*Chapter 5*

# Habitat Relations of the California Spotted Owl

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The California spotted owl's distribution spans a latitudinal range similar in extent to that of the northern spotted owl (Johnsgard 1988). It occurs at higher elevations than the northern subspecies, however, and portions of the overall population exist in "island" subpopulations on isolated mountain ranges in southern California (Gutiérrez and Pritchard 1990). It also occurs within sight of the Los Angeles Basin, with one of the largest human populations in North America. Grinnell and Miller (1944) first recognized that California spotted owls occupy a variety of forest types. The extent of this variety has been documented by Laymon (1988), Bias (1989), Neal et al. (1989), Call (1990), Call et al. (1991), LaHaye et al. (1992a), and Bias and Gutiérrez (1992). In this chapter we summarize the patterns of habitat variation and habitat use across most of the range of the California spotted owl.

## Study Areas and Methods

### Sierra Nevada

Six major studies have described habitat relations of California spotted owls in four general areas spanning the length of the Sierra Nevada (fig. 5A). From north to south, these four study areas were: (1) The Lassen Study Area (Zabel pers. comm.), which included primarily high-elevation (5,500-7,200 feet) forests of red fir and white fir (Rundel et al. 1977) and secondarily some lower-elevation habitats dominated by pines and Sierran mixed-conifer forests (see color photos 5-1 and 5-4 at the end of this chapter). The area was a mosaic of selectively logged, clearcut, and uncut stands (old-growth). (2) The Tahoe Study Area (Call 1990) was primarily in mid-elevation mixed-conifer forest (Rundel et al. 1977) at 2,200-5,200 feet. The past history of logging there resulted in a diverse patchwork of different stand ages, types, and densities. (3) The Eldorado Study Area (Laymon 1988, Bias 1989, Lutz 1992) extended from low- and mid-elevation mixed-conifer forest to higher-elevation fir forest (1;000-7,400 feet) (color photos 5-11, 5-12, and 5-18). Logging history has varied there because of the pattern of land ownership-about 40 percent of the land was in private industrial forests that occupied alternate sections in a "checkerboard" pattern with federal lands (Bias and Gutiérrez 1992). Laymon's study included winter observations of migrant owls that moved from their higher-elevation nesting habitats to foothill riparian/hardwood forests as low as 1,100 feet. These latter sites should not be construed as representative of owl sites in the Sierran conifer zone. (4) The Sierra Study Area, in the Sierra National Forest (NF) (Verner et al. 1991), included two distinct habitat types-one dominated by mixed-conifer forest at elevations ranging from about 4,500 to 7,500 feet, the other dominated by hardwoods in oak-pine woodlands and relatively dense riparian/hardwood forests at elevations from about 1,000 to 3,500 feet. Only this study area included breeding populations both in high-elevation conifer forests and riparian/hardwood forests at low elevations (color photos 5-21 and 5-22).

### Southern California

Several habitat studies have been done on isolated mountain ranges in southern California (fig. 5A). Here we discuss only one major study area-the San Bernardino, which encompassed almost the entire owl population in the San Bernardino Mountains (LaHaye et al. 1992b). It was the largest of the isolated "island" populations of spotted owls in California. The San Bernardino Study Area included numerous habitat types (see Thorne 1977) because it ranged in elevation from 2,500 to about 9,000 feet (color photos 5-34 to 5-37).

The habitat of two isolated populations studied by Gutiérrez and Pritchard (1990), on-Mount San Jacinto and Palomar Mountain (fig. 5A) (color photos 5-39 to 5-42, and 5-44), had lower diversity than the San Bernardino Study Area and involved much smaller owl populations. Barrows (1980) reported observations at five roost sites of pairs or individuals on four mountains in southern California. In addition to these investigations, qualitative assessments of habitat have been made by U.S. Department of Agriculture, Forest Service (FS) biologists from the various NFs in southern California, but especially from the Los Padres NF (Sandburg and Winter 1989) (color photos 5-29 to 5-32, and 5-38). Observations of owls by forest biologists were part of their normal duties, and did not include designation of specific study area boundaries.

### Photo Series

A set of color photographs of California spotted owl habitat from throughout the subspecies' range augments our text descriptions of habitats. These photographs, presented as a set at the end of this chapter, were taken from June to September 1991 during field trips by the Technical Assessment Team. The purpose of the trips was to become directly familiar with the full range of variation in the habitat occupied by this owl.

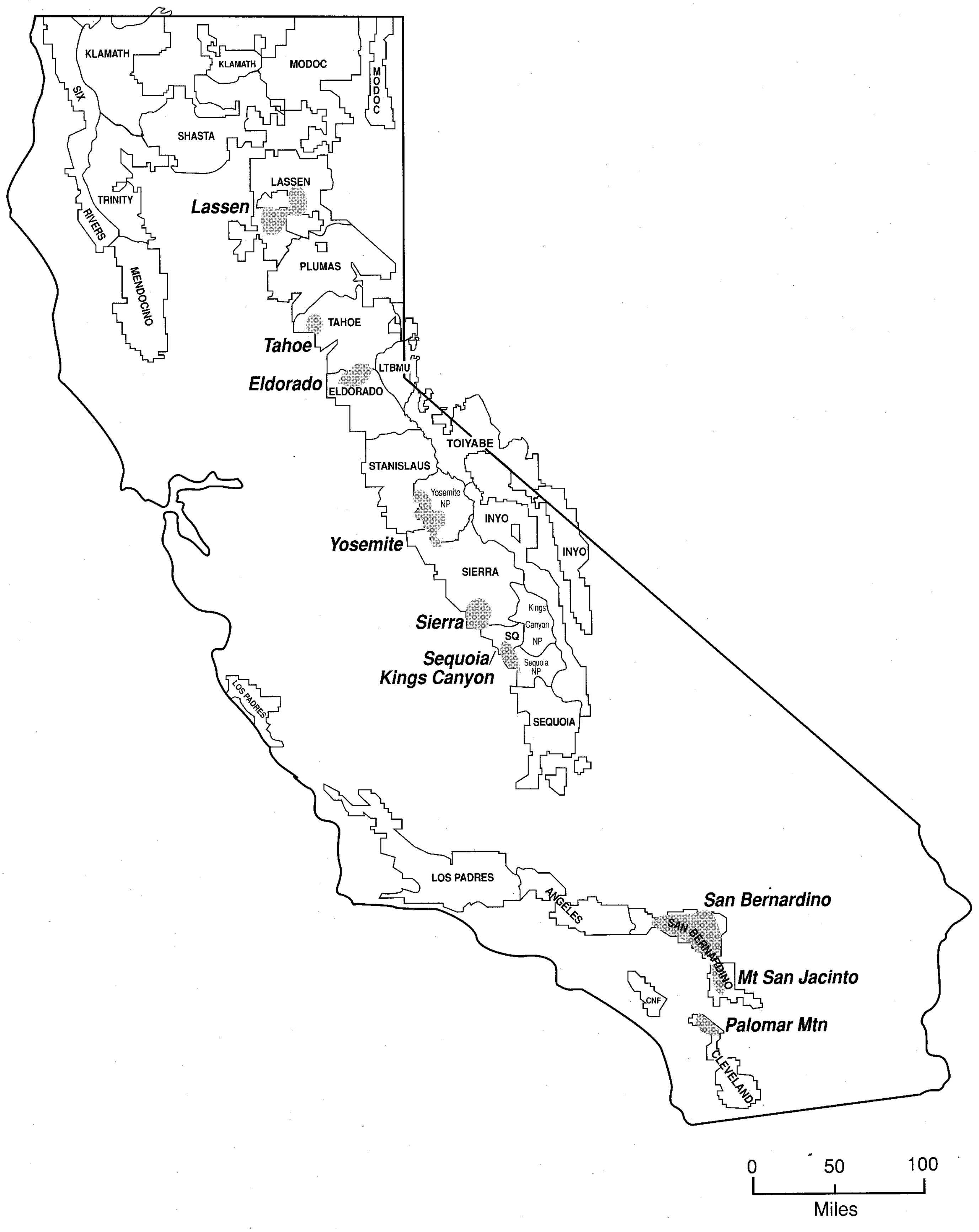


Figure 5A-Locations of radio-tracking and demographic study areas for California spotted owls.

# Conifer Forests of the Sierra Nevada and Southern California

## *Patterns of Habitat Use at a Landscape Scale*

California spotted owls use forested habitats almost exclusively (color photos 5-1 to 5-48). Only one record is available of a pair nesting in a tree not closely surrounded by a stand of other trees. That pair nested in a residual snag in a clearcut on the Sierra NF, although relatively dense stands of oaks were within 160 feet of the nest and the young moved there shortly after they left the nest (Yamanaka pers. comm.). Spotted owls have occasionally foraged in relatively open areas, such as shrubfields, meadows, or plantations, but this is exceptional. Call (1990), for example, found such habitats to be used significantly less than expected, based on availability in the Tahoe Study Area. We included these observations only to illustrate that California spotted owls occasionally occur in habitats that do not meet all their life history requirements (that is, they are unsuitable). It is important to note that one cannot infer suitability from the occasional presence of owls in a habitat.

### Data at a Landscape Scale

Each of the seven Sierra Nevada NFs provided the following information on detected owl nests ($n$ = 148): (1) timber type and size of the stand in which the nest was located, based on verified database mapping in their Land Management Plans (LMPs); (2) the same information as in (1) for each stand polygon that bordered the nest stand and was in a timber type used for foraging, roosting, or nesting; and (3) a map of the nest and adjacent stands. Stands bordering nest stands were primarily M2G, M3N, M4N, M3G, M4G, R3N, R4N, R3G, and R4G (codes for timber strata are defined in table 1C and in Appendix B). The estimated number of acres in habitat types listed in table 5A were based on the most recent FS inventory data (Fiske, pers. comm.).

### Selective Use of Forest Types

Based only on those habitat types in which nests had been observed and verified, we found a significant difference between habitats selected for nesting stands and the overall distribution of available habitats in Sierran NFs (table 5A, fig. 5B). A 95-percent Bonferroni interval test (see Neu et al. 1974, Byers and Steinhorst 1984) on the forest types contributing to this difference (table 5A) showed that, based on availability of different forest stand types, spotted owls in the Sierra Nevada nested more than expected in mixed-conifer stands with medium- to large-sized trees [24 to 36+ inches in diameter at breast height (d.b.h.)], stands with a wide range of tree sizes overall (5 to 60+ inches in d.b.h.), and medium (40-69 percent) (stand type M4N) to high (70-100 percent) total canopy cover (stand type M4G). Forty-five percent of all nest stands in Sierran conifer forests, however, were in the M4N and M4G habitat types. All other habitat types that we evaluated were used equal to or less than their proportional availability (table 5A).

**Table 5A**-*Distribution of California spotted owl nest habitat types compared with proportions of available habitats in the Sierra Nevada.*

| | | 95 percent Bonferroni interval | | | | |
|---|---|---|---|---|---|---|
| Habitat Type[1] | Sample size | Lower | Point estimate | Upper | Available | Result |
| M2G[2] | 2 | 0 | 0.0135 | 0.0390 | 0.0209 | U = A[3] |
| M3P | 10 | 0.0121 | 0.0676 | 0.1231 | 0.2369 | U < A |
| M3N,G | 44 | 0.1962 | 0.2973 | 0.3984 | 0.2501 | U = A |
| M4P | 10 | 0.0121 | 0.0676 | 0.1231 | 0.1418 | U < A |
| M4N,G | 67 | 0.3426 | 0.4527 | 0.5628 | 0.2005 | U > A |
| R3P | 2 | 0 | 0.0135 | 0.0390 | 0.0448 | U < A |
| R3N,G | 3 | 0 | 0.0203 | 0.0514 | 0.0522 | U < A |
| R4N,G | 10 | 0.0121 | 0.0676 | 0.1231 | 0.0464 | U = A |
| **Total** | **148** | | | | | |

[1] See figure 5B for distribution of habitat types that were signficantly different ($x^2$ = 79.9, df = 7, $P$ < 0.05) between used and available types.

