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NESTS OF NORTHERN SPOTTED OWLS ON THE OLYMPIC PENINSULA, WASHINGTON

ERIC D. FORSMAN[1] AND ALAN R. GIESE[1]

ABSTRACT.—We located 155 nests in 82 territories occupied by Northern Spotted Owls (*Strix occidentalis caurina*) on the Olympic Peninsula, Washington. All nests were in trees. Of 116 nests that were measured, 105 were in cavities and 11 were in external platforms on tree limbs. Cavity nests were typically in large holes in the side of the trunk or in the broken top of the trunk. Aspect of cavity entrances was non-random, with the majority of cavities facing east-north-east. Location of nest trees did not differ from expected values for slope aspect or position on slope. Proportions of nest sites in different percent slope categories differed from availability, with more nests than expected in the higher percent slope categories. Nests usually were in stands with high overall canopy closure (≥ 70%), but canopy closure in the immediate vicinity of the nest varied from 35–90%. Most nests (87%) were in multilayered stands dominated by large trees. Nests in younger stands were typically in stands where remnant old trees were present. Owls changed nests between successive nesting events in 80% of all cases. Changes in pair members on a territory did not influence the frequency with which pairs switched to a new nest tree in the next nesting year. Based on observed rates of attrition, the expected life span of nests was 120 years.
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Spotted Owls (*Strix occidentalis*) use a variety of structures for nests, including cavities, platforms constructed by other birds or mammals, platforms that are the result of natural accumulations of debris, and ledges on cliffs or cave walls (Bent 1938, Forsman et al. 1984, LaHaye 1988, Buchanan et al. 1993). In most regions, nesting is limited primarily to trees (Forsman et al. 1984, LaHaye 1988, Buchanan et al. 1993, Folliard 1993). Nesting on ledges on cliffs or cave walls is largely restricted to rocky canyons in the southwestern United States and Mexico (Dickey 1914, Ligon 1926, Bent 1938, Ganey 1988). However, two nests on cliffs have been observed in western Oregon (M. Brown pers. comm., J. Niles pers. comm). Although there have been no studies in which use versus availability of different nest types have been tested, it appears that the types of nests used are influenced by availability and possibly regional differences in climatic conditions.

With the exception of reports by Buchanan (1991) and Buchanan et al. (1993, 1995), relatively little information is available on characteristics of nests used by Northern Spotted Owls (*S. o. caurina*) in Washington. During a long-term study of demographic characteristics of Northern Spotted Owls on the Olympic Peninsula in western Washington (1987–

[1] USDA Forest Service, Pacific Northwest Research Laboratory, 3200 SW Jefferson Way, Corvallis, Oregon 97331, and Dept. of Fisheries and Wildlife, Oregon State Univ., Corvallis, Oregon 97331.

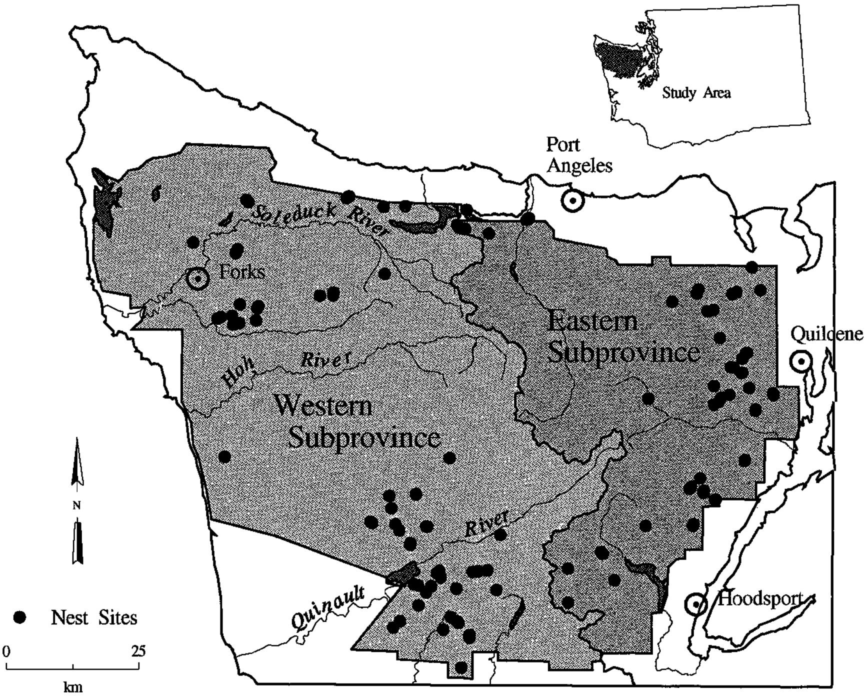

FIG. 1. Location of 116 nest trees used by Northern Spotted Owls on the Olympic Peninsula study area in northwestern Washington. In some cases a single dot may represent more than one nest because nests were very close together. We subdivided the area into western and eastern subprovinces based on differences in precipitation and vegetation.

