The Condor 97:684-693

HABITAT CONFIGURATION AROUND SPOTTED OWL SITES IN NORTHWESTERN CALIFORNIA[1]

JOHN E. HUNTER AND R. J. GUTIÉRREZ
Department of Wildlife, Humboldt State University, Arcata, CA 95521

ALAN B. FRANKLIN
Department of Fishery and Wildlife Biology, Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO 80523

Abstract. During each breeding season between 1988 and 1992, nests and daytime roosts were located for most territorial members of a contiguous population of Northern Spotted Owls (*Strix occidentalis caurina*) in northwestern California. Using Landsat imagery, we compared the amount of five land cover types, mature and old-growth forest fragmentation, and seral stage heterogeneity within 800 m (200 ha) circular plots around nest, roost, and random sites. This plot size was based on the observed spatial distribution of owl sites (one-half the average nearest-neighbor distance between territory centers) within the study area. Nest and roost sites were characterized by lower amounts of nonvegetated and herbaceous land cover, and greater amounts of mature and old-growth coniferous forest which was less fragmented than random sites. Mean amounts of mature and old-growth forest within 200 ha radius plots were 94.1 ha, 92.0 ha, and 71.8 for nest, roost, and random sites, respectively. The area of other land cover types was similar between owl and random sites. All habitat variables were similar at nest and roost sites. To evaluate the influence of spatial scale, habitat variables around nest and random sites also were estimated within eight concentric circular plots ranging from 800 to 3,600 m radii. Differences between nest and random sites in the amount and fragmentation of mature and old-growth forest were significant ($P < 0.01$) out to 1,200 m. Differences in the amount of nonvegetated and herbaceous, and seral stage heterogeneity were significant ($P < 0.05$) out to 1,200 m and 800 m, respectively. These results indicate that spatial scale of sampling is important and will affect analytical results. Our findings from the Klamath Physiographic Province of California were similar to results from comparable studies in Oregon and Washington.

Key words: Northern Spotted Owl; Strix occidentalis caurina; *Strigiformes; habitat use; Landsat; landscape ecology; northwestern California.*

INTRODUCTION

Northern Spotted Owl (*Strix occidentalis caurina*) nest and roost sites typically are found at locations that have complex forest structure (Barrows 1981, Forsman et al. 1984, LaHaye 1988, Solis and Gutiérrez 1990). While complex forest structure can occur in younger stands, in the Pacific northwest it is most common in late seral stage coniferous forests (i.e., mature and old-growth; U.S.D.I. 1992). Not only are Spotted Owl sites usually found within patches of late seral stage forest (Blakesley et al. 1992), but studies in Oregon and Washington demonstrate that Spotted Owl sites are surrounded by greater amounts and less fragmented mature and old-growth than random sites (Ripple et al. 1991a, Meyer et al. 1992, Lehmkuhl and Raphael 1993, Johnson 1993).

Despite the evidence that Spotted Owls select mature and old-growth forest at a variety of spatial scales, the existence of this relationship in the Klamath Physiographic Province of California has been questioned (California Forestry Association 1993). Therefore, we evaluated habitat configuration around nest and roost sites in a contiguous population of Northern Spotted Owls within the Klamath Physiographic Province of northwestern California. We compared the arrangement and the amounts of different land cover types around Spotted Owl nest and roost sites (i.e., used sites), and random sites (i.e., available sites).

STUDY AREA

The 292 km² Willow Creek Study Area (WCSA) consisted primarily of public lands, and was lo-

---

[1] Received 25 October 1994. Accepted 4 April 1995.

TABLE 1. Definition of land cover classes used to map the Willow Creek Study Area, northwestern California, 1990.

Class	Definition
Water	Water.
Nonvegetated and herbaceous	Total canopy closure < 30%. Greater than 50% of ground cover comprised of forbs, grass, rock, soil, and woody plants <2.5 cm dbh.
Brush	Total canopy closure < 30%. Greater than 50% of ground cover comprised of brush, conifer, and hardwood species ranging from 2.5 to 12.6 cm dbh.
Pole and medium conifer	Total canopy closure ≥ 30%. More than 50% of conifer basal area comprised of trees ranging from 12.7 to 53.2 cm dbh.
Mature and old-growth	Total canopy closure ≥ 30%. More than 50% of conifer basal area comprised of trees ≥53.3 cm dbh.
Hardwood	Total canopy closure ≥ 30%. More than 80% of basal area comprised of hardwood trees >12.6 cm dbh.

cated south of the town of Willow Creek, in Humboldt County, California. Approximately 90% of the vegetation at the WCSA consisted of Mixed Evergreen Forest (Küchler 1977, Franklin et al. 1990). The overstory consisted of Douglas-fir (*Pseudotsuga menziesii*), with a midstory dominated by tanoak (*Lithocarpus densiflora*), Pacific madrone (*Arbutus menziesii*), canyon live oak (*Quercus chrysolepis*), and other hardwoods. Elevations above 1,200 m were dominated by Klamath Montane Forest (Küchler 1977), which was characterized by white fir (*Abies concolor*), incense cedar (*Libocedrus decurrens*), and pine (*Pinus* spp.) associations. Scattered xeric sites, mostly at lower elevations, consisted of Oregon Oak Forest (Küchler 1977), dominated by Oregon white oak (*Quercus garryana*). Intensive timber harvesting, primarily clearcut logging, began in the 1950s and along with natural environmental conditions created a mosaic of successional vegetation.