[2] Habitat codes correspond to FS timber strata labels: M = mixed-conifer, R = red fir; 2 = pole-sized trees (<12 inches in d.b.h.), 3 = small sawtimber (trees 12-24 inches in d.b.h.), 4 = medium and large sawtimber (24-40 and >40 inhces in d.b.h.); G = 70+ percent canopy cover, N = 40-69 percent canopy cover; P = 0-39 percent canopy cover.

[3] U = A; current evidence does not indicate a difference between use and availability.
U < A; used less than expected.
U > A; used greater than expected.

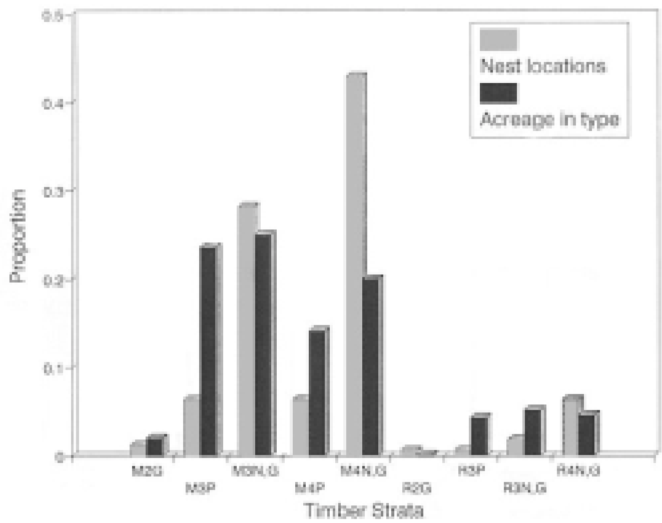


**Figure 5B**-Nest locations *(n* = 148) and proportional availability of different timber strata (see Appendix B or table 5A for definitions of strata codes).

In addition to the strata listed in table 5A and figure 5B, four nests were in pure stands of ponderosa pine (one each in P3N, P4P, P3G, and P4G) and eight nests in hardwood types. Because of a lack of consistency among NFs in typing these timber strata, we could not develop reliable estimates of their acreages available, or of their associated nests. Consequently, these nests were omitted from the analysis of use-versus-availablity presented in table 5A. Ponderosa pine types commonly include hardwood components, but these are not considered in timber inventories. As a result, a site with ponderosa pines in the overstory and an understory of hardwoods would be judged by its stratum label to be unsuitable for nesting (and possibly even for foraging) by the owls, even though that may not be the case. Although we lack the needed data to perform rigorous statistical tests, it is our firm biological understanding that pine stands with high canopy closure and a significant hardwood component are excellent owl habitat. Not only do they have all of the necessary structural components, but also they are in an elevational zone where the distributions of woodrats and flying squirrels overlap. The presence of a rich and diverse prey base, proper structural characteristics, and relatively mild climatic conditions may well make these sites among the highest quality owl habitat in the Sierra Nevada. We believe, therefore, that at least the P4G strata is selected for nesting by owls, in excess of its availability.

Bias and Gutiérrez (1992) found that nesting and roosting owls on the Eldorado Study Area almost exclusively used mixed-conifer stands with medium (M3G) to large (M4G) timber and at least 70 percent canopy cover (color photos 5-11 and 5-18). The M4G stands were more abundant on public than on private land in the study area, and the owls used public lands for nesting and roosting significantly more than they used private lands. Gutiérrez and Pritchard (1990) found that spotted owls on Mount San Jacinto used conifer and riparian/hardwood forests (color photos 5-41 and 5-42) significantly more than expected, based on their availability, and that owls on Palomar Mountain used primarily conifer or mixed forests of conifers and hardwoods (color photos 5-39 and 5-40).

### Density of Owl Sites in Relation to Amount of Suitable Habitat

Based on intensive surveys for owls by NF personnel and others, owl densities in U.S. Geological Survey quadrangles (1:24,000; $n$ = 49) in the zone of mid-elevation, Sierran mixed-conifer forests were significantly, but weakly, correlated with the percentage of forests having medium-sized and larger trees and high canopy closure ($R^2$ = 0.38, $P < 0.05$; fig. 5C). We interpreted these relations cautiously, however, because survey effort was not uniform among the survey units and error exists in the type mapping of mixed-conifer habitat by the FS (Call 1990, Bias and Gutiérrez 1992, G. N. Steger pers. observ.). Nevertheless, this analysis suggested that, as with nest stands, owl densities were higher in areas with a higher proportion of dense stands and large trees.

## *Patterns of Habitat Use at a Home-Range Scale*

Here we report results of various studies that have compared attributes of sites used for nesting, roosting, and foraging with the same attributes measured at sites randomly selected from the surrounding forest. Only results of studies done in conifer forests of the Sierra Nevada and San Bernardino Mountains are reported here. Methods used to measure habitat attributes varied among the studies. Although direct statistical comparisons could not be made across all studies, we believe all methods provided objective, quantitative estimates of the attributes in local owl habitats.

All workers except Laymon (1988) used consistent methods within their studies, and workers from three study areas (Tahoe--Call 1990, Eldorado-Bias 1989, and San Bernardino--LaHaye et al. 1992a) used consistent methods among the studies. Workers from these latter three studies used a variable circular-plot design, using basal area prisms that resulted in an increasing plot size with increasing diameters of trees, an estimation procedure commonly used by foresters for estimating

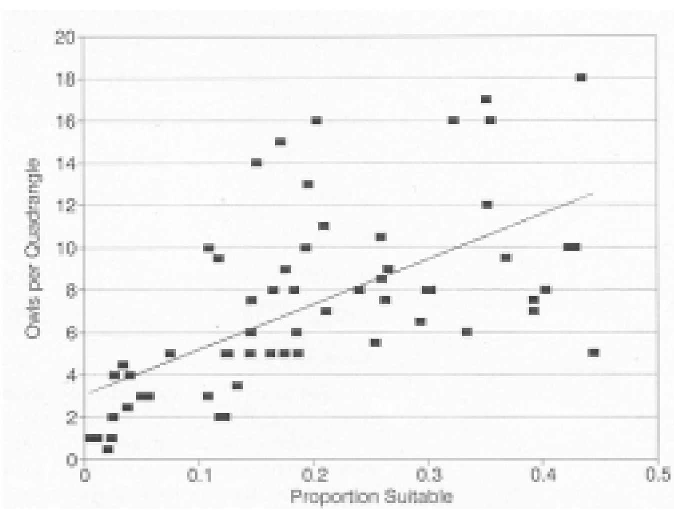


**Figure 5C**-Density of owl sites in the Sierra Nevada *(n*= 49) in relation to the proportion of habitat considered to be suitable for spotted owls in U.S. Geological Survey quadrangles (1:24,000).

Although our conclusions from studies in the Tahoe Study Area were basically the same as those reported by Call (1990) and Call et al. (1991), some details of our results differed slightly because we eliminated from Call's sample of random points all locations with <40 square feet per acre in basal area of softwoods. Eliminating recent clearcuts and shrubfields allowed more meaningful biological comparisons with foraging sites. In addition, we subsampled the sample of foraging sites by eliminating, at random, all but one location from each owl, or owl pair, in a given day.

In addition to studies that compared habitat attributes between random sites and sites used by owls, B. B. Bingham (pers. observ.) and Steger and Eberlein (pers. comm.) sampled nest stands in the Lassen Study Area and the Sierra Study Area, respectively, but not in comparison with random sites. In these studies, vegetation at nest sites was sampled using strip transects arranged perpendicular to one another and centered on the nest tree. Beginning 32.8 feet from the center of the nest tree, the long axes of four strip transects (32.8 by 113.7 feet-total area sampled = 0.30 acre) radiated on four sides of the nest tree along perpendicular lines through the nest tree. No vegetation data were collected within the 32.8 by 32.8 foot square centered on the nest tree.

Finally, Steger and Eberlein (pers. comm.) sampled habitats, by canopy-cover class (0-39 percent, 40-69 percent, and 70+ percent), throughout the radio-tracking portion of the Sierra Study Area, based on stratified random samples of habitat polygons in both the foothill riparian/hardwood and mixed-conifer portions of the study area. Their method used four sets of nested plots randomly located in each polygon. Plots were 16.4 by 328 feet for all trees and snags, 32.8 by 328 feet for trees >35.4 inches in d.b.h., and 65.6 by 328 feet for snags >15.7 inches in d.b.h.

## Differences Among Methods

Laymon (1988), Bias (1989), and LaHaye et al. (1992a) all used tree-centered plots for the evaluation of the nest sites, but they did not center random plots on trees. This method introduced a potential bias in the comparisons between nest/roost sites and random locations. It also had the potential to bias the inferences drawn concerning stand attributes based on nest locations. Data from Call (1990), B. B. Bingham (pers. observ.), and Steger and Eberlein (pers. comm.) did not have this bias.

The magnitude of any bias introduced by centering on a large tree is related to the density of similar trees in the surrounding stand and the size of the sample plot. One way to envision the bias is to ask how likely it is that a random plot (of identical size and shape) in the same stand would sample either the nest tree or another tree having similar size and condition. We would expect samples centered on nest trees to be more strongly biased than roost locations-roosts are often in small trees in dense stands, whereas nest trees are generally larger than trees in the surrounding stand (for example, tables 5B-5D).

Based on plot size, Laymon's (1988) data may be the most biased. He used small (0.17-acre), fixed plots and all of his owl-use plots, including foraging locations, were tree-centered. Bias (1989) and LaHaye et al. (1992a) both used variable-plot methods with a basal area factor (BAF) of 20. This sampling technique has the advantage that plot size increases with the size of the nest tree. For a tree 40 inches in d.b.h., the plot size is 0.44 acres; it is nearly an acre for a 60-inch tree.

Estimating the Bias-We could not repeat these studies or obtain all the raw data for re-analysis. We could, however, estimate the probable magnitude of the statistical bias due to tree-centering and determine the extent to which it changed the inferences drawn from these analyses. For Bias (1989) and LaHaye et al. (1992a), we corrected for total basal area simply by removing the nest/roost tree. When prism sampling, overall basal area can be determined simply by counting the number of "count trees" in the plot. Each counted tree represents a certain basal area per acre, as determined by the BAF. With a BAF of 20, for instance, each tree represents 20 square feet basal area per acre (BA/acre). At nest and roost sites, Bias obtained an average of 251 and 294 square feet BA/acre, respectively (table 5B), and LaHaye et al. reported 223 and 267 square feet BA/acre for nest and roost sites, respectively (table 5C). On average, Bias and LaHaye et al. were "counting" between 11 and 15 trees in each sample plot. Removing the nest tree from the basal area calculation would remove only one tree from each plot, a reduction of 20 square feet BA/acre. This suggests a range from 203 to 274 square feet BA/acre in their nest and roost stands.

While this decrease is not large, we believe it probably exceeds the potential bias of including the nest or roost tree in the sample. For example, if the nest tree were not within the plot, most likely other trees would be. The basal area of these trees would, in part, compensate for the removal of the nest tree. To obtain better estimates of the true bias, we analyzed nest site data from B. B. Bingham (pers. observ.) and Steger and Eberlein (pers. comm.). These data were taken in the vicinity of the nest tree but did not include the nest tree. We added the nest tree and recomputed live tree and snag basal area. For Bingham's data, live tree basal area was increased by about 7 square feet BA/acre and was not significantly different from the original estimate ($P = 0.18$). Basal area for the largest diameter-class, however, was shifted by 16.4 square feet BA/acre ($P = 0.002$). Similarly, snag basal area was significantly overestimated by including the nest snag in the sample. For Steger's and Eberlein's data, live tree basal area was increased about 4 square feet/acre, not significantly different from the original estimate ($P = 0.17$). Snag basal area was increased 5 square feet/acre, not significantly different from the original estimate ($P = 0.36$).