1994), we located 155 nest trees, some of which were used in multiple years. Herein, we describe characteristics of a sample of those nests, including rates of nest attrition and frequency of reuse of nests.

STUDY AREA AND METHODS

The study area included the entire Olympic Peninsula (Fig. 1). Most field work occurred on lands administered by the USDA Forest Service, but we also monitored some pairs of owls within the Olympic National Park and on lands administered by the Washington Department of Natural Resources. The Olympic Peninsula is a mountainous region characterized by a wet, maritime climate and dense coniferous forests. Mean annual precipitation is highly variable, ranging from 115 cm at Quilcene on the east side of the peninsula (USDA Forest Service records for 1985–1995) to 365 cm on the west side of the peninsula (U.S. National Park Service records for 1987–1992).

Forests on the peninsula are generally dominated by mixtures of western hemlock, (*Tsuga heterophyla*), western redcedar (*Thuja plicata*), sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menziesii*) and Pacific silver fir (*Abies amabilis*). Western hemlock, western redcedar, and Sitka spruce predominate in more mesic areas, and Douglas-fir predominates on drier sites. Pacific silver fir occurs at a broad range of elevations but becomes increasingly dominant at higher elevations.

History of nest use was determined by monitoring the same owl territories each year. Pairs were checked several times each year to determine their nesting status and to locate nest trees. Owls were marked with unique color bands, which made it possible to determine movements between alternate nests and to determine when pair members were replaced by new individuals. Nests were located by observing owls as they carried prey into cavities or platforms (Forsman 1983).

The 155 nests located included 132 on the Olympic National Forest, 13 in the Olympic National Park, four on lands administered by the Washington Department of Natural Resources, five on private lands, and one on the Quinault Indian Reservation. We measured 116 nest trees in 70 territories. The number of nest trees measured per territory was one (33 territories), two (28 territories), or three (9 territories). We climbed 86 nest trees in order to measure dimensions of nest cavities or platforms and measured 30 from the ground, with no nest dimensions taken. Selection of nests for measurement was not random. We simply measured as many nests as we could, incidental to the other objectives of our study. To assess whether types of nests used by spotted owls differed between the wet coastal region of the peninsula and the comparatively drier east slope of the Olympic Mountains, we stratified the study area for some analyses (Fig. 1).

We used a metric tape or clinometer to measure vertical distances. Tree diameter at breast height (DBH) was measured 1.4 m above ground, except that trees with swollen bases were measured immediately above the swelling. Tree diameter at nest height (DNH) was measured at the level of the nest. If the tree had secondary tops, the number of tops was recorded. Secondary tops were limbs that grew upward and formed a new top after the original top of the tree broke off or died. Trees were classified as alive if they had any live limbs, regardless of whether the nest was in a live portion of the tree or not.

Nest types were classified as side cavities, top cavities or external platforms. A side cavity was a hole in the side of a tree trunk. A top cavity was a hole or depression in the broken top of a tree bole that was accessed through the top of the bole. External platform nests were accumulations of sticks or other debris located on limbs outside a tree bole.

Nest entrance width and height were defined as the horizontal and vertical dimensions of the entrance in centimeters. These parameters were measured only for nests with obvious horizontal and vertical entrance limits. Such measures were not applicable to external nest platforms or to cavity nests with large, irregular shaped entrances. Cavity depth was the vertical distance from the cavity entrance to the cavity floor. Platform depth applied only to external platform nests and was the vertical distance from the bottom of the nest structure to the top edge of the structure. Mean diameter of each cavity or external platform was estimated by taking two measurements at right angles to each other across the cavity or platform and dividing the sum by two.

Percent cover above the nest was visually estimated as overhead cover from the perspective of an owl in the nest, including contributions from cavity structure and overhanging vegetation. All estimates of percent cover above the nest were made by the same observer, and were thus not subject to among-observer variation. Entrance aspect was an azimuth from the center of the tree through the center of the cavity opening or across the center of the nest platform (for external nests).

Each nest stand was assigned to one or more structural categories depending on the size distribution of the trees. Categorizations of nest stand structure were based on visual inspection rather than on exhaustive measurements. Canopy closure within a 30 m radius of the nest tree was estimated visually. Elevations were recorded using altimeters or USGS maps. Other variables recorded were slope azimuth, slope gradient (in percent), and position of nests relative to topographic position on slope (lower third, middle third, upper third). We used χ^2 tests to determine if slope aspect, slope percent, or topographic position of nests differed from what was available (Marcum and Loftsgaarden 1980). Expected values for categories of slope aspect, slope percent, and topographic position were determined from a random sample of 200 30-m^2 grid cells on a digital elevation map of the Olympic National Forest. Aspects were grouped into eight 45° classes, and slopes were grouped into seven 15% classes. The Rayleigh test (Batschelet 1981) was used to test whether azimuths of nest entrances were randomly distributed.

