Research Article

Roosting Habitat Use and Selection By Northern Spotted Owls During Natal Dispersal

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ABSTRACT We studied habitat selection by northern spotted owls (*Strix occidentalis caurina*) during natal dispersal in Washington State, USA, at both the roost site and landscape scales. We used logistic regression to obtain parameters for an exponential resource selection function based on vegetation attributes in roost and random plots in 76 forest stands that were used for roosting. We used a similar analysis to evaluate selection of landscape habitat attributes based on 301 radio-telemetry relocations and random points within our study area. We found no evidence of within-stand selection for any of the variables examined, but 78% of roosts were in stands with at least some large (>50 cm dbh) trees. At the landscape scale, owls selected for stands with high canopy cover (>70%). Dispersing owls selected vegetation types that were more similar to habitat selected by adult owls than habitat that would result from following guidelines previously proposed to maintain dispersal habitat. Our analysis indicates that juvenile owls select stands for roosting that have greater canopy cover than is recommended in current agency guidelines. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS dispersal habitat, logistic regression, northern spotted owl, radio-telemetry, *Strix occidentalis caurina*, Washington.

Habitat selection by adult spotted owls has been studied in many different areas and forest types (e.g., Forsman et al. 1984, 2005, Laymon 1988, Carey et al. 1992, Ward et al. 1998, Hamer et al. 2007). In contrast, habitat selection by dispersing juvenile spotted owls has received relatively little attention (Miller et al. 1997, Buchanan 2004). In the absence of data to the contrary, Thomas et al. (1990:310) assumed that juvenile spotted owls could successfully disperse through landscapes dominated by young forests with canopy cover as low as 40%. This assumption has been questioned but never tested (Buchanan 2004).

Since it was listed as threatened in 1990, the northern spotted owl (*Strix occidentalis caurina*) has continued to decline in most areas within its range (Forsman et al. 2011). The decline is thought to be due to continued habitat loss and competition with the barred owl (*S. varia*), which has invaded much of the range of the northern spotted owl during the last century (Livezey 2009, Wiens 2012). Although dispersal dynamics could also be contributing to the continued decline of spotted owl populations (Lande 1988, Doak 1989, Lamberson et al. 1994), the types of habitat used during natal dispersal remain largely unexplored (except see Miller et al. 1997). In the absence of quantitative

data, managers have had little choice but to rely on the assumptions made by Thomas et al. (1990).

In 1995–1997, we quantified vegetation characteristics at roosts used by radio-marked juvenile spotted owls on the east slope of the Cascades in Washington, USA. Our objectives were to determine if stand attributes differed between plots used for roosting and random plots within the same stands, and to determine if vegetation and/or topographic attributes differed between forest stands used for roosting and randomly selected stands within the landscape. Because most studies indicate that adult spotted owls select for forests with large trees and high canopy cover (e.g., Forsman et al. 1984, Carey et al. 1992, Hamer et al. 2007), we predicted that dispersing juveniles would select similar forest stands. Our objective was to use the observed associations between dispersing owls, different vegetation attributes, and topographic characteristics to make inferences regarding the relative suitability of different forest types and topographic attributes for dispersal habitat.

STUDY AREA

We radio-marked juvenile owls in the Cle Elum, Naches, and Leavenworth Ranger Districts of the Wenatchee National Forest on the east slope of the Cascades, Washington, USA. This region was dominated by moun-tainous terrain covered by mixed-conifer forests of Douglas-fir (*Pseudotsuga menzesii*), grand fir (*Abies grandis*), and ponderosa pine (*Pinus ponderosa*; Lillybridge et al. 1995).

Subalpine areas above about 1,800 m were dominated by mountain hemlock (*Tsuga mertensiana*), subalpine fir (*Abies lasiocarpa*), and subalpine larch (*Larix lyalli*). Elevations ranged from 670–2,084 m, and average annual precipitation near the center of the study area (47.19°N 120.93°W) was 54 cm in 1991–1997 (National Oceanic and Atmospheric Administration 2001). Most precipitation fell in winter, primarily as snow.

