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NEST SITES AND NESTING HABITAT OF THE NORTHERN SPOTTED OWL IN NORTHWESTERN CALIFORNIA¹

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Abstract. We located 69 Spotted Owl (*Strix occidentalis caurina*) nests in northwestern California. Spotted Owls nested in eight different tree species of which 83% were located in Douglas-firs (*Pseudotsuga menziesii*). Sixty percent of the nests were located in broken-top trees, whereas cavity and platform nests each accounted for 20%. Minimum nest tree ages averaged 288 years (range 57–688) with 42% of the trees having minimum ages of > 300 years. Owls nested in forests that were structurally different than forests available to them. These stands were characterized by large (> 90 cm dbh) conifers, a hardwood understory, and a variety of tree sizes. Nest sites appeared to be located in pockets of even older forest containing disfigured trees of advanced age which provided suitable nesting structures.

Key words: nest sites, nesting habitat, Northern Spotted Owl, old-growth conifer forests, *Strix occidentalis caurina*.

INTRODUCTION

Conservation of the Spotted Owl (*Strix occidentalis*) has been controversial because of the economic value associated with the trees within its habitat (Gutiérrez et al. 1995). Forsman et al. (1984), Forsman and Giese (1997), and Hershey et al. (1998) have described nest trees and nesting habitat in mesic forests occurring in western Oregon and Washington. Buchanan et al. (1993, 1995) and Everett et al. (1997) provided similar descriptions from drier forests in eastern Washington. Here, we provide detailed information on Northern Spotted Owl (*S. o. caurina*) nests and nesting habitat in the southern portion of its range, in northwestern California, in order to better understand habitat selection patterns and to facilitate conservation planning for this subspecies.

METHODS

STUDY AREA

Our study area was located in northwestern California and included the Klamath Mountains and Coast Ranges from the Oregon border south 455 km to southern Marin County. The study area was selected to sample nest sites and nest stands throughout the range of the Northern Spotted Owl in California.

The climate was Mediterranean, characterized

by hot, dry summers and cool, moist winters. Average annual rainfall ranged from approximately 50 cm in the southern portion of the study area to greater than 250 cm in the northern portion (Kahrl 1979).

Topography of the study area varied from low rolling hills in the south to steep rugged mountains in the north. Elevations ranged from sea level to 2,743 m. The vegetation within the study area was quite diverse, ranging from beach and dune (Barbour and Johnson 1988) and coastal salt marsh (MacDonald 1988) to montane and subalpine vegetation (Sawyer and Thornburgh 1988). However, Spotted Owls generally only inhabited low to middle elevation conifer forests (U.S. Dept. Interior 1982, Forsman et al. 1984, Gutiérrez et al. 1995).

LOCATING NESTS

We located nests using procedures described by Forsman (1983) and Franklin et al. (1996). Once owls were located during night-time surveys, one of the adults was fed mice and followed to the nest as it delivered the prey to either an incubating/brooding female or nestling. Additional nest sites were located by cooperating biologists.

NEST TREE MEASUREMENTS

We recorded information on seven variables to describe each nest tree (LaHaye 1988), of which we present data on the three most important measurements. In addition, 50 nest trees were increment bored (Ferguson 1970) to estimate minimum ages. Because Spotted Owls often nest

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in broken-top trees, we also estimated the number of years since the main stem broke by examining the extracted increment cores and locating the change in growth rate associated with the reduction in crown foliage. We counted tree rings directly and did not extrapolate ring counts to the unsampled portion of the core radii, because there is no accurate method for predicting tree age from partial tree radii. Thus, our counts represented minimum tree ages.

NEST MEASUREMENTS

We climbed 26 nest trees to measure nest characteristics. The diameter of the nesting surface was estimated using a measuring tape on four axes that divided the surface into eight approximately equal parts. Percent cover above the nesting surface was estimated with a spherical densiometer (Lemmon 1956) by placing the instrument at the center of the nest. In addition, the azimuth from the nest to all shelter trees was recorded. A shelter tree was defined as any tree that was taller than the nesting surface and within 10 m of the nest.