The study area contained rugged, mountainous terrain and three third-order drainages. Winters were typically cool and wet, while summers were hot and dry (Franklin et al. 1990). This area was representative of the Klamath Physiographic Province of the Northern Spotted Owl (Thomas et al. 1990). Franklin et al. (1990) provided a more detailed description of the study area.

METHODS

LAND COVER MAPPING

We used Landsat Thematic Mapper digital imagery to map land cover on the WCSA. Scene 5225218174, which was acquired by Landsat-5 on 1 May 1990, was chosen because it was cloud free, and the acquisition date was near the midpoint of the study period. Land cover data from a single date was considered adequate because only 2.1% of the study area was logged during the study period (Hunter 1994). Each grid-cell in the imagery was 25 m × 25 m (625 m^2); this resolution was maintained during all phases of analysis.

Our land cover classification represented seral stages of coniferous forest (Table 1). These broad classes represented cover types that were comparable to categories derived during previous owl studies at WCSA (Franklin et al. 1990, Solis and Gutiérrez 1990, Blakesley et al. 1992). Using more narrowly defined land cover classes also would have reduced the power and accuracy of our comparisons of use versus availability (White and Garrott 1986). Spectral similarities between structurally similar seral stages of coniferous forest also limited our ability to differentiate between some seral stages (e.g., between mature and old-growth). Within our study area, old-growth stands had larger diameter trees than did mature stands, however, mature and old-growth stands were otherwise structurally similar (Solis and Gutiérrez 1990). Due to the spatial resolution of the Landsat data, much of the surface water within the study area was not mapped. Therefore, we did not test for differences in the area of water between owl and random sites.

Reference vegetation data were collected at 120 non-random plots. Plot locations were purposely located in an attempt to encompass the full spectrum of vegetative and physiographic conditions that existed on the study area. Hunter (1994) provided a complete description of the variables and methods used at vegetation plots. Other reference data included a set of color 1:15,820 aerial photographs acquired 25 June 1990, and personal knowledge of the study area. Reference data were used during image classification to identify clustering areas and to evaluate spectral classes.

The MicroImage (Version 4.0) software package (Terra-Mar Resource Information Services, Inc., Mountain View, CA 94043) was used to classify the Landsat imagery. We used a hybrid approach to image classification, which combined elements of both supervised and unsupervised techniques (see Lillesand and Kiefer 1987: 687). Guided clustering (Walsh 1980, Fox et al. 1992) with the Euclidean distance algorithm was used (Richards 1986) to develop spectral statistics for known areas. These spectral classes with the maximum likelihood classifier (Jensen 1986, Lillesand and Kiefer 1987) were used to classify a portion of the study area, which was then evaluated with reference data. Those spectral classes which performed well in the classification were retained. This was an iterative, trial-and-error process of developing spectral classes and testing their effectiveness. When spectral classes adequately defined the target land cover classes while maintaining low spectral variability, we used the maximum likelihood algorithm for a full classification of the WCSA. Those scattered grid-cells which remained unclassified were classified with a supervised Euclidean distance classifier (Jensen 1986). Following the final classification, spectral classes were combined into their respective land cover classes.

Random vegetation plots were located at points ($n = 55$) distributed throughout the study area; these data were used after image classification to assess the accuracy of the final land cover map. Random points were plotted on 1:24,000 topographic maps and located in the field using terrain associations and altimeter readings in conjunction with at least one compass bearing and distance estimate from a known location. Four vegetation plots, each 25 m apart and arrayed in a north-south oriented square pattern, were arranged around each of the random points. Data for the four plots were pooled, and the land cover at each random point was designated as belonging to a specific class based on the criteria in Table 1. The land cover class at each point was compared to the predominate land cover in the nine grid-cells (75 m × 75 m) around each corresponding point on the final land cover map. This three by three grid-cell sampling unit was used to reduce the differences between vegetation plot data and mapped land cover which were due to errors in coordinate accuracy of maps and navigation errors resulting from locating plots in the field. We estimated map accuracy by the percent of agreement between the actual land cover at random points and mapped land cover at corresponding random points (Story and Congalton 1986). Overall map accuracy of the final Landsat classification was estimated to be 76.4%; the accuracy of the mature and old-growth component of the final map was estimated to be 83.6%. These estimates of accuracy were probably underestimates due to the influence of other sources of error not associated with the classification (Congalton and Green 1993). The accuracy of our land cover map was similar to those reported for other Landsat mapping efforts in forested mountainous terrain. For example, Fiorella and Ripple (1993) had 78.3% overall map accuracy for their forest successional stage map of a portion of the Central Cascades Range of Oregon. Congalton et al. (1993) reported a 82.3% overall map accuracy for their old-growth map of National Forests and Parks west of the Cascades in Oregon and Washington. Effects of classification errors on analytical results are unknown. Hunter (1994) provided additional information on the methods used to map land cover and estimate accuracy.