Land ownership in much of the study area was characterized by a checkerboard pattern of alternating square-mile sections of public and private land (Jensen et al. 1995). Historically, management of both public and private lands was largely for lumber production, which resulted in a highly fragmented patchwork of forest age classes. In general, privately owned lands were managed with a greater emphasis on lumber production than public lands and were more heavily logged. However, even on federal lands, most closed-canopy stands within the study area were mixed-age stands that had a long history of selective logging, wildfire, and insect damage.

METHODS

Capture and Monitoring of Owls

We defined natal dispersal as the movements of an owl from the time it left the natal site until it joined the breeding population (Howard 1960). The typical dispersal pattern for spotted owls is to initially make relatively extensive, rapid movements away from the natal area in the first winter after hatching (Miller et al. 1997, Forsman et al. 2002). To document this phase, we attached radio transmitters (Holohil Systems Ltd., Model RI-2C, Carp, Ontario, Canada) to 128 juvenile spotted owls between late July and August 1995, shortly before they dispersed from their natal areas (Forsman et al. 2002). Transmitters weighed 5 g, had a life expectancy of 9 months, and were glued and tied to the central rectrices (Reid et al. 1996). This study was conducted under the auspices of Oregon State University Institutional Animal Care and Use Committee (IACUC) protocol number 3628.

After juveniles left their natal areas, we relocated them by triangulation of radio signals taken from at least 3 locations using a portable receiver and a hand-held 2-element Yagi antenna. If we could not find owls by ground search, we relocated them using a fixed-wing airplane and then resumed tracking them from the ground (Forsman et al. 2002). We often triangulated an approximate location and then homed in on the signal to visually locate the owl in its roost tree. For the within-stand analysis of roost versus random plots, we used only locations in which we visually located owls or their roost trees. For the landscape-scale analysis, we included only locations where the error polygon formed by the intersection of ≥3 telemetry bearings was <1 ha, or where the owl was visually located.

Nearly all the owls that we radiomarked confined their movements to the xeric east slope of the Cascades. We excluded the few individuals ($n = 4$) that dispersed onto the mesic west slope of the Cascades from the analysis because the sample was not large enough to compare among different climatic zones.

We obtained almost all locations (96%) included in our analysis during fall through early spring (Sep–Mar) when owls were either actively dispersing or settled in temporary home ranges (Forsman et al. 2002). We relocated owls approximately every 2 weeks, and tracked them for up to 2 years if they survived the first year of life and if we were able to recapture them to install new transmitters. Because tracking periods were not equal for all owls, we collected more locations for some owls than others. To minimize potential bias from using more locations from some owls than others, we randomly selected a sample of 5 relocations over the entire study for those owls for which we had >5 relocations, and used a repeated measures design (see below). This subsample included 301 roost locations (172 visuals, 129 triangulations) from 97 owls.

We did not directly estimate telemetry error in this study, but in 2 other studies in which we used the same telemetry methods on spotted owls, the median distance between estimated and actual owl locations was 100 m (mean = 140 ± 17 m; Forsman et al. 2005). This estimate is comparable to other studies of spotted owls (Carey et al. 1992, Zabel et al. 1995, Glenn et al. 2004). Though the relatively large errors associated with triangulations were of concern, we assumed for purposes of this study that misclassification errors due to telemetry error were similar in all vegetation types, and that the overall assessment of use of different vegetation types was correct.

Roost Site Data

We measured vegetation attributes at 76 roosts used by 34 owls. We did not randomly choose the stands selected for measurement but measured as many stands as we could, given logistical and funding constraints. In each of the 76 stands, we measured 1 set of nested plots centered on the roost tree and another set of nested plots centered on a randomly located point. We determined random plot centers by mapping the boundaries of each roost stand in a geographic information system (GIS), and then randomly selecting an x-y grid intersection as the center of the random plot. We then established random plots by navigating to the random point with a global positioning unit (Trimble Navigation Limited, model Pathfinder Pro XL, Sunnyvale, CA) and selecting the nearest tree >10 cm diameter at breast height (dbh) as the center of the plot.

