	1.01	0.08
II	0.27	0.70	0.40	0.59	0.095
III	0.06	0.20	0.14	0.38	0.43
IV	0.49	1.10	0.14	0.83	<0.001
All decay classes	1.29	1.42	1.44	1.42	0.520

^a dbh in cm.

^b I = fully intact; II = bole intact or broken, some branches and bark missing; III = bole intact or broken near top, no bark or branches remaining; IV = bole broken at or below midpoint, no bark or branches remaining, sapwood soft.

random sites in volume of downed wood of any decay class (Table 5). All classes of downed wood and snags at nest and random sites exhibited considerable variation among the 5 sample plots; the coefficient of variation among sites ranged from 132 to 601% for snags and from 97 to 159% for downed wood.

DISCUSSION

Determinants of Habitat Selection

We inferred habitat selection among spotted owls within stands used for nesting by comparing nest sites and random sites within stands. We recognize that habitat structures that were not different between nest and random sites in

our analyses (e.g., vegetational closure) might influence habitat selection at stand or landscape scales (Johnson 1980, Forsman et al. 1984, La-LaHaye 1988). Carey (1985) listed several hypotheses that may explain the association between spotted owls and forests. Hypotheses that might explain within-stand nest site selection include factors that are associated with thermoregulatory benefits, optimal foraging efficiency, or an antipredator strategy.

If prey abundance and/or availability influenced nest site selection, habitat structures associated with prey should be more abundant at nest sites than random sites. Large volumes of snags and coarse woody debris have been associated with old-growth forests (Franklin et al.

Table 3. Paired-sample (*t*-test, Wilcoxon test) comparison of basal area (m²/ha) of live trees at spotted owl nest and random sites in the eastern Cascades, Washington, 1988–90 (*n* = 62).

Species	Nest		Random		P
	\bar{x}	SD	\bar{x}	SD	
Douglas-fir	20.8	13.3	18.3	14.3	0.02
Grand fir	9.3	9.4	8.8	7.4	0.85
Ponderosa pine	3.4	4.8	2.7	4.7	0.24
Western hemlock	1.9	6.9	2.0	10.8	0.65
Western larch ^a	1.2	1.9	1.3	2.1	0.44
Western redcedar ^b	0.8	3.0	0.5	1.5	0.73
Other ^c	1.0	2.5	2.0	4.7	0.02
Hardwoods ^d	0.1	0.4	0.1	0.3	0.51
Total	38.5	15.5	35.8	17.8	0.087

^a *Larix occidentalis*.

^b *Thuja plicata*.

^c Species include lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), western white pine (*Pinus monticola*), noble fir (*Abies procera*), and Pacific silver fir (*A. amabilis*).

^d Species include big-leaf maple (*Acer macrophyllum*), Douglas maple (*A. glabrum*), vine maple (*A. circinatum*), red alder (*Alnus rubra*), Columbia hawthorne (*Crataegus columbiana*), black cottonwood (*Populus trichocarpa*), and Scouler willow (*Salix scouleriana*).

Table 4. Paired-sample (*t*-test, Wilcoxon test) comparison of mean tree densities (no./ha) by species and diameter class (dbh) at spotted owl nest and random sites on the eastern slope of the Cascade Mountains, Washington, 1988–90 (*n* = 62).

Species	Diameter class ^a									
	10–34		35–60		61–84		85–110		111–135	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Douglas-fir										
Nest	115.0	142.3	49.0	46.8	15.5	16.8	2.0	3.8	0.5	2.8
Random	95.8	104.5	38.3	41.8	14.5	18.5	3.3	5.8	0.8	2.0
<i>P</i>	0.40		0.03		0.48		0.25		0.85	
Grand fir										
Nest	157.8	150.5	20.5	25.5	4.3	9.3	0.3	2.0	0	
Random	144.0	129.8	19.5	21.5	3.5	6.0	0.08	0.8	0	
<i>P</i>	0.80		0.60		0.93					
Ponderosa pine										
Nest	8.0	29.5	5.0	9.3	3.8	5.5	0.8	2.3	0.2	1.0
Random	4.3	9.3	3.8	13.8	3.0	7.3	0.8	2.0	0.2	0.8
<i>P</i>	0.50		0.61		0.03		0.48		0.56	
Western larch										
Nest	9.8	26.8	4.0	8.3	0.5	2.0	0.08	0.8	0	
Random	7.0	16.5	3.5	5.8	1.0	3.3	0.18	1.0	0	
<i>P</i>	0.72		0.82		0.41		0.56			
Western redcedar										
Nest	5.3	19.2	0.8	2.3	0.8	3.3	0.5	2.3	0	
Random	4.3	12.5	2.0	7.8	0.18	1.0	0.18	1.0	0	
<i>P</i>	0.73		0.37		0.48		0.59			
Western hemlock										
Nest	11.8	39.0	4.3	14.5	1.0	4.3	0.8	5.0	0.3	2.0
Random	10.5	36.8	2.3	9.0	1.3	8.5	0.5	4.5	0.3	2.0
<i>P</i>	0.64		0.15		0.95					
Hardwoods ^b										
Nest	5.0	15.2	0.2	0.9	0		0		0	
Random	5.2	10.5	0.2	1.3	0		0		0	
<i>P</i>	0.74									
Other conifers ^c										
Nest	10.8	29.0	2.5	6.9	0.6	3.9	0		0	
Random	21.2	53.9	2.8	8.6	0.3	1.2	0.2	0.9	0	
<i>P</i>	0.075		0.59		0.48					