B. B. Bingham (pers. observ.) and Steger and Eberlein (pers. comm.) used fixed plots of 0.3 acres. These plots were smaller than the plots associated with large d.b.h. classes using a BAF of 20, but not greatly so. We believe these data can be used to make reasonable inferences concerning the magnitude of bias in the results of Bias (1989) and LaHaye et al. (1992a). Laymon's (1988) plots were about half the size of those used by Bingham and by Steger and Eberlein, so the potential for bias is therefore greater.

Conclusions-Given their sampling methods, results from Bias (1989) and LaHaye et al. (1992a) should be interpreted with a number of cautions. The overall basal area figures and basal area for all trees >16 inches in d.b.h. would not be significantly

**Table 5B**-*Habitat characteristics (mean and percent Coefficient of Variation) of California spotted owl nest* (n *=11) and roostsites* (n *= 29), and random sites (public land,* n *=328) in the Eldorado Study Area, central Sierra Nevada (Bias 1989).*

| | Nest sites | | Roost sites | | Random sites | |
|---|---|---|---|---|---|---|
| | Mean | Percent CV | Mean | Percent CV | Mean | Percent CV |
| **Physiographic attributes** | | | | | | |
| Percent slope | 26.1 | 46.8 | 30.1 | 58.3 | 32.3 | 61.2 |
| Elevation (feet) | 4,900.0 | 18.6 | 4,561.0 | 14.6 | 4,728.3 | 18.1 |
| **Structural attributes** | | | | | | |
| Percent cover | 89.3 | 16.1 | 95.6[a] | 3.9 | 79.2 | 32.0 |
| Basal area (square feet per acre) | | | | | | |
| Hardwoods | 38.3 | 69.1 | 43.6 | 60.9 | 61.3 | 138.1 |
| Softwoods | 234.4 | 43.8 | 268.4[a] | 44.0 | 151.6 | 80.2 |
| **Total live** | **251.0** | **25.1** | **293.7[a]** | **37.0** | **173.4** | **70.5** |
| Snag | 52.7[a] | 45.8 | 52.7[a] | 72.8 | 37.0 | 134.2 |
| Basal area (square feet per acre, by d.b.h. class)[1, 2] | | | | | | |
| 3.9-4.8 | 5.5 | - | 7.4 | - | 3.9 | - |
| 4.9-10.7 | 14.5 | - | 24.4 | - | 44.7 | - |
| 10.8-20.6 | 89.9 | - | 90.3 | - | 61.9 | - |
| 20.7-35.5 | 91.0 | - | 82.7 | - | 52.4 | - |
| >35.5 | 110.9 | - | 95.1 | - | 42.6 | - |
| Downed woody debris (percent cover, by diameter class in inches) | | | | | | |
| 1-11.8 inches | 12.1 | 57.8 | 10.2 | 69.0 | 11.2 | 122.6 |
| >11.8 inches | 2.7 | 87.0 | 2.6 | 187.8 | 3.9 | 244.6 |

[a] Significantly different from the corresponding random sample, at the 0.001 level of significance (1-way ANOVA, using Scheffe test for multiple comparisons).
[1] Diameter at breast height, in inches.
[2] CVS could not be computed for these data.

**Table 5C**-*Habitat characteristics (mean and percent Coefficient of Variation) of California spotted owl nest* (n *= 131) and roost sites* (n *= 43), and random sites* (n *= 296) in the San Bernardino Study Area, southern California (LaHaye et al. 1992a).*

| | Nest sites | | Roost sites | | Random sites | |
|---|---|---|---|---|---|---|
| | Mean | Percent CV | Mean | Percent CV | Mean | Percent CV |
| **Physiographic attributes** | | | | | | |
| Percent slope | 51.2[a] | 50.8 | 54.7[a] | 44.6 | 32.3 | 68.8 |
| Elevation (feet) | 6,052.0[a] | 20.9 | 6,299.2[a] | 18.5 | 6,942.3 | 14.7 |
| **Structural attributes** | | | | | | |
| Percent cover | 76.9[a] | 21.3 | 83.6[a] | 15.3 | 52.2 | 50.5 |
| Basal area (in square feet per acre) | | | | | | |
| **Total live** | **222.7[a]** | **41.7** | **266.7[a]** | **35.2** | **124.2** | **68.8** |
| Snag | 21.4[a] | 120.9 | 20.9[a] | 123.3 | 7.8 | 217.3 |
| Dead-topped trees | 12.2 | 143.3 | 15.7 | 99.1 | 7.0 | 224.6 |
| Hardwoods (by d.b.h. class)[1] | | | | | | |
| 0-5.9 | 5.2 | 263.0 | 10.5 | 182.8 | 14.8 | 245.2 |
| 6.0-11.8 | 13.1 | 207.1 | 32.7 | 182.3 | 14.8 | 230.3 |
| 11.9-17.7 | 14.4 | 224.6 | 25.7 | 163.9 | 3.5 | 356.0 |
| >17.7 | 19.6 | 151.0 | 28.8 | 162.5 | 3.1 | 391.6 |
| **Total** | **52.31** | **129.5** | **97.61** | **119.5** | **36.2** | **169.0** |
| Softwoods (by d.b.h. class) | | | | | | |
| 0-9.8 | 12.2 | 178.1 | 16.6 | 160.5 | 13.1 | 207.1 |
| 9.9-19.7 | 27.0 | 123.8 | 41.4 | 128.4 | 24.8 | 135.7 |
| 19.8-29.5 | 46.2 | 100.3 | 43.6 | 117.4 | 21.8 | 127.8 |
| >29.5 | 85.4 | 77.1 | 67.1 | 67.7 | 29.2 | 124.1 |
| **Total** | **170.4[a]** | **58.9** | **168.6[a]** | **68.5** | **88.0** | **85.1** |

[a] Significantly different from the corresponding random sample, at the 0.001 level of significance (Mann-Whitney *U* test).
[1] Diameter at breast height, in inches.

**Table 5D**-*Habitat characteristics of California spotted owl roost sites in summer* (n =*120*), *fall* (n = *78*), *and winter* (n = *61*), *and at random sites throughout summer/ fall* (n = *120*) *and winter* (n = *66*) *in the Eldorado Study Area, central Sierra Nevada (Laymon 1988). Note that all winter data were obtained in low-elevation, oak-pine forests, where the birds migrated for the winter (see Chapter 4).*

| | Roost sites | | | | Random sites | | Roost sites in winter | | Random sites in winter | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Summer | | Fall | | Summer/fall | | | | | |
| | Mean | Percent CV | Mean | Percent CV | Mean | Percent CV | Mean | Percent CV | Mean | Percent CV |
| **Physiographic attributes** | | | | | | | | | | |
| Percent slope | 18.1[a] | 36.3 | 21.1[a] | 35.6 | 23.4 | 46.8 | 26.8[a] | 36.4 | 19.9 | 30.6 |
| **Structural attributes** | | | | | | | | | | |
| Percent cover | 85.8[a] | 6.4 | 75.2 | 9.4 | 67.9 | 29.0 | 63.5[b] | 12.9 | 29.7 | 32.8 |
| Basal area (square feet per acre) | | | | | | | | | | |
| Hardwoods | 20.9 | 79.8 | 12.6[a] | 106.5 | 26.1 | 146.0 | 18.7[b] | 56.7 | 7.0 | 126.9 |
| Softwoods | 330.7[a] | 21.6 | 259.7[a] | 25.9 | 163.8 | 62.6 | 57.1[b] | 65.1 | 29.2 | 78.8 |
| **Total live[1]** | **351.6** | - | **272.3** | - | **189.9** | - | **75.8** | - | **36.2** | - |
| Snags | 41.4[a] | 57.6 | 47.5[a] | 60.8 | 17.4 | 246.4 | 35.7[b] | 168.3 | 19.6 | 63.2 |
| Downed woody debris (tons per acre, by log diameter class)[2] | | | | | | | | | | |
| 0-3 inches | 0.82 | 0.30 | 0.90 | 0.32 | 0.82 | 0.74 | 0.23[b] | 0.78 | 0.18 | 0.50 |
| >3 inches | 12.16[a] | 0.59 | 10.53 | 0.72 | 9.36 | 1.39 | 1.56[b] | 1.55 | 0.62 | 1.44 |

[a] Significantly different from corresponding random sites in summer/fall, at the 0.05 level of significance (Student's *t* test).
[b] Significantly different from corresponding random sites in winter, at the 0.05 level of significance (Student's *t* test).
[1] The sum of softwood and hardwood basal areas. Data were not available to compute a percent Coefficient of Variation for this variable.
[2] Assumes a specific gravity of 0.4 for downed woody debris.

biased. Basal area in the largest diameter-class would, however, be overestimated, by perhaps as much as 20 square feet BA/acre. Similarly, snag basal area would be overestimated by perhaps 10 square feet BA/acre. Laymon's (1988) basal area data should be viewed with caution. For all of these studies, we have no reason to believe that estimates of canopy closure were affected by tree-centering (for example, see table 5B).

No important changes in inferences made from results of these studies were associated with these biases, although it is possible that the statistical significance of certain test results could be altered. It is important to note that in Bias (1989) and LaHaye et al. (1992a) the statistically significant basal area differences from random samples were associated most strongly with sites of roost trees, where we do not expect tree-centering to have as much impact as at nest tree sites. It is also worth noting that the statistical results presented by Call (1990), B. B. Bingham (pers. observ.), and Steger and Eberlein (pers. comm.) were not based on tree-centered plots.

## Nest and Roost Sites

Physiographic Attributes-Mean elevation at nest sites in conifer forests increased -from about 5,300 feet in the northern Sierra Nevada to 6,000 feet in southern California-about coincident with low- to mid-elevation mixed-conifer zones. Nests at the highest elevations were in red fir forests in the Sierra Nevada and white fir forests in the San Bernardino Mountains. No nests have been located in subalpine forests anywhere in California.

Blakesley et al. (1992) reported that nest sites of northern spotted owls in northwestern California tended to be on steeper slopes and in the lower third of canyons. This pattern was true for the California spotted owl only in the San Bernardino Study Area (table 5C). Based on statistical methods for analyzing data from circular distributions (Zar 1984, p. 422-469), the mean aspects of nesting, roosting, and random sites were not significantly different in the San Bernardino Mountains (LaHaye et al. 1992-). Assuming equal availability of aspects, significantly more nest sites in the Sierra Nevada were located on north aspects and fewer on southwest aspects than expected ($n$ = 148; $P$ < 0.001; fig. 5D). These results should be viewed with caution, however, as we cannot evaluate the validity of the assumption that all aspects were equally available.

Roost sites used by California spotted owls were similar in structure and composition to those used for nesting, although we know less about owl roosting habitat than nesting habitat. Some spotted owls have repeatedly used the same roost sites, suggesting that they have narrow selection patterns for roosting (Barrows and Barrows 1978, Barrows 1980, Steger and Eberlein pers. comm.) or that they tend to return to familiar or favorable roosts.