At each roost and random point, we used a 12.6-m radius plot (area = 0.05 ha) to estimate the density/ha of all trees >10 cm dbh and all saplings that were 5–10 cm dbh. We used a 17.8-m radius plot (0.1 ha) to record all live or dead trees >50 cm dbh. For trees >10 cm dbh, we recorded species, dbh, tree height, bole height (height to the first live limb), top condition (broken or intact), number of secondary tops, and presence or absence of fire scars. We calculated quadratic mean diameter (QMD) as $\sqrt{BA/n*0.0000785}$ where BA = basal area (m^2), and n = number of dominant and codominant trees in the stand. For each Douglas-fir tree, we also recorded whether there was visible evidence (deformed

limbs) of dwarf mistletoe (*Arceuthobium douglasii*) infection (Hawksworth 1977).

We recorded the dbh, height, and decay class (Cline et al. 1980) of all dead trees >3 m tall (hereafter referred to as snags). We calculated volume of snags as the frustum of a cone (a cone with the end truncated) in which the diameter at the top of the frustum was estimated based on a taper rate of 1.2 cm/m (Spies and Franklin 1991). We recorded the number of cut stumps within the 0.1-ha plot for 2 diameter classes: 25–50 cm and >50 cm.

We used the line-intercept method to estimate shrub cover on 4 transects in the 0.1-ha plot (Parker and Savage 1944). We summed distances covered by low shrubs (≤1 m high) and high shrubs (>1 m high) along each transect and recorded the dominant species of shrub. We estimated ground cover by dead wood (logs) as the proportion of the transect covered by logs ≥10 cm in diameter. We measured ground cover and density of tree seedlings (1–5 cm dbh) in 2 subplots (1-m radius) located 9 m from the plot center. We estimated mean canopy closure with a moosehorn densiometer (Bonner 1967) at 9 m and 17.8 m from the plot center on each of the 4 shrub transects for a total of 8 estimates per plot. Hereafter, we will refer to estimates taken with the moosehorn densiometer as canopy closure, and estimates taken from aerial photography as canopy cover (Jennings et al. 1999). At each of the primary plots, we recorded whether the plot center was located within 50 m of a talus opening ≥10 ha in area. We recorded disturbance categories in each plot (fire, logging, blowdown, commercial thin, within 75 m of a recent clear-cut, other). We also measured slope aspect and percent slope at each plot. Because we measured 35 roost plots when the ground was covered by snow, we had incomplete data for 17 variables, such as percent cover by logs and shrubs.

Landscape Data

We developed a vegetation map from a 1997 Landsat Thematic Mapper image with a pixel size of 25 m (Neiman 1998). The original vegetation map included a density layer of 4 tree classes, and a 17-class vegetation structural layer. We combined these 2 layers to create a layer with 4 vegetation cover types. These types were shrub/sapling/pole (canopy cover 0–100% and QMD <20); moderate canopy (forest with canopy cover 40–70%); closed canopy (forests with canopy cover >70%); and non-habitat, which included open canopy forest (<40% canopy cover), meadows, shrub-steppe, agricultural areas, and rock. We used forest harvest records from the United States Forest Service, Washington State Department of Natural Resources, and private land-owners to correct pixel values in areas of forest that were cut after the study began, but prior to the recording of the 1997 satellite image.

We used GIS software to produce a value for each 25-m pixel based on 4 attributes: 1) the vegetation type of the majority of pixels in a 3 × 3-cell neighborhood around each focal pixel (described above); 2) topographic position (TOPO), defined as the percentile of the range of elevation within 1 km of the focal pixel, with values from 0 for valley floor to 1 for hilltop

(Singleton et al. 2010); 3) solar insolation (SOLAR), measured in annual mean daily watt-hours as calculated by the ARCGIS Solar Analyst extension (Singleton et al. 2010); and 4) percent slope (SLOPE). For the vegetation type attribute, we used the average of the 3 × 3-cell neighborhood to compensate for the possibility of spatial errors in the telemetry locations and to remove solitary pixel values or smooth the vegetation map. Barred owls have been shown to use forests on lower topographic positions and on gentler slopes than expected (Gremel 2005, Singleton et al. 2010, Wiens 2012) and appear to be displacing spotted owls into steeper and higher elevation areas (Gremel 2005). Thus, we included the TOPO and SLOPE variables in our models to determine if these variables helped to describe habitat used by dispersing juveniles. The SOLAR metric was a non-circular, continuous measurement of slope and aspect, and incorporated topography and the amount of direct sunlight striking the ground at the latitude of each pixel (Singleton et al. 2010). Adult spotted owls in our study area tended to avoid open forests on south-aspects (Forsman et al. 1990), so we used the SOLAR variable to evaluate whether dispersing juveniles also avoided stands with high SOLAR values.

