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CHARACTERISTICS OF OLD-GROWTH FORESTS ASSOCIATED WITH NORTHERN SPOTTED OWLS IN OLYMPIC NATIONAL PARK

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Abstract: The relationship between northern spotted owls (*Strix occidentalis caurina*) and old-growth forests is well established, but there are few studies indicating which particular characteristics of these forests are most important to spotted owls. Thus, we compared characteristics of forests at owl response and non-response sites across Olympic National Park to identify the specific features which best predict daytime presence of northern spotted owls in relatively pristine forest. At 32 owl response sites and 230 non-response sites we measured 9 structural and species composition variables thought to be important to spotted owls. Based on these variables, we used stepwise logistic regression to develop models predicting the presence or absence of spotted owls. The accuracy of classifying a given site as a response or non-response site was quite high: 57% and 80% better than chance alone for the eastern and western sides of the Park, respectively. Spotted owls tended to roost and/or nest in stands with high vertical canopy layering; snag diameter also was related to spotted owl occurrence. We conclude that managers should focus increased attention on canopy layering and snag diameter as predictors of spotted owl presence in unharvested forests.

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Northern spotted owls have been strongly linked to old-growth forests in the Pacific Northwest (e.g., Forsman et al. 1984, Carey et al. 1990, Ripple et al. 1991). It is important, however, to know the specific components of old-growth forests most closely associated with owl presence or absence before making decisions regarding habitat and management needs of this federally designated threatened species. Previous studies that have specifically examined the relationship

between owls and particular habitat variables (Solis 1983, Sisco and Gutiérrez 1984, Laymon and Barrett 1986, Solis and Gutiérrez 1990) have taken place in areas containing a mosaic of natural and human-altered environments. Conclusions from these studies are useful for showing habitat choices made by owls in disturbed settings, but logged areas may not contain the full complement of historical habitat characteristics. A generalized test for the best predictors of owl occurrence should include the full spectrum of undisturbed structural and compositional characteristics, thereby identifying the most critical variables from a complete range of choices.

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Forests in Olympic National Park are largely free of human-caused disturbance and vary from communities of large trees near sea level to sub-alpine forests in the mountainous interior (Fonda and Bliss 1969). We sampled both forests and owl presence across a vegetation gradient from near sea level to timberline to ascertain which particular components of old-growth forest are most consistently selected by northern spotted owls for daytime use.

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STUDY AREA

Our study area encompassed 3,670 km² of the mountainous interior portion of Olympic National Park (hereafter referred to as "the Park") in northwestern Washington. Few roads penetrate this area, and elevation ranges from 100 m to 2,458 m. The Bailey Range roughly bisects the Park, creating a distinct rainshadow along the eastern side (Fonda and Bliss 1969, Fonda 1974). Annual precipitation averages about 100 cm on the eastern side and about 400 cm on the western side. The precipitation gradient and associated differences in vegetation prompted separate analyses of eastern and western sides.

In the study area, we established 56 segments of trail or road totalling 347 km in 9 different drainages. These transects were chosen as representative of low to high elevation forests in several different regions of the Park. Although logistics limited us to trails or roads and prevented random sampling, we chose transects that varied in distance to streams, slopes, aspects, and forest vegetation types (Mills et al. 1988, Fredrickson et al. 1989). Thus, we sampled transects representing eastern and western side elevational gradients from the Park's lowland bound-

ary to timberline. No transects passed through areas of recent major forest disturbance.

METHODS

Spotted Owl Sampling

We surveyed transects for spotted owls between mid-April and late July 1988–90, the time of year when nesting and fledging activities facilitate their detection (Forsman 1983, Forsman et al. 1984). We used standard owl sampling procedures (Forsman et al. 1984) to call for owls every 400 m (0.25 mi) along transects between dusk and dawn. Nighttime responses are often from foraging owls that range widely, whereas daytime responses are generally by owls that are at a roost or nest site (E. D. Forsman, U.S. For. Serv., pers. commun.). Therefore, daytime locations estimate nesting and roosting habitat more conservatively. For every nighttime owl response we detected, we made at least 2 attempts to find the owl during the day. The protocol for day locations was to return to the nighttime response site and walk >1 km in all directions while mimicking owl calls. Daytime responses separated by >400 m were considered different responses.