LAND COVER ANALYSIS

The WCSA was the site of a long-term demographic study of Spotted Owls, in which the entire area was intensively surveyed for owls each year. As a result, the identity and locations of a high percentage of territorial owls were known (Franklin et al. 1990, Franklin 1992). For this study, we used data collected from 1988 through 1992. During each breeding season (April to August) during our study period, the entire WCSA was surveyed for Spotted Owls by nighttime calling. During daytime searches, roosting owls were visually located and individually identified using color bands (Franklin et al. 1990). Nests were located while determining reproductive status. Nest and roost locations were plotted on 1:24,000 topographic maps in the field using terrain associations and altimeter readings in conjunction with at least one compass bearing and distance estimate to a known location. Annual nest and roost locations represented all known territorial owls within the WCSA. Individual owls were considered to belong to a specific territory when they were repeatedly located in a given area. Field methods followed Forsman (1983) and Franklin et al. (1990).

We used program IDRISI (Eastman 1992), a grid-based geographic information system (GIS), to extract land cover data from the final land cover map. We measured the area (ha) of each land cover type, an index of the fragmentation of mature and old-growth forest, and an index of seral stage heterogeneity at nest, roost, and random sites. We estimated the fragmentation of mature and old-growth forest using a variation of the fragmentation index introduced by Ripple et al. (1991b). For each circular plot, we calculated the mean distance of each non-mature and old-growth grid-cell from a grid-cell of mature and old-growth. Higher mean values represented higher levels of fragmentation. Lehmkuhl and Raphael (1993) used a similar version of this index to measure fragmentation around Spotted Owl sites on the Olympic Peninsula, Washington. Using the proportions of each of the six land cover types within plots, we calculated seral stage heterogeneity using Simpson's (1949) index of diversity. This heterogeneity index was more sensitive to the area of each land cover type present than it was to the number of land cover types present (Magurran 1988). We measured the area of land cover types, and the indices of fragmentation and heterogeneity within 800 m, 1,200 m, 1,600 m, 2,000 m, 2,400 m, 2,800 m, 3,200 m, and 3,600 m radii concentric circular plots, which with the GIS we used, corresponded to 200 ha, 451 ha, 803 ha, 1,255 ha, 1,807 ha, 2,461 ha, 3,217 ha, and 4,070 ha plot sizes, respectively.

Spotted Owls may repeatedly nest or roost in the same general area, and commonly roost near active nests. Spotted Owls also are often site tenacious over long periods of time (Forsman et al. 1984). These behaviors may result in a lack of independence among sites within a given territory, both within a single year and between years. As a result, for each territory where nesting occurred during the study period, only one nest site was selected randomly for analysis. We also randomly selected one roost site from each territory. In order to maintain independence between nest and roost sites, only roosts from years in which no nesting occurred were considered.

In use versus availability studies such as ours, the designation of which habitat components were actually available to the organism could have considerable influence on the inference (Johnson 1980). Because there was markedly different floristic composition at higher elevations within the WCSA, we eliminated from consideration four random points which fell at elevations greater than the maximum elevation (1,350 m) observed at an owl nest or roost site during the study period. Using this criterion, 50 random points were selected for analysis. Thus, the population to which we felt inferences could be made consisted of territorial Spotted Owls on public lands in the Klamath Province of northwestern California below 1,350 m elevation.

Statistical tests on habitat variables were first performed on data from circular plots that had a radius most closely approximating one-half the average nearest-neighbor distance between the centers of Spotted Owl territories. We considered this plot size to be biologically meaningful because it represented an estimate of territory spacing within this contiguous population of owls. It also served to reduce overlap between adjacent plots. The selection of sites used to measure nearest-neighbor distances between territory centers was constrained by the problems of independence discussed above. Therefore, we only measured distances between 1990 territory centers; we chose this particular year because it was the midpoint of the study period. The center of each 1990 territory was estimated by selecting a single site from that year which best represented the center of activity for that territory (Ganey 1991). The order of priority for selecting this location for each territory was: (1) nest site; (2) pair roost site; (3) most frequently-used roost site; (4) female roost site; and (5) male roost site. We measured the nearest-neighbor distances between these territory centers on 1:24,000 scale topographic maps.