Within study areas, roost and nest sites were similiar in elevation and slope (tables 5B and 5C), probably because the owls often roosted near a nest site (LaHaye et al. 1992a). All of the roosting California spotted owls found by Barrows (1980) were on north-facing slopes. Studies in the Sierra Nevada (Laymon 1988, Bias 1989) and in the San Bernardino Mountains (W. S. LaHaye pers. observ.), however, did not reveal a significant

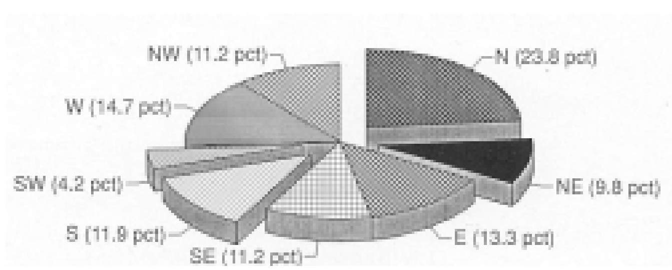


**Figure 5D**-Proportions of nest sites on slopes facing different directions from all nest sites located on National Forests within the range of the California spotted owl ($n$ = 143).

difference in mean aspect between roost sites and random locations. The owls studied by Barrows (1980) were in habitats at low elevation, where the dense-canopied stands selected by the owls would be found most often on north-facing slopes.

Structural Attributes-Mean canopy cover at nest and roost sites, for the three studies that measured these variables (tables 5B-5D), was consistently higher than the canopy cover at random samples-on average, about 20 percent higher. Canopy closure at nest sites was not significantly higher than at random locations in the central Sierra Nevada (table 5B), but it was significantly higher in the San Bernardino Mountains (table 5C). Roost sites had significantly ($P$ = 0.001) higher canopy closure than random sites in all three studies.

Mean softwood basal area was also consistently higher at nest and roost sites in all three studies. Total live tree BA/acre averaged 127 square feet greater in nest and roost stands than at random sites. As with canopy closure, measures of basal area were more often significantly different between roost sites and random sites than between nest sites and random sites (tables 5B-5D). In all cases allowing a statistical comparison, roost sites had significantly more total live tree basal area and basal area of softwoods than random locations. At nest sites, total live tree basal area and softwood basal area were consistently higher than at random sites in both studies reporting these results (tables 5B and 5C), significantly so for both attributes in the San Bernardino Study Area (table 5C).

Tree size-class data were available for nesting and roosting sites in the Eldorado NF (table 5B) and the San Bernardino NF (table 5C) and for nest sites in the Sierra and Lassen NFs (table 5E). In the Eldorado NF, nest sites averaged 111 square feet BA/acre in trees >35.5 inches in d.b.h. Nest sites in the San Bernardino NF had, on average, >85 square feet BA/acre in trees >29.5

**Table 5E**-*Habitat characteristics (mean and percent Coefficient of Variation) of spotted owl nest sites in the Lassen Study Area (n = 24), southern Cascade region of northern California (B. B. Bingham pers. observ.), and the Sierra Study Area (n = 11), southern Sierra Nevada (Steger and Eberlein pers. comm.).*

| | Lassen Study Area | | Sierra Study Area | |
|---|---|---|---|---|
| | Mean | Percent CV | Mean | Percent CV |
| **Physiographic attributes** | | | | |
| Percent slope | 25.8 | 51.6 | 7.9 | 66.2 |
| Elevation (feet) | 5,599.6 | 8.0 | 4,840.0 | 7.9 |
| **Structural attributes** | | | | |
| Percent cover | 85.2 | 9.8 | 85.6 | 13.8 |
| Live trees[1] | | | | |
| Basal area (square feet per acre) | | | | |
| **Total** | **243.8** | **36.7** | **185.8** | **73.3** |
| Stems per acre (d.b.h. class in inches)[2] | | | | |
| 5-10 | 93.2 | 72.0 | 96.3 | 73.3 |
| 11-20 | 60.3 | 50.8 | 35.9 | 43.7 |
| 21-35 | 17.1 | 73.8 | 16.6 | 57.0 |
| >35 | 8.0 | 86.7 | 5.2 | 88.7 |
| Stems per acre (height class in feet) | | | | |
| 13-25 | 14.8 | 251.7 | 99.0 | 101.9 |
| 26-39 | 44.3 | 87.1 | 35.0 | 60.1 |
| 40-53 | 34.2 | 84.4 | 25.1 | 65.3 |
| 54-79 | 42.4 | 83.4 | 35.0 | 62.3 |
| 80-105 | 20.8 | 92.3 | 10.4 | 90.9 |
| 106-131 | 13.2 | 70.6 | 9.2 | 135.3 |
| 132-157 | 6.7 | 160.1 | 6.4 | 215.2 |
| 158-183 | 1.8 | 172.0 | 2.1 | 145.2 |
| >183 | 0.4 | 358.7 | 0.6 | 222.5 |
| Snags | | | | |
| Basal area (square feet per acre) | | | | |
| **Total**[3] | **47.5** | **85.0** | **33.0** | **167.2** |
| Large[4] | 21.3 | 119.1 | 19.5 | 131.8 |
| Stems per acre (d.b.h class in inches) | | | | |
| 5-10 | 8.8 | 171.4 | 20.2 | 146.5 |
| 11-20 | 7.7 | 185.8 | 5.8 | 109.9 |
| 21-35 | 5.9 | 79.5 | 2.5 | 151.8 |
| >35 | 2.8 | 130.8 | 1.2 | 222.0 |
| Downed woody debris (tons per acre, by log diameter-class)[5] | | | | |
| 11-20 inches | 3.2 | 103.2 | 2.5 | 78.6 |
| 21-35 inches | 7.7 | 94.4 | 5.1 | 131. |
| >35 inches | 11.4 | 100.7 | 13.5 | 128.5 |

[1] Only live trees with d.b.h. >4 inches.
[2] Diameter at breast height, in inches.
[3] Snags >4 inches in d.b.h., and ≥4.6 feet tall (Lassen Study Area) or ≥6.6 feet tall (Sierra Study Area).
[4] Snags ≥15 inches in d.b.h. and ≥20 feet tall.
[5] Only logs >10 inches in diameter at the large end. Assumes a specific gravity of 0.4 for downed woody debris.

inches in d.b.h. Nest sites in the Sierra and Lassen NFs averaged five and eight stems per acre >35 inches in d.b.h., respectively. These data, when combined with the analysis of nest-site preferences based on timber strata (table 5A, fig. 5B), demonstrate that a significant large-tree component is present in most owl nest stands.

At nest sites, basal areas were highest in the large-tree classes (>24 inches in d.b.h.) and decreased through each of the smaller size-classes (tables 5B and 5C). This often resulted in multi-storied nest stands dominated by larger trees with a well-developed understory (for example, color photo 5-27). The vertical stratification in these stands was not as extensive as that observed in nest stands of the northern spotted owl in northwestern California (LaHaye 1988, Solis and Gutiérrez 1990, B. B. Bingham pers. observ.).

Percent canopy cover, total live tree basal area, softwood basal area, hardwood basal area, and snag basal area were generally greater at owl roost sites than at random locations (tables 5B-5D). As at nest sites, the basal area of trees at roost sites was concentrated in the large size-classes, but with trees of all sizes resulting in multi-storied canopies.

Many of these parameters exhibited a large degree of variability, and the differences between habitat used by spotted owls and random locations may or may not have been statistically significant within a given study. The data were, however, consistent and mutually supportive among all studies. California spotted owls in these various studies chose to nest and roost in stands that were denser than average and that contained a large-tree component. Most nest sites were selected in dense mixed-conifer stands with average quadratic mean diameters of canopy trees >24 inches in d.b.h. We know of no data that contradict these findings.

## Size of Activity Centers

Activity centers are areas within which owls find suitable nesting sites and several suitable roosts, and in which they do a substantial amount of their foraging. Using the sample of nest trees from conifer forests in the Sierra Nevada (*n* = 148), we estimated the sizes of stands containing the nest trees and the cumulative size of each nest stand plus all adjoining stands that were of a timber type used equal to or greater than its availability (table 5A). These adjoining stands may make important contributions to activity centers, because the owls have direct access to them. In some instances, nesting pairs may even spend more time in one or more of the adjoining stands than they do within the stand containing their nest.

The mean size of nest stands was 99.9 acres (SD = 114.9 acres) and the median was about 65 acres. The mean size of the nest stand plus adjacent stands was 306.7 acres (SD = 386.6 acres) and the median was about 265 acres. Numerous roosts would be available in the nesting and adjoining stands. Cumulative distribution functions for these two variables provide two important insights (fig. 5E). The majority of nest stands were smaller than 100 acres, but, in contrast, the majority of nest-plus-adjacent stands exceeded 200 acres.

Based on results of radio-tracking studies, the latter variable provides a better estimate of the size of activity centers. An estimate of the area used for foraging in an activity center may be approximated by the area that includes half of the nighttime (foraging) locations of owls during the breeding period, as estimated by the adaptive kernel method (Worton 1989). In the radio-tracking study in the Sierra NF (G. N. Steger pers. observ.), this averaged 317 acres (SD = 202; *n* = 9) in 1987, 296 acres (SD = 110; *n* = 7) in 1988, and 310 acres (SD = 127; *n* = 9) in 1989. These estimates were not independent from year to year, because some of the same individuals' home ranges were included in 2 or 3 of the years. In the radio-tracking study in the Lassen NF (Zabel pers. comm.), the average was 788 acres (SD = 347; *n* = 10) in 1989-90. In all cases, only birds with at least 20 nighttime locations were used for these estimates.

## Nest Sites on Private Timberlands

Hofmann and Taylor (1992) reported general habitat conditions at 18 nest sites on industrial forest lands in the northern (*n* = 4), central (*n* = 5), and southern (*n* = 9) Sierra Nevada. Fourteen of the pairs nested successfully, but the report did not indicate the proportion of all owls found on private lands that nested or the proportion that fledged young. The owls nested in a variety of forest stands, ranging from sparse (5 percent) to high (86 percent) cover by multi-storied stands with large-diameter trees. Reported values of site attributes were within ranges given above for nest sites in NFs. Overall, 60-65 percent of the area within a radius of 1,000 feet of nests had "dense" canopy cover. No other structural habitat features were reported.

Taylor (1992) provided additional information on the habitat associations of owls nesting on industrial forest lands in the Sierra Nevada. Based on a sample of 28 nests, Taylor found "...a clear pattern of dominance of nest sites by medium and large d.b.h. stands..." and the data to clearly indicate "...that owls nest in areas with moderate-to-dense canopy closure" (Taylor 1992, p. 9). These results are consistent with those reported in tables 5B-5D.

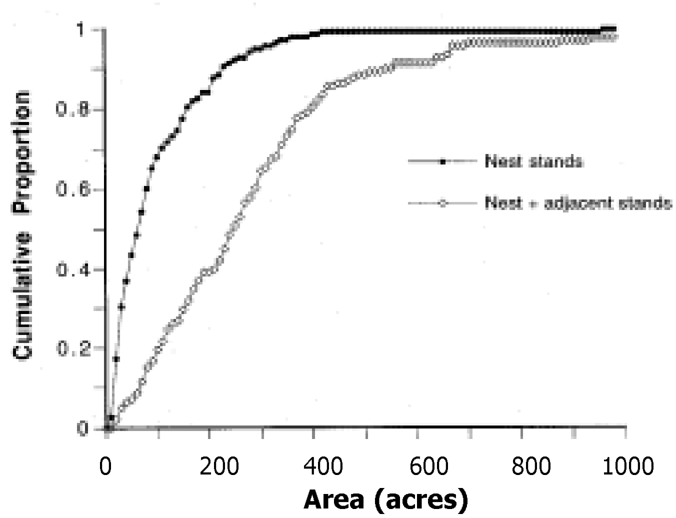


**Figure 5E**-Cumulative distribution of nest stands, and nest stands plus adjacent stands, arranged by size. Adjacent stands were restricted to those timber types used equal to, or greater than, their availability (*n* = 138).