^a dbh in cm.

^b Species include big-leaf maple, Douglas maple, vine maple, red alder, Columbia hawthorne, black cottonwood, and Scouler willow.

^c Species include lodgepole pine, Engelmann spruce, western white pine, noble fir, and Pacific silver fir.

1986) and with spotted owl nest sites west of the Cascade Mountain crest (Gutiérrez 1985, LaHaye 1988). Northern flying squirrels (*Glaucomys sabrinus*), a major prey species for northern spotted owls (Forsman et al. 1984), nest and

den in cavities in large snags (Weigl and Osgood 1974). Other small mammals are associated with coarse woody debris on the forest floor (Maser and Trappe 1984). In our study, densities of large snags and volumes of coarse woody debris

Table 5. Paired-sample (*t*-test, Wilcoxon test) comparison of downed wood volume (m³/ha ± SD) according to decay class at spotted owl nest and random sites on the eastern slope of the Cascade Mountains, Washington, 1988–90 (*n* = 62).

Decay class ^a	Nest		Random		<i>P</i>
	\bar{x}	SD	\bar{x}	SD	
I	51.81	134.58	22.60	35.91	0.21
II	58.10	62.04	57.46	55.78	0.75
III	77.83	81.69	79.35	88.21	0.74
IV	80.59	71.09	76.02	106.29	0.13
All classes	268.33	239.19	235.43	182.90	0.46

^a I = fully intact; II = bole intact or broken near top, some bark and branches missing; III = most branches and all bark missing; IV = all branches and bark missing, bole oval to flat and collapsing.

did not differ between nest and random sites. Thus, our data suggest that food supplies or foraging efficiency may have little influence on within-stand nest site selection.

We speculate that canopy height is important to nest site selection by increasing the owls' detectability of predators. Spotted owls typically nest in mistletoe-infected clumps of branches or abandoned northern goshawk (*Accipiter gentilis*) nests low in the canopy of dominant or codominant trees (Buchanan et al. 1993) in areas with a greater canopy height of dominant and/or codominant trees. We believe this nest placement provided protection from predators above while maximizing visibility in the understory. This may be important if open nests (particularly goshawk nests) in this region are more vulnerable to predators than are cavity nests (Ricklefs 1969); however, our sample of cavity nests was too small to adequately test for an association between canopy position and nest type. Spotted owls probably select nest sites to optimize among various benefits associated with energy balance and predator avoidance (Newton 1979, Cody 1985).

Forest Dynamics

In the eastern Cascades, spotted owls nested in a wide range of stand ages (54–700 yr) and structures. Stands in the stem exclusion, understory reinitiation, and old-growth phases of successional development often included ponderosa pine, Douglas-fir, and western larch as canopy dominants, whereas grand fir occupied suppressed, intermediate, and codominant canopy positions. These attributes are functions of site disturbance history and forest stand dynamics (Oliver 1981, Larson 1986, Cobb 1988).

Stand dynamics and the resulting forest structure were influenced by wildfires at 89% of the nest sites examined. Although we can make few conclusions about the extent or intensity of fires, >50% of the nest sites were <130 years old and contained few or no residual trees, indicating they were in pockets or stands previously destroyed by wildfire. However, some sites contained residuals that survived what were otherwise stand-replacement fires. The abundance of 10–60-cm diameter grand fir trees in the subcanopy is consistent with compositional and structural changes in other mixed conifer forests after the onset of fire suppression (Antos and Habeck 1981). Research is needed to address landscape changes associated with fire suppres-

sion in mixed conifer forests and perhaps to model the distribution and abundance of spotted owls in pre- and postfire suppression eras.

In our study, approximately 46% of the nest stands had been partially logged, 2 as recently as 15 years prior to nesting. Most of these harvests, however, occurred >40 years prior to our study. Intermediate and suppressed trees experience greater growth following partial harvests, and some understory reinitiation may occur at this time (Oliver 1981). Partial harvests in the WNF may have helped to maintain some Douglas-fir regeneration, but the most significant effects of such overstory removal in an era of fire suppression included promoting a dense grand fir understory and perhaps the spread of dwarfmistletoe.