We designated owl response and non-response sites after a transect was sampled 3 times at night, and daytime occupancy was assessed. All sightings of owls made during the day were designated as response sites; non-response sites included all other locations on the transects where owls were called at night. Calling sites where an owl was heard at night but not during the day, as well as sites immediately adjacent, were deleted from analyses because their status as response/non-response sites was ambiguous. Although site designation was based on only 3 nighttime surveys, Azuma et al. (1990) noted that 86% of the owls detected on U.S. Forest Service lands in Washington and Oregon were found during the first 3 of 6 nighttime surveys. We did not consider non-response sites as necessarily unsuitable environments because these areas may well have been used for foraging, dispersal, or even nesting and roosting at other times or in other years. We simply presumed that there were characteristics of response sites that caused owls to choose these areas for roosting and nesting over other available locations.

We included as response sites 10 daytime locations that were not on the sampling transects, but were discovered fortuitously by us or other biologists. Three of these were in the Park, and seven were in pristine forests contiguous with

and <3 km from the Park boundary. To assure that these locations could be pooled with the responses obtained on the transects, we compared the mean values of each structural variable (see below) in the transect versus non-transect response plots. Based on *t*-tests corrected for table-wide significance via a sequential Bonferroni test (Rice 1989), there were no differences ($P > 0.2$) for any variable between transect and non-transect plots. Therefore, all response locations were pooled.

Habitat Sampling

We collected information on 9 habitat variables at each owl response and non-response site. Habitat sampling at owl non-response sites was centered from 25 to 100 m off the road or trail, with the direction and exact distance from the owl calling site randomly determined. To reduce error based on single point measurements at an expected small number of response sites, we sampled habitat at 3 locations for each daytime response site. The first sampling location was randomly centered 1–15 m from the roost or nest tree, and the other two were centered 50 m away in randomly chosen directions. Measurements in the 3 sampling locations at each response site were averaged to give a site mean for analysis.

We employed several types of measurements to quantify the 9 habitat characteristics. Based on the point-center quarter method (Cottam and Curtis 1956), we obtained average diameter of snags (SNDBH) and indices to distance between snags (SNDIS) and between trees (TRDIS). Density of large trees was assessed by counting the number of trees >80 cm dbh on a 0.1-ha circular plot (BIGT). The percent cover of downed logs (LOG) and the percent cover of vascular plants less than 2 m tall (GCOV) were ascertained with a modified reconnaissance plot (Franklin et al. 1970) fixed at 0.05 ha.

We visually estimated overhead canopy cover at different heights from the center of the reconnaissance plot (see Vales and Bunnell 1988 for favorable comparison between this and more objective methods). Potential bias was minimized by careful instruction on the dangers of observer expectancy bias (Mills and Knowlton 1989), by calibrating observers, and by preventing any observer from sampling a majority of plots at any given elevation or vegetation type. We recorded, in 10% cover classes, the percent of the sky covered by canopy in each of the following vertical layers: 2–10 m, 11–20

m, 21–30 m, 31–40 m, and >40 m. All 5 overhead layers were summed to calculate an index to vertical canopy layering (VERT) that incorporated the height of the stand as well as the amount and the distribution of foliage in the canopy. Because this index was calculated by summing percent coverage of individual layers, no single layer contributed >100 to the indexed value. The first vertical layer (2–10 m) assessed openness of the lower canopy and therefore was included as a separate variable (LAY1) in the habitat analyses. Total overhead canopy cover was not included as a variable because it was highly correlated with VERT, and preliminary logistic regression analyses with VERT consistently performed much better than similar analyses with total cover.