We overlaid 152 test points on a digital aerial photograph to test the accuracy of our vegetation categories. To further assess the accuracy of the canopy cover attribute, we overlaid a grid of 25 equally spaced dots at 385 test points on a digital aerial photograph, and assigned a value for canopy cover based on the proportion of dots that intersected with vegetation. Overall accuracy of the vegetation type map versus aerial photo interpretation was 67% with a fuzzy accuracy rate of 73% (Woodcock and Gopal 2000). Producer's accuracy for canopy cover was 75%, 48%, and 63% and within 10% of the reference grid value 84%, 72%, and 73% of the time for closed canopy, moderate canopy, and non-habitat, respectively.

Selection Analyses

Roost site analysis.—To assess owl selection at the roost site scale, we used a binary response variable (roost plot vs. random plot in the roost stand) and logistic regression (PROC GENMOD, SAS Institute, Inc., Cary, NC) to obtain the β coefficients of an exponential resource selection function (RSF). We used the repeated measures to block variances by owl because we measured >1 plot for some owls and we wanted to control for any lack of independence among plots. We ranked models using quasi-likelihood (QIC; Pan 2001) and considered whether the 95% confidence intervals on relative risk overlapped 1 to evaluate the strength of evidence for specific model effects.

We conducted 2 separate analyses with separate model rankings because snow conditions prevented us from measuring all covariates for each variable of interest. First, we compared models relating single factors of canopy closure, canopy closure diversity as estimated by coefficient of variation (SE/mean CV) of canopy closure readings, number of Douglas-fir/ha, number of large (>50 cm dbh) trees/ha, and quadratic mean diameter of dominant or codominant trees between used versus random plots (Table 1). Because snow

Table 1. Means ($\bar{x}$) and standard errors of variables measured in 76 forest stands used for roosting by juvenile northern spotted owls during natal dispersal on the eastern slope of the Cascades, Washington, USA, 1995–1997. Variables used in our roost site analysis are indicated with dagger (†).

Variable	Roost plots		Random plots	
	$\bar{x}$	SE	$\bar{x}$	SE
Elevation (m)	1,139.00	23.00	1,151.00	25.00
Slope (%)	46.00	2.00	44.00	2.00
Aspect (degrees)	284.00		278.00	
Canopy closure (%)†	66.00	2.00	63.00	2.00
CV[a] of canopy closure†	0.58	0.05	0.64	0.05
Saplings/ha	255.00	28.00	362.00	45.00
Snag basal area (m²/ha)	5.70	0.89	6.70	0.93
Basal area Douglas-fir (m²/ha)	19.10	1.90	18.10	1.60
Basal area other conifers (m²/ha)	18.70	1.90	19.20	1.80
Basal area all conifers (m²/ha)	37.80	2.30	37.20	1.90
Quadratic mean diameter (cm)[b]†	44.00	1.70	46.00	1.70
Douglas-fir (no./ha)†	183.00	20.00	179.00	16.00
Large Douglas-fir (no./ha)[c]	18.00	3.00	22.00	3.00
Large other conifers (no./ha)[c]	18.00	3.00	19.00	3.00
All large conifers (no./ha)[c]†	36.00	5.00	41.00	4.00
All conifers/ha	432.00	21.00	442.00	22.00
Mean dbh of Douglas-fir[d] (cm)	38.00	3.00	33.00	2.00
CV of mean dbh of Douglas-fir[d]	0.29	0.02	0.35	0.02
Mean dbh of other conifers[d] (cm)	27.00	1.00	26.00	1.00
CV of mean dbh of other conifers[d]	0.39	0.02	0.42	0.02
Mean dbh of all conifers[d] (cm)	32.00	1.00	31.00	1.00
CV of mean dbh all conifers[d]	0.47	0.01	0.50	0.02
Trees with secondary tops (no./ha)	21.00	3.00	21.00	3.00
Trees with broken tops (no./ha)	22.00	3.00	38.00	4.00

[a] CV = coefficient of variation (SE/mean).

