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NEST-SITE SELECTION AND REPRODUCTIVE SUCCESS OF CALIFORNIA SPOTTED OWLS

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ABSTRACT.—We evaluated quality of nesting habitat and nest-site selection of an insular population of California Spotted Owls (*Strix occidentalis occidentalis*). We assessed habitat structure for successful and unsuccessful nests from 103 independent territories at three spatial scales, and habitat selection by comparing nest stand structure with identical variables from random points. Fledging success was unrelated to nest type, nest tree, nest stand characteristics, or habitat type. However, nest productivity was greatest in lower elevation oak/big-cone fir habitat (1.7 fledglings per successful nest). Nest stands were characterized by greater variation in tree size, higher canopy closure, and greater basal area of large trees compared with random points. We were able to differentiate consistently between nest and random points using discriminant function models (≈79% correct classification). Our results confirm previous observations that California Spotted Owls will use a variety of habitats, but these habitats are consistently characterized by greater structural complexity compared with available habitat. *Received 24 May 1996, accepted. 30 Sept. 1996.*

Conservation of the Spotted Owl (*Strix occidentalis*) is controversial because of its affinity for economically important, late seral-stage conifer forests (Gutiérrez et al. 1995). Both Northern and Mexican Spotted Owls (*S. o. caurina*, *S. o. lucida*, respectively) are Federally listed threatened species because of past and projected habitat loss (U. S. Department of Interior 1990, 1993). In contrast, the California Spotted Owl (*S. o. occidentalis*) is not currently under consideration for Federal protection, presumably because it inhabits a variety of habitat types other than late seral-stage conifer forests and there is no evidence for decline in the largest population occurring in the Sierra Nevada (Verner et al. 1992). Nevertheless, at least one insular population of California Spotted Owls is declining rapidly (LaHaye et al. 1994).

Even though California Spotted Owls have been observed in a variety of habitat types, we do not know which of these are preferred habitats. More importantly, we do not know what contribution each habitat type represents to the overall viability of the subspecies. For instance, territorial displacement may force individuals to use less preferred habitats (Van Horne 1983). Individuals in suboptimal habitats may represent sink populations (Pulliam 1988), and while sink populations may help to stabilize a regional population (or metapopulation), they would not be viable by themselves (Pulliam and Danielson 1991).

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In this study we evaluated habitat selection and habitat quality of an insular population of California Spotted Owls. We incorporated measures of fitness (reproductive success and productivity) to evaluate the relative quality of habitat characteristics and different habitat types that the owls were using. We also evaluated habitat selection by comparing owl nest stands to random points throughout the San Bernardino Mountains.

STUDY AREA AND METHODS

The California Spotted Owl occurs as insular populations in southern California (LaHaye et al. 1994) with the largest of these island populations in the San Bernardino Mountains. This mountain range, which is part of the Transverse Range Geologic Province (Norris and Webb 1990), includes a large elevation gradient (800 m to 3500 m) as well as the majority of habitats used by the subspecies throughout its geographic range. Mean annual precipitation ranges from less than 20 cm to more than 100 cm and is strongly influenced by elevation, topography, and rain shadow effects (Minnich 1988). The vegetation is diverse ranging from Mojave Desert scrub (Vasek and Barbour 1977) at lower elevations to alpine (Major and Taylor 1977) on San Gorgonio Mountain. Most Spotted Owls occupy mixed conifer forests between 1000 m and 2500 m elevation.

Owl survey methods.—We located Spotted Owls and assessed their reproductive activity following methods of Franklin et al. (1996). Nests were located by following male owls to nest trees or by observing females leaving or entering nests. To minimize disturbance we did not measure nesting habitat until after juveniles fledged. Nests were classified as platform, cavity or broken-top (LaHaye 1988). Broken-top nests were typically found near the breakpoint of a broken trunk. Cavity nests were usually formed by a large branch tearing free of the main stem. Both of the above nest types required advanced heart rot for proper development. Platform nests were either abandoned stick nests constructed by other animals or natural accumulations of debris in the branches.

Vegetation measurement.—We measured vegetation characteristics using a variable circular plot (Mueller-Dombois and Ellenberg 1974) at nest and random locations. Random points were selected from universal transverse mercator coordinates throughout forest habitat in the San Bernardino Mountains. At nest and random points we estimated basal area of trees using a 20-factor basal area prism (Dilworth 1981). We measured the height and diameter at breast height (dbh) of each tree tallied with the prism. Diameter estimates were then grouped for further analysis with the conifer dbh classes sapling (0.1–25.0 cm), pole (25.1–50.0 cm), medium (50.1–75.0 cm) and large (>75.0 cm). Hardwood dbh classes were similar except we based them on 15 cm intervals instead of 25 cm intervals. We estimated percent canopy closure using a concave, spherical densiometer (Lemmon 1957). Other habitat characteristics were measured using standard techniques (see LaHaye 1988). Nests were also classified by their location in mixed conifer forests above 1800 m (*Pinus jeffreyi*, *P. ponderosa*, *P. lambertiana*, *Abies concolor*), oak/big-cone fir forest below 1500 m (*Quercus chrysolepis*, *Pseudotsuga macrocarpa*) and mid-elevation conifer/hardwood habitat.