We tested for differences between nest, roost, and random one-half nearest-neighbor sized plots using resampling-based, multiple testing procedures in PROC MULTTEST in SAS (SAS Institute 1992). In this procedure, we used *t*-tests for means with the randomization option to resample the data with replacement 1,000 times. Use of the randomization option did not require the assumption of an underlying population. We tested all of the variables simultaneously using the following a priori linear contrasts (tests): nest versus random, roost versus random, nest versus roost, and nest combined with roost versus random. *P*-values resulting from the analysis were

TABLE 2. Landscape characteristics within 800 m radius (200 ha) plots around Spotted Owl nest, roost, and random sites, in northwestern California, 1988–1992.

Variable[a]	Nest sites (n = 33)		Roost sites (n = 45)		Random sites (n = 50)		Exact P-value
	Mean	SD	Mean	SD	Mean	SD	
Land cover type (ha)							
Nonvegetated and herb	9.2A	6.8	9.6A	7.7	17.0B	15.9	0.012
Brush	20.8	17.7	21.1	16.9	28.0	24.4	0.555
Pole and medium	23.3	9.7	26.1	12.2	25.2	13.8	1.000
Mature and old-growth	94.1A	26.2	92.0A	27.0	71.8B	28.1	0.003
Hardwood	53.0	18.6	51.6	19.3	57.6	20.9	0.841
Landscape indices							
Fragmentation	26.3A	12.6	28.0A	16.5	39.7B	27.3	0.019
Heterogeneity	0.648	0.091	0.645	0.081	0.692	0.064	0.058

[a] Means sharing the same letter within a row did not differ ($P < 0.05$) based on multiple t-tests with adjusted P-values.

exact and adjusted for correlations between variables on the same plot and for correlations between tests. Essentially, this analysis was analogous to a one-way MANOVA without any underlying distributional assumptions (Westfall and Young 1993). For those habitat variables in which test results suggested differences at this plot size, nest and random data from each of the additional concentric circular plot sizes were compared with Mann-Whitney tests (Zar 1974). The purpose of this analysis was to estimate the plot size at which habitat variables were no longer significant. In addition, this analysis illustrated the gradient of change in habitat characteristics with increasing distance away from owl sites.

RESULTS

Between 1988 and 1992, 50 unique Spotted Owl territories were identified within the WCSA. Of the 70 nest sites and 306 roost sites located, 33 and 45 sites respectively, were randomly selected for analysis. Forty unique territories were present during 1990. The mean nearest-neighbor distance between 1990 Spotted Owl territory centers was 1,579 m (SD = 525, n = 40, range 540 to 3,400 m). Because one-half of this distance was 790 m, we used the 800 m radius (200 ha) plots to make initial comparisons in habitat characteristics between nest, roost, and random sites.

There was less area of nonvegetated and herbaceous cover in 200 ha plots around Spotted Owl nest and roost sites than around random sites, while nest and roost sites had similar areas of nonvegetated and herbaceous (Table 2). Nest, roost, and random sites did not differ with respect to amount of brush, pole and medium conifer forest, and hardwood forest (Table 2). Owls used nest and roost sites that had more mature and old-growth forest than was available throughout the landscape, but nest and roost sites had similar amounts of mature and old-growth forest (Table 2). The area of mature and old-growth forest within 200 ha plots ranged from 42.3 to 162.3 ha, 32.8 to 146.2 ha, and 8.4 to 136.5 ha around nest, roost, and random sites, respectively. Mature and old-growth forest fragmentation also was lower around nest and roost sites than around random sites (Table 2), with nest and roost sites having similar levels of fragmentation (Table 2). Differences in seral stage heterogeneity between nest, roost, and random sites were not statistically significant at $\alpha = 0.05$. However, the observed P-value of 0.058 did not strongly support the null hypothesis of no difference and heterogeneity at nest and roost sites appeared lower than at random sites (Table 2).

Significant differences ($P < 0.01$) between nest and random sites were present out to 1,200 m for the amount and fragmentation of mature and old-growth forest (Table 3). The amounts of nonvegetated and herbaceous cover and seral stage heterogeneity were different ($P < 0.05$) out to 1,200 m and 800 m, respectively (Table 3). The precise distance at which habitat configuration was no longer different between nest and random sites was not determined.

Within the range of plot sizes that we estimated habitat characteristics around owl sites, the percentage of nonvegetated and herbaceous increased, while the percentage of mature and old-growth forest decreased (Fig. 1). Levels of fragmentation and heterogeneity around owl sites

TABLE 3. Mann-Whitney test statistics from comparisons of habitat characteristics within 8 concentric circular plots around Spotted Owl nest and random sites in northwestern California, 1988–1992.

