CHARACTERISTICS OF NEST TREES AND NEST SITES OF CALIFORNIA SPOTTED OWLS IN CONIFEROUS FORESTS OF THE SOUTHERN SIERRA NEVADA

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ABSTRACT: We described 86 nest sites of California spotted owl (*Strix occidentalis occidentalis*) and tested for differences in vegetation structure at nest locations in conifer-dominated stands in 2 study areas, the Sierra National Forest (SNF) and Sequoia and Kings Canyon National Parks (SNP), California. All nests were between 1061 and 2414 m in elevation, 52 were side-cavity nests, 18 top-cavity nests, and 9 platform nests. All nests were in live trees (69) or snags (17): 41 in fir (*Abies* spp.), 17 in black oak (*Quercus kelloggii*), 14 in pine (*Pinus* spp.), and 14 in giant sequoia (*Sequoiadendron giganteum*). Nest trees had a mean diameter of 118.5 cm (SD = 32.1), except for giant sequoia which were much larger in diameter (462.9, SD = 144.5 cm). Pines were the only species where we detected a significant difference ($P = 0.0001$) in diameter of nest trees between study areas, with larger diameter nest trees located on the SNP. Nest sites were evenly distributed topographically, from near the ridge tops to the bottoms of drainages. Slopes and aspects at nest sites differed ($P < 0.05$) between study areas with the SNF having the greatest number of nests in the 0-10% slope class on north and west aspects, while the SNP had the greatest number in the 10-20% slope class on east aspects. Nest sites in both study areas had dense canopy cover (89%) with multiple vegetative layers. Overall, nest site characteristics on the SNF and SNP were similar despite the long history of timber harvest on the SNF and the lack of harvest on SNP.

Key words: California spotted owl, nest sites, nest structures, Sequoia and Kings Canyon National Parks, southern Sierra Nevada, *Strix occidentalis occidentalis*

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California spotted owls (*Strix occidentalis occidentalis*) in the Sierra Nevada do not build their own nests; they rely on naturally occurring cavities, platforms from natural accumulation or constructed by birds or mammals, and rock ledges (Verner et al. 1992, Steger et al., in press). Cavity nest sites are more common (66%) in conifer vegetation types (Verner et al. 1992) whereas platform nests are more common (59%) in the oak woodlands (Steger et al., in press). In conifer forests broken tops and cavities develop in old trees, and about one-third of all nests are found in snags (Verner et al. 1992). Use of rock ledges for nesting sites is rare in the Sierra Nevada with only 1 recent report (Steger et al., in press).

Information on nest sites used by California spotted owls suggests that nests are located in a variety of vegetation types and tree species (Verner et al. 1992, LaHaye et al. 1997, Steger et al., in press). Characteristics such as high basal area of trees, dense canopy cover, and presence of large decadent trees appear to be more critical to successful nesting (Bias and Gutiérrez 1992, Verner et al. 1992) than nest type, species of nest tree, or vegetation type (LaHaye et al. 1997). However, nests studied to date have been on National Forests where nest site availability may have been influenced by historic timber harvest. Descriptions of nest sites not affected by timber harvest, such as on National Parks, may offer additional information about the habitat characteristics associated with nesting. Our paper describes the characteristics of nest trees, nest structures, associated vegetation, and physical attributes at spotted owl nest sites in the southern Sierra Nevada conifers from the Sierra National Forest and Sequoia and Kings Canyon National Parks, and compares nest site characteristics between National Forest lands and National Park lands.

STUDY AREA

Our study was conducted in the southern Sierra Nevada in the Sierra National Forest (SNF) and Sequoia and Kings Canyon National Parks (SNP), California (Fig. 1). The SNF and SNP study areas covered 526 km^2 and 259 km^2, respectively; both ranged in elevation from 1060 to 3040 m. Spotted owl nests sampled in our study were within giant sequoia (*Sequoiadendron giganteum*) and mixed-conifer vegetation, which included montane hardwood-conifer, ponderosa pine, Sierra mixed-conifer, white fir, and red fir vegetation as described in Mayer and Laudenslayer (1988).