[b] Quadratic mean diameter ($\sqrt{BA/n} * 0.0000785$) of dominant and co-dominant conifers where BA = basal area (m²), and n = number of dominant and co-dominant trees in the stand.

[c] Dbh indicates diameter at breast height (cm). Approximate dbh of trees in the small, medium, and large size classes was 10–30–cm, 31–50 cm, and >50 cm, respectively.

[d] Average and coefficient of variation (CV = SE/mean for dbh estimates are from the 0.05-ha plot).

prevented us from collecting data on all variables on all plots, we used a reduced data set ($n = 40$) to compare selection models based on log cover, coefficient of variation of log cover, snag volume/ha, and dwarf mistletoe rating (Table 2).

Landscape-scale analysis.—To assess habitat selection at a population level, we used a use versus available approach equivalent to a Design II study as described in Manly et al. (2010). We defined the area available for use by spotted owls as the polygon formed by a 1.5-km buffer around the minimum convex polygon containing all owl locations. We then used program Hawth's Tools (Beyer 2004) to generate 301 random points within this polygon to sample the available habitat. Four random locations could not be classified by the vegetation layer, leaving 297 random points to compare to the 301 owl locations. We used logistic regression to obtain the β coefficients of an exponential RSF likelihood model based on used and available points drawn from a population of all resource units in a particular landscape (Johnson et al. 2006, Lele et al. 2013, McDonald 2013). Because we had multiple locations (up to 5) from some owls, we used PROC GENMOD in SAS with a repeated measures statement (REPEATED = SUBJECT) to block variances by owl, and used generalized estimating equations (GEE) to estimate parameter values (Fieberg et al. 2010). We ranked models by quasi-likelihood under the independence model criterion (QIC; Pan 2001), in the same manner as ranking models by Akaike's Information Criterion (AIC; Akaike 1973, Burnham and Anderson 1998).

In a preliminary analysis, we examined habitat attributes at 500–1,500 m from owl locations, and found that habitat in the immediate vicinity of the owl location most consistently differentiated owl roosts from random points. Thus, we confined the current analysis to the pixel value at the roost. We examined 5 single-factor models, including intercept-only (null model), vegetation type, slope, solar insolation, and topographic position. In addition to the QIC rankings, we used the degree to which the 95% confidence interval surrounding the relative risk overlapped 1 to evaluate the direction and strength of evidence for specific model effects, with confidence limits broadly overlapping 1 indicating no effect. We did not have a priori expectations regarding whether any of these covariates in combination would best explain owl roost locations. So to avoid a large, uninformed model set resulting from every possible combination of covariates in 2-, 3-, 4-, and 5-factor models, we initially evaluated single-factor models in comparison to the intercept-only model. If any of the single factor models were within 2 QIC and included 95% confidence limits on the relative risk that did not overlap 1, we combined covariates into multi-factor models.

RESULTS

Roost Site Analysis

We summarized 43 variables at roost and random plots after first standardizing density measurements to units/ha (Tables

Table 2. Means ($\bar{x}$), and 95% confidence intervals (CI) of understory variables in stands used by juvenile northern spotted owls during dispersal and random plots in the same stand, on the eastern slope of the Cascades, Washington, USA, 1995–1997. Measurements of variables were restricted to 40 stands that were free of snow. Variables used in our roost site analysis are indicated with dagger (†).