Statistical analysis.—We explored differences between successful and unsuccessful nests across three spatial scales. If one or more fledglings were produced at a nest, then it was classified as successful. At the smallest scale, we tested for independence between nest success and both nest type and nest tree characteristics (dbh, nest height, tree height). We then expanded the analysis to nest stand variables and finally we considered patterns of nest success between broad habitat categories. We also evaluated differences in nest productivity (average number of fledglings/successful nest) at the broadest scale. In order to avoid pseudoreplication, only one nest site per owl territory was used in our analyses. When data appeared normally distributed we used parametric statistics for our comparisons, otherwise nonparametric tests were used. For multiple pairwise comparisons we adjusted our significance level using a 95% Bonferroni interval to avoid excessive Type I error (Neter et al. 1990) and used Tukey's studentized range test for significant ANOVAs. We compared slope aspects (compass bearings) using circular statistics (Batschelet 1981).

In order to examine differences in forest structure, we calculated the standard deviation for all tree dbh measurements at each sample point. This standard deviation was then treated as a random variable and used to examine differences in variability of tree size between nest and random points. We excluded points where less than two trees were present (1 nest and 33 random sites). This is a conservative test of tree structure differences because Spotted Owl sites usually contain more trees than random sites.

We tested Spotted Owl nest-site selection by comparing 29 vegetation variables from nest points with corresponding values from random points. We also assessed our ability to classify Spotted Owl nesting habitat using a series of discriminant function models (DFMs) (Capen et al. 1986, Call et al. 1992). The DFMs were restricted to five variables that were significantly different between nest and random points ($P < 0.002$) and minimally correlated ($r < 0.6$, Spearman rank test; percent slope, percent canopy closure, hardwood basal area, conifer basal area). Using these five variables we constructed a series of 25 nonparametric DFMs based on a randomly selected subsample of nest and random points (approximately 76 of each type). The DFM algorithm used a k-nearest neighbor density function ($k = 20$, SAS 1989). The ability to discriminate between random and nest points was then evaluated by examining the classification rate for the data set used to construct each DFM (cross-validation) and the ability of each DFM to classify correctly the remaining nest and random points (independent points from approximately 25 nest and 221 random sites). Percent correct classification rates were tested for significance using Cohen's Kappa statistic (Titus et al. 1984).

RESULTS

Between 1987 and 1994 we located 216 California Spotted Owl nests at 103 sites occupied by territorial owls. All nests were in trees and the elevation of nest sites ranged from 885 m to 2560 m. We found nests in ten different tree species (71% conifer, 29% hardwood, Table 1) and the majority (59%) of these nests were platforms. For the 103 independent nests (one from each territory) we found that the average Spotted Owl nest was located 16.1 m (standard deviation, $s = 6.9$) above ground in a tree that was 24.4 m ($s = 9.1$) tall with a dbh of 90.8 cm ($s = 27.6$). Platform nests were located in trees having a dbh ($\bar{x} = 75.0$ cm, $s = 34.9$) that was significantly smaller than either cavity nest trees ($\bar{x} = 108.3$ cm, $s = 29.1$) or broken-top nest trees ($\bar{x} = 122.3$ cm, $s = 29.0$, $F = 18.2$, df $= 102$, $P < 0.0001$). No platform nests were found on snags (i.e., standing dead trees), whereas 13.5% of broken-top nest trees and 23.1% of cavity nest trees were snags. Mean slope aspects where nest and random points occurred ($\phi = 348°$, $r = 0.45$, N $= 103$; $\phi = 341°$, $r = 0.23$, N $= 296$, respectively) were not significantly different ($P > 0.05$).

TABLE 1

NEST TREE SPECIES AND NEST TYPE FOR ALL NESTS USED BY CALIFORNIA SPOTTED OWLS IN THE SAN BERNARDINO MOUNTAINS, CALIFORNIA (1987–1994)

		Percent nest types		
Tree species	Number of nests (%)	Platform	Cavity	Broken-top
Abies concolor	75 (34.7)	34.5	13.8	51.7
Alnus rhombifolia	3 (1.4)	66.7	0.0	33.3
Calocedrus decurrens	19 (8.8)	89.4	5.3	5.3
Pinus coulteri	1 (0.5)	0.0	100	0.0
P. jeffreyi or *P. ponderosa*	29 (13.4)	58.6	34.5	6.9
P. lambertiana	19 (8.8)	57.9	36.8	5.3
Pseudotsuga macrocarpa	29 (13.4)	34.5	13.8	51.7
Quercus chrysolepis	34 (15.7)	67.6	23.5	8.8
Q. kelloggii	7 (3.2)	0.0	85.7	14.3
Total	216	58.8	24.1	17.1

Thirty-nine percent of the owl territories occurred in higher elevation mixed conifer forests, while 41% occurred in oak/big-cone fir forests. Twenty percent of the territories were in mixed conifer/hardwood habitat (Table 2).