## Foraging Sites

Attributes of foraging habitats used by California spotted owls have been estimated in only two studies (Laymon 1988, Call 1990). In both studies, the range of habitat structures used by the owls was greater in foraging habitats than in nesting and roosting habitats. Laymon (1988, p. 100) concluded that the majority of spotted owl foraging locations in his Eldorado study were on sites with medium to large trees (in Laymon's classification, these were trees >24 inches in d.b.h.) and dense canopy closure (60 to 100 percent). They significantly selected for stands with trees >24 inches in d.b.h. and canopy cover of 40 to 59 percent, based on availability. On the other hand, they used stands significantly less than expected that had (1) trees in the 11- to 24-inch d.b.h. group and 60 to 100 percent cover, and (2) trees >24 inches in d.b.h. and canopy cover of 10 to 39 percent. Laymon (1988, p. 115) also reported that the owls in his study selected "foraging sites with more and larger snags."

Call (1990, p. 30) concluded that the owls in his Tahoe NF study area used clearcuts, shrubfields, and plantations significantly less than expected ($P$ = 0.01), based on availability. They used medium timber (11-20 inches in d.b.h.) in proportion to availability ($P$ = 0.51), and they used large timber (20-35 inches in d.b.h.) significantly more than expected ($P$ = 0.01). In addition, the probability of an owl's using large timber was significantly greater than of its using medium timber ($P$ = 0.003). Based on vegetation sampled at foraging locations by Call (1990, p. iv), a "discriminant function analysis indicated that the owls selected habitats with late-successional stand characteristics including mature and old-growth timber [>35 inches in d.b.h.], multiple vegetation strata, and high live timber basal area." The combined results from Laymon's and Call's studies suggest that spotted owls in these Sierran conifer forests tended to forage in stands of intermediate to older ages.

Based on three canopy-closure classes (see table 5F), owls in the Sierra Study Area used stands with 70+ percent canopy closure significantly more and stands with 0-30 percent canopy closure significantly less than expected (Verner et al. 1991; also see Chapter 6).

Physiographic Attributes-Laymon (1988) found that random sites were significantly steeper than foraging sites during both summer and fall in the Eldorado Study Area (table 5G), but Call (1990) found no difference in the Tahoe Study Area (table 5H).

**Table 5F**-*Structural attributes of habitats (mean and percent Coefficient of Variation, by canopy cover class) used by California spotted owls during radio-tracking studies in the mixed-conifer zone of the Sierra Study Area, southern Sierra Nevada (Steger and Eberlein, pers. comm.).*

| | 0-39 percent canopy cover ($n$ =64) | | 40-69 percent canopy cover ($n$ = 35) | | 70+ percent canopy cover ($n$ = 21) | |
|---|---|---|---|---|---|---|
| | Mean | Percent CV | Mean | Percent CV | Mean | Percent CV |
| Percent canopy cover | | | | | | |
| By densiometer | 26.5[a] | 67.6 | 60.0[b] | 23.9 | 73.7[c] | 14.0 |
| By aerial photo | 21.0[a] | 49.9 | 52.9[b] | 16.7 | 74.8[c] | 6.8 |
| Basal area (square feet per acre) | | | | | | |
| Green trees | 61.4[a] | 84.2 | 172.2[b] | 41.3 | 211.3[c] | 20.7 |
| Snags | 4.7[a] | 137.0 | 12.1[b] | 76.3 | 13.9[b] | 64.1 |
| Hardwoods (by d.b.h. class)[1] | | | | | | |
| 0-4.7 inches | 0.1[a] | 300.0 | 0.3 | 200.0 | 0.6[b] | 269.2 |
| 4.8-10.6 inches | 0.7[a] | 280.0 | 1.5[b] | 144.1 | 2.0[b] | 104.1 |
| 10.7-20.5 inches | 1.1[a] | 250.0 | 2.0 | 188.9 | 1.6[b] | 141.0 |
| 20.6-35.4 inches | 0.6 | 323.1 | 1.3 | 313.8 | 2.0 | 233.3 |
| >35.5 inches | 0.1 | 800.0 | 0.6 | 442.9 | 0.0 | 0.0 |
| **Total** | **2.6[a]** | **193.3** | **5.6[b]** | **160.9** | **6.2[b]** | **109.4** |
| Softwoods (by d.b.h. class)[1] | | | | | | |
| 0-4.7 inches | 1.7[a] | 137.5 | 3.7[b] | 107.1 | 4.4[b] | 72.4 |
| 4.8-10.6 inches | 7.2[a] | 107.8 | 13.9[b] | 70.8 | 21.2[c] | 46.6 |
| 10.7-20.5 inches | 15.4[a] | 99.2 | 39.5[b] | 45.3 | 54.5[c] | 38.2 |
| 20.6-35.4 inches | 22.6[a] | 107.9 | 63.2[b] | 60.8 | 74.0[b] | 60.0 |
| >35.5 inches | 12.0[a] | 148.0 | 46.3[b] | 79.4 | 51.0[b] | 75.7 |
| **Total** | **59.0**[a] | **84.2** | **166.5**[b] | **43.9** | **205.2**[c] | **21.1** |
| Shrubs per acre | 3.7[a] | 325.5 | 18.0[b] | 293.7 | 8.4 | 250.9 |
| Downed woody debris (tons/acre, by log diameter-class)[2] | | | | | | |
| 11-20 inches | 2.1[a] | 88.9 | 3.2[b] | 75.5 | 3.1[b] | 74.2 |
| 21-35 inches | 4.0[a] | 102.1 | 4.7[b] | 100.7 | 6.9[b] | 83.7 |
| >35 inches | 3.3[a] | 213.3 | 9.3[b] | 144.7 | 8.2[b] | 106.1 |

[a,b,c]Values in the same row with different alpha superscripts are different at the 0.05 level of significance (one-way ANOVA).
[1] Diameter at breast height, in inches.
[2] Assumes a specific gravity of 0.4 for downed woody debris.

Structural Attributes-Percent canopy cover, softwood basal area, total live tree basal area, snag basal area, and the amount of large, downed woody debris were generally greater at foraging than at random sites (tables 5G and 5H). Stand measurements reported for the Sierra Study Area were not related to specific foraging locations of spotted owls, so they could not be used to compare attributes at foraging locations with those at random locations. Total basal areas reported in the Sierra Study Area (table 5F) in stands with 40-69 percent and 70+ percent canopy cover were comparable to those at foraging sites reported by Call (1990) for the Tahoe Study Area and by Laymon (1988) for the Eldorado Study Area. That was not the case, however, for stands with 0-39 percent canopy cover in the Sierra Study Area. Conifers were the dominant component of basal area in all locations studied (tables 5F-5H). Point estimates for softwood, hardwood, and snag basal areas also were generally less in foraging than at roost and nest sites.

### Selection Patterns of Radio-tagged Birds

Where significant patterns of habitat selection were observed among radio-tagged owls, results were consistent with those from the studies reported here. In the Lassen and Sierra Study Areas, some radio-tagged owls used denser stands and were associated with larger trees more than expected on the basis of availability. Only one bird used stands in the lowest canopy-cover class more than expected, and none did so for small tree classes (Chapter 6).

Results of Call's (1990) and Laymon's (1988) studies, reported earlier in this chapter, tend to show stronger selection for habitat attributes by foraging owls than suggested by studies reported in Chapter 6. We believe this resulted from differences between studies in their scale of measurements. Call and Laymon sampled habitats at or very near actual locations where owls foraged. Studies reported in Chapter 6, on the other hand, characterized the entire stand in which a given owl foraged, thus lacking the localized scale used by Call and Laymon.

## Patterns of Habitat Use at a Stand Scale

### Nest Types

All recently located nests of California spotted owls have been in trees, but some early records exist of nests found in other locations. For example, records obtained from the Western Foundation of Vertebrate Zoology (Kiff pers. comm.) included notes on 14 nests located between 1889 and 1947. Five were on cliff ledges, one was in a pigeon coop, and eight were in hardwood trees. The pigeon coop nest was composed of "manure," hay, and feathers in a deserted coop under a roof supported by four posts. This nest contained four eggs-only one of two clutches of that size ever reported for spotted owls (see Johnsgard 1988).

Quantitative information on nest trees and nest sites were provided by each of the seven NFs in the western Sierra Nevada and the four southern California NFs. This database was supplemented with identical information from four of the major study areas (Lassen--Blakesley pers. comm.; Eldorado-Moen pers. comm.; Sierra and Sequoia/Kings Canyon--G. N. Steger pers. observ.; and San Bemardino--W. S. LaHaye pers. observ.).

**Table 5G**-*Habitat characteristics (mean and percent Coefficient of Variation) of California spotted owl foraging locations in summer (n = 120) and fall (n = 79), and at random locations throughout summer/fall (n = 120) in the Eldorado Study Area, central Sierra Nevada (Gaymon 1988).*

| | Foraging sites | | | | Random sites in summer and fall | |
|---|---|---|---|---|---|---|
| | Summer | | Fall | | | |
| | Mean | Percent CV | Mean | Percent CV | Mean | Percent CV |
| **Physiographic attributes** | | | | | | |
| Percent slope | 19.4[a] | 90.3 | 17.9[a] | 86.9 | 23.4 | 46.8 |
| **Structural attributes** | | | | | | |
| Percent cover | 66.8 | 32.0 | 61.6 | 45.5 | 67.9 | 29.0 |
| Basal area (square feet per acre) | | | | | | |
| Hardwoods | 16.6[a] | 172.9 | 9.2[a] | 275.2 | 26.1 | 146.0 |
| Softwoods | 200.4[a] | 69.0 | 196.1 | 74.1 | 163.8 | 62.6 |
| **Total live[1]** | **217.0** | - | **205.3** | - | **189.9** | - |
| Snags | 23.1 | 216.9 | 28.8 | 208.8 | 17.4 | 246.4 |
| Downed woody debris (tons per acre, by log diameter-class)[2] | | | | | | |
| 0-3 inches | 0.80 | 0.75 | 0.83 | 0.82 | 0.82 | 0.74 |
| >3 inches | 11.84 | 1.67 | 13.76[a] | 1.43 | 9.36 | 1.39 |

[a] Significantly different from the corresponding random sites, at the 0.05 level of significance (Student's *t*-test).
[1] The sum of softwood and hardwood basal areas. Data were not available to compute a percent Coefficient of Variation for this variable.
[2] Assumes a specific gravity of 0.4 for downed woody debris.

**Table 5H** *Habitat characteristics (mean and percent Coefficient of Variation) of foraging* (n *= 158) and random sites* (n= *256) from six California spotted owl home ranges in the Tahoe Study Area, central Sierra Nevada (Call 1990).*

| | Foraging sites | | Random sites | |
|---|---|---|---|---|
| | Mean | Percent CV | Mean | Percent CV |
| **Physiographic attributes** | | | | |
| Percent slope | 28.4 | 58.1 | 27.4 | 63.0 |
| Elevation (feet) | 3,852.0 | 12.5 | 3,888.0 | 13.9 |
| **Structural attributes** | | | | |
| Percent canopy cover | 91.8[a] | 12.4 | 85.2 | 47.1 |
| Basal area (square feet per acre) | | | | |
| Hardwoods | 23.9 | 161.0 | 20.2 | 153.5 |
| Softwoods | 154 .9[a] | 52.7 | 129.8 | 52.3 |
| **Total live** | **178.7[a]** | **43.7** | **150.6** | **44.1** |
| Snags | 15.3[a] | 154.6 | 10.1 | 169.6 |
| Basal area (square feet per acre, by d.b.h. class)[1] | | | | |
| 3.9-4.8 inches | 1.6 | 374.5 | 2.2 | 379.2 |
| 4.9-10.7 inches | 25.5 | 119.9 | 27.6 | 116.9 |
| 10.8-20.6 inches | 52.8 | 79.7 | 51.8 | 86.2 |
| 20.7-35.5 inches | 67.1[a] | 81.1 | 49.5 | 94.7 |
| >35.5 inches | 32.1[a] | 104.9 | 19.7 | 149.14 |
| Downed woody debris (percent cover, by diameter class) | | | | |
| 1-11.8 inches | 5.86 | 82.1 | 4.5 | 103.3 |
| >11.8 inches | 3.26 | 184.8 | 1.7 | 195.9 |

[a] Significantly different from the corresponding random sites, at the 0.005 level of significance (Student's *t*-test).