Variable[b]	Plot radius (m)[a]							
	800	1,200	1,600	2,000	2,400	2,800	3,200	3,600
Nonveg & herb	2.02*	2.17*	1.79	1.60	1.52	1.54	1.55	1.70
Mature & old	3.39**	2.79**	2.02*	1.57	1.33	1.07	0.72	0.72
Fragmentation	3.09**	2.75**	1.85	1.38	1.18	0.84	0.86	0.88
Heterogeneity	2.29*	1.86	1.14	1.06	1.09	0.74	0.43	0.43

[a] 800 m, 1,200 m, 1,600 m, 2,000 m, 2,400 m, 2,800 m, 3,200 m, and 3,600 m radii plots correspond to 200 ha, 451 ha, 803 ha, 1,255 ha, 1,807 ha, 2,461 ha, 3,217 ha, and 4,070 ha plot sizes, respectively.

[b] Nonveg & herb—Nonvegetated, herbs, and woody plants < 2.5 cm dbh; Mature & old—≥53.3 cm dbh conifers.

* $P < 0.05$; ** $P < 0.01$ for two-tailed tests.

both increased with increasing plot size (Fig. 2). Like other measures of landscape pattern (Turner et al. 1989), the heterogeneity index we used increased with increasing plot size, even for random plots (Fig. 2). Nevertheless, like the other variables, heterogeneity at owl and random sites converged rather that stabilizing at different levels. This supports the inference that owl sites are more homogeneous than random sites at smaller spatial scales. These data illustrated the influence spatial scale can have on estimates of habitat characteristics.

DISCUSSION

We think the 200 ha plot was the most appropriate size for our comparisons because it was based on the observed spatial distribution of owl sites. Our analysis on the effects of different plot sizes suggests that consideration of biologically-derived spatial scale is important and will affect analytical results.

We documented that Spotted Owls in the Klamath Physiographic Province of California nest and roost at sites with greater amounts of mature and old-growth forest which are less fragmented than what was generally available on the landscape. This pattern also has been documented in Oregon and Washington (Ripple et al. 1991a, Meyer et al. 1992, Lehmkuhl and Raphael 1993). Spotted Owls in these more northern areas, however, occupied sites with even greater amounts of mature and old-growth than our study. Several possible reasons exist to explain this difference. We examined a contiguous population, in contrast to the other studies which used individual owl sites throughout a much larger landscape. If owl sites used in their analyses were located in conjunction with timber sale planning, they could have been biased towards sites with greater amounts of older forest. Another possibility is a differential response of owls to habitat configuration within the California Klamath Province. Nevertheless, the general patterns were similar.

Any response of Spotted Owl populations to changes in habitat configuration could be delayed due to the presence of non-territorial "floaters" (Franklin 1992), and because they are site tenacious and have long lifespans (Forsman et al. 1984). Other factors also may make it difficult to determine critical levels of habitat reduction and fragmentation. In interior northwestern California, dusky-footed woodrats (*Neotoma fuscipes*) are the predominate food resource for the Spotted Owl (Ward 1990), and are most abundant in sapling/brushy poletimber, followed by seedling/shrub and old-growth stands (Sakai and Noon 1993). While mature and old-growth forests are more open and thus may permit more efficient foraging by Spotted Owls (U.S.D.I. 1992), areas of early seral stage habitat may act as sources for dispersing woodrats (Ward 1990, Sakai and Noon 1993). The low significance level we observed in the difference between seral stage heterogeneity at owl and random sites could be evidence of these opposing influences on habitat use. That is, the presence of untreated (no herbicide spraying or brush removal) regenerating clearcuts (10–25 years old) may temporarily increase local prey populations, delaying the effects of reductions in nesting and roosting habitat. If all cover types other than mature and old-growth forest were of low value to owls, then differences in seral stage heterogeneity should have been more similar to differences in mature and old-growth forest fragmentation. Meyer et al. (1992) found, in contrast to old-growth fragmentation, that none of their indices of seral stage heterogeneity (diversity, dominance, contagion, fractal dimension, and patchiness) were different be-