The annual survival rate of nest trees (ϕ) was estimated by calculating the average proportion of known nest trees that survived each year. The estimated mean life expectancy of nest trees from the time they were first located was calculated using the formula $-1/\ln\phi$ (Brownie et al. 1978:204).

RESULTS

We found 155 nests in 82 different owl territories, including 24 territories where pairs nested only once, 19 where pairs nested in two different years, 23 where pairs nested in three years, 11 where pairs nested in four years, and four territories where pairs nested in five years, and one territory where a pair nested in six years. Two pairs nested twice in the same year after initial nesting attempts failed (Forsman et al. 1995). The total number of different nest trees per territory ranged from 1–4. Thirty-three territories had one nest, 29 had two nests, 16 had three nests, and four had four nests. All nests were in trees.

Nest characteristics.—We measured 116 nests in 70 different territories, including 65 nests in 40 territories in the western subprovince of the peninsula and 51 nests in 30 territories in the eastern subprovince (Fig. 1). Of the nests that were measured, 62 (53.4%) were in side cavities, 43 (37.1%) were in top cavities, and 11 (9.5%) were in external platforms. Frequency of use of different nest types differed between the eastern and western subprovinces of the peninsula (χ^2 = 19.4, 2 df, $P \leq 0.001$), with nests in side cavities predominating in the western subprovince (71%), and nests in top cavities predominating in the eastern subprovince (51%). Percent cover directly above the nest averaged slightly higher in the western subprovince than in the eastern subprovince (Table 1) ($t = -2.31$, 92 df, $P = 0.015$).

Nest trees that were measured included 40 western hemlock, 36 Douglas fir, 33 western red cedar, two Pacific silver fir, two grand fir (*Abies grandis*), one Sitka spruce, one western white pine (*Pinus monticola*), and one unknown species. Ninety nests (78%) were in live trees and 26 (22%) were in dead trees. Frequency of occurrence in different tree species did not differ between nests in live trees, and nests in dead trees (χ^2 = 1.72, 3 df, $P = 0.633$).

Of 90 nests in live trees, 67 (74%) were located above the lowest live limb (i.e., in the crown of the tree), and 23 (26%) were located below

TABLE 1

MEASUREMENTS OF NESTS AND NEST TREES USED BY NORTHERN SPOTTED OWLS ON THE OLYMPIC PENINSULA, WASHINGTON, SUBDIVIDED BY PHYSIOGRAPHIC SUBREGION

	E. subregion			W. subregion			Entire sample		
Variable	N	$\bar{x}$	SE	N	$\bar{x}$	SE	N	$\bar{x}$	SE
Nest height (m)	43	23.2	1.72	63	23.5	1.12	106	23.2	0.96
Tree height (m)	44	33.1	2.01	62	46.0	1.29	106	40.6	1.28
Bole height (m)[a]	26	19.6	1.59	54	20.1	0.96	80	19.9	0.82
DBH (cm)[b]	46	107.2	6.31	64	157.7	8.20	110	136.6	5.93
DNH (cm)[b]	30	69.3	4.52	57	105.6	6.00	87	93.1	4.61
No. secondary tops[c]	42	1.0	0.24	62	1.4	0.20	104	1.2	0.15
Avg. nest diameter (cm)	31	43.9	2.40	55	46.3	1.16	86	45.4	1.14
Percent cover above nest	37	82.2	3.00	57	90.0	1.89	94	86.9	1.68
Cavity depth (cm)[d]	24	28.0	8.73	52	10.8	2.16	76	16.2	3.23
Platform depth (cm)[e]	7	21.0	2.05	2	23.5	3.50	9	21.6	1.71
Entrance width (cm)[f]	11	24.0	3.16	40	25.2	1.74	51	24.9	1.51
Entrance height (cm)[f]	7	95.7	51.89	41	88.5	10.29	48	89.5	11.28

[a] Height to first live limb.
[b] DBH and DHN indicate diameter of tree at breast height and nest height, respectively.
[c] Number of live tree tops developing subsequent to the development of the original tree top.
[d] Distance from cavity entrance to floor of cavity.
[e] Distance from top to bottom of external platform type nests.
[f] Entrance dimensions apply to nests in cavities only.

the crown. When both live and dead trees were included, 67 of 116 nests (58%) were in the crown of a live tree. Mean DBH of nest trees was 136.6 cm (SE = 5.93, range = 30–379 cm). On average, total height, DBH and DNH of nest trees were larger in the western subprovince than in the eastern subprovince ($t_{HT} = -5.39$, $P < 0.001$ $t_{DBH} = -4.88$, $P < 0.001$, $t_{DNH} = -4.84$, $P < 0.001$) (Table 1).