[b] Significantly different from the corresponding random sites, at the 0.001 level of significance (Mann-Whitney *U* test).

[1] Diameter at breast height.

Based on nest locations in trees, we recognize five nest types that are used regularly by spotted owls in the Sierra Nevada and southern California (table 5I). (1) Cavity nests (color photo 5-3) are placed in natural cavities resulting from decay, usually in the heartwood of a large, old tree. Cavities large enough for owl nests can form where large branches tear out of the trunk of the tree (side cavities). (2) Broken-topped trees and snags (color photo 5-8) may develop depressions via decay, or they may persist without much decay but still provide a broad enough surface for the owls to lay their eggs. (3) Platform nests (color photo 5-14) are those placed on remnant platforms built by other species (for example, goshawks, ravens, or tree squirrels), or on debris accumulations in densely branching structures of trees. (4) Dwarf mistletoe brooms are often dense enough that they form a suitable nest substrate. (5) "Undefined" nest types are those that do not clearly fall into types 1-4 or for which we lack data. In spite of the variety of nest types used by these owls, the nest trees are still generally larger than other trees within the same stand (see below, table 5K). The large trees most often selected for nest sites by California spotted owls also exhibited signs of old age. Forty-three percent of the nests were in large decay cavities, and another 16 percent were on broken-topped trees or snags (for example, color photo 5-8). Many other nests were placed on limb deformities that supported debris platforms.

Among 276 nests located recently, most of them in NFs in the Sierra Nevada and southern California, nest type varied markedly in different parts of the owl's range (table 5I). In particular, cavity nests dominated nest types in both northern and southern Sierran conifer forests, but platforms were most common in conifer forests of southern California, perhaps as a result of differences in the availability of nesting substrates (see LaHaye 1988). Patterns on industrial forest lands in the Sierra Nevada were similar, but with a greater proportion of platform nests. Based on a sample of 16 nests, half were cavity and half were platform type (Taylor 1992). Northern spotted owls in Oregon nested primarily in tree deformities (Forsman et al. 1984). A similar pattern was found among northern spotted owls in northwestern California (LaHaye 1988), but platform nests were more frequent in the southern part of that study area.

Forsman et al. (1984) reported that young northern spotted owls from several platform nests in Oregon left their nests several days earlier than young from cavity nests. Because they were younger and less able to climb, they spent longer on the ground than young from cavity nests. Forsman et al. speculated that, as a result, these young may have experienced higher predation while on the ground than young from cavity nests. LaHaye et al. (1992a), however, found no differences in overall nesting success among broods produced in cavity nests, broken-topped nests, or platform nests in the San Bernardino Mountains.

Table 5I-*Characteristics of nest trees used by California spotted owls, by major habitat type, based on data from all study areas except the Tahoe, and from all relevant National Forest files, 1986-1991.*

| General habitat type | Number of nests | Tree condition: Alive | Tree condition: Snag | Nest type[1]: CA | BT | PL | MI | UN | Nest tree: Conifer | Nest tree: Hardwood |
|---|---|---|---|---|---|---|---|---|---|---|
| Northern Sierran Conifer | 83 | 61 | 22 | 55 | 9 | 15 | 4 | 0 | 79 | 4 |
| Southern Sierran Conifer | 41 | 29 | 12 | 27 | 4 | 2 | 2 | 4 | 29 | 12 |
| Southern California Conifer | 139 | 128 | 11 | 33 | 28 | 78 | 0 | 0 | 109 | 30 |
| Riparian/hardwood forests | 13 | 13 | 0 | 5 | 3 | 5 | 0 | 0 | 0 | 13 |

[1]CA = cavity, BT = broken-top, PL = platform, MI = dwarf mistletoe, UN = undefined.

**Table 5J**-*Tree species used as nest sites by the California spotted owl, based on data from all study areas except the Tahoe, and from all relevant National Forest files, 1986-1991.*

| General habitat type | White fir | Red fir | Douglas-fir | Bigcone Doug-fir | Incense-cedar | Sugar pine | Jeffrey pine | Ponderosa pine | Black oak | Live oak | White alder | Other[1] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Northern Sierran Conifer | 22 | 9 | 21 | 0 | 7 | 16 | 2 | 8 | 3 | 0 | 0 | 1 |
| Southern Sierran Conifer | 12 | 5 | 1 | 0 | 1 | 2 | 2 | 5 | 12 | 0 | 0 | 1 |
| Southern California Conifer | 45 | 0 | 0 | 21 | 15 | 10 | 17 | 0 | 5 | 22 | 3 | 1 |
| Riparian/hardwood forests | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 5 | 2 | 3 |

[1]One nest each was in giant sequoia, Coulter pine, blue oak, tanoak, cottonwood, and California sycamore.

**Table 5K**-*Nest stand and nest tree characteristics of California spotted owls, by general habitat type (mean ± SD), based on data from all study areas except the Tahoe, and from all relevant National Forest files, 1986-1991.*

| General habitat type | Elevation (feet) | Total canopy cover (percent) | Nest tree d.b.h.[1] (inches) | Nest tree height (feet) | Nest height (feet) |
|---|---|---|---|---|---|
| Northern Sierran conifer | 5,284 ± 922<br>*n* = 65 | 75.4 ± 17.2<br>*n* = 28 | 43.5 ± 14.7<br>*n* = 81 | 96.8 ± 36.7<br>*n* = 75 | 64.9 ± 25.7<br>*n* = 75 |
| Southern Sierran conifer | 5,750 ± 1355<br>*n* = 41 | 75.5 ± 27.4<br>*n* = 17 | 46.7 ± 19.6<br>*n* = 41 | 95.0 ± 52.7<br>*n* = 40 | 57.5 ± 31.0<br>*n* = 40 |
| Southern California conifer | 6,002 ± 1270<br>*n* = 137 | 79.3 ± 17.7<br>*n* = 131 | 37.0 ± 13.9<br>*n* = 139 | 87.5 ± 33.3<br>*n* = 139 | 56.5 ± 23.2<br>*n* = 139 |
| Riparian/hardwood forests | 2,618 ± 1271<br>*n* = 13 | 89.3 ± 10.6<br>*n* = 6 | 29.5 ± 16.6<br>*n* = 13 | 55.0 ± 23.5<br>*n* = 13 | 38.4 ± 14.0<br>*n* = 13 |

[1]Diameter at breast height.

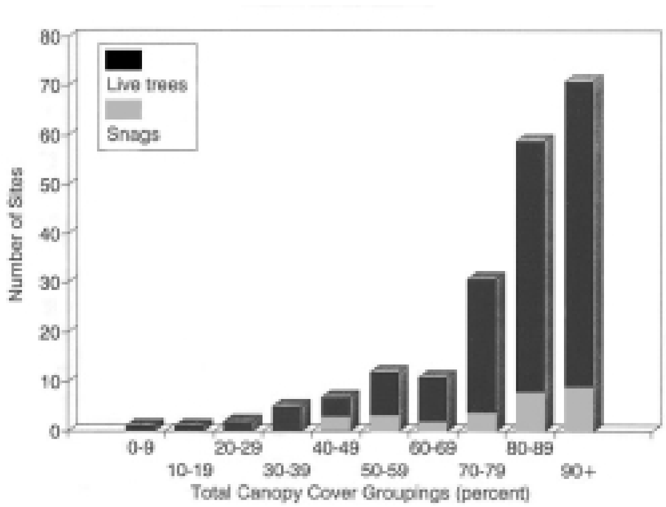


**Figure 5F**-Number of nest sites, by canopy-cover class; nests in snags and live trees are differentiated (*n* = 201).

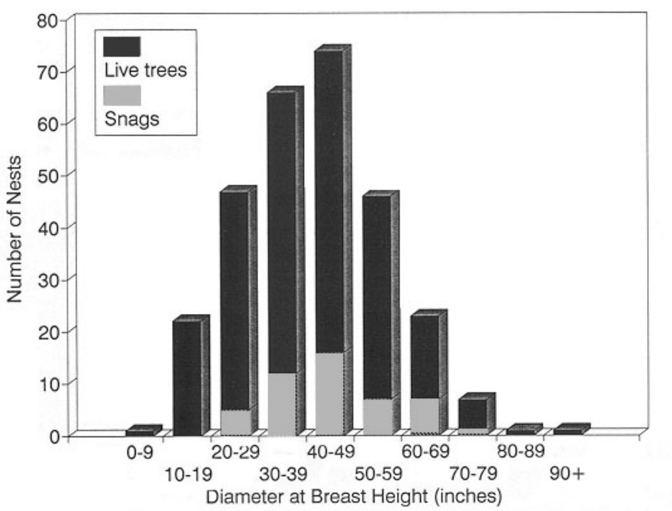


**Figure 5G**-Number of live trees and snags, by stem diameter-class, used for nest sites by California spotted owls (*n* = 288).

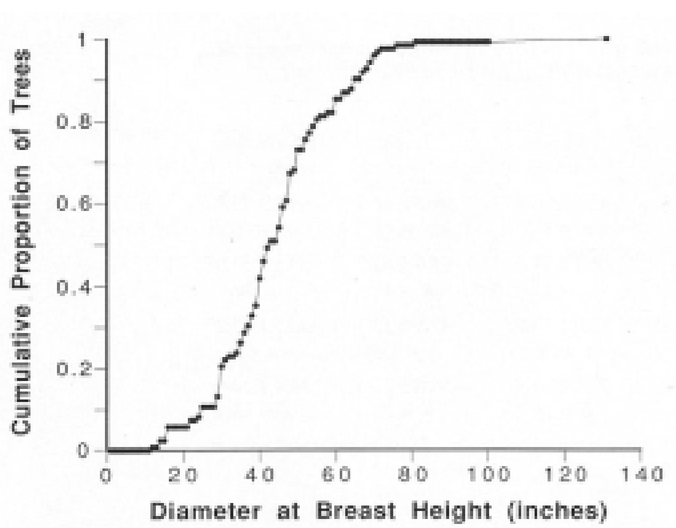


**Figure 5H**-Cumulative distribution of nest trees in the Sierra Nevada conifer zone, arranged by diameter at breast height (*n* = 122).

## Nest Trees

Ten species of conifers and seven species of hardwoods accounted for all recent nest sites reported for California spotted owls (table 5J). Nest trees were typically in stands with high canopy cover-75.4 percent in Sierran conifer and 79.3 percent in southern California conifer forests (table 5K; see fig. 5F). These estimates compared favorably with those reported above for nest stands (tables 5B and 5C). Eighty-three percent of all nests in the conifer forests were in living trees (fig. 5G) and 82 percent were in conifers. These trees were very large, averaging about 90 feet tall (range 25-262 feet) and 41 inches in d.b.h. (range 9-81 inches), with means slightly higher in Sierran than in southern California conifer forests (table 5K). More than 75 percent of all nest trees were larger than 30 inches in d.b.h. (fig. 5H). Results from surveys of nest sites on industrial forest lands also showed that owls nested in large trees. Based on a sample of 17 nests from the Sierra Nevada conifer zone, nest tree d.b.h. averaged 41.8 inches (Taylor 1992).

The d.b.h. of nest trees in our current sample was significantly greater than that of conifers in general in the Sierra Nevada *even in 1900* ($\chi^2$ = 167, df = 6, $P$ < 0.001; fig. 5I), based on trees on plots measured by Sudworth (1900) prior to extensive logging. Interestingly, the diameter distribution of white fir trees used as nest sites by owls was not significantly different ($\chi^2$ = 7.469, df = 5, $P$ > 0.10; fig. 5J) from that of white firs measured by Sudworth. The white fir comparison is appropriate because that was the most common nest tree species used by California spotted owls (table 5J). Comparison of the sample of nest trees from Sierran conifer forests to the current diameter distribution in the M4G timber strata on the Tahoe NF also shows extensive selection for large-diameter trees (fig. 5K). To the extent that the Tahoe NF sample is representative of this timber strata in the Sierra Nevada, selection for large trees for nesting is clearly evident.