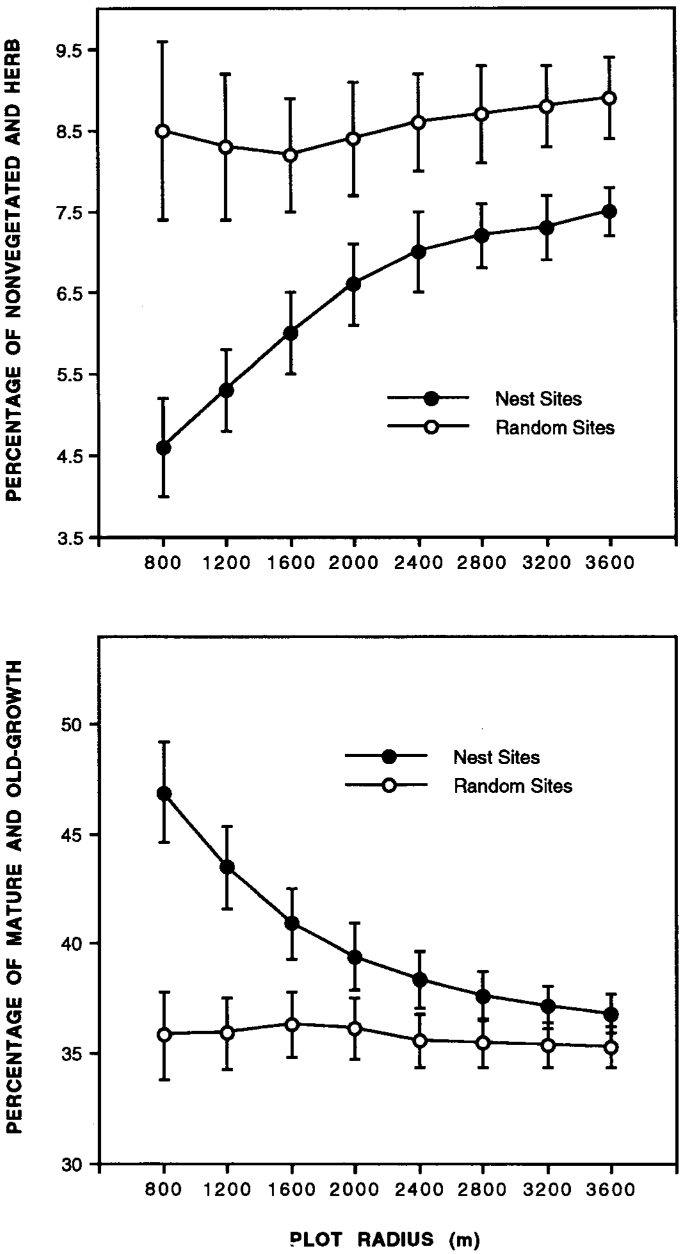

FIGURE 1. Percentage of area (mean ± 1 SE) in nonvegetated and herbaceous, and in mature and old-growth within eight concentric circular plots around Spotted Owl nest sites, and random sites in northwestern California, 1988–1992.

tween owl and random sites. Chávez-León (1989) also found that habitat interspersion was similar between owl sites and surrounding areas.

Besides prey availability, landscape configuration also may influence Spotted Owl habitat use patterns in other ways. Given that Spotted Owls have a relatively narrow thermal neutral zone (Ganey et al. 1993), the selection for sites within older, more dense stands may facilitate thermoregulation (Barrows 1981). Microcli-

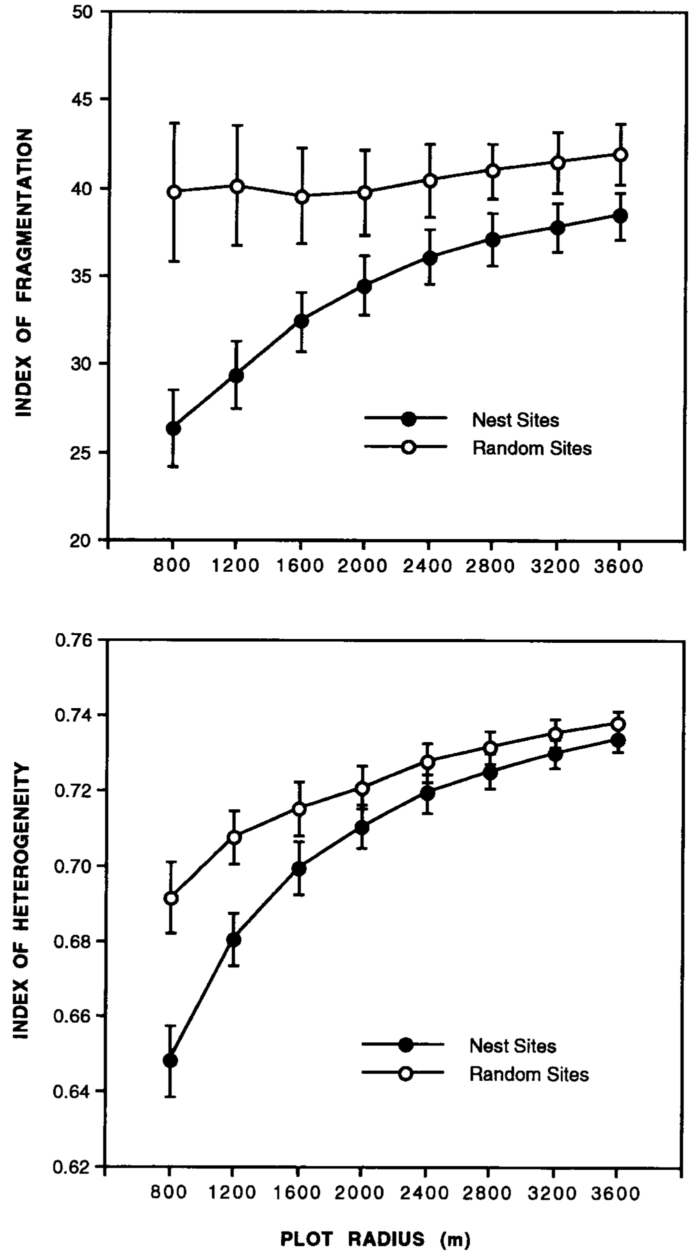

FIGURE 2. Indices of fragmentation and heterogeneity (mean ± 1 SE) within eight concentric circular plots around Spotted Owl nest sites, and random sites in northwestern California, 1988–1992.

