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OLD-FOREST DISTRIBUTION AROUND SPOTTED OWL NESTS IN THE CENTRAL CASCADE MOUNTAINS, OREGON

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Abstract: Unlike previous spotted owl (*Strix occidentalis*) habitat association studies, we restricted our inquiry to the old-forest type and thus explored the association of spotted owls with habitat distribution as opposed to habitat type. We compared old-forest distribution around 126 northern spotted owl (*S. o. caurina*) nests in 70 pair territories, 14 nonreproductive spotted owl activity centers, and 104 points drawn randomly from old forest (closed canopy, >80 yr) in the central Cascade Mountains of Oregon. We quantified the percentage of old forest within 50 concentric circular plots (0.1–5.0-km radii) centered on each analyzed point, and we used logistic regression to make spatially explicit inferences. Owl nests were surrounded by more old forest in plots with 0.2–0.8-km radii ($P < 0.05$). Results suggested the landscape scales most pertinent to northern spotted owl nest-site positioning in this study were (in descending order) (1) the surrounding 15 ha (approx 200-m radius), (2) the surrounding 30–115 ha (approx 300–600-m radius), (3) the surrounding 200 ha (800-m radius), and (4) possibly the surrounding 700 ha (1,500-m radius). Nests were associated with higher proportions of old forest near the nest, implying that the arrangement of habitat was important for nest-site selection, positioning, or both. The 70 territories of nesting owls had more old forest on average than did the 14 nonreproductive owl sites, and the probability that a pair nested at least once during the study was positively associated with area of old-forest habitat in all radii studied. Because spotted owls in the central Cascade Mountains of Oregon are known to have home ranges that average 1,769 ha, our results apply to nest-site location on the landscape and not to the amount of habitat necessary for pair persistence or successful reproduction.

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Numerous habitats at association studies have examined relations between northern spotted owls (hereafter, spotted owl) and old forests (Forsman et al. 1984, Thomas et al. 1990, Ripple et al. 1991*b*, Bart and Forsman 1992, Lehmkuhl and Raphael 1993, Hunter et al. 1995, Ripple et al. 1997). Researchers conducting these

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studies identified, without exception, a strong association between owl occupancy and mature and old-growth forests (hereafter, old forests), or forests with structural characteristics of old forests. Although the presence and amount of structurally complex forests are important to spotted owl occupancy, relatively little is known about whether the distribution of those forests, relative to spotted owl nest sites, affects nest-site selection, survival, and reproduction of individual spotted owl pairs.

Spotted owls are central-place foragers, use large amounts of old-forest habitat, and their use of space is explained by optimal foraging theory (Carey and Peeler 1995). We hypothesized that reproductively active spotted owl pairs located nests to maximize the amount of old forest available and selected landscapes where the proportion of old-forest habitat was centrally weighted or "clumped" in its general arrangement. To test this hypothesis, we compared habitat characteristics around spotted owl nests to random locations in old forest. Restricting random locations to old forest allowed inference regarding selection of habitat distribution or configuration as opposed to selection of habitat class. Our study differs from previous spotted owl habitat use studies in this regard. We predicted that the amount of old forest around spotted owl nests and random old-forest points would be similar in small plot sizes, but that spotted owl nests would have significantly more old forest in larger plot sizes, indicating an association with higher amounts or "clumps" of old forest within a given area. Finally, as plot sizes became very large, the amounts of old forest around both sets of points would, necessarily, become similar.

Also, we hypothesized that the amount of old forest available to a pair of spotted owls influenced their reproductive potential. To test this hypothesis, we compared the amount of old forest around nesting pairs versus sites occupied by spotted owls that were nonreproductive during the period of study. We predicted that reproductive pairs would have greater amounts of old forest immediately surrounding them than would nonreproductive spotted owls.

We used logistic regression to make scale-specific inferences regarding landscape composition by constructing models that used the percentage of old forest in variously sized circular plots as explanatory variables. We thus identified those spatial scales at which the area of old forest was most associated with spotted owl occupancy as represented by nest locations.