METHODS

Nest trees were located from 1990 through 1996 using methods described by Forsman (1983). Data were collected at all known nest sites. Nest tree species and condition (live tree or snag) were recorded. The diameter of each nest tree was measured at breast height (DBH) (1.37 m) with a diameter tape. Heights of the nest tree and nest were measured with a clinometer. Nest types were described as top cavity, side cavity, or platform formed by an existing raptor nest, broken top, or mistletoe broom. Aspect; slope; position on slope; elevation; and distance to, and type of, nearest water and road was recorded at each nest site. Vegetation measurements were taken around each nest from 4, 0.028-ha strip plots, each starting 5 m from the bark of the nest tree and radiating outward 30 m in each cardinal direction. Canopy cover was measured at 5, 10, and 25 m from the nest tree along each strip plot using a spherical densiometer; means of these measurements were calculated to estimate the canopy cover for the plot. Trees were defined as live woody vegetation >2 m tall, while snags were all dead trees >13 cm DBH and >2 m tall. Trees or snags with half or more of the bole rooted inside the strip plot were identified to species; their DBH and height were measured, and they were grouped into 30-cm stem-diameter classes. Basal areas (m^2/ha), number of stems/ha, and means of heights were calculated. Volume (m^3) and tons/ha of large woody debris (logs >24 cm in diameter at the large-end) within the plot were calculated by measuring the length and diameters at each end. Live woody vegetation <2 m tall was considered to be shrub cover and grouped by conifer, hardwood, shrub (evergreen or deciduous), and fern. Ground cover was classified as rock, soil, large litter (5-24 cm in diameter), small litter (<5 cm in diameter), herb, grass, moss, and lichen. Shrub cover and ground cover were measured along 30-m line intercepts through the middle of each strip plot. Line intercept measurements were

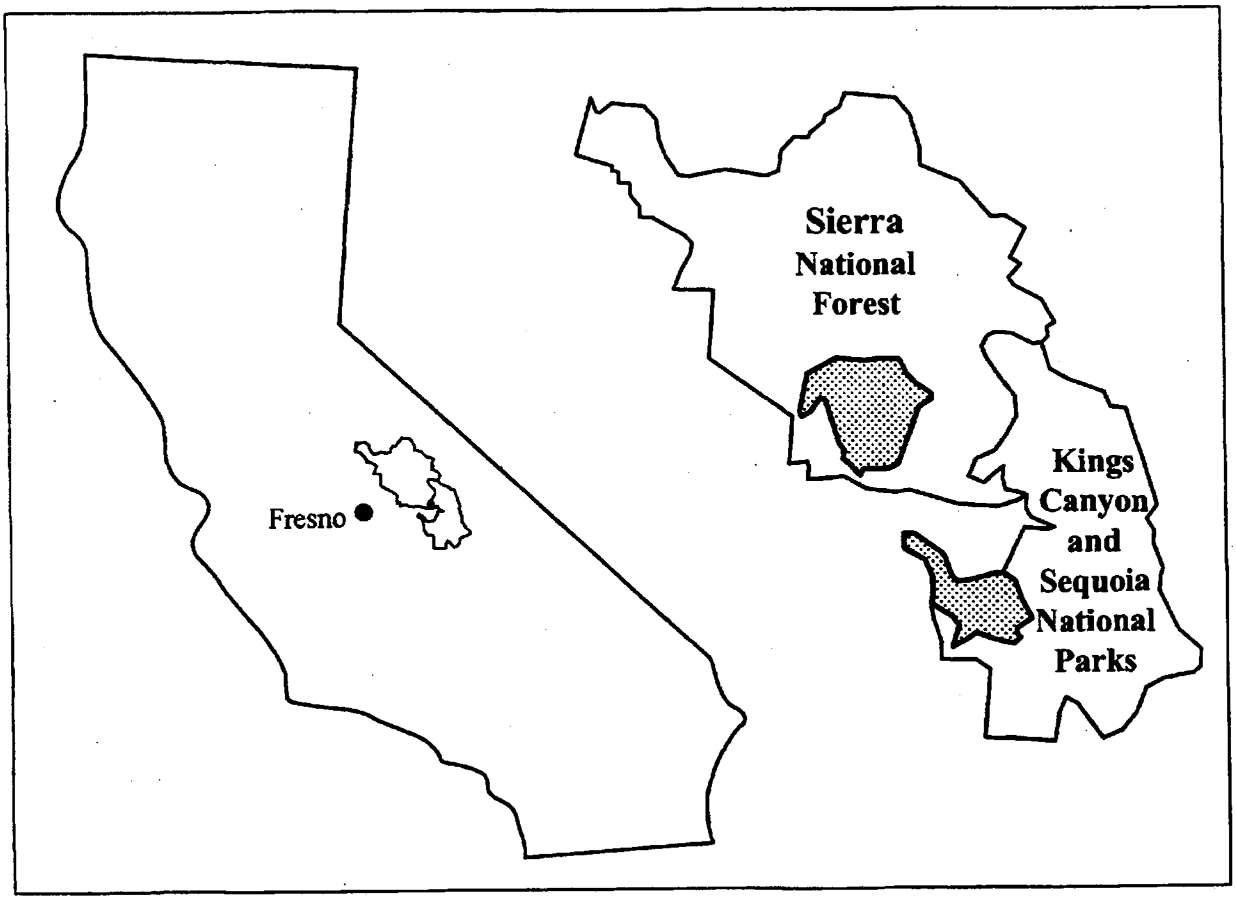

Fig. 1. Locations of study areas in Sierra National Forest (SNF) and Sequoia and Kings Canyon National Parks (SNP), California.

reported as the percent of the line covered by each of the categories.