The significant inference from these results is that California spotted owls in conifer forests today are selecting nest trees from among the few remaining trees that are as large as or larger than average trees in 1900, before extensive logging began to remove the largest trees from the forest. When this pattern is coupled with the past and projected future trends of large trees in the Sierra Nevada (Chapter 13), it is reasonable to hypothesize large-diameter trees as a current or potentially limiting factor sometime in the future. That is, even if large trees are not currently limiting, we have reason to be concerned that they could soon be limiting if specific constraints on their removal are not invoked in the near-term.

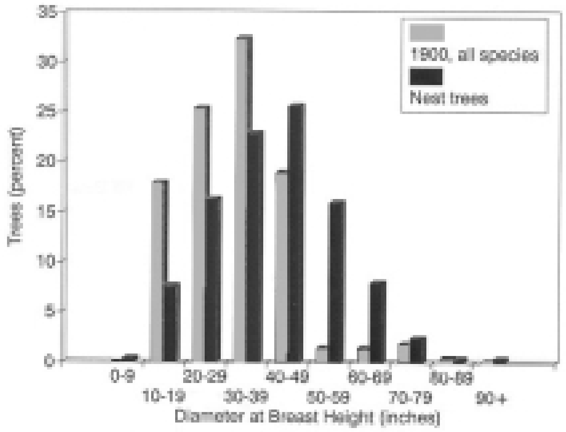


**Figure 5I-**Proportions of nest trees (recent) and trees available in stands in 1900 (Sudworth 1900), by stem diameter-class.

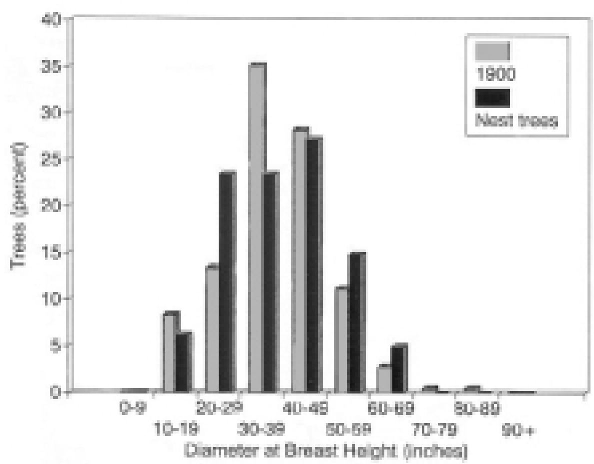


**Figure 5J-**Proportions of nest trees (recent) that were white firs, and white firs available in stands in 1900 (Sudworth 1900), by stem diameter-class.

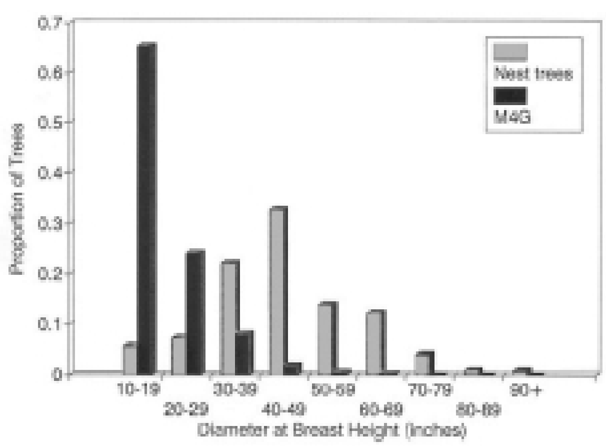


**Figure 5K-**Proportion of nest trees (recent) in Sierran conifer forests (*n* =122) and trees currently available in M4G stands on the Tahoe NF, by stem diameter-class.

# Foothill Riparian/Hardwood Forests

Measurements of winter foraging sites and foraging stand attributes in foothill riparian/hardwood forests were available for the Eldorado Study Area (Laymon 1988) and the Sierra Study Area (Steger and Eberlein pers. comm.) (tables 5D and 5L). Because sample sizes were small, these analyses should be considered as preliminary at this time. Point estimates suggest about the same range of values for percent canopy cover as observed in the conifer forests at higher elevations (compare tables 5D, 5F, and 5L). Basal areas of green trees and snags were considerably less, and shrub density was much higher in the hardwood type than in the conifer forest. Based on Laymon (1988), and a comparison of tables 5F and 5L, together with considerable on-site experience with these habitats, we found that riparian/hardwood forests dominated by oaks tended to have less canopy layering than most sites in the Sierran mixed-conifer and ponderosa pine/hardwood types (color photos 5-23 and 5-25). Multiple layers were present, however, in the mixed-hardwood forests in southern California, where spotted owls occur in narrow riparian corridors in steep-sided canyons, as in the Los Padres NF (color photo 5-28). Tables 5D and 5L also suggest less downed woody debris in the low-elevation hardwood type, compared to conifer forests.

Nest sites in riparian/hardwood forests averaged about 2,600 feet in elevation. No pattern was evident in the types of nests found in these forests (table 5I), but the sample size was too small to establish a pattern if one existed. All of the nests located were in hardwoods that averaged 55 feet tall (range 16-98 feet) and 30 inches in d.b.h. (range 13-72 inches) (table 5K).

Collectively, these data indicate that owl habitat in the foothill/riparian forests was characterized by both lower live tree basal area and lower canopy cover than higher-elevation sites in the conifer zone. The high closure measured at nest sites in the foothill zone (table 5K) may represent a highly localized phenomenon-one uncharacteristic of stands in this area in general. Furthermore, in the foothill habitats, the average nest-tree d.b.h. was smaller (table 5K) and platform nests were more common (table 5I) than in the conifer zone. Given these contrasts, the structure of owl habitats in foothill riparian/hardwood forests appeared to be substantially different from that in mixed-conifer forests. We caution that no data exist that suggest that stand basal areas, cover classes, and nest-tree sizes used in the foothill/riparian zone would, if created in the conifer zone, provide suitable owl habitat. Indeed, owls that migrated to low-elevation sites for the winter moved back upslope and chose dense stands with large trees in the mixed-conifer forest as summer habitat (table 5D).

**Table 5L**-*Structural attributes of habitats (mean and percent Coefficient of Variation, by canopy cover class) used by California spotted owls during radio-tracking studies in the riparian/hardwood zone of the Sierra Study Area, southern Sierra Nevada (Steger and Eberlein pers. comm.).*

| | 0-39 percent canopy cover (*n* = 7) | | 40-69 percent canopy cover (*n* = 5) | | 70+ percent canopy cover (*n* = 8) | |
|---|---|---|---|---|---|---|
| Structural Attributes | Mean | Percent CV | Mean | Percent CV | Mean | Percent CV |
| Percent canopy cover | | | | | | |
| By densiometer | 36.3[a] | 39.4 | 67.26 | 11.8 | 74.3[b] | 16.3 |
| By aerial photos | 15.9[a] | 66.8 | 59.06 | 11.6 | 80.0[c] | 5.8 |
| Basal area (square feet per acre) | | | | | | |
| Green trees | 20.0[a] | 80.0 | 50.1[b] | 51.5 | 65.6[b] | 67.1 |
| Snags | 0.9[a] | 175.0 | 4.1 | 87.2 | 5.0[b] | 80.7 |
| Hardwoods (by d.b.h. class)[1] | | | | | | |
| 0-4.7 inches | 1.4[a] | 124.2 | 4.6[b] | 48.1 | 6.5[b] | 91.9 |
| 4.8-10.6 inches | 6.7 | 115.0 | 18.8 | 37.4 | 19.0 | 30.7 |
| 10.7-20.5 inches | 5.9 | 97.8 | 12.9 | 61.5 | 20.0 | 113.7 |
| 20.6-35.4 inches | 5.1 | 125.0 | 8.5 | 80.9 | 12.0 | 129.1 |
| >35.5 inches | 1.0 | 262.5 | 5.4 | 150.0 | 1.3 | 279.3 |
| **Total** | **20.0[a]** | **79.4** | **50.2[b]** | **51.4** | **58.7[b]** | **65.3** |
| Softwoods (by d.b.h. class)[1] | | | | | | |
| 0-4.7 inches | 0 | 0 | 0 | 0 | 0.1 | 200.0 |
| 4.8-10.6 inches | 0 | 0 | 0 | 0 | 0.3 | 300.0 |
| 10.7-20.5 inches | 0 | 0 | 0 | 0 | 2.3 | 219.2 |
| 20.6-35.4 inches | 0 | 0 | 0 | 0 | 4.4 | 281.0 |
| >35.5inches | 0 | 0 | 0 | 0 | 0 | 0 |
| **Total** | **0** | **0** | **0** | **0** | **7.0** | **258.1** |
| Shrubs per acre | 105.0 | 198.8 | 69.0 | 62.5 | 127.0 | 144.4 |
| Downed woody debris (tons per acre, by log diameter-class)[2] | | | | | | |
| 11-20 inches | 0.09 | 264.4 | 0.10 | 223.5 | 0.68 | 164.1 |
| 21-35 inches | 0 | | 0.41 | 223.7 | 0.45 | 187.5 |
| >35 inches | 0 | | 0 | | 0 | |

[a,b,c] Values in the same row with different alpha superscripts are different at the 0.05 level of significance (one-way ANOVA).

[1] Diameter at breast height, in inches.

[2] Assumes a specific gravity of 0.4 for downed woody debris.

# Discussion

## General Patterns of Habitat Use

The first specimen of the spotted owl was collected by Xantus (1859) in the Tehachapi Mountains of southern California. This bird was likely found in the closed-canopied, riparian/hardwood forests common to the Fort Tejon region. Following this first documented sighting by Europeans, many reports of California spotted owls appeared in the literature over the next 80 years (see Grinnell and Miller 1944, Gould 1974). These reports and several nest records at the Western Foundation of Vertebrate Zoology (Kiff pers. comm.) indicated that California spotted owls in past decades used both conifer and hardwood habitats, and were found consistently in densely forested areas.

More recent observations and studies document the habitat associations of this bird throughout its range and in a quantitative fashion. These results suggest some general patterns about habitat use by California spotted owls. First, they use a broader array of habitats than used by the northern spotted owl. Second, within the general habitat types selected, they use forest patches that are complex in structure relative to what is available (for example, many trees in different diameter-classes and high canopy closure). Third, California spotted owls appear to select remnants of the older Sierran and San Bernardino conifer forests that have managed to survive 200-400 years to the present time (see table 5M). Especially for nesting and roosting, present data from several different sources suggest that most California spotted owls select dense stands with very large, presumably old trees. Fourth, although habitat attributes associated with California spotted owls at their nest and roost sites parallel those associated with northern spotted owls, foraging habitat used by the California subspecies appears to be much more variable than for its northern relative. Indeed, the considerable range in variation found in habitats used by California spotted owls is well-illustrated by the photos at the end of this chapter. In spite of this variation, however, results of studies reported in this chapter firmly establish that these owls use their forested environment in a nonrandom fashion.