mates in mature and old-growth stands can be influenced up to 250 m away from edges (Chen et al. 1990), and evidence suggests that Northern Spotted Owls select nest and roost sites averaging >200 m from edges (Johnson 1993). Therefore, owls may be using sites with more contiguous mature and old-growth in order to reduce thermoregulatory costs. This influence may be less important in younger stands with residual large trees or in coastal areas which experience lower summer temperatures. Potential nest structures also would presumedly be more plentiful in areas with greater amounts of mature and old-growth forest. Less fragmented nest and roost habitat also may afford fewer contacts with competitors and predators which favor more open habitats such as Barred Owls (*Strix varia*), Great Horned Owls (*Bubo virginianus*), Common Ravens (*Corvus corax*), and Red-tailed Hawks (*Buteo jamaicensis*; U.S.D.I. 1992, Johnson 1993). It should be noted that while we combined mature and old-growth, our results do not necessarily indicate that they are of equal quality as Spotted Owl habitat.

Almost every aspect of Spotted Owl ecology has been contested by biologists and special interest groups. In a recent petition to de-list the Northern Spotted Owl from its threatened status, the California Forestry Association (1993) asserted that Spotted Owls in Northern California are flexible in their habitat use patterns and fully occupy conifer-dominated forests of all ages. Our data suggests that such assertions may be incorrect for public lands in the Klamath Province in California, and that occupancy by owls is significantly influenced by the amount and distribution of older forests within the landscape. Further, the California Klamath Province owl population contributes significantly to the larger regional owl population (Gutiérrez 1994). It is therefore prudent to continue to base conservation decisions on empirical information rather than speculation.

ACKNOWLEDGMENTS

L. Fox III assisted with image processing, and R. T. Golightly and B. R. Noon reviewed earlier drafts of this paper. J. A. Blakesley, D. Delaney, D. Fix, C. Jewett, C. A. Moen, A. Padilla, J. Woodford and others assisted with field work. Personnel at the Six Rivers National Forest provided much appreciated support. Partial funding was provided by the USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Cooperative Agreement No. PSW-90-0013CA, and the California Department of Fish and Game, California Environmental License Plate Fund and California Native Species Enhancement Account, Nongame Bird and Mammal Section, Job II.A.2.

LITERATURE CITED

BARROWS, C. W. 1981. Roost selection by Spotted Owls: an adaptation to heat stress. Condor 83: 302–309.

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.

CALIFORNIA FORESTRY ASSOCIATION. 1993. A petition to remove the Northern Spotted Owl in California from the list of threatened species. Unpublished document, California Forestry Association, Sacramento, CA.

CHÁVEZ-LEÓN, G. 1989. Characteristics of fragmented habitat used by the Northern Spotted Owl (*Strix occidentalis caurina*) in northwestern California. M.Sc.thesis, Humboldt State Univ., Arcata, CA.

CHEN, J., J. F. FRANKLIN, AND T. A. SPIES. 1990. Microclimatic pattern and basic biological responses at the clearcut edges of old-growth Douglas-fir stands. Northwest Environ. J. 6:424–425.

CONGALTON, R. G., AND K. GREEN. 1993. A practical look at the sources of confusion in error matrix generation. Photogram. Eng. Remote Sens. 59:641–644.

CONGALTON, R. G., K. GREEN, AND J. TEPLY. 1993. Mapping old growth forests on National Forest and Park lands in the Pacific northwest from remotely sensed data. Photogram. Eng. Remote Sens. 59:529–535.

EASTMAN, J. R. 1992. IDRISI user's guide, version 4.0. Clark Univ., Graduate School of Geography, Worcester, MA.

FIORELLA, M., AND W. J. RIPPLE. 1993. Determining successional stage of temperate coniferous forests with Landsat satellite data. Photogram. Eng. Remote Sens. 59:239–249.

FORSMAN, E. D. 1983. Methods and materials for locating and studying Spotted Owls. U.S. Forest Serv. Gen. Tech. Rep. PNW-162. Portland, OR.

FORSMAN, E. D., E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildl. Monogr. 87:1–64.

FOX, L., III, J. A. SIEGEL, AND P. E. HARDWICK. 1992. Defining maximum spectral information in Landsat, thematic mapper, digital imagery, p. 90–97. *In* ASPRS/ACSM Annual Meeting and Convention: symposium proceedings. American Society for Photogrammetry and Remote Sensing, Bethesda, MD.

FRANKLIN, A. B., J. P. WARD, R. J. GUTIÉRREZ, AND G. I. GOULD. 1990. Density of Northern Spotted Owls in northwest California. J. Wildl. Manage. 54:1–10.