Nest sites in giant sequoia groves from both study areas were grouped together. All other sites were considered mixed-conifer and were analyzed by study area (SNF conifer and SNP conifer). A 2-sample *t*-test was used to evaluate differences between the vegetative measurements around nest sites only on the mixed-conifer sites. All nest sites were grouped into 4 aspect categories: north (315° to 45°), east (46° to 134°), south (135° to 224°), and west (225° to 314°); slopes at nests were classified by 10% categories. Both aspect and slope at nest sites were tested (χ) against an expected slope and aspect of the landscape generated from U.S.G.S. digital elevation model of the study areas.

RESULTS

Nest Characteristics

Eighty-six nests were located, 50 in SNF and 36 in SNP. All were found in live trees (69) or snags (17): 41 in fir (*Abies concolor* and *A. magnifica*), 17 in black oak (*Quercus kelloggii*), 14 in pines (*Pinus ponderosa, P. jeffreyi, P. lambertiana*), and 14 in giant sequoia (Table 1). We identified 70 cavity nests (52 side cavities and 18 top cavities) and 9 platform nests of the 79 sites where nest type was determined (Table 1).

Height of nest trees averaged 46 m (±19 SD); giant sequoias were the tallest while black oaks were the shortest (Table 1). Nest heights averaged 26 m (±11). Nests tended to be in the upper half of the nest tree (nest heights averaged 64% of tree heights) except in giant sequoia

Table 1. Structural attributes of nests and nest trees southern Sierra Nevada, California, 1990-96.

Study area		Tree height (m)		Nest height (m)		Nest structure[a]	
Species	*n*	$\bar{x}$	SD	$\bar{x}$	SD	platform	cavities
Sierra National Forest							
True fir[b]							
Snags	8	33	9	27	11	0	8
Live trees	18	47	12	28	8	4	13
Black oak							
Snags	2	11	3	10	2	0	2
Live trees	13	26	7	13	3	0	12
Yellow pine[c]							
Snags	1	55		22		0	1
Live trees	2	35	6	15	3	1	1
Sugar pine							
Live trees	6	40	10	25	7	1	4
Sequoia and Kings Canyon National Parks							
True fir[b]							
Snags	3	48	14	37	18	0	3
Live trees	12	44	6	31	3	2	8
Black oak							
Live trees	2	15	5	8	1	1	1
Sugar pine							
Snags	3	54	5	30	1	0	3
Live trees	2	45	10	30	2	0	1
Giant sequoia							
Live trees	14	78	10	37	11	0	13

[a] Seven nest structures were not determined.

[b] Includes white fir and red fir.

[c] Includes ponderosa pine and Jeffery pine.

where nests tended to be just below the middle of the tree (49% of tree heights).

Diameter of nest trees varied from black oak with the smallest mean DBH to giant sequoia with the largest (Table 2). Diameters were similar for species between study areas except for *Pinus* spp., which were significantly ($P = 0.0001$) larger in the SNP than in SNF. Mean DBH of platform nest trees (114 cm ± 24) did not differ ($P = 0.84$) from the mean DBH of trees that supported cavity nests (116 cm ± 35) excluding nests in giant sequoias.

Site Characteristics

Owl nest sites ranged from 1061 to 2414 m in elevation. Nest sites were found on slopes ranging from 2 to 68% (x = 29 ±16%). Slopes at nest sites in the SNF differed significantly ($\chi^2 = 43.4$, 6 df, $P < 0.005$) from those in the SNP. Also, slopes derived from the landscape model differed significantly from the observed slopes at nests within each study area (SNF $\chi^2 = 18.9$, 9 df, $P < 0.025$ and SNP $\chi^2 = 44.3$, 9 df, $P < 0.005$). The SNF had the greatest number of nests in the 1-10% slope class while the SNP had the more in the 11-20% class (Fig. 2).

Nest sites were distributed topographically from near the ridge tops to the bottom of drainages in both study areas (Table 3). No significant difference was found between SNF landscape aspects and its corresponding nest sites ($\chi^2 = 4.1$, 3 df, $P > 0.1$). Aspects at nest sites did differ significantly between study areas ($\chi^2 = 9.8$, 3 df, $P < 0.05$), and the landscape aspects in SNP differed ($\chi^2 = 13.1$, 3 df, $P < 0.005$) from SNP nest sites. Owls nested on east (39%) and west (36%) aspects in SNP, whereas more nests were on south (32%) and west (40%) aspects on SNF (Fig. 3).