Variable	Roost plots $\bar{x}$	Roost plots 95% CI	Random plots $\bar{x}$	Random plots 95% CI
Proportion of plots with:				
Small stumps[a]	0.26	0.12–0.43	0.26	0.12–0.43
Large stumps[a]	0.29	0.14–0.46	0.26	0.12–0.43
No disturbance	0.38	0.23–0.54	0.48	0.32–0.64
Fire scarred trees	0.33	0.19–0.49	0.60	0.43–0.75
Logging[b]	0.30	0.17–0.47	0.33	0.19–0.49
Blowdown forest	0.05	0.01–0.17	0.08	0.02–0.20
A clearcut within 75 m	0.08	0.02–0.20	0.25	0.13–0.41
Pre-commercial thinning	0.03	0.00–0.13	0.05	0.00–0.17
Other disturbance[c]	0.08	0.02–0.20	0.05	0.00–0.17
Talus slope within 50 m	0.08	0.02–0.20	0.05	0.00–0.17
Low shrubs	0.38	0.23–0.54	0.45	0.29–0.62
High shrubs	0.43	0.27–0.59	0.38	0.23–0.54
Proportional cover by logs†	0.03	0.01–0.04	0.04	0.03–0.05
CV of log cover[d]†	0.74	0.53–0.95	0.71	0.52–0.89
Mean log diameter in cm	29 (27)	24–34	27 (28)	24–32
CV of log diameter	0.32	0.24–0.41	0.32	0.25–0.39
Snag volume (m³)†	57.00	35–78	69.00	44–94
Seedling density (no./ha)	6,369	1,150–1,1586	23,885	9,380–38,391
Dwarf mistletoe rating[e]†	2.50	1.99–3.01	2.80	2.33–3.27

[a] Diameters of small and large stumps were 25–50 cm and ≥50 cm, respectively. Sample size includes 35 roost/random plot pairs for which we had stump data.
[b] Logging was indicated by stumps present in the plot. We did not determine age of stumps.
[c] Other disturbances included plots with ≥1 of the following disturbances: old road through plot, adjacent to a road cut, adjacent to a natural opening, firewood cutting in plot, historical beaver activity.
[d] Coefficient of variation calculated as SE/mean.
[e] From 39 stands where the same observer recorded dwarf mistletoe in Douglas-fir in both roost and random plots. Values were summarized for dominant and codominant trees.

1 and 2). In the roost site analysis, none of the 9 single-factor models were appreciably better than the intercept-only models (Table 3), and all 95% confidence intervals on estimates of relative risk overlapped 1. Although there appeared to be little selection for within-stand structure, most stands used for roosts (78%) had ≥10 trees/ha that were large trees (>50 cm dbh). Although canopy closure did not differ between roost and random plots, the average canopy closure at roost plots was high (66 ± 2%).

Landscape-Scale Analysis
In the landscape analysis, the model that included vegetation type (TYPE) accounted for more than 99% of the evidence by QIC weight (Table 4). Using the non-habitat type as the reference category, we found that the closed canopy type was most highly selected (95% CI for relative risk = 4.5–13.2 times as great as the non-habitat type). The second most selected vegetation type was the moderate canopy type (95% CI for relative

Table 3. Ranking of models by quasi-likelihood under the independence criterion (QIC) for roost site scale analysis of roosting habitat used by dispersing juvenile northern spotted owls on the eastern slope of the Cascades, Washington, USA, 1995–1997. We also provide ΔQIC and QIC weights (QIC wt).

Model	QIC	ΔQIC	QIC wt
All plots combined			
Intercept-only	210.72	0.00	0.31
All large conifers (no./ha)	211.01	0.30	0.27
Quadratic mean diameter(cm)[a]	211.34	0.63	0.23
CV[b] of canopy closure	211.80	1.09	0.18
Douglas-fir (no./ha)	212.61	1.89	0.12
Canopy closure	212.77	2.05	0.11
Snow-free plots only			
Dwarf mistletoe rating	109.58	0.00	0.38
CV[b] of log cover	110.11	0.53	0.29
Intercept-only	110.90	1.32	0.20
Snag volume(m³)	112.38	2.80	0.09
Proportional cover by logs	114.33	4.75	0.03

[a] Quadratic mean diameter ($\sqrt{BA}/n*0.0000785$)of dominant and co-dominant conifers where BA = basal area (m²), and n = the number of dominant and co-dominant trees in the stand.
[b] CV = coefficient of variation (SE/mean).