When only nests in live trees were included, the majority (83%) of nests in top cavities were in trees with secondary tops. Only 53% of nests in side cavities and 50% of nests in external platforms occurred in trees with secondary tops. When both live and dead trees were included, the percent of nests in trees with secondary tops was 65% for top cavity nests, 44% for side cavity nests, and 50% for external platforms ($\chi^2 = 3.93$, 2 df, $P = 0.140$).

Mean entrance dimensions of cavities were 24.9 cm (width) and 89.6 cm (height) (Table 1). However, entrance dimensions were recorded only for cavities that had well-defined entrances. As a result, our mean entrance dimensions did not represent many cavities that were accessed through large, irregular shaped holes that were formed when tops or large limbs broke off of trees. Nests of the latter type were typically entered through a long crack of variable width in the side of the tree or through the jagged

TABLE 2

MEASUREMENTS OF SPOTTED OWL NESTS IN CAVITIES AND EXTERNAL PLATFORMS ON THE OLYMPIC PENINSULA, WASHINGTON

Variable	Cavity nests			Platform nests[a]			Comparison of means[b]	
	N	$\bar{x}$	SE	N	$\bar{x}$	SE	t	P
Nest height (m)	95	23.3	1.02	11	24.1	3.00	−0.27	0.791
Tree height (m)	95	40.7	1.36	11	39.8	3.99	0.21	0.837
Bole height (m)[c]	70	19.9	0.87	10	20.2	2.66	−0.13	0.896
DBH (cm)[d]	99	141.8	6.15	11	88.7	15.74	2.77	0.007
DNH (cm)[d]	79	97.1	4.74	8	53.4	10.73	2.86	0.005
Avg. nest diamter (cm)	76	45.3	1.15	10	48.0	4.59	−0.76	0.449
Percent cover above nest	83	87.0	1.79	11	86.2	5.02	0.12	0.906
No. secondary tops	94	1.2	0.15	10	1.7	0.75	−0.98	0.332

[a] Platforms on tree limbs.
[b] 2-tailed *t*-test. Data on percent cover were log-transformed for *t*-tests.
[c] Height to first live limb.
[d] DBH and DHN indicate diameter of tree at breast height and nest height, respectively.

top of a tree with a broken bole. Entrance dimensions of cavities did not differ between the eastern and western subprovinces ($t_{width} = -0.32$, 49 df, $P = 0.748$; $t_{ht} = 0.14$, 48 df, $P = 0.896$). The distribution of nest cavity entrance azimuths was non-random, with the majority of nests facing east-north-east (mean angle = 72°, SE = 7.5, $r = 0.2021$, $P = 0.038$, N = 94).

Height of the cavity entrance above the cavity floor averaged 16.2 cm (SE = 3.23, median = 4.5 cm) and ranged from 0-66 cm with a single exceptional value of 203 cm (Table 1). In the latter case, the owls accessed the bottom of the cavity by hopping down a ladder-like series of old branch cores that projected into the hollow interior of the tree.

On average, cavity nests occurred in larger trees than external platform nests (Table 2). Variables that did not differ between cavity nests and external platform nests were nest height, total tree height, bole height, percent cover directly above the nest, mean number of secondary tops, and average diameter of nests (Table 2).

The nest substrate in cavity nests typically consisted of a decomposing mixture of wood, bark, conifer needles, twigs, and insect tillings. Small amounts of moss or lichens were sometimes mixed with the debris. In all cases, it appeared that substrate accumulations were the result of decomposition of the interior of the tree and/or debris falling into the cavity. Nests typically contained remains of prey and pellets forming a layer up to 7 cm deep. Eggshell fragments were rarely found in nests except in conjunction with nest failures.

Of 11 nests classified as external platforms, five were old stick nests that appeared to have been built by Common Ravens (*Corvus corax*) or Northern Goshawks (*Accipiter gentilis*), three were on debris platforms on large clumps of deformed limbs caused by dwarf mistletoe (*Arceuthobium* spp.) infections, and three were collections of debris that accumulated where a tree split into multiple tops. The nest substrate in external platform nests was typically a decomposing mixture of tree bark, conifer needles, twigs, lichens, and moss.

Site characteristics.—Of 116 nests measured, 82 (71%) were in forests characterized by multi-layered canopies where the dominant overstory trees were ≥ 100 cm DBH. Twenty-two nests (19%) were in multi-layered forests dominated by 50–99 cm DBH trees that included scattered individuals or patches of large (≥ 100 cm DBH) old trees. Three nests (2%) were in relatively even-aged forests of 50–99 cm DBH trees, and nine nests (8%) were in forests that included a mosaic of small trees (DBH = 13–49 cm) and larger trees (DBH ≥ 50 cm).