Generally, nest sites were >100 m from open water and from the nearest road in both study areas, although 3 nests were located <10 m of improved roads (Table 3). On the SNF, 49 of the 50 nest sites had evidence of past logging (cut boles, stumps, limb debris) whereas only 2 of the 36 sites on the SNP had logging debris.

Canopy cover at all nest sites averaged 90% (± 10%, range = 37-99%) and did not differ between study areas ($t = 1.63$, 83 df, $P = 0.11$; Table 3). Nest sites found in red firs had the lowest average canopy cover at 78% (± 5.3%).

Of the 86 nest sites measured, 66 (77%) were in mixed conifer vegetation types and 20 (23%) were in sequoia stands (19 on SNP and 1 on SNF). Structural attributes of the vegetation around nests varied among sites and between study areas (Tables 4 and 5). The nest sites we measured had multiple layers of vegetation canopy. Live trees at nest sites averaged 874 (± 656) stems/ha. The SNF conifer had significantly ($P < 0.01$) greater numbers of stems and basal area within the 31 to 60 cm diameter class than SNP conifer. Overall, we found that most nest sites had numerous small conifer stems (<30 cm in DBH), although the SNF conifer sites had more stems in the size classes <30 to 60 cm and fewer large stems (61 to >91 cm) than SNP conifer sites (Table 4).

Table 2. Diameter of nest trees of California spotted owls on the Sierra National Forest and Sequoia and Kings Canyon National Parks study areas, southern Sierra Nevada, California, 1990-96.

	All nest trees			Live trees			Snags		
Study area Species	*n*	cm	SD	*n*	cm	SD	*n*	cm	SD
Sierra National Forest									
True fir	26	127	20	18	129	20	8	121	34
Black oak	15	88	23	13	93	21	2	58	19
Pines	9	95 [a]	21	8	92	20	1	123	
Sequoia and Kings Canyon National Parks									
True fir	15	131	20	12	131	19	3	131	25
Black oak	2	63	32	2	63	32	0	—	—
Pines	5	172 [a]	20	2	163	17	3	177	22
Giant sequoia	14	463	145	14	463	145	0	—	—

[a] Significant difference in diameter between study areas ($t = 6.69$ $P = 0.0001$).