Nest success.—At the two smaller spatial scales (i.e., nest tree and nest stand) we found no significant differences between successful nests (N = 77) and unsuccessful nests (N = 26) (F and χ^2 tests, $P > 0.05$). Nest success also was independent of habitat type ($\chi^2 = 1.7$, df = 2, $P = 0.4$), but productivity was not. We found more juvenile Spotted Owls fledged from nests located in the oak/big-cone fir forests when compared with the mixed conifer and conifer/hardwood forests (Wilcoxon rank test, $\chi^2 = 7.3$, df = 2, $P = 0.026$, Table 2).

Characteristics of nesting habitat.—In general, nest sites were multi-

TABLE 2

HABITAT TYPES AND FLEDGING SUCCESS FOR CALIFORNIA SPOTTED OWL NESTS LOCATED IN THE SAN BERNARDINO MOUNTAINS, CALIFORNIA (1987–1994)

Habitat type	Number of nests (% successful)	Average fledglings per nest (s)[a]	Average fledglings per successful nest[b] (s)
Oak/big-cone fir	42 (81)	1.39 (0.87)	1.72 (0.61)
Conifer/hardwood	21 (67)	0.98 (1.05)	1.46 (0.97)
Mixed conifer	38 (76)	0.95 (0.77)	1.31 (0.58)

[a] Standard deviation.
[b] Nest productivity.

TABLE 3
SUMMARY OF VEGETATION VARIABLES THAT WERE SIGNIFICANTLY DIFFERENT BETWEEN RANDOM POINTS AND CALIFORNIA SPOTTED OWL NEST POINTS IN THE SAN BERNARDINO MOUNTAINS, CALIFORNIA (1987–1994)

	Nest points (N = 103)		Random points (N = 296)	
Habitat variable	Mean[a]	% CV[b]	Mean	% CV
Percent canopy closure	79.3	22.3	52.4	49.9
Percent slope	54.2	49.8	32.1	68.7
Broken-top tree basal area[c]	2.9	174.3	0.5	322.9
Snag basal area	4.8	116.7	1.8	217.8
Hardwood basal area (30.1–45 cm dbh)	3.2	216.7	0.9	332.8
Hardwood basal area (>45 cm dbh)	4.9	144.7	0.8	380.4
Total conifer basal area	37.1	59.5	20.1	85.8
Conifer basal area (50.1–75 cm dbh)	9.6	100.3	4.9	130.1
Conifer basal area (>75 cm dbh)	19.1	77.4	6.7	124.2

[a] Includes zero values for all variables.
[b] Percent coefficient of variation.
[c] Square meters per hectare.

storied stands composed of both conifers and hardwoods (Table 3). In addition, basal areas for large conifers and hardwoods, broken-top trees and snags were significantly higher in nest stands than in random locations. Nest points had a greater mean standard deviation for tree sizes than random points ($\bar{x}$ = 30.9, s = 11.6, N = 102; $\bar{x}$ = 23.0, s = 12.8, N = 263, respectively; t = 5.6, $P < 0.0001$) showing that nest stands had greater variability in tree sizes.

We were able to differentiate consistently between nest and random points based on our DFMs (Table 4). Overall rates of correct classification were very similar for both cross-validation and independent classification schemes (≈79%, $P < 0.0003$). There was greater variation in the correct classification for independent nests which was not surprising given the smaller sample size for this group (average N = 26; Table 4). Overall variation in correct classification was low (coefficient of variation < 10%).