Estimated mean canopy closure in the vicinity of the nest tree ranged from 30–95% ($\bar{x}$ = 70%, SE = 1.44, N = 104) and did not differ significantly (t = 1.50, 102 df, P = 0.136) between the eastern subprovince ($\bar{x}$ = 72.6, SE = 2.43, N = 41) and western subprovince ($\bar{x}$ = 68.2, SE = 1.75, N = 63). Of 13 nest sites with estimated canopy closure ≤ 50%, all were in or adjacent to small natural openings in stands that otherwise had high (≥ 70%) canopy closure.

In the western subprovince, 63 of 65 (97%) nest trees were in forests in which the majority of trees in the overstory and understory were western hemlock, and two (3%) were in forests dominated by Douglas-fir. Western redcedar was present in variable numbers in nearly all stands. Sitka spruce and Pacific silver fir were common associates on lowland and upland sites, respectively.

In the eastern subprovince, 37 nests (73%) were in forests in which the majority of trees in the overstory were Douglas fir, and 14 (27%) were in forests dominated by western hemlock. Common associates in Douglas-fir stands were western hemlock, western redcedar, and Pacific silver fir, with the silver fir component generally increasing with elevation. Stands dominated by western hemlock typically included variable amounts of western redcedar, Douglas-fir, and Pacific silver fir. Grand fir (*Abies grandis*) was a relatively uncommon overstory component in a few low-elevation nest sites in the eastern subregion.

In both subprovinces, western white pine, grand fir, red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophylum*) were present in many nest stands, usually in small amounts. Red alder was typically limited to areas along streams or swampy areas.

TABLE 3

PROPORTIONS OF SPOTTED OWL NEST LOCATIONS AND RANDOM LOCATIONS IN DIFFERENT PHYSIOGRAPHIC CATEGORIES ON THE OLYMPIC PENINSULA, WASHINGTON, 1987–1994

Variable	Nests[a]	Random	95% CI[b]
Slope aspect			
North	0.108	0.140	
Northeast	0.171	0.105	
East	0.090	0.120	
Southeast	0.126	0.155	
South	0.117	0.125	
Southwest	0.108	0.120	
West	0.144	0.140	
Northwest	0.135	0.095	
Slope gradient (%)			
0–14	0.129	0.140	−0.106, 0.084
15–29	0.086	0.165	−0.168, 0.010
30–44	0.129	0.205	−0.177, 0.025
45–59	0.155	0.210	−0.161, 0.512
60–74	0.216	0.180	−0.076, 0.148
75–89	0.164	0.065	0.006, 0.192
90+	0.121	0.035	0.007, 0.165
Position on slope			
Lower third	0.500	0.450	
Middle third	0.345	0.400	
Upper third	0.155	0.150	

[a] Sample sizes for nest variables were 111 (aspect) and 116 (% slope, slope position). Sample size for random samples was 200.

[b] Ninety five percent confidence intervals are presented only for variables that had significant χ^2 tests for use versus availability. Intervals indicate whether a category was used more than expected (interval is positive), less than expected (interval is negative) or in proportion to availability (interval overlaps 0).

Location of nest trees did not differ from expected values for slope aspect (χ^2 = 5.17, 7 df, P = 0.64) or position on slope (χ^2 = 0.99, 2 df, P = 0.61) (Table 3). Proportions of nest sites in different percent slope categories differed from availability, with more nests than expected in the steeper percent slope categories (χ^2 = 22.61, 6 df, P = 0.001) (Table 3).

Elevation at nest sites ranged from 104–975 m in the western subprovince and 114–1189 m in the eastern subprovince. When nests were grouped into 150 m elevation bands, the distribution of nests differed in the eastern and western subprovinces (χ^2 = 35.6, 7 df, P <0.001, Fig. 2). The proportion of nests above 600 m elevation was 59% in the eastern subprovince, compared to only 10% in the western subprovince. In both regions, upper elevations at which nests were located generally corresponded with the transition to stands that were largely dominated by Pa-