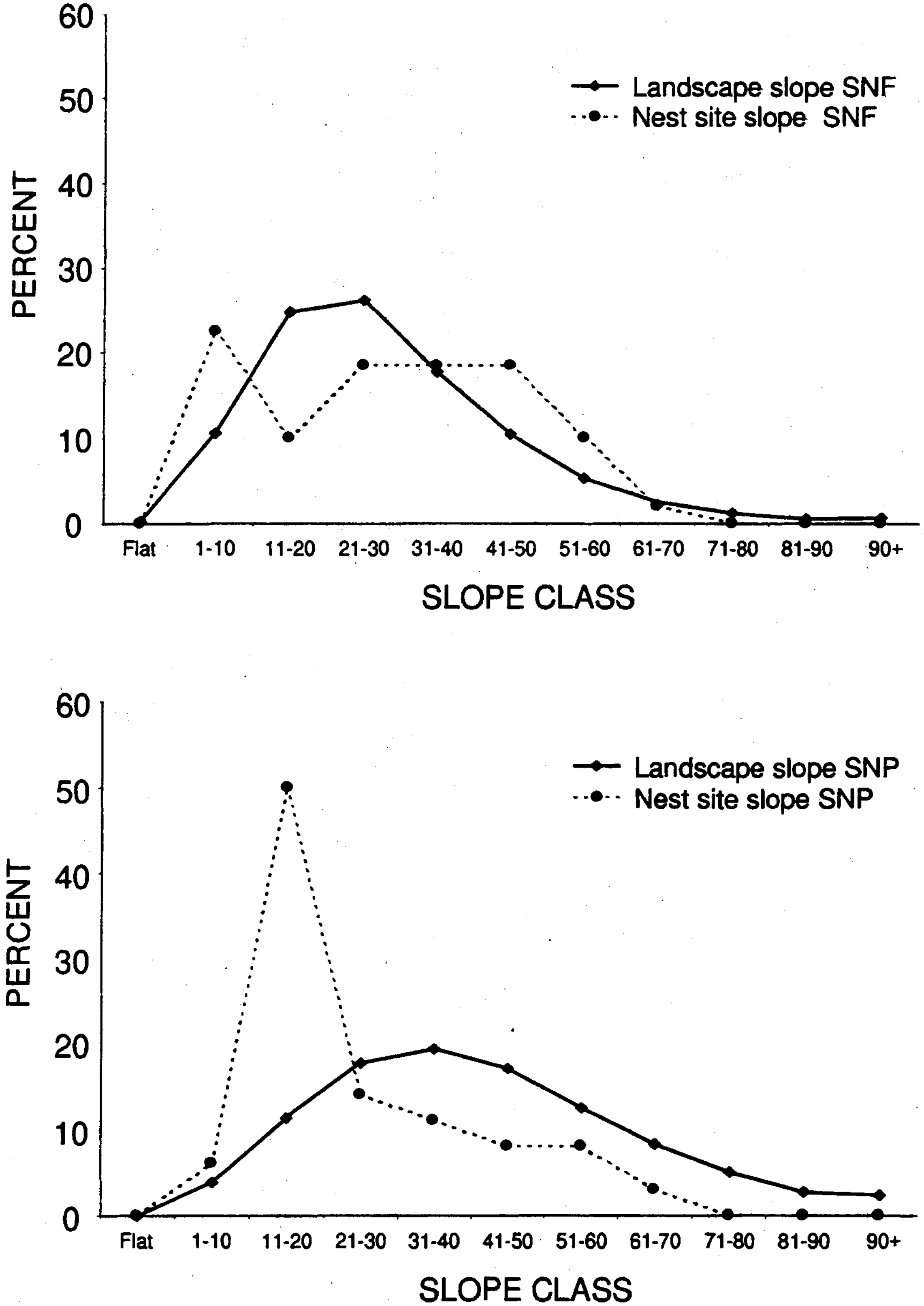

Fig. 2. Proportion of 86 California spotted owl nest sites and landscape slopes derived from U.S.G.S. digital elevation model by 10% slope classes on the Sierra National Forest (SNF, top) and Sequoia and Kings Canyon National Parks (SNP, bottom), southern Sierra Nevada, California.

We also found that <5% of the trees from around the nest sites had diameters larger than the mean nest tree diameter except in the 20 sequoia sites. In the sequoia sites about 10% of the sampled trees were larger than the nest trees.

Total basal area of all live trees did not differ significantly (t =1.29, 64 df, P = 0.20) between the SNF conifer (75.9 m^2/ha) or SNP conifer (67.8 m^2/ha) (Table 4). The giant sequoia sites had the greatest total basal area (104 m^2/ha) mainly from large diameter (>91 cm) trees. Conifers with diameters ranging from <30 to 60 cm accounted for 50% of the basal area in SNF conifer, 38% in SNP conifer, and 21% in giant sequoia sites.

Plant species >2 m tall, other than conifers, accounted for approximately 21% of the live stems on both study areas, and 6% of the total basal area (Table 4). The majority of these other species were of small diameter (<30 cm in DBH), and stem density varied greatly between plots. A significant difference (P = 0.05) in the number of small diameter trees (<30 cm) was detected between the SNF conifer and SNP conifer sites (Table 4). Overall, the SNF conifer had fewer small nonconifer stems (<30 cm) but more large nonconifer stems than the SNP conifer and giant sequoia sites.

Nest sites averaged 60 (±41.3) snags/ha with about half (33 ±28.0) being small (<30 cm in DBH) conifers (Table 5). The SNF conifer sites had significantly (P = 0.04) more small snags (<30 cm in DBH), while the SNP conifer sites had significantly (P = 0.006) more large snags (>91 cm in DBH). Basal area of snags was significantly (P = 0.02) greater in the SNP conifer than in the SNF conifer mainly as a result of the larger diam-