We recognized three nest types: broken-top, cavity, and platform. Broken-top nests were located in trees whose bole had broken, thereby providing a nesting surface near the top of the remaining stub. Cavity nests were defined as any nest that the owls accessed through an entrance on the side of the bole, which were not obvious broken-top nests. A platform nest was any accumulation of sticks or debris that provided a suitable nesting surface. Platform nests included abandoned animal nests and debris traps such as branches infected with mistletoe (*Phoradendron* sp.).

HABITAT MEASUREMENTS

Detailed vegetation information was obtained from 44 nest stands to quantify differences between habitat used for nesting and other forested habitat within 1,500 m of each nest sampled. Nesting habitat data were collected at four sample points 25 m from each nest in each cardinal direction. Spacing of samples was established to characterize nest stands without having large diameter nest trees necessarily dominate the samples. Additionally, four sample points were located in each cardinal direction and at a random distance between 200 m and 1,500 m from the nest tree to represent available habitat. This sampling was designed to address nest level habitat

selection occurring within a hypothetical Spotted Owl home range. In each nest stand, four sample points were measured within both nesting and available habitat to increase the number of points available for use in the assessment of model stability (see below). At each sample point, information also was collected to provide a general physiographic description and a detailed description of the vegetation (LaHaye 1988).

Bitterlich's variable-radius method (Mueller-Dombois and Ellenberg 1974) using an English measure, 20 basal area factor angle, was used to determine which trees would be included in the sample (Dilworth and Bell 1985). Ground cover was measured by recording cover values of trees < 10 cm diameter at breast height (dbh), shrubs, herbs, litter, and coarse woody debris along one 22.9-m line intercept per sample point (LaHaye 1988). Canopy closure was estimated with a spherical densiometer by averaging 16 readings collected in the vicinity of each sample point (LaHaye 1988).

DATA ANALYSES

We used Kruskal-Wallis tests to examine univariate intergroup differences (Zar 1974) of habitat variables with a significance level adjustment for multiple comparisons (Rice 1990). We used variance ratio tests (Zar 1974) for assessing group differences among nest types. We used circular statistics (the mean angle [ϕ] and the measure of concentration [r], Batschelet 1981) to evaluate slope aspects at nest trees, nest aspects, and azimuths from the nests to shelter trees. The measure of concentration indicated the degree of clustering of sample values around the mean angle (e.g., when all sample points have the same value, $r = 1.0$). Means (\pm SD) are reported below.

We used Pearson product-moment correlation coefficients (Nie et al. 1975) to assess colinearity between variables. Variables with correlation coefficients ≥ 0.60 were noted and the variable that provided the most meaningful biological interpretation was retained and the other was removed from further analyses.

Power or log transformations were conducted on variables that were not normally distributed. Data transformation was accomplished using the Box-Cox transformation (Sokal and Rohlf 1981).

We used stepwise discriminant analysis

TABLE 1. Description of Spotted Owl nests and nest trees in northwestern California. Means \pm SD (*n*).

Variable	Nest type		
	Broken-top	Cavity	Platform
Diameter at breast height (cm)	138 \pm 8.0 (35)	157 \pm 11.6 (15)	119 \pm 9.5 (14)
Tree height (m)	39 \pm 2.4 (35)	43 \pm 3.5 (15)	43 \pm 4.9 (14)
Nest height (m)	28 \pm 1.8 (35)	26 \pm 3.0 (15)	21 \pm 1.9 (13)
Percent cover at nest	85 \pm 16.6 (13)	100 \pm 0.0 (6)	85 \pm 3.1 (3)

(Klecka 1982) to explore differences between nesting habitat and forested habitat within 1,500 m of each nest. A random sample of 44 nest stand and 44 available habitat sample points (one of each from each unique nest stand) was used to construct each discriminant function. A new random, but not independent, sample of 44 nest and 44 available habitat sample points (one of each from each unique nest stand) exclusive of the sample points used to construct the discriminant function, was used to generate the classification matrices. Only sample points that occurred in forested habitat were used. All analyses contained groups with equal sample sizes and the group variance/covariance matrices were evaluated for homogeneity using Box's test (Nie et al. 1975).

We used the method described by Capen et al. (1986) to evaluate discriminant models when some or all of the assumptions of stepwise discriminant analysis are not met. The models were evaluated by replicating the process twenty times and assessing the stability of the classification rates, the variable loading pattern, and the structure coefficients. We calculated chance corrected classification rates (Titus et al. 1984) to assess the statistical significance of the classification success using the results of the pooled stepwise discriminant analysis.