STUDY AREA

The study was conducted on the west slope of the Cascade Mountain Range in Oregon and included portions of the Blue River, Mckenzie Bridge, and Sweet Home ranger districts of the Willamette National Forest, as well as some interspersed private holdings. Spotted owls have been studied intensively in this area since 1975. The east side of the study area was bordered by the Three Sisters and Mt. Washington wilderness areas. Privately owned land and land administered by the Bureau of Land Management bordered the west side. The boundaries of the study area were defined by the minimum convex polygon formed by adding a 3.4-km buffer (the maximum plot radius used by Ripple et al. [1991*b*]) to the outermost spotted owl activity centers we sampled.

Topography was typical of the Western Cascades Province (Franklin and Dyrness 1973), with mountainous terrain deeply dissected by rivers and streams. Elevations ranged from 400 to 1,500 m. The climate was maritime with wet, mild winters and dry, warm summers. Climatological data collected at the primary meteorological station (elevation 426 m) in the H. J. Andrews Experimental Forest (the center of the study area) during the period of 1973–84 yielded a mean annual temperature of 8.5°C, with monthly ranges from 0.6°C in January to 17.8°C in July (Greenland 1994). Average annual precipitation was 2,302 mm, 71% of which fell from November through March. Mean annual precipitation was greater at higher elevations (e.g., 2,785 mm at 1,203 m) and was often in the form of snow in the winter months, with snow packs forming above 1,050 m and persisting into June in some years (Bierlmaier and McKee 1989, Greenland 1994).

The study area was located within the Western Hemlock (*Tsuga heterophylla*) Zone, the most extensive vegetation zone in western Oregon (Munger 1930, Franklin and Dyrness 1973). Vegetation was dominated by forests of Douglas-fir (*Pseudotsuga menziesii*), western hemlock, and western redcedar (*Thuja plicata*). Approximately 49% of the area had been clearcut and converted to young (approx ≤40 yr) conifer plantations or was otherwise not suitable as spotted owl nesting habitat. The remainder was dominated by 200–750-year-old forests, with some interspersed stands of 100–200-year-old trees.

Very little timber harvest occurred on the study area until after World War II. The majority of harvests since that time have been clearcuts (Ripple et al. 1991*a*). Consequently, the forests were easily classified because they tended to be either <40 years old (poor habitat for spotted owls) or >200 years (excellent habitat for spotted owls).

METHODS

Habitat Classification

Cohen et al. (1995) defined and mapped 12 land-cover classes on the study area from a 1988 Landsat Thematic Mapper image. Pixel resolution of the image was 25 × 25 m, overall accuracy was 82%, and accuracy of individual classes was 56–100% (Cohen et al. 1995). We reclassified their 12 classes into 4 habitats that were ecologically relevant to spotted owls: (1) old forest (closed canopy ≥80 yr), (2) young forest (closed canopy <80 yr), (3) nonhabitat (all other terrestrial classes), and (4) water. Reclassification increased overall accuracy to 93% (88–100% for individual classes) because most of the error in the interpreted image was in the younger forest age classes (Cohen et al. 1995). For further details of image processing and habitat classification see Swindle (1998).

Reclassification of the image yielded an underestimate of the amount of old forest on the landscape when compared to Ripple et al. (1991*b*) who used aerial photo interpretation to estimate area of old forest in the same vicinity. To partially correct this problem, we smoothed the image by performing a 2-pixel radius, moving circular-window, majority SCAN procedure (Earth Resource Data Analysis Systems, Atlanta, Georgia, USA). The smoothing process effectively removed all patches <0.4 ha in size. Nearly half (50.8%) of the landscape was classified as old forest, 29.7% as nonhabitat, and 19.1% as young forest. Smoothing the image resulted in an increase of old forest by nearly 3%, a reduction of about 2% of young forest and <1% of nonhabitat.

Spotted Owl Nests and Activity Centers

We used a Global Positioning System (GPS; Model PRO XL with TDC2 data logger; Trimble Navigation, Sunnyvale, California, USA) to determine Universal Transverse Mercator (UTM) coordinates for 126 nest trees in 70 spotted owl territories. We also determined site centers at 14 additional territories that had evidence of consistent occupancy during the study but where spotted owls did not nest or at least did not produce any young. In the latter cases, we used the actual roost location closest to the geographic mean of all known roost locations in the territory as the site center. The 84 spotted owl territories were surveyed for occupancy for ≥4 years during 1987–95 as part of another study (Miller et al. 1996).