We derived community type (COMMUN) at each site by combining the species composition of the ground cover and of the 5 canopy layers, and running these data through the 2-way indicator species analysis in TWINSpan (Hill 1979, Gauch 1982). TWINSpan produces hierarchical classifications representing environmental gradients found among the samples, and can be used to define the various community types.

Statistical Analyses

Because our vegetation plots could be classified as associated with owl responses and non-responses instead of only response and random, we used stepwise logistic regression to predict whether an owl would respond at a given location based on specific habitat characteristics (Afifi and Clark 1984, Dixon et al. 1988). Because disparate group sizes may obscure the predictive value of the model and the individual variables (B. R. Noon, U.S. For. Serv., Arcata, Calif., pers. commun.), and our data included far more non-response than response sites, we randomly subsampled from the non-response group the same number of sites as were found in the response group. This procedure was repeated 20 times for both the eastern and western side data, with a predictive model generated for each subsampling.

We assessed goodness-of-fit for the 40 predictive models using the Hosmer-Lemeshow (HL) test (Dixon et al. 1988, Hosmer and Lemeshow 1989). A low *P*-value indicated poor correspondence between the estimated and expected probabilities. The HL test *P* was <0.1 for only five of 20 eastern side runs and two of 20 western side runs, indicating that most of the

Table 1. Structural habitat variables sampled at spotted owl daytime sites, Olympic National Park, 1988–90.

Variable ^a	Eastern side				Western side			
	Response n = 21		Non-response n = 136		Response n = 11		Non-response n = 94	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
TRDIS (m)	4.2	0.9	4.7	2.3	5.5	1.0	6.1	2.5
SNDIS (m)	14.0	4.8	14.5	10.8	17.5	7.9	23.4	15.3
SNDBH (cm)	52.4	16.0	39.1	20.0	72.4	23.1	91.3	41.2
LOG (%)	5.8	3.9	7.4	6.5	6.6	4.0	6.7	4.9
GCOV (%)	46.5	22.0	52.4	30.6	69.2	18.7	70.9	24.7
VERT	200.4	29.4	161.9	60.2	238.3	26.0	177.2	66.9
L1 (%)	45.3	18.6	44.6	27.7	49.8	13.8	46.7	29.2
BIGT	4.0	2.6	3.5	4.0	4.9	1.1	4.7	2.9

^a TRDIS—tree distance, SNDIS—snag distance, SNDBH—snag diameter at breast height, LOG—percent cover of logs, GCOV—percent cover of vascular plants <2 m tall, VERT—index to vertical canopy layering, L1—cover of lowest canopy layer, BIGT—number of trees >80-cm diameter breast height on 1,000-m² plot.

predictive models fit the logistic model reasonably well.

To determine percent of response and non-response sites correctly classified by the logistic model, we chose probability cutpoints that simultaneously maximized the total classification accuracy and that of the response group, while insuring a classification accuracy for the non-response group of at least 50%. Such a method of choosing cutpoints is appropriate for 2 reasons. First, the critical issue in spotted owl conservation and management is correct identification of potential owl sites (response sites). Secondly, some non-response sites may, in fact, be suitable for owls for daytime activities. Our approach placed a premium on determining how well the models predicted owl occurrence, while permitting increased incorrect classification of non-response sites.

We examined the importance of particular habitat variables by counting the number of

times that each variable was chosen by the stepwise procedure, regardless of the order of inclusion, in our 20 model runs.

RESULTS

Analyses were based on 230 non-response and 32 response sites (Table 1; Appendix). The responses came from >24 different owls or owl pairs, thereby reducing independence problems arising from concentrating response plots in the territory of few individuals (Capen et al. 1986).

The 20 different iterations for the eastern and western sides of the Park indicated high predictive ability for classifying owl habitat as a response or non-response site. For the eastern side, the average classification accuracy for all sites was 78.5% (SD = 6.6); this classification was on average 57% better than that expected by chance alone (Titus et al. 1984). The mean classification accuracy of eastern side non-response sites alone was 67.9% (SD = 11.0), whereas that of response sites was 89.0% (8.5).