Table 4. Ranking of models by quasi-likelihood under the independence criterion (QIC) for landscape-scale analysis of roosting habitat used by dispersing juvenile northern spotted owls on the eastern slope of the Cascades, Washington, USA, 1995–1997. We also present ΔQIC and QIC weights (QIC wt). Covariates are type = cover type (shrub–sapling, moderate canopy, closed canopy, or non-habitat), topo = topographic position, solar = solar insolation, and slope = percent slope within a 25-m^2 pixel of the owl relocation.

Model	QIC	ΔQIC	QIC wt
Type	754.77	0.00	1.00
Topo	822.10	67.33	0.00
Solar	830.74	75.97	0.00
Intercept-only	833.91	79.15	0.00
Slope	834.88	80.12	0.00

risk = 1.89–8.8 times), followed by the shrub and sapling type (95% CI for relative risk = 1.63–5.69 times).

DISCUSSION

Roost Site Selection

In contrast to the assumption that stands with relatively open canopies provide suitable dispersal habitat for spotted owls, our results suggest that dispersing juveniles selected stands for roosting that had relatively high canopy closure ($\bar{x} = 66 \pm 2\%$). One qualification on our results is that we used a moosehorn densiometer to estimate canopy closure as opposed to estimating canopy cover with aerial photos; these 2 methods are not directly comparable because estimates of canopy closure with a moosehorn densiometer are typically lower than estimates of canopy cover based on remotely sensed data. In our case, we found that estimates based on the moosehorn averaged $13.8 \pm 1.7\%$ less than estimates of canopy cover derived by superimposing a dot grid over aerial photos of the roost stands.

Although spotted owls did not strongly select for tree diameter at the roost site scale, most stands selected for roosting by dispersing juveniles had ≥10 large trees/ha. We did not determine the age of the large trees in roost plots, but an earlier study in our study area (R. Schellhass, U.S. Forest Service, unpublished data) estimated the average age of a 50-cm dbh tree was approximately 140 years old. Selection for stands with some attributes of older forest was not unexpected given that Miller et al. (1997) found that dispersing juvenile spotted owls in western Oregon used old forests more than other forest types and did not roost in non-forest areas. In our study, these stands were selected at the patch scale, or third-order selection (Johnson 1980). Two hypotheses could explain why dispersing owls selected closed-canopy stands. First, several researchers (Barrows 1981, Forsman et al. 1984, Weathers et al. 2001) have shown that temperature and precipitation appear to influence selection for roost trees and attributes within a roost tree, such as perch height and percent overhead cover. Thus, owls could be selecting for these roost attributes at a finer scale than our roost plots, and selection for stands with large trees could increase the odds of finding these micro-site attributes.

Second, juvenile northern spotted owls may have selected for closed-canopy forest because their preferred prey were most abundant in old forests or in areas where there was a mosaic of old forests and openings (Carey et al. 1992, Ward et al. 1998, Lehmkuhl et al. 2006a, b). Our sampling design did not allow for a comparison between roosting and foraging because our data were limited to roost locations. However, because spotted owls tend to use similar forest types for roosting and foraging (Forsman et al. 1984, Carey et al. 1992, Herter et al. 2002), one would expect to see selection for older forests for roosting if the owls are also foraging in the same stands.

Some researchers have found that northern spotted owls often forage near edges between old forest and other forest types but roost in adjacent stands with denser canopy cover (Zabel et al. 1995, Glenn et al. 2004, McDonald et al. 2006). Also, Forsman et al. (1984) found that the proportional use of old forest was higher for roosting than foraging. Thus, if dispersing owls use a broader range of forest types for foraging than for roosting, our roost stand characteristics may not have described the full range of forest types used for foraging.

Our estimates of average basal area in roost stands used by juvenile spotted owls were similar to estimates from earlier studies of adult spotted owls in the eastern Cascades of Washington (Buchanan et al. 1995; G. King, Yakama Indian Nation, unpublished data), but our estimate of average canopy closure at roosts (66%) was lower than was reported for spotted owl nest sites in earlier studies conducted in the same region as our study (75%–93%; Buchanan et al. 1995; G. King, unpublished data; Herter et al. 2002). It is unclear if these differences were real or were due to small sample sizes or differences in methods used to estimate canopy closure. G. King (unpublished data) and Buchanan et al. (1995) used spherical densiometers to measure canopy closure, which tend to produce higher estimates than moosehorn densiometers (Bunnell and Vales 1990, Cook et al. 1995).