The pixel containing each site center was identified on the classified GIS image. Of the 126 nest trees, 113 (89.7%) were located in pixels classified as old forest, 7 (5.6%) were located in young forest, and 6 (4.7%) were in pixels classified as nonhabitat. Five of the 13 points were incorrectly classified because of the smoothing process (i.e., they were classified as old forest prior to smoothing). Three nests were located in young forest stands but in remnant old-growth trees ≥122 cm diameter at breast height (dbh). Similarly, the 5 remaining nests, correctly classified in nonhabitat pixels, were in old-growth trees ≥102 cm dbh. We found that 4 of these trees were in or near rock outcrops, talus, or quarry, and 1 was near the edge of a stand of sapling trees.

Random Point Selection

We selected a sample of old-forest pixels (hereafter, old-forest random points) from the image by generating a list of random UTM coordinates. We rejected UTM coordinates falling on non-U.S. Forest Service land, designated Wilderness Areas, or outside the study area boundaries; 104 pixels met these criteria.

Habitat Analysis

Fifty concentric, nonoverlapping, circular ring-plots were overlaid on each of the 126 spotted owl nests, 14 nonreproductive spotted owl activity centers, and 104 old-forest random points. Each of the 50 ring-plots averaged 4 pixels (100 m) in width and ranged from 0.1 to 5.0 km in radius (outer edge). We chose a ring width of 100 m for convenience and because analyses using other ring widths were conducted but did not change our conclusions (Swindle 1998). The percentage of each cover class around each point was calculated in each of the 50 nonoverlapping rings and in each of the 50 inclusive circles. The 126 spotted owl nests were grouped into 70 territories by obtaining the average habitat values for those territories with >1 nest. The territories were identified by concurrent demographic research where nearly all territorial individuals were monitored annually (Miller et al. 1996). Because of the large area of spotted owl territories and affinity of spotted owls to nonoverlapping core areas, allocating nests to territories was obvious and straightforward.

Statistical Design and Analyses

This was an observational "case-control" study (Ramsey and Schafer 1997) to compare landscapes around spotted owl nests to old-forest random points. Similar to Ramsey et al. (1994), we used logistic regression for our comparisons. To understand how the amount or percentage of old-forest habitat surrounding a given point affected the probability of that point being a spotted owl nest, we estimated the ratio of the odds that a site surrounded by a given percentage of old forest was a nest versus the odds that a site surrounded by no old forest was a nest. We thus estimated the probability that a site was a spotted owl nest via a general model structure as a linear-logistic model

$$p = \frac{e^y}{1 + e^y}.$$

Under this general model, y represented 1 of 3 linear equations that compared the percentages of old forest between the groups in (1) circles, (2) 100-m-wide rings, and (3) a circle of a given size plus the next larger ring:

$$\beta_0 + \beta_1(\% \text{ old forest in Circle } x), \quad (1)$$

$$\beta_0 + \beta_1(\% \text{ old forest in Ring } x), \quad (2)$$

and

$$\beta_0 + \beta_1(\% \text{ old forest in Circle } x) + \beta_2(\% \text{ old forest in Ring } x + 1), \quad (3)$$

where x represents the circle or ring number ranging from 1 to 50 (Fig. 1). Hereafter, we refer to these models as circle-plot (1), ring-plot (2), and circle + ring analyses (3).

We increased our ability to detect an effect by using an a priori minimum sample size formula (Ramsey and Schafer 1997). This approach was analogous to an a priori determination of statistical power, although the approach was confidence interval driven (see Ramsey and Schafer 1997) and entailed specifying an expected standard deviation, confidence level, and effect size. We used the standard deviation of the mean amount of old forest around nest sites in the 1,826-ha (2.4 km) plots studied by Ramsey et al. (1994), a confidence level of 95%, and an arbitrarily chosen effect size (expressed as a desired odds ratio) of 5:1.

For each model set, we produced a graph of the percentage of old forest in plots, and a graph of odds. We created the graphs of odds to show the increase in the probability that a given point is a nest site for each 10% increase in the amount of old forest in a circle (or ring) of a given radius by exponentiating the calibrated regression coefficient (i.e., $e^{(10)\beta}$; Ramsey and Schafer 1997:568–571, 599–604).