All classification accuracy values were higher for the western side. Total classification accuracy averaged 90.2% (SD = 10.3), an average of 80% better than chance alone (Titus et al. 1984). The average classification accuracy for non-response sites was 86.4% (SD = 15.1), whereas that of response sites was 94.1% (SD = 8.8).

Only 2 variables, the index to vertical canopy layering (VERT) and the diameter of snags (SNDBH), were chosen on the majority of the model runs (Table 2), implying that these variables were important when predicting whether owls used a particular site for nesting or roosting. Vertical canopy layering was higher in response sites than non-response sites (Table 1). Snag di-

Table 2. Number of times habitat variables entered logistic stepwise regression models in 20 iterates for eastern and western sides of Olympic National Park, 1988–90.

Variable ^a	Eastern side	Western side
VERT	13	17
SNDBH	11	15
BIGT	4	8
COMMUN	5	6
TRDIS	5	2
L1	4	2
SNDIS	2	2
GCOV	1	1
LOG	4	0

^a VERT—index to vertical canopy layering, SNDBH—snag diameter at breast height, BIGT—number of trees >80-cm diameter breast height on 1,000-m² plot, COMMUN—community type, TRDIS—tree distance, L1—cover of lowest canopy layer, SNDIS—snag distance, GCOV—percent cover of vascular plants <2 m tall, LOG—percent cover of logs.

iameter was less consistent, with snags larger at response than non-response sites on the eastern side and the opposite trend on the western side. Overall, snags were much smaller on the eastern side of the Park (Table 1), such that snags in eastern-side response sites were smaller than snags in western-side response or non-response sites.

We recognize concerns regarding variable inclusion and overfit in stepwise logistic regression models (e.g., James and McCulloch 1990). With regard to overfit, whereby classification accuracy is artificially inflated by the small contribution of relatively unimportant variables, we are unaware of quantitative criteria that balance the clarity gained from removing potentially overfit variables against the resulting reduction in classification accuracy. Nevertheless, we explored how classification accuracy changed after removing a variable from stepwise models with 3–6 variables (no models had >6 variables). Elimination of variables other than the vertical canopy index or snag diameter generally reduced classification accuracy by a small amount (0–5%). If the vertical canopy index was deleted from a stepwise model, the classification accuracy generally dropped by 15–25%; omitting snag diameter had a wider range of effect, with classification accuracy decreasing by <5% to >15%. The relatively large decrease in classification accuracy when the vertical canopy index or snag diameter was removed reinforced our conclusion that these variables were important predictors of owl presence. Conversely, the generally small decreases in classification accuracy upon removal of other variables indicated that the stepwise procedure did not highly inflate classification accuracy by overfitting. Our results (Table 2) are reported directly from the stepwise runs, without adjustment for overfit.

Although the community types determined by the indicator species analysis were chosen on a minority of stepwise regression runs, we observed a variety of habitat types with owl responses (Appendix; see also Snetsinger et al. 1991). The highest proportion of response locations were in silver fir–western hemlock and Douglas fir–western hemlock community types.

DISCUSSION

Our finding that vertical canopy layering and snag diameter were important contributors to models that accurately predict whether an owl will be present at a given owl calling site during

the day differs from studies in a mosaic of disturbed and undisturbed forests, where owls roosted in stands with higher canopy closure, lower herb and shrub cover, and higher basal area of large conifers (Solis and Gutiérrez 1990). In our study, vertical canopy layering was a much better predictor of spotted owl presence than total canopy cover, and factors such as tree size, vegetation and log cover, and tree species composition were relatively unimportant predictors.