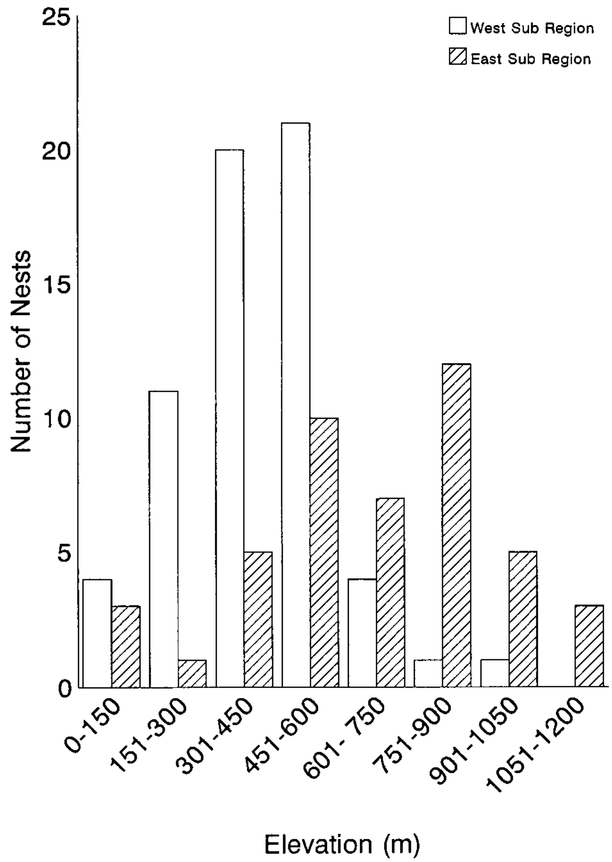

FIG. 2. Distribution of 108 Spotted Owl nests by elevational zone on the Olympic Peninsula, Washington, 1987–1994.

cific silver fir. Due to differences in temperature and precipitation this transition occurred at about 900 m in the western subprovince and 1200 m in the eastern subprovince (Henderson et al. 1989).

Site history.—Of 116 nest trees measured, three became nonfunctional during the study. In two cases, the tree fell down. In one case, the tree remained standing but the cavity collapsed. The average annual survival rate of nest trees from 1987–1993 was 0.992 (SE = 0.003). Estimated mean life expectancy of nest trees from the time they were first located was 124 years.

Although their historical nests were usually still intact, owl pairs changed nests in 88 of 118 (75%) sequential nesting attempts. This calculation was based on the entire sample of 155 nests, and all years of data for all pairs that nested in ≥ 2 yrs. Frequency of switching to different nests in different years did not differ between pairs that underwent a change in a pair member versus pairs that did not change members ($\chi^2 = 0.190$, 1 df, $P = 0.663$). Use of a different nest following replacement of a pair member was 80% following a male replacement (N = 10) and 60% following a female replacement (N = 10) ($\chi^2 = 0.952$, 1 df, $P = 0.329$).

The frequency with which pairs changed nests in sequential nesting years did not differ between 17 cases in which pairs failed at nesting (0.765) and 83 cases in which pairs nested successfully (0.699) ($\chi^2 = 0.298$, 1 df, $P = 0.585$). This comparison did not include two pairs that failed and renested in the same year. In the latter cases, both pairs moved to a new nest for their second nesting attempt.

At 40 territories where we observed at least two nest change events, we found that at least 40% of the time pairs changed back to a nest that had been used in previous years. The median distance between alternate nests was 0.52 km (range = 0.03–3.36 km, N = 92). At 46 territories where we confirmed two or more nests used in different years, the area of the smallest circle that encompassed all of the known nests ranged from 0.001–8.87 km^2 (median = 0.33 km^2).

DISCUSSION

Species of trees used for nesting on the peninsula were about equally divided among western hemlock (35%), Douglas-fir (31%) and western red cedar (28%). In contrast, some studies in other regions have reported the majority of nests in Douglas-fir (Forsman et al. 1984, LaHaye 1988, Buchanan et al. 1993). In managed stands in California, 35% of nests were in redwoods (*Sequoia sempervirens*), 27% were in Douglas-fir, 17% were in grand fir, and 13% were in hardwoods (Folliard 1993:31). The considerable variation in species composition of nest trees in different regions suggests that selection is based primarily on the presence of a suitable cavity or platform rather than tree species.

The proportion of nests in dead trees on the Olympic Peninsula (23%) was higher than has been reported from study areas in Oregon (4%), the Washington Cascades (12%), and managed stands in northern California (10%) (Forsman et al. 1984:31, Buchanan et al. 1993:5, Folliard 1993: 30). We do not know if this reflected a difference in the relative abundance of suitable nests in live vs. dead trees, or was due to other factors.

The proportion of nests in external platforms on the Olympic Peninsula (10%) was considerably lower than has been reported for other regions. For example, external platform nests comprised 19% of nests in samples from western Oregon (Forsman et al. 1984:32), and 50–80% of nests in samples from the east slope of the Cascades in Oregon and Washington (Forsman et al. 1984:32, Buchanan et al. 1993:5). It is unclear whether the high proportion of nests in cavities on the Olympic Peninsula is simply a function of availability. An alternative hypothesis is that Spotted Owls on the Olympic Peninsula actually select for cavity type nests because they provide more protection from the frequent heavy rains that occur during the nesting season.