Landscape-Scale Selection

To facilitate dispersal of spotted owls between reserves of old forest, Thomas et al. (1990:310) recommended that at least 50% of the land area between reserves should be covered by forests with average tree diameter ≥11 inches (28 cm), and average canopy closure ≥40%. This so called "50–11–40 rule" has been widely used as a baseline for forest management within the range of the northern spotted owl. For example, the regulatory definitions of spotted owl dispersal habitat established by the Washington State Forest Practices Board (WSFPB 2011) include forest stands with 1) ≥50% canopy closure; 2) ≥50 conifer trees/acre (124/ha) with dbh ≥6 inches (15 cm) in even-aged stands or ≥4 inches (10 cm) in uneven-aged stands; 3) average tree height ≥65 feet (20 m); and 4) a total tree density of ≤200 trees per acre (494/ha; WSFPB 2011, WAC 222-16-085). Although our data on canopy closure cannot be directly translated into canopy cover values, our mean estimate of canopy closure from plots at roosts (66%), which was likely an underestimate of canopy

cover, was considerably higher than the minimum values recommended by Thomas et al. (1990) or WSFPB (2011). Our estimate of average conifer tree density of 432 trees/ha from the roost site analysis was near the WSFPB guideline of 494 trees/ha, but the minimum tree diameters in the WSFPB rules were over 2 times smaller than mean values in the roost plots used by spotted owls in our study.

Dispersing owls could benefit from selecting older, closed-canopy stands for roosting. The amount of older forest in territories of adult spotted owls, particularly around core areas, is positively associated with annual survival (Olson et al. 2004, Dugger et al. 2005). These older, closed-canopy forest stands are important sources of prey (Lehmkuhl et al. 2006*a,b*) and possibly have microhabitat conditions that enable spotted owls to successfully disperse across the landscape until they acquire a territory. Should these types of stands become rare or highly fragmented, the ability of owls to disperse across the landscape would be diminished, contributing to population declines (Forsman et al. 2011).

Dispersing juvenile spotted owls often use areas around the periphery of home ranges of resident adults (Forsman et al. 2002). This suggests that all habitat may not be equally available to dispersing owls because some areas may be more heavily defended than others. If all areas within our study area were not equally accessible to dispersing juveniles, we may have overestimated what was available. This is a common issue in use-available studies but is virtually impossible to account for (Aarts et al. 2008, Beyer et al. 2010). A possible method to compensate for this problem would be to incorporate a movement parameter in the analysis (e.g., Fieberg et al. 2010), but we had insufficient data to do so.

The accuracy of our landscape-scale canopy cover measurements was moderate compared to a visual assessment of an aerial photo of the same areas. Based on our finding of selection for closed-canopy forest, we believe that the quality of roosting habitat for dispersing spotted owls in Washington is a continuum that ranges from low (open canopy forest) to high (closed-canopy forest), and we caution that the upper and lower values of the canopy cover categories that we used for our landscape-scale analysis should not be viewed as absolute limits in defining dispersal habitat.

MANAGEMENT IMPLICATIONS

Buchanan (2004) summarized a number of different management strategies and definitions of dispersal habitat that have been proposed to facilitate dispersal of juvenile spotted owls. Among these, the rather minimal management guidelines in Thomas et al. (1990) have been widely used as the primary prescription for providing dispersal habitat for spotted owls. Based on our study, we recommend that managers should pursue a strategy that exceeds the canopy cover guidelines recommended by Thomas et al. (1990) when managing dispersal habitat for spotted owls. Based on our estimate of mean canopy closure (66%), and our estimate of mean canopy cover from overlaying a dot grid on the same areas (approx. 14% larger), we recommend that the target for

canopy cover in stands managed for dispersing spotted owls should be at least 80%.

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