Vertical canopy layering is a function of both the height of trees and the amount of cover in all layers. Proposed advantages of a multi-layered canopy have included thermoregulation in both summer (Barrows and Barrows 1978, Barrows 1981) and winter (Forsman et al. 1984), and increased foraging efficiency and abundance of prey such as northern flying squirrels (*Glaucomys sabrinus*) (Carey 1985, Gutiérrez 1985), a favored species on the Olympic peninsula (Forsman et al. 1989).

The consistency with which snag diameter was chosen in the stepwise models signifies that it is also an important contributor to predicting daytime occurrence of owls. It is possible that the region-specific trends (i.e., snags larger at response sites than non-response sites on the eastern side vs. the opposite on the western side) indicate an optimal size of snag for hunting or foraging for prey; however, our data do not address this question.

We cannot attribute much importance to the other variables, which were seldom chosen by the stepwise procedure. Because community type is included among these rarely chosen variables, managers concerned with conserving owl habitats through silvicultural treatments or set-asides should focus their efforts on stand structure more than species composition, except as species composition influences eventual stand structure. It is, however, noteworthy that a forest type often ignored in consideration of typical spotted owl habitat, montane silver fir–western hemlock communities, had the highest proportion of response locations among the various community types in our study.

RESEARCH IMPLICATIONS

We believe that although total canopy cover is currently easier to measure from aerial and satellite imagery, it cannot replace the index of vertical canopy layering in assessing the probability of northern spotted owl occupancy.

However, total canopy cover in conjunction with canopy depth as measured from aerial or satellite imagery (Short and Williamson 1986, Martens et al. 1991) may prove to be useful predictors.

We acknowledge that there are dangers in basing habitat-use studies solely on presence/absence criteria. Our sites may have been classified as non-response for reasons other than habitat preference (Johnson 1981, Van Horne 1983, Verner et al. 1986). Also, even if suitability of the site is identified correctly in terms of presence or absence, it is still not known how well the animals reproduce and survive, so one cannot verify habitat quality. Because of these concerns and because the generality of our conclusions is unknown, our work should undergo validation before it becomes part of management practice (Johnson 1981, Noon 1986), particularly on areas outside Olympic National Park.

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Appendix. Community types comprising the variable COMMUN and entering the stepwise logistic regression as a measure of plant species composition at owl response and non-response sites, Olympic National Park, 1988–90.

Community type ^a	Response sites	Total sites	% of total ^b
Sitka spruce-vine maple/oxalis ^c	0	12	0.0
Sitka spruce-western hemlock/oxalis ^c	2	23	8.7
Western hemlock-Sitka spruce-Douglas fir-western red cedar/oxalis ^c	4	29	13.8
Silver fir-subalpine fir-mountain hemlock-Alaska yellow cedar	0	9	0.0
Silver fir-western hemlock/huckleberry ^c	10	52	19.2
Western hemlock	1	8	12.5
Western hemlock-Douglas fir ^c	2	26	7.7
Douglas fir-Western hemlock/Western hemlock-salal ^c	13	69	18.8
Douglas fir-Western hemlock/salal	0	24	0.0
Subalpine fir-Alaska yellow cedar	0	6	0.0
Alaska yellow cedar-willow subalpine fir	0	4	0.0

^a Species are presented as primary canopy species/ground cover species; scientific names: Alaska yellow cedar (*Chamaecyparis nootkatensis*), Douglas fir (*Pseudotsuga menziesii*), huckleberry (*Vaccinium* spp.), mountain hemlock (*Tsuga mertensiana*), oxalis (*Oxalis oregana*), salal (*Gaultheria shallon*), silver fir (*Abies amabilis*), Sitka spruce (*Picea sitchensis*), subalpine fir (*Abies lasiocarpa*), vine maple (*Acer circinatum*), western hemlock (*Tsuga heterophylla*), willow (*Salix* spp.), western red cedar (*Thuja plicata*).

^b Refers to the percentage of all sites in that vegetation type that had spotted owl responses.

^c Most stands in these community types contained structural characteristics commonly used to define old-growth forests.