FRANKLIN, A. B. 1992. Population regulation in Northern Spotted Owls: theoretical implications for management, p. 815–827. *In* D. R. McCullough and R. H. Barrett [eds.], Wildlife 2001: populations. Elsevier Applied Science, London, England.

GANEY, J. L. 1991. Developing and testing a predictive model for Mexican Spotted Owl habitat. Ph.D.diss., Northern Arizona Univ., Flagstaff, AZ.

GANEY, J. L., R. P. BALDA, AND R. M. KING. 1993. Metabolic rate and evaporative water loss of Mexican Spotted and Great Horned Owls. Wilson Bull. 105:645–656.

GUTIÉRREZ, R. J. 1994. Changes in the distribution and abundance of Spotted Owls during the past century. Stud. Avian Biology 15:293–300.

HUNTER, J. E. 1994. Habitat configuration around Spotted Owl nest and roost sites in northwestern

California. M.Sc.thesis, Humboldt State Univ., Arcata, CA.

Jensen, J. R. 1986. Introductory digital image processing: a remote sensing perspective. Prentice-Hall, Englewood Cliffs, NJ.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, D. H. 1993. Spotted Owls, Great Horned Owls, and forest fragmentation in the central Oregon Cascades. M.Sc.thesis, Oregon State Univ., Corvallis, OR.

Küchler, A. W. 1977. The map of the natural vegetation of California, p. 908–938. *In* M. Barbour and J. Majors [eds.], Terrestrial vegetation of California. J. Wiley and Sons, New York.

LaHaye, W. S. 1988. Nest site selection and nesting habitat of the Northern Spotted Owl (*Strix occidentalis caurina*) in northwestern California. M.Sc.thesis, Humboldt State Univ., Arcata, CA.

Lehmkuhl, J. F., and M. G. Raphael. 1993. Habitat pattern around Northern Spotted Owl locations on the Olympic Peninsula, Washington. J. Wildl. Manage. 57:302–315.

Lillesand, T. M., and R. W. Kiefer. 1987. Remote sensing and image interpretation. J. Wiley and Sons, New York.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton Univ. Press, Princeton, NJ.

Meyer, J. S., L. L. Irwin, and M. S. Boyce. 1992. Influence of habitat fragmentation on Spotted Owl site location, site occupancy, and reproductive status in western Oregon. Unpublished document, National Council of the Paper Industry for Air and Stream Improvement, Corvallis, OR.

Richards, J. A. 1986. Remote sensing digital image analysis: an introduction. Springer-Verlag, Berlin.

Ripple, W. J., D. H. Johnson, K. T. Hershey, and E. C. Meslow. 1991a. Old-growth and mature forests near Spotted Owl nests in western Oregon. J. Wildl. Manage. 55:316–318.

Ripple, W. J., G. A. Bradshaw, and T. A. Spies. 1991b. Measuring forest landscape patterns in the Cascade Range of Oregon, USA. Biol. Conserv. 57:73–88.

Sakai, H. F., and B. R. Noon. 1993. Dusky-footed woodrat abundance in different-aged forest in northwestern California. J. Wildl. Manage. 57:373–382.

SAS Institute. 1992. SAS/STAT software: changes and enhancements, release 6.07. SAS Tech. Rep. P-229. SAS Institute, Cary, NC.

Simpson, E. H. 1949. Measurement of diversity. Nature 163:688.

Solis, D. M., Jr., and R. J. Gutiérrez. 1990. Summer habitat ecology of Northern Spotted Owls in northwestern California. Condor 92:739–748.

Story, M., and R. G. Congalton. 1986. Accuracy assessment: a user's perspective. Photogram. Eng. Remote Sens. 52:397–399.

Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. A conservation strategy for the Northern Spotted Owl. U.S. Gov. Printing Off., Washington, DC.

Turner, M. G., R. V. O'Neill, R. H. Gardner, and B. T. Milne. 1989. Effects of changing spatial scale on the analysis of landscape pattern. Landscape Ecol. 3:153–162.

U. S. Department of the Interior. 1992. Draft recovery plan for the Northern Spotted Owl. U. S. Fish and Wildlife Service, Portland, OR.

Walsh, S. J. 1980. Coniferous tree species mapping using LANDSAT data. Remote Sensing of Environ. 9:11–26.

Ward, J. P., Jr. 1990. Spotted Owl reproduction, diet and prey abundance in northwest California. M.Sc.thesis, Humboldt State Univ., CA.

Westfall, P. H., and S. S. Young. 1993. Resampling-based multiple testing: examples and methods for *p*-value adjustment. J. Wiley and Sons, New York.

White, G. C., and R. A. Garrott. 1986. Effects of biotelemetry triangulation error on detecting habitat selection. J. Wildl. Manage. 50:509–513.

Zar, J. H. 1974. Biostatistical analysis. Prentice Hall, Englewood Cliffs, NJ.