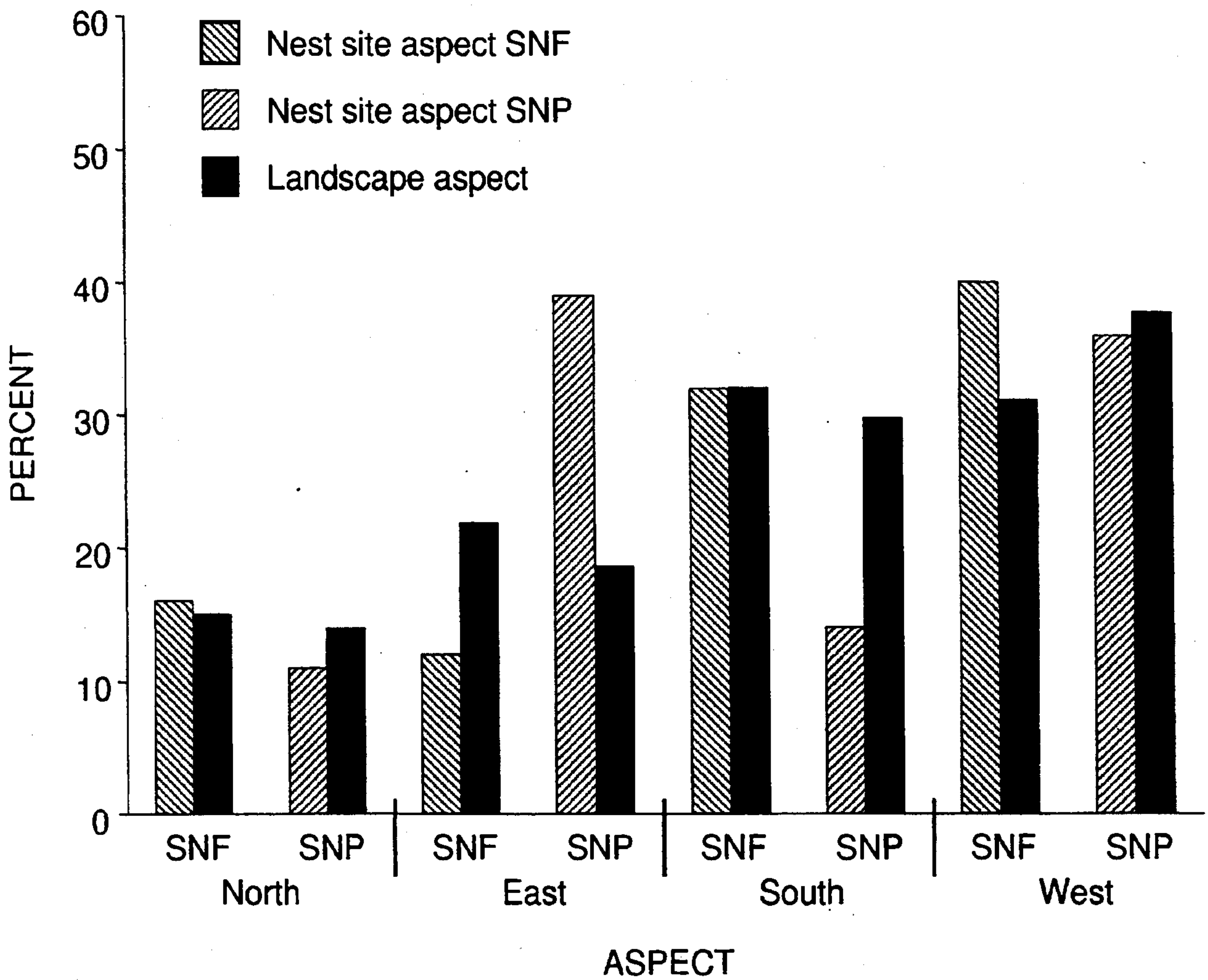

Fig. 3. Proportion of 86 California spotted owl nest sites and landscape aspects derived from U.S.G.S. digital elevation model in 4 aspect classes on the Sierra National Forest (SNF) and Sequoia and Kings Canyon National Parks (SNP), southern Sierra Nevada, California.

eter (> 91 cm) snags. Downed woody debris did not differ significantly ($P < 0.06$) between SNF conifer and SNP conifer (Table 5).

The shrub and ground cover at owl nest sites was similar in both study with only 3 of the 13 attributes measured differing significantly between study areas (Table 5). Generally, we found about 10-17% cover of small shrubs and ferns. Ferns differed significantly ($P < 0.0001$) between SNF conifer and SNP conifer sites as did small litter ($P = 0.05$) and herbaceous vegetation ($P = 0.01$) (Table 5).

DISCUSSION

In our study of nest sites we found only slight differences between the SNF where timber has been harvested for the last 100 years, and the SNP, which has had little or no harvesting of timber. Both study areas had similar basal areas of live trees and dense canopy cover at nest sites which has been identified as being critical to successful nesting (Bias and Gutiérrez 1992, Verner et al. 1992). In the SNF, 98% of the nest sites had logging activity which may be the cause of the increased numbers and basal area of small diameter conifers on that study area. Yet, enough large-diameter trees, mainly firs and oaks, were present to support a high rate of cavity nesting.

Table 3. Physiographic attributes of California spotted owl nest sites on the Sierra National Forest (SNF) and Sequoia and Kings Canyon National Parks (SNP) study areas, southern Sierra Nevada, California, 1990-96.

Physiographic attribute	SNF	SNP
Mean elevation (m)	1748	1892
Mean slope (%)	30	28
Canopy cover (%)	91	89
No. of nests by:		
topographical position		
upper 1/3 of slope	13	15
middle 1/3 of slope	18	8
lower 1/3 of slope	19	13
distance to water (m)		
<10	3	1
10-30	5	4
30-100	12	9
>100	30	22
distance to road (m)		
<10	2	1
10-30	4	2
30-100	9	4
>100	35	29

The selection of cavities for nesting sites may depend on cavity availability, which typically become more frequent as trees age and become decadent. If cavities are associated with larger, older trees, then platform nests might occur in smaller diameter trees were suitable cavity nests may not be as available. High rates of platform nest use have been reported for the California spotted owl (Steger et al., in press), Mexican spotted owl (*S. o. lucida*) (Seamans and Gutiérrez 1995), and northern spotted owl (*S. o. caurina*) (Buchanan et al. 1993) in hardwood and mixed-conifer forests. In these studies the average nest tree diameters were smaller than those reported for nest trees in conifer forests where cavity nesting is more common. In our study areas, both cavity and platform nest trees had large diameters.