RESULTS

NEST TREE LOCATION

Sixty-nine Spotted Owl nest trees were located. Elevation at nest sites ranged from 36 to 1,507 m. However, 50 (71.4%) of the nests were located between 500 m and 1,200 m elevation. Forty-seven (68.1%) nests were located on the lower half of the slope on which they occurred. The mean distance to water from nest trees was 117.3 \pm 110 m.

The mean angle of the slope aspects at Spotted Owl nests was 58 \pm 72°. The measure of

concentration was 0.21, indicating that the mean angle was not significantly different than random. The mean percent slope was 49 \pm 18%.

NEST CHARACTERISTICS

Broken-top nests (*n* = 41, 60%) were the most commonly used nest type, while cavity nests (*n* = 14) and platform nests (*n* = 14) accounted for 20% each. Mean nest aspect was southerly (201 \pm 67°, *n* = 42) but did not differ from a random distribution (*r* = 0.31). The mean azimuth to shelter trees from nests was 30 \pm 91° with *r* = 0.001. Thus, shelter trees also were distributed randomly. Average nest surface diameter was 53 \pm 16 cm (*n* = 17) for broken-top nests, 42 \pm 14 cm (*n* = 6) for cavity nests, and 46 \pm 14 cm (*n* = 3) for platform nests; the differences were not significant ($F_{2,23} = 1.03$, *P* = 0.37).

NEST TREE CHARACTERISTICS

Spotted Owl nests were located in eight tree species. Eighty-three percent were located in Douglas-fir trees (*Pseudotsuga menziesii*), 9% in redwoods (*Sequoia sempervirens*), and less than 2% each in Bishop pine (*Pinus muricata*), tan oak (*Lithocarpus densiflorus*), canyon live oak (*Quercus chrysolepis*), black oak (*Q. kelloggii*), chinquapin (*Chrysolepis chrysophylla*), and white fir (*Abies concolor*).

We found no significant differences in dbh ($F_{2,61} = 2.62$, *P* = 0.08), tree height ($F_{2,61} = 0.56$, *P* = 0.57), nest height ($F_{2,60} = 1.86$, *P* = 0.16), or percent cover at the nest ($F_{2,19} = 2.75$, *P* = 0.09) among trees containing the three nest types (Table 1).

Minimum tree ages obtained from 50 nest trees averaged 288 \pm 129 years and ranged from 57 to 688 years. In addition, 70% and 42% of the nest trees had minimum ages exceeding 200 and 300 years, respectively. The average number of years since the bole broke on broken-top nest trees was 135 \pm 73 years (*n* = 20).

TABLE 2. Means (\pm SD) for variables used in the univariate analyses of Spotted Owl nest stands and available habitat in northwestern California.

Variable	Habitat type	
	Nest	Available
Shrub cover (%)	9.0 \pm 10.2	8.5 \pm 11.2
Herb cover (%)	16.3 \pm 13.6	14.4 \pm 14.3
Litter cover (%)	68.4 \pm 14.8	72.3 \pm 14.2
Small woody debris (%) ^a	11.6 \pm 7.9	10.3 \pm 6.3
Large woody debris (%) ^b	5.9 \pm 7.2	5.2 \pm 5.9
Canopy closure (%)	75.0 \pm 10.4	75.9 \pm 14.4
Tanoak ba ^c	4.4 \pm 4.8	2.6 \pm 3.1
Madrone ^d ba	1.8 \pm 2.3	1.7 \pm 2.1
Live Oak ba	0.9 \pm 2.4	1.9 \pm 3.8
Broken-top Douglas-fir ba	1.5 \pm 1.7	0.8 \pm 1.4
Douglas-fir snag ba	1.4 \pm 1.7	0.2 \pm 0.7 ^e
Conifer ba, 1–30 cm dbh	3.1 \pm 2.4	2.7 \pm 1.9
Conifer ba, 31–60 cm dbh	2.4 \pm 3.3	1.8 \pm 2.0
Conifer ba, 61–90 cm dbh	3.8 \pm 6.0	2.1 \pm 1.8
Conifer ba, >90 cm dbh	10.7 \pm 3.6	4.3 \pm 3.5 ^e
Hardwood ba, 1–20 cm dbh	3.3 \pm 3.1	4.4 \pm 3.5
Hardwood ba, 41–60 cm dbh	2.2 \pm 2.1	1.1 \pm 1.4 ^e

^a Dead and down, less than 0.30 m in diameter.