Availability of different nest types does appear to influence nest selection by Spotted Owls (LaHaye 1988, Folliard 1993). Folliard (1993:51) noted that "Generally, platform nests tended to be used more often in even-aged stands with few or no residual trees remaining." On the east slope of the Washington Cascades, where many stands had been thinned to remove large old trees, 80% of nests examined by Buchanan et al. (1993) were in platforms. These observations suggest that, where large trees with cavities have been removed or are otherwise lacking, and where heavy precipitation is not a common occurrence during the nesting season, platform nests provide a viable alternative for Spotted Owls, if adequate numbers of platforms are present.

Without some sort of overhanging cover, nests in the top of broken off trees are likely to be more exposed to the elements than nests in side cavities. Therefore, we hypothesized that the proportion of nest trees with secondary tops should be higher for nests in top cavities than for nests in side cavities. Although there appeared to be a trend in this direction, the differences were not significant. Thus, while Spotted Owls do appear to select nests with good overhead cover on the Olympic Peninsula, the presence of secondary tops does not appear to be a reliable indicator of this.

Mean nest tree height, nest height, and nest tree dbh on the Olympic Peninsula were about the same as, or slightly greater than, was reported for Oregon and northern California (Forsman et al. 1984, LaHaye 1988, Folliard 1993), but were considerably greater than values reported for the east slope of the Cascades in Washington (Buchanan 1991, Buchanan et al. 1993). The considerable variation in these parameters among regions suggests that size of the tree or height of the nest are relatively less important in nest selection than the presence of a suitable cavity or platform.

Forsman et al. (1984) noted that cavity nests used by Spotted Owls in Oregon tended to be in the upper two-thirds of the canopy while platforms tended to be in the lower third. Buchanan et al. (1993) noted that cavity nests on the east slope of the Cascades were located at all levels in the forest canopy, whereas most platform nests were in the lower third of the canopy. In our sample, nests were found at all levels in the forest canopy, but the majority of both cavity nests (88%) and platform nests (82%) were in the lower two-thirds of the canopy. We do not know if this reflected selection by the owls or simply reflected the availability of nests. However, the preponderance of platform nests in the lower two-thirds of the canopy is likely explained by availability; large limbs capable of supporting large platform nests tend to be located in the lower part of tree boles, and debris platforms tend to form in the lower canopy as a result of materials falling from above.

Selection for cavities that opened to the east-northeast could possibly be explained by the fact that storms on the Olympic Peninsula typically approach from the west-southwest. However, since we did not have data on the actual availability of cavities with respect to entrance aspect, we could not discount the possibility that selection was based on availability.

Mean width of cavity entrances on the Olympic Peninsula was slightly less than in Oregon (30 cm; Forsman 1983:32) and was slightly above the upper end of the range reported by (Folliard 1993:28) for managed stands in northern California (15–23 cm). The smallest entrance we measured was 16 × 18 cm, which is similar to the smallest entrance found in California (15 × 18 cm; Folliard 1993:28). Mean diameter of nests on the Olympic Peninsula (45 cm) is similar to values reported for Oregon (50 cm; Forsman et al. 1984:32) and California 52 cm; Folliard 1993: 28). Folliard (1993) noted that width of the nest platform did not differ according to nest type, a result supported by our observations. Although we recorded one cavity that was 203 cm deep, most cavities used by Spotted Owls are less than 100 cm deep (this study, Forsman et al. 1984). Infrequent use of deeper cavities may be a function of availability or may be because owls find it difficult to climb in and out of such cavities.

The fact that nest sites in our study did not differ from expected values for slope aspect or position on slope suggests that these variables were relatively unimportant in nest site selection on the Olympic Peninsula. Although we found higher than expected proportions of nests on steeper slopes, we are unsure whether this represented selection by the owls. It is possible that the distribution of suitable owl nesting habitat was skewed towards the steeper slope categories as a result of historical patterns of forest management in which harvest on steep, unstable slopes was avoided. In northwestern California, Blakesley et al. (1992) also found no differences between observed and expected values for slope aspect at Spotted Owl nest sites. In contrast to our findings, Blakesley et al. (1992) found no differences between observed and expected values for percent slope at nests and found that owls nested on the upper third of slopes less than expected and nested on the lower third of slopes more than expected. Although they did not have data on the availability of different slope categories in their study areas, some investigators have compared the distribution of slope azimuths at nests with a uniform distribution (Forsman et al. 1984) or random distribution (LaHaye 1988, Buchanan 1991, Folliard 1993). In these cases, some investigators have found significant differences (LaHaye 1988), while others have not (Forsman et al. 1984, Buchanan 1991, Folliard 1993).