One area of concern that needs to be monitored is the difference in the diameter of pines that were used for nesting in SNF compared to the diameter of pines used in SNP. We contend that the reduced diameter of pines on the SNF is a result of selective cutting of that species. McKelvey and Johnson (1992) described a pattern of partial cutting that typically removed only the largest most merchantable trees in the National Forests prior to the 1980s. The pines, mainly sugar pine and ponderosa pine, were and still are economically valuable and are often selected for harvest in the SNF study area. As these commercially desirable, large-diameter trees become less available there may be a tendency to start harvesting the large firs that were left from the previous selective cuttings. This may reduce the number of potential cavity nest sites and impact reproduction on the SNF study area. Currently, reproduction on both study areas was found to be similar with SNF producing 0.65 young per pair checked for reproduction and the SNP producing 0.62 (Steger, unpubl. data).

Gutiérrez et al. (1992) suggested, with caution, that significantly more nests located in the Sierra Nevada were on north aspects and fewer on southwest. Our data gave mixed results, with greater use of east aspects in SNP and north and west aspects in SNF. Nesting on the lower third of the slope and use of primarily northern aspects have been reported for all spotted owl subspecies, although this type of activity is not consistent across all studies (Blakesley et al. 1992, Buchanan et al. 1993, Gutiérrez et al. 1992, LaHaye 1988, Seamans and Gutiérrez 1995, Steger et al., in press). Use of northern aspects and drainages may play a role in thermoregulation (Barrows and Barrows 1978) or may be selection for densely canopied sites such as in the foothill riparian and oak woodlands of the southern Sierra Nevada (Steger et al., in press). Use of steep slopes (Forsman and Giese 1997) and the lower third of drainage bottoms (Blakesley et al. 1992) may be a result of past logging practices, where moderate slopes and ridge tops were more accessible and harvestable thus reducing large trees and therefore potential nesting sites. Our findings of heavier use of low to moderate slopes may be the result of large numbers of suitable nest trees through the landscape as in SNP where timber harvest was minimal. Or it may be the harvesting techniques in the SNF study areas where large less merchantable trees (true fir and black oak) were left scattered over the landscape providing suitable nest sites.

The selection of white fir as nest trees has been documented by Gutiérrez et al. (1992) and LaHaye et al. (1997); they found fir had the highest frequency of use followed by pines, oaks, and *Pseudotsuga* spp. For its limited availability, we found that giant sequoia was the most frequently used species. Firs, including white fir and red fir, were frequently used in both study areas followed by black oak and then pines on SNF and pines then black oak on SNP.

In the Sierra Nevada about 30% of the nests occured in snags (Verner et al. 1992). Use of snags in our study was slightly lower at 20%. With the concern for forest health, fire—mainly prescribed fire—is being reintroduced into the Sierra Nevada. The effects on the numbers of snags and their suitability as nesting structures is unknown, but burning can change snag structure and population (W. F. Laudenslayer, Jr. pers. comm.).

Another aspect of forest health is the removal or reduction of species which are considered competitors with pines, such as white fir and black oak. In the SNF, 82% of the nest trees were large-diameter firs and oaks at elevations from 1060 to 2040 m, the zone of selective cutting of pines. As managers reduce these competing species they need to recognize the potential for nesting sites of spotted owls and retain those trees that show decadence, cavities, hollow trunks, and hollow limbs. Future monitoring will help determine whether management aimed at restoring health and biological diversity to the forest ecosystem affects spotted owl nest-site selection and if changes in nest selection result in changes in reproductive performance.

Table 4. Live tree characteristics at California spotted owl nest sites on the Sierra National Forest (SNF) conifer sites (n = 49), Sequoia and Kings Canyon National Parks (SNP) conifer sites (n = 17), and sites on both study areas within giant sequoia forests (Sequoia) (n = 20) in the southern Sierra Nevada, California, 1990-96.