^b Dead and down, greater than or equal to 0.30 m in diameter.

^c Basal area in m² ha⁻¹.

^d *Arbutus menziesii*.

^e Significant difference between habitat types ($\alpha = 0.005$).

HABITAT CHARACTERISTICS

We located Spotted Owl nests in three forest types. Mixed evergreen forest ($n = 32$), mixed conifer forest ($n = 6$), and redwood forest ($n = 6$). Sample sizes from the mixed conifer and redwood forests were too small for independent analyses. Therefore, we combined the data from all three forest types for all habitat analyses.

We measured 123 vegetation variables at 352 sample points in 44 nest stands. We reduced the original 123 variables to 17 (Table 2) by eliminating variables whose frequency of occurrence was too limited to be useful in the analyses and by removing variables which were highly correlated with other variables. None of the remaining 17 variables were normally distributed. Because transformations resulted in little or no improvement, we used the untransformed vari-

ables in all analyses. In addition, the variance/covariance matrices were strongly heterogeneous ($F_{6,887547} = 15.44$, $P < 0.001$). Between-group univariate analyses indicated three variables that were significantly different between nest stands and random habitat (Table 2). The three significant variables were conifer basal area (> 90 cm dbh), hardwood basal area (41–60 cm dbh), and basal area of Douglas-fir snags.

The three variables used by the stepwise discriminant analysis to differentiate nest stands from random habitats were conifer basal area (> 90 cm dbh), hardwood basal area (41–60 cm dbh), and basal area of Douglas-fir trees with broken tops (Table 3). Over 70% of all sample points combined were correctly classified by the discriminant models (Table 3). The results of the chance-corrected classification evaluation showed

TABLE 3. Variable loading pattern and classification rates from 20 stepwise, discriminant analyses of Spotted Owl nesting habitat in northwestern California.

Variable	Frequency of occurrence in random subsamples	Mean structure coefficient \pm SD	Classification results	
			Group	% correct \pm SD
Conifer ba ^a , > 90 cm dbh	20	0.88 \pm 0.08	Nest	67.2 \pm 5.8
Hardwood ba, 41–60 cm dbh	12	0.43 \pm 0.10	Available	75.7 \pm 6.4
Broken-top Douglas-fir ba	8	0.59 \pm 0.09	Overall	71.4 \pm 3.1

^a Basal area in m² ha⁻¹.

the classification rates of the discriminant model to be significantly better than random ($Z = 149.3$, $P < 0.001$), and the variable loading pattern, structure coefficients, and classification rates to be relatively stable (Table 3).

DISCUSSION

Virtually every aspect of Spotted Owl ecology has been contested by special interest groups, particularly habitat selection and population dynamics (Gutiérrez et al. 1996). Unambiguous studies of owl habitat selection are difficult to execute because of the scale and expense required for a proper experimental design. However, both comparative studies and studies effected in a variety of situations can provide insight into general patterns of habitat selection even though they may be correlative in nature. If patterns are consistent, it lends generality to the inferences about habitat selection. Our research suggests that Northern Spotted Owls do not require a specific type of nest structure to initiate nesting. It must only be a structure large and stable enough to support a female and her eggs/brood. However, the forest in which the owl chooses to nest is very different from available habitat within its home range. These forests regularly contain the types of structures the owl will accept as nesting substrates.

Although Spotted Owl nests in northwestern California were located at a variety of elevations, > 94% occurred below 1,218 m. This observation supported Forsman et al.'s (1984) and Gutiérrez et al.'s (1992) contention that Spotted Owls in general have an upper elevational limit that corresponds to the ecotone separating mid-elevation forests from subalpine forests. However, this boundary is probably the result of the availability of suitable habitat and prey rather than a physiological limit.