The mean and range of canopy closure at nest sites in Oregon ($\bar{x}$ = 69%, SE = 2.65, range = 35–91) (Forsman et al. (1984:30), were nearly identical to measurements from the Olympic Peninsula ($\bar{x}$ = 70%, SE = 1.44, range = 30–95%). Although canopy closure at nests in Oregon and on the Olympic Peninsula was highly variable, Folliard (1993) and Buchanan et al. (1993) stressed the consistency of high canopy cover at Spotted Owl nest sites in their study areas. We are unsure to what extent canopy closure estimates can be compared among study areas, because estimates may have been influenced by differences in methodology or observers.

In contrast to the low rate of attrition of nests on the Olympic Peninsula, Forsman et al. (1984) noted a relatively high rate of attrition of nest trees in Oregon. Of eight nests that became unusable in the Oregon study, four fell down, three were cut down during logging operations, and one cavity collapsed. Although he did not mention overall attrition rates of nests, Folliard (1993) noted that platform nests in northern California were especially ephemeral in nature.

The tendency of Spotted Owls on the Olympic Peninsula to use different nests in different nesting years contrasts with reports from other regions indicating frequent reuse of the same nests in different years (e.g., Forsman et al. 1984, Ganey 1988). This behavior did not appear to be influenced by turnover of pair members or by success or failure of nests in prior years. We do not know of any obvious factors that should have caused owls on the peninsula to use alternate nests more frequently than owls in other regions.

Habitat selection by spotted owls is likely influenced by a variety of factors, including prey availability, availability of suitable nests and roosts, and presence of escape cover. Use of nest stands by Spotted Owls on the Olympic Peninsula appears to be almost entirely restricted to stands of large trees or younger stands in which there are residual old trees. Retention of small clusters of live trees in harvest units may provide future nesting habitat in stands that would otherwise be uninhabitable by Spotted Owls.

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LITERATURE CITED

BATSCHELET, E. 1981. Circular statistics in biology. Academic Press, London, England.

BENT, A. C. 1938. Life histories of North American birds of prey. Part 2. U.S. National Museum Bull. 170.

BLAKESLEY, J. A., A. B. FRANKLIN, AND R. J. GUTIÉRREZ. 1992. Spotted owl roost and nest site selection in northwestern California. J. Wildl. Manage. 56:388–392.

BROWNIE, C. D. R. ANDERSON, K. P. BURNHAM, AND D. S. ROBSON. 1978. Statistical inference from band recovery data—a handbook. USDI Fish and Wildl. Serv., Resource Publ. No. 131.

BUCHANAN, J. B. 1991. Spotted owl nest site characteristics in mixed conifer forests of the eastern Cascade Mountains, Washington. M. Sc. thesis, Univ. of Washington, Seattle.

———, L. L. IRWIN, AND E. L. MCCUTCHEN. 1993. Characteristics of Spotted Owl nest trees in the Wenatchee National Forest. J. Raptor Res. 27:1–7.

———, ——— , AND ———. 1995. Within-stand nest site selection by Spotted Owls in the eastern Washington Cascades. J. Wildl. Manage. 59:301–310.

DICKEY, D. R. 1914. The nesting of the Spotted Owl. Condor 16:193–202.

FOLLIARD, L. 1993. Nest site characteristics of Northern Spotted Owls in managed forests of northwest California. M.S. thesis, Univ. of Idaho, Moscow.

FORSMAN, E. D. 1983. Methods and materials for locating and studying Spotted Owls. USDA For. Serv. Gen. Tech. Rept. PNW-162.

———, A. GIESE, D. MANSON, S. SOVERN, AND D. R. HERTER. 1995. Renesting by Spotted Owls. Condor 97:1078–1080.

———, E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildl. Monogr. 87.

GANEY, J. L. 1988. Distribution and habitat ecology of Mexican Spotted Owls in Arizona M.S. thesis. Northern Arizona University, Flagstaff.

GUTIÉRREZ, R. J. 1985. An overview of recent research on the Spotted Owl. Pp. 39–49 *in* Ecology and management of the Spotted Owl in the Pacific Northwest (Gutiérrez, R. J., and A. B. Carey, eds.). USDA For. Serv. Gen. Tech. Rept. PNW-185.

HENDERSON, J. A., D. H. PETER, R. D. LESHER, AND D. C. SHAW. 1986. Forested plant associations of the Olympic National Forest. USDA For. Serv. Ecol. Tech. Paper R6-ECOL-TP 001-88.

LAHAYE, W. 1988. Nest site selection and nesting habitat of the Northern Spotted Owl in northwest California. M.Sc. thesis, Humboldt State University, Arcata.

LIGON, J. S. 1926. Habits of the Spotted Owl (*Syrnium occidentale*). Auk 43:421–429.

MARCUM, C. L. AND D. O. LOFTSGAARDEN. 1980. A nonmapping technique for studying habitat preferences. J. Wildl. Manage. 44:963–968.