	SNF conifer		SNP conifer		Sequoia sites		*t*-test[a]	*P*
Attributes DBH/size class	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Live trees (basal area in m^2 per ha)								
Conifers <30 cm	20.0	14.0	13.0	8.0	11.0	10.0	1.69	0.09
31-60 cm	15.0	7.0	11.0	4.0	10.0	8.0	2.35	0.02
61-90 cm	14.0	9.0	16.0	10.0	14.0	6.0	0.72	0.47
>91 cm	21.0	18.0	23.0	16.0	67.0	87.0	0.41	0.68
Other <30 cm	1.9	3.0	2.9	4.0	1.6	4.0	1.10	0.27
31->91 cm	3.7	6.4	1.1	2.9	0.0	0.0	1.57	0.12
Total basal area	75.9	23.7	67.8	17.5	104.4	83.8	1.29	0.20
Live trees (stems per acre)								
Conifers <30 cm	615.0	462.0	489.0	342.0	358.0	361.0	1.03	0.31
31-60 cm	102.0	46.0	72.0	7.0	68.0	44.0	2.52	0.01
61-90 cm	34.0	34.0	38.0	25.0	32.0	14.0	0.63	0.53
>91 cm	19.0	16.0	22.0	13.0	26.0	19.0	0.52	0.60
Other <30 cm	90.0	192.0	226.0	336.0	148.0	309.0	2.04	0.05
31->91 cm	16.0	28.1	9.0	22.5	0.0	0.0	0.91	0.37
Total live trees	876	515	855	528	627	610	0.14	0.89
Height (m)								
Live trees <30 cm	12.0	3.0	11.0	2.0	14.0	9.0	0.46	0.64
31-60 cm	25.0	5.0	24.0	4.0	27.0	7.0	1.04	0.30
61-90 cm	35.0	9.0	37.0	9.0	39.0	12.0	1.47	0.15
>91 cm	39.0	19.0	45.0	13.0	53.0	16.0	1.07	0.29

[a] Two sample *t*-test between mixed-conifer sites on the SNF and SNP.

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Table 5. Snags, down logs, shrubs, and ground cover characteristics of California spotted owl nest sites on the SNF conifer (n = 49), SNP conifer (n = 17), and sites with Sequoia forests (n = 20) in the southern Sierra Nevada, California, 1990-96.

		SNF conifer		SNP conifer		Sequoia sites		*t*-test[a]	*P*
Attributes	DBH/size class	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Snags (basal area in m^2 per ha)									
Conifers	13-30 cm	1.4	1.4	0.7	0.7	0.8	0.6	2.02	0.05
	31-60 cm	2.0	2.8	1.3	2.2	2.3	2.8	0.88	0.38
	61-90 cm	1.4	2.4	2.8	3.6	3.1	3.5	1.77	0.08
	>91 cm	3.6	6.7	9.8	8.9	13.7	24.4	3.04	0.003
Other species (All)		0.4	1.1	0.3	0.8	0.1	0.1	0.37	0.71
Total Snag BA		8.7	9.1	14.9	10.4	19.9	25.5	2.31	0.02
Snags (stems per ha)									
Conifers	13-30 cm	47	48	23	21	28	20	2.08	0.04
	31-60 cm	14	18	8	13	15	17	1.29	0.20
	61-90 cm	3	6	6	8	7	8	1.76	0.08
	>91 cm	3	6	9	8	8	8	2.84	0.006
Other species (All)		6	13	3	5	1	2	0.81	0.42
Total Snags		74	60	49	29	58	35	1.65	0.10
Woody debris									
Logs >24 cm (tons/ha)[b]		72.9	55.0	105.3	66.1	168.0	190.2	1.88	0.06
Logs >24 cm (m^3/ha)		161.0	121.0	232.0	146.0	370.0	419.0	1.88	0.06
Shrub cover (%)									
Conifer		1.8	2.7	1.3	2.0	2.7	5.4	0.77	0.44
Hardwood		0.5	1.4	1.1	1.9	1.3	3.8	1.44	0.16
Evergreen		5.5	9.8	6.4	13.8	5.7	10.9	0.27	0.79
Deciduous		2.3	3.4	1.9	4.0	4.2	5.9	0.40	0.69
Fern		0.5	1.1	6.2	8.4	1.8	2.7	4.68	0.0001
Total Shrub cover		10.6	10.6	16.8	14.1	13.1	12.5	1.91	0.06
Ground cover (%)									
Rock		2.5	0.6	1.2	0.5	1.6	2.0	1.30	0.20
soil		3.2	4.4	3.8	6.6	0.7	0.9	0.40	0.69
Large litter		4.4	3.7	6.0	4.1	6.4	3.7	1.43	0.16
Small litter		86.2	9.0	80.8	10.8	83.5	6.4	2.03	0.05
Herbaceous		1.3	2.4	4.5	7.4	4.6	4.3	2.62	0.01
Grass		0.4	0.7	1.4	3.5	0.3	0.2	1.86	0.07
Moss		0.2	0.6	0.5	0.9	0.2	0.3	1.52	0.13
Lichen		0.2	1.0	0.1	0.2	0.1	0.1	0.38	0.71

[a] Two sample t-test between mixed-conifer sites on the SNF and SNP.

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

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