We found the majority of our nests on the lower portions of slopes as others have (Blakesley et al. 1992, Seamans and Gutiérrez 1995, Hershey et al. 1998). Sawyer et al. (1988) recognized that lower slopes and river terraces were the most productive habitats in northwestern California. Thus, these areas would be more likely to provide the large trees and forest structure used by Spotted Owls for nesting. Fire also may be less frequent in stream bottoms which would enhance tree survival. Similarly, this study and others (Forsman et al. 1984, Folliard 1993) noted that Spotted Owls select nests near

surface water which is more likely to occur at the bottom of slopes.

Nest stands in our study and on the Olympic Peninsula (Forsman and Giese 1997) were located on markedly steeper slopes than those reported from Oregon (Forsman et al. 1984), eastern Washington (Buchanan et al. 1995), and coastal northwestern California (Folliard 1993). These differences probably are explained by the physiographic differences among these study areas. Thus, steep slopes are not an ecological requirement for the Spotted Owl throughout its range.

Spotted Owl nest trees in this study were quite old. The mean estimated, extracted core radius (0.47) indicated that typically only half of the core radii were extracted in our samples. Thus, actual tree ages were substantially older than the recorded ring counts. Doubling the extracted core ring counts for a crude estimate of tree age indicated that 84% of the nest trees were greater than 300 years old. Gutiérrez et al. (1992) reported similar ages for California Spotted Owl (*S. o. occidentalis*) nest trees in southern California. In addition, over half (55%) of the broken-top nest trees in our study were estimated to have broken more than 100 years ago. In contrast, Buchanan et al. (1993) found Spotted Owls nesting in trees ranging from 66–700 years old with a median age of 137 years. Similarly, Seamans and Gutiérrez (1995) reported relatively younger aged ($\bar{x} = 163.6$ years) nest trees used by Mexican Spotted Owls (*S. o. lucida*) in New Mexico. Thus, nest tree ages vary among regions and forest types occupied by this species.

We chose to divide nests identified in this study into three nest types. Several authors (Forsman et al. 1984, Buchanan et al. 1995, Hershey et al. 1998) did not distinguish between broken-top and cavity nests, and lumped these two into a tree-deformity nest type. The use of tree-deformity nests seems to be correlated with either age of the forests or the management of those forests. For example, this study, Forsman et al. (1984), Forsman and Giese (1997), and Steger et al. (1997) found tree-deformity nests to be the most common nesting structures in older forests of northwestern California, Oregon, the Olympic Peninsula, and the Sierra Nevada, respectively. In contrast, Buchanan et al. (1995) and Folliard (1993), both working in younger forests created by logging or fire, located the majority of nests in platform structures. Thus,

the type of nest structure locally available to the owl may be less critical than other requirements such as prey availability, suitable habitat, etc. Hence, these findings are not consistent with the nesting hypothesis as the basis for habitat selection (Gutiérrez 1985).

The overall selection pattern of microhabitat structure we observed was consistent with all other studies of Spotted Owl habitat selection throughout its range (Northern Spotted Owl: Buchanan et al. 1995, Everett et al. 1997, Gutiérrez et al. 1998, Hershey et al. 1998; California Spotted Owl: Gutiérrez et al. 1992, LaHaye et al. 1997; Mexican Spotted Owl: Seamans and Gutiérrez 1995). Spotted Owls in this study selected nesting habitats with a large-diameter conifer overstory which contained a significant component of deformed trees and was subtended by an understory of large hardwoods. These results, coupled with high variation in tree diameters in nesting areas, demonstrate that the owls are using more complexly structured forest of older age than was available in the landscape. Our study area spanned much of the Northern Spotted Owl's range in California. Thus, the patterns we observed in combination with those of other habitat studies suggest the generality that the structure of the forest is as important as its age. However, complex forest structure, disfigured trees, and hence, habitats used for nesting by this owl, tend to become more common as a forest ages.

In conclusion, Spotted Owls in northwestern California appeared to be selecting nests in remnant patches of older trees that escaped past fires or other natural catastrophes allowing the trees to achieve a size and age that was more advanced than trees in the surrounding forest. Therefore, to provide nests and nesting habitat for future Spotted Owl generations, it may be critical to conserve not only these remnant stands but also patches of forest spared by future wild fires and other disruptive events.

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