Mistletoe is estimated to occur in 40% of all stands east of the Cascade crest in Washington (Knutson and Tinnin 1980). We observed dwarfmistletoe at 70 of 83 sites. Although we found no differences in mistletoe ratings between nest and random sites, we believe that this is an important habitat feature at stand and landscape levels because the adventitious growth of branches resulting from mistletoe infection are commonly used by spotted owls for nesting substrate (Buchanan et al. 1993) and also may be an important nesting substrate for northern flying squirrels (Mowrey and Zasada 1984).

MANAGEMENT IMPLICATIONS

A history of disturbance (fire, forest pathogens, logging) resulted in variable nest site conditions across the region. Despite this variability, a single factor, fire suppression, is common to the entire eastern Cascades Province. Since the onset of fire suppression in the WNF, an extended fire-free interval has resulted in changes in stand structure, species composition, and effects of forest pathogens (Agee and Edmonds 1992). Concomittant suppression of a natural regime of frequent, low intensity ground fires has increased the probability of large-scale or stand-replacement fires because fuel levels and structural continuity have been enhanced (Agee and Edmonds 1992). Thus, management efforts to control fire may have increased the amount of suitable habitat in the landscape, but simultaneously resulted in a greater risk of habitat loss due to catastrophic fire. Consequently, the management dilemma, if this scenario is true, is to derive a balance between conserving short- and long-term habitat for owls while developing

a more stable forest landscape that is less likely to be adversely affected by pathogens and fire. Judicious management experiments using prescribed fire and innovative silvicultural techniques may reduce risks of wildfire in mixed-conifer forests while sustaining forest habitat and spotted owl populations (Thomas et al. 1990).