DISCUSSION

Habitat selection in Spotted Owls has been studied extensively (Gutiérrez et al. 1995). The extent of inference, however, is usually limited in these studies for many reasons (Wolff 1995). For example, logistical and financial constraints of field research often restrict selection studies to small sample sizes (e.g., Solis and Gutiérrez 1990, Carey et al. 1990, Call et al. 1992) and pseudoreplicated designs (e.g., Solis and Gutiérrez

TABLE 4

PERCENT CORRECT CLASSIFICATION RATES FOR 25 DISCRIMINANT FUNCTION MODELS (DFM) COMPARING CALIFORNIA SPOTTED OWL NEST POINTS WITH RANDOM POINTS IN THE SAN BERNARDINO MOUNTAINS, CALIFORNIA (1987–1994)

Type of DFM	Mean percent correct classification (% CV)	Range	N[a]	Kappa
Cross-validation[b]				
Nest	82.6 (3.6)	74.6–87.5	77	
Random	78.2 (6.3)	67.9–86.1	76	
Total	80.4 (3.8)	74.2–85.4	153	0.61*[c]
Independent[d]				
Nest	83.1 (8.8)	71.9–95.7	26	
Random	77.7 (3.3)	73.1–81.7	220	
Total	78.2 (2.8)	74.8–82.7	246	0.35*

[a] Mean sample size; actual sample size will vary slightly between each DFM.
[b] Includes only those points that were used to formulate the DFM.
[c] Proportion of points that are correctly classified over the number of correct classifications expected by chance; *, $P < 0.0003$.
[d] Independent classifications only include points that were not used to formulate the DFM.

1990, Call et al. 1992). Habitat studies rarely account for temporal variation and the scale of investigation is usually limited to one or two spatial scales (e.g., Lemkule and Raphael 1993, Hunter et al. 1995). Habitat studies rarely include a full range of available habitats (i.e., include extremes). Finally, habitat quality is rarely assessed using some measure of fitness (Van Horne 1983).

We investigated habitat selection in an entire population of Spotted Owls over eight years at several spatial scales. Our extensive survey efforts have allowed us to sample 95% of all territories consistently in the San Bernardino Mountains each year since 1989 (LaHaye et al. 1994) which includes all habitat types used by the owls. The extent of our sampling avoided pseudoreplication and allowed us to evaluate two measures of fitness (reproductive success and productivity) as indicators of habitat quality.

Nest-site selection.—Spotted Owls selected large trees in which to nest which is consistent with observations throughout their range (LaHaye 1988, Bias and Gutiérrez 1992, Gutiérrez et al. 1992, Seamans and Gutiérrez 1995). Owls in our study also differentially used platform structures as nest sites. The use of platform nests, however, does not appear to be related to nesting success. Thus, selection for nest type may be related to availability of the different nest types; something which we were unable to estimate (see also LaHaye 1988).

Nest habitat characteristics.—Spotted Owls in our study showed a pattern of habitat selection similar to other populations where the owls selected habitats with a structure different than what was generally available to them (e.g., Solis and Gutiérrez 1990, Bias and Gutiérrez 1992, Gutiérrez et al. 1992). Nest sample points were characterized by more complex vegetative structure (greater variation in tree sizes, larger trees, higher canopy closure). Our DFM models demonstrated that the multivariate distribution of habitat characteristics for nest and random points were quite dissimilar. Some overlap, however, is evident between these distributions as we would expect since some random points were in fact suitable owl habitat in terms of stand structure. Of course, it was not possible to determine which of these characters, if any, was the reason for habitat selection. Nevertheless, it appeared that the Spotted Owls were behaving as habitat specialists at the scale of nest habitat selection.

Habitat quality.—Spotted Owls were equally likely to fledge juveniles in all three habitats, but breeding owls located in the lower elevation oak/big-cone fir habitat produced more fledglings per nest. This is consistent with earlier reports that showed a negative relationship between productivity and elevation (Bart and Forsman 1992). Given the potential for improved fitness in the oak/big-cone fir habitat, we would predict that owls would select this habitat preferentially. This appears to be the case; Smith (1995) estimated the ecological densities for this same population to be 0.43, 0.20 and 0.11 owls/km^2 for oak/big-cone fir, conifer/hardwood, and mixed conifer, respectively. Higher densities may reflect smaller territory sizes which could result from increased prey densities associated with higher mast production at lower elevations. Thus, owls may have more energy to invest in reproduction in the lower elevation oak/big-cone fir habitat. Ultimately, we will need data on survivorship and reproductive success of fledglings from each of these habitat types before we can assess their true contribution to the total population of California Spotted Owls in the San Bernardino Mountains.

There is a potential for increased disturbance of Spotted Owl habitat associated with the burgeoning human population in southern California (McKelvey and Weatherspoon 1992). In particular, as demand for housing and general suburban expansion continues in San Bernardino County, the lower elevation oak/big-cone fir habitat may be the first to be impacted. Smith (1995) has shown a strong negative association between habitat fragmentation and occurrence of Spotted Owls. Thus, human disturbance is likely to fragment these important habitats and negatively affect what appears to be the most productive segment of the San Bernardino Spotted Owl population.

We infer from our study results that although Spotted Owls used a variety of habitat types, they selected forests that were different from available habitat. Further there appears to be differential fledgling productivity attributable to different habitats, but not to nest structure *per se.* Therefore, we conclude that Spotted Owls are structural habitat specialists inhabiting areas of differing qualities.

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