**Table 5M-***Core data (mean ±SD) and ages of nest trees used by California spotted owls in the San Bernardino Mountains; sample sizes are in parentheses beneath means and SDs.*

| Trees | D.b.h.[1] | Tree height[2] | Nest height[2] | Core age in years | Mean percent of total radius cored |
|---|---|---|---|---|---|
| All trees | 41 ± 13.0 | 103 ± 32.9 | 65 ± 4.3 | 230 ± 93.8 | 69 ± 26.4 |
| | (30) | (30) | (30) | (29) | (29) |
| White fir | 41 ± 11.7 | 91 ± 25.1 | 65 ± 19.2 | 238 ± 68.2 | 70 ± 20.1 |
| | (14) | (14) | (14) | (14) | (14) |
| Sugar pine | 37 ± 17.6 | 90 ± 31.2 | 53 ± 22.0 | 217 ± 43.1 | 46 ± 48.2 |
| | (3) | (3) | (3) | (3) | (3) |
| Jeffrey pine | 40 ± 14.8 | 116 ± 37.9 | 68 ± 27.8 | 223 ± 143.1 | 78 ± 26.3 |
| | (8) | (8) | (8) | (8) | (8) |
| Incense-cedar | 46 ± 15.8 | 131 ± 29.0 | 83 ± 27.5 | 193 ± 111.0 | 64 ± 31.4 |
| | (3) | (3) | (3) | (3) | (3) |
| Bigcone Douglas-fir | 48 ± 16.1 | 115 ± 54.5 | 42 ± 28.3 | 320 ± 0.0 | 48 ± 0.0 |
| | (2) | (2) | (2) | (1) | (1) |

[1] Diameter at breast height, in inches.
[2] Height in feet.

The association between the variable habitats used by California spotted owls and their population effects is not well understood. For example, we do not know if the birds survive and reproduce equally well in each of the many habitat types where they are found. We strongly suspect, however, that populations in some of those habitats are "sources" (reproduction exceeds replacement needs within the population, so surplus young are produced which emigrate to other areas) and populations in others are "sinks" (where reproduction is generally insufficient to replace local losses, so maintenance of the population requires immigration from other areas). We also do not know if spotted owls in the Sierra Nevada evolved in a more heterogeneous environment than was the case for northern spotted owls. Spotted owls evolving in different environments may exhibit different adaptive responses (for example, see Gutiérrez and Pritchard 1990). Although we do not yet know the answers to some of these critical questions, we infer that human-induced habitat changes (for example, from logging) may adversely affect the owls and lead to population declines.

California spotted owls in conifer forests exhibited significant overuse of M4G stands at the landscape scale. These are dense (70+ percent canopy cover) mixed-conifer forests with canopy trees averaging ≥24 inches in d.b.h. This pattern of selectivity was corroborated by comparisons with random locations of stands used for nesting, roosting, and foraging in the conifer forest. The vast majority of birds used sites with greater canopy cover, total live tree basal area, basal area of softwoods and hardwoods, and snag basal area than found at random sites. These are attributes that we would expect to find in M4G stands. Finally, selection of nest sites and nest trees by the owls further corroborates the findings from analyses at other scales of resolution. A high proportion of nest sites, especially in Sierran conifer forests, were in natural cavities or in broken-topped trees or snags. Trees used for nest sites were significantly larger and probably older than available in the general forest matrix, even in M4G stands. This pattern suggests that, currently, most nest trees are surviving remnants from forests of past centuries.

## Is the Owl A Habitat Specialist?

In spite of the fact that the owl used a range of habitat conditions, we believe it should be characterized as a specialist. For example, we observed that 80 percent of all nest trees were located in stands with canopy cover of at least 70 percent. The average (and median, and modal) d.b.h. of nest trees in the Sierra Nevada was about 45 inches, but only 2 percent of all trees greater than 10 inches in d.b.h. in M4G stands on the Tahoe NF were in the 40-49 inch d.b.h. group. By specialist we mean an animal that shows a clear selection for certain habitats or habitat attributes. Two assumptions we invoked in our analyses were (1) the pattern of habitat usage we observed was not constrained by any other species, and (2) the use of a habitat type significantly in excess of its availability reflects selection. The degree to which these assumptions were met is unknown. It is possible, for example, that the California spotted owl's pattern of habitat use was influenced by competition with another raptor species. Also, the methods we used can be misleading if, for example, the preferred habitat is also the most common habitat. Regarding these two possibilities, we have no data that suggest direct competitive interactions with other raptor species, and the habitat used most commonly for nesting (M4G) is uncommon (about 20 percent, based on FS inventory data) in the Sierran landscape.

We do not claim dependence by the spotted owl upon any given habitat type or attribute. Further, we do not contend that our data, at this time, indicate that any given habitat type or attribute is "required," in the sense that its absence would lead to the owl's extinction. But we do believe that the habitat distribution patterns of the majority of owls, given the constraints of availability and possible biotic interactions, currently reflect optimal choices. If better choices were available, natural selection would act to remove those individuals making the wrong choice.

Based on our definition of a specialist and the operational manner in which we identified selection, we believe we have made the best use of the available data to craft a set of recommendations intended to secure future options for managing the species. We have based our inferences on what the majority of the owls selected from among choices in their habitats, and assumed that these choices reflected the most important attributes to retain in future landscapes.

## Recommendations

Translating all the habitat association patterns into a general characterization of nesting, roosting, and foraging stands that should be suitable for spotted owls in conifer forests is difficult. It is also risky! All too often, suggestions offered tentatively are misconstrued to be the last and definitive word on the matter. Even with these misgivings, however, we offer here some tentative estimates of stand attributes, based mainly on tables 5B-5H. Given these caveats, the tabulation below may be a fair, initial representation of the range of mean values of some attributes in suitable habitat for spotted owls in Sierran mixed-conifer forests. Most values in the tabulation generally reflect the range of means from the various studies reported in this chapter. We have combined values for nesting and roosting stands, because (1) they tend to be very similar, (2) spotted owls commonly roost within the stands that include their nests, and (3) we believe that a stand suitable for nesting would also provide conditions satisfying the roosting needs of the owls.

| | Nesting and roosting stands | Foraging stands |
|---|---|---|
| Percent canopy cover[1] | 70-95 | 50-90 |
| Total live tree basal area[2] | 185-350 | 180-220 |
| Total snag basal area | 30-55 | 15-30 |
| Basal area of large snags[3] | 20-30 | 7-17 |
| Downed woody debris[4] | 10-15 | 10-15 |

[1] Mostly in canopy ≥30 feet high, including hardwoods.
[2] Square feet per acre.
[3] Dead trees ≥15 inches in d.b.h. and ≥20 feet tall.
[4] Tons per acre.

The values for total snag basal area are high and reflect sampling of all, or nearly all, dead trees by various workers. We believe, however, that relatively small snags have little value in terms of spotted owl habitat. Snags need to be large enough to accommodate nest sites for medium to large cavity-nesting birds and den sites for flying squirrels. In addition, larger snags take longer than small snags to decompose after they have fallen. We consider snags that are at least 15 inches in d.b.h. and 20 feet tall to be near the smaller end of suitability for owl habitat. In two comparisons of total snag basal area with the basal area of "large" snags (≥15 inches in d.b.h. and ≥20 feet tall (table 5E), large snags comprised 45 percent and 59 percent of the total. Snag values in the above tabulation could be adjusted accordingly to estimate the basal area of large snags in owl habitats. This limited analysis suggests that owl nest and roost sites have from about 19 to 31 square feet basal area of large snags, and foraging sites have from 7 to 17. Because we recommended an interim approach to management for spotted owls in the Sierra Nevada (Chapter 1), one based on the concept of preserving all options for future management of spotted owls, we recommend maintaining at least 20 square feet basal area of large snags wherever possible in owl habitat. Based on current information, this standard appears to be appropriate for maintenance of suitable nesting and roosting sites. It is at the lower end of estimates for nesting and roosting sites and slightly above the upper end of estimates for foraging sites.

Estimates of the mass of downed wood in owl nesting, roosting, and foraging sites ranged from 10.5 to 24.7 tons per acre, with a mean of 17.4 and a standard deviation of 5.3. (Based on values in tables 5D-5G, and on approximations of tons/acre from values given in tables 5B and 5H.) Most of this was in pieces at least 11 inches in diameter. We believe that much of this has managed to accumulate because of effective fire suppression in Sierran conifer forests during the past 80-90 years, so these quantities probably exceed what was present during presettlement times. Fuels management specialists from R5 and from NFs in the Sierra Nevada have assured us that the fuel loads indicated by the average in owl habitats represent a significant hazard vis-à-vis the intensity of fires and the likelihood of stand-destroying fires. Consequently, we believe that a compromise is needed between fire threats and what the data indicate to be typical quantities of large logs in owl habitats. We suggest a range of 10-15 tons per acre, in the largest logs available, and believe it is inadvisable to retain logs smaller than 11 inches in diameter to attain this level. This range is at the low end of the values observed in owl habitats.

## Research Considerations

Despite the considerable amount of study already done in an effort to estimate habitat-use patterns by spotted owls, we still have limited knowledge about this critical aspect of the bird's ecology. This is particularly true relative to the relations between habitat and demographic variation. This is the case largely for three reasons. First, research on this subspecies was slow in getting started, because most of the early concern was directed at the northern spotted owl. Funds available for research on the California spotted owl have not been sufficient to allow studies of their prey, or even to complete a full inventory of all habitats where the owl is likely to occur. Second, most definitive studies of the California spotted owl were initiated in 1986 or later. Coincidentally, this was when the current drought began (fig. 4H), making it impossible to determine whether observed results from owl studies should be interpreted primarily in relation to changing habitat conditions, to the drought, or both. Third, knowledge about different gradations in habitat suitability must be based on habitat-specific studies of the owl's demography--whether or not they reproduce well enough in a given habitat to equal or exceed annual mortality rates.

Demographic information on owl populations in a variety of different habitats will take many years to obtain and will depend on monitoring demographic trends through both wet and dry climatic periods. We should continue to build on existing demographic studies to attain some of the information needed, because they already have an accumulating database. We also need to consider a range of options for adding other demographic studies. In particular, we see great potential for demographic studies on lands of some of the major commercial timber companies whose forest practices differ in important ways. These are ad hoc experiments (Bias and Gutiérrez 1992) on the effects of different management regimes on the owls.

Every effort should be made to establish consistent methods, attributes to be measured, data forms, and analytical procedures to be used by all researchers on California spotted owls. Failing adoption of standard methods and so on, quantitative relations among different techniques should be developed to ease interpretation of data from different studies. Finally the efficiency and utility of different techniques should be explored to encourage adoption of a uniform protocol for basic information collection in the field.

The "Achilles heel" of wildlife management is separating correlation and causation. All analyses of habitat described in this paper are based on correlational studies. That is, we observe a particular variable, such as canopy closure, to be consistently high at owl sites relative to available sites, but we do not know if that variable is the reason why owls are present at the site. They may be there because canopy closure is usually associated with a different stand attribute, one that we have not measured and one that may be too subtle to quantify. Hence, we do not know if changes in canopy closure will consistently result in a functional response by owls inhabiting a site. The fact that we have not demonstrated cause-and-effect relations, however, does not dilute the power of these documented trends. Rather, it tempers our recommondations about managing for functional owl habitat.

Controlled experiments, in which one or more attributes are changed and subsequent functional responses of the owls are documented, are the best way to identity cause-and-effect relations. Experimentation in certain fields of science is the rule (for example, see Platt 1964). Experiments in natural ecosystems, however, are generally orders of magnitude more complicated and less controllable than experiments in fields like chemistry, physics, or molecular biology. Nevertheless, the widespread logging of forests for commodity production provides a possibility of undertaking ecological experiments on owl responses to changes in habitat. Experiments can occur at two spatial scales--the landscape (that is, a collection of owl home ranges) and the site (within a forest patch occupied by an owl or pair of owls). The critical question to be asked is: Do the changes in spatial arrangement or the structure and composition of habitats affect the owl's ability to survive and reproduce? Formulation of specific experiments should be based on empirical information generated from natural history studies (see above) and the creative application of results from modeling habitat conditions observed in natural history studies. The success of experiments in discerning alternative outcomes will determine their potential for applying a management system to a larger landscape.

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