LITERATURE CITED

- AGEE, J. K., AND R. L. EDMONDS. 1992. Forest protection guidelines for the northern spotted owl. Pages 181–244 in U.S. Department of Interior. Recovery plan for the northern spotted owl—final draft. Vol. 2. U.S. Gov. Print. Off., Washington, D.C.
- ANTOS, J. A., AND J. R. HABECK. 1981. Successional development in *Abies grandis* (Dougl.) Forbes forests in the Swan Valley, western Montana. *Northwest Sci.* 55:26–39.
- ARNO, S. F. 1976. The historic role of fire on the Bitterroot National Forest. U.S. For. Serv. Res. Pap. INT-187. 29pp.
- BATSCHLET, E. 1981. Circular statistics in biology. Academic Press, New York, N.Y. 371pp.
- BERGIN, T. M. 1991. A comparison of goodness-of-fit tests for analysis of nest orientation in western kingbirds (*Tyrannus verticalis*). *Condor* 93:164–171.
- BUCHANAN, J. B., L. L. IRWIN, AND E. L. MCCUTCHEM. 1993. Characteristics of spotted owl nest trees in the Wenatchee National Forest. *J. Raptor Res.* 27:1–7.
- CAREY, A. B. 1985. A summary of the scientific basis for spotted owl management. Pages 100–114 in R. J. Gutiérrez and A. B. Carey, eds. Ecology and management of the spotted owl in the Pacific Northwest. U.S. For. Serv. Gen. Tech. Rep. PNW-185.
- CHAN, S. S., R. W. MCCREIGHT, J. D. WALSTAD, AND T. A. SPIES. 1986. Evaluating forest vegetative cover with computerized analysis of fisheye photographs. *For. Sci.* 32:1085–1091.
- CLINE, S. P., A. B. BERG, AND H. M. WIGHT. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *J. Wildl. Manage.* 44:773–786.
- COBB, D. F. 1988. Development of mixed western larch, lodgepole pine, Douglas-fir, grand fir stands in eastern Washington. M.S. Thesis, Univ. Washington, Seattle. 99pp.
- CODY, M. L., EDITOR. 1985. Habitat selection in birds. Academic Press, Orlando, Fla. 558pp.
- FORSMAN, E. D., E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the spotted owl in Oregon. *Wildl. Monogr.* 87. 64pp.
- FRANKLIN, J. F., AND C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. U.S. For. Serv. Gen. Tech. Rep. PNW-8. 417pp.
- , F. HALL, W. LAUDENSLAYER, C. MASER, J. NUNAN, J. POPPINO, C. J. RALPH, AND T. SPIES. 1986. Interim definitions for old-growth Douglas-fir and mixed-conifer forests in the Pacific Northwest and California. U.S. For. Serv. Res. Note PNW-447. 7pp.
- GUTIÉRREZ, R. J. 1985. An overview of recent research on the spotted owl. Pages 39–49 in R. J. Gutiérrez and A. B. Carey, eds. Ecology and management of the spotted owl in the Pacific Northwest. U.S. For. Serv. Gen. Tech. Rep. PNW-185.
- HAWKSWORTH, F. G., AND D. WIENS. 1972. Biology and classification of dwarf mistletoes (*Arceuthobium*). U.S. For. Serv. Agric. Handb. 401, Washington, D.C. 234pp.
- HINDS, W. T. 1984. Towards monitoring of long-term trends in terrestrial ecosystems. *Environ. Conserv.* 11:11–18.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- KNUTSON, D. M., AND R. TINNIN. 1980. Dwarf mistletoe and host tree interactions in the managed forests of the Pacific Northwest. U.S. For. Serv. Gen. Tech. Rep. PNW-111. 19pp.
- LAHAYE, W. 1988. Nest site selection and nesting habitat of the northern spotted owl in northwest California. M.S. Thesis, Humboldt State Univ., Arcata, Calif. 111pp.
- LARSON, B. C. 1986. Development and growth of even-aged stands of Douglas-fir and grand fir. *Can. J. For. Res.* 16:367–372.
- MARTIN, T. E., AND J. J. ROPER. 1988. Nest predation and nest-site selection of a western population of the hermit thrush. *Condor* 90:51–57.
- MASER, C., AND J. M. TRAPPE, EDITORS. 1984. The seen and unseen world of the fallen tree. U.S. For. Serv. Gen. Tech. Rep. PNW-164. 56pp.
- MOSHER, J. A., K. TITUS, AND M. R. FULLER. 1987. Habitat sampling, measurement, and evaluation. Pages 81–97 in B. A. Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird, eds. Raptor management techniques manual. *Natl. Wildl. Fed. Sci. Tech. Ser.* 10, Washington, D.C.
- MOWREY, R. A., AND J. C. ZASADA. 1984. Den tree use and movements of northern flying squirrels in interior Alaska and implications for forest management. Pages 351–356 in W. R. Meehan, T. R. Merrell, and T. A. Hanley, eds. Fish and wildlife relationships in old-growth forests. *Am. Inst. Fish Res. Biol.*, Juneau, Alas.
- NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, S.D. 399pp.
- NOON, B. R. 1981. Techniques for sampling avian habitats. Pages 42–52 in D. E. Capen, ed. The use of multivariate statistics in studies of wildlife habitat. U.S. For. Serv. Gen. Tech. Rep. RM-87.
- OLIVER, C. D. 1981. Forest development in North America following major disturbances. *For. Ecol. Manage.* 3:153–168.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* 9:1–48.
- SHAPIRO, S. S., AND M. B. WILK. 1965. An analysis of variance test for normality. *Biometrika* 52:591–611.
- SOLLINS, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Can. J. For. Res.* 12:18–28.
- SPIES, T. A., AND J. F. FRANKLIN. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington.

- Pages 91–107 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep. PNW-285.
- SPURR, S. H., AND B. V. BARNES. 1980. Forest ecology. Third ed. John Wiley and Sons, New York, N.Y. 687pp.
- THOMAS, J. W., E. D. FORSMAN, J. B. LINT, E. C. MESLOW, B. R. NOON, AND J. VERNER. 1990. A conservation strategy for the northern spotted owl. U.S. For. Serv., U.S. Bur. Land Manage., U.S. Fish and Wildl. Serv., U.S. Natl. Park Serv. U.S. Gov. Print. Off., Washington, D.C. 427pp.
- U.S. DEPARTMENT OF INTERIOR. 1992. Recovery plan for the northern spotted owl—final draft (2 vols.). U.S. Gov. Print. Off., Washington, D.C. 812pp.
- WEIGL, P. D., AND D. W. OSGOOD. 1974. Study of the northern flying squirrel *Glaucomys sabrinus* by temperature telemetry. *Am. Midl. Nat.* 92: 482–486.
- WELLNER, C. A. 1984. History and status of silvicultural management in the interior Douglas-fir and grand fir forest types. Pages 3–10 in D. M. Baumgarter and R. Mitchell, eds. Silvicultural management strategies for pests of the interior Douglas-fir and grand fir forest types. Washington State Univ. Coop. Ext., Pullman.
- WILKINSON, L. 1988. SYSTAT: the system for statistics. SYSTAT, Evanston, Ill. 822pp.
- ZAR, J. H. 1984. Biostatistical analysis. Second ed. Prentice Hall, Englewood Cliffs, N.J. 718pp.

Received 3 August 1993.

Accepted 18 October 1994.

Associate Editor: Ryan.