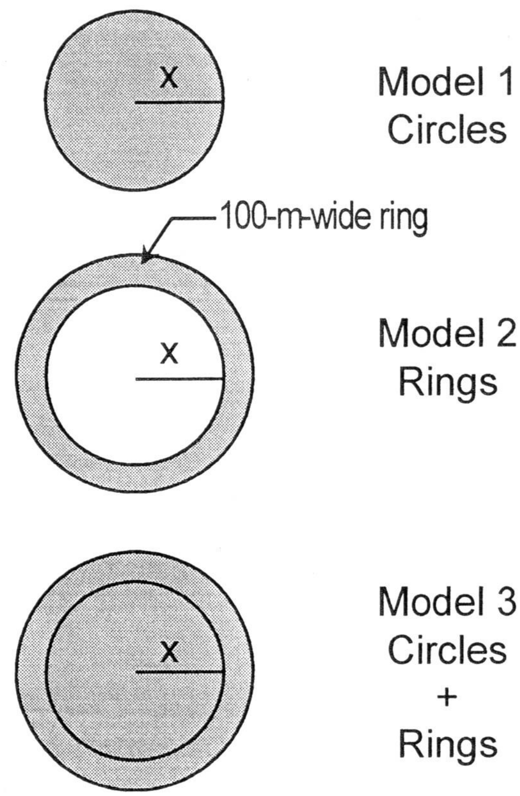

Fig. 1. Plots used for habitat sampling and analyses for northern spotted owl nests, nonreproductive activity centers, and old-forest random points in the central Cascade Mountains, Oregon, 1987–95. Circle and ring plots were numbered 1 to 50 and thus ranged from 0.1 to 5.0 km. Note that the nonshaded centers of Model 2 are not analyzed. Model 3 has the structure of (Circle x) + (Ring x + 1), and rings are 0.1 km wide.

RESULTS

The comparison of spotted owl nest sites and points randomly drawn from old forest indicat-

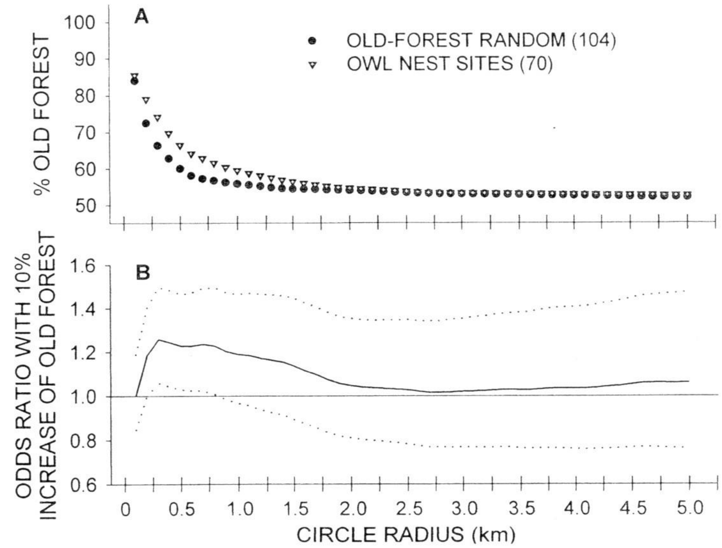

Fig. 2. Old forest in 50 concentric circle-plots around northern spotted owl nest sites and old-forest random points in the central Cascade Mountains, Oregon, 1987–95. (A) Percentage of old-forest, and (B) odds associated with a 10% increase of old-forest = $e^{(10)\beta}$. The dotted lines in (B) indicate 95% confidence intervals.

ed, in addition to the amount, that the distribution of old-forest habitat was important and served as a good predictor for spotted owl occupancy and nest-site selection. The comparison of spotted owl nest sites with activity centers of spotted owls that did not nest during the study indicated a possible relation between amount of habitat and reproductive performance. However, our confidence in this finding is tempered by low sample size and study design limitations.

As hypothesized, the circle-plot analyses indicated the amount of old forest around spotted owl nests was similar to points randomly drawn from old forest in the smallest circle plots (<0.2 km), differed ($P < 0.05$) in medium-size plots (0.2–0.8 km), and was similar in large plots (>0.8 km; Figs. 2A,B).

Spotted owl nests were associated with clumped arrangements of old forest. The ring-plot analyses indicated there was more old forest around nest sites than around old-forest random points from 0.1–0.6 km ($P \leq 0.10$; Figs. 3A,B). The relation was strongest from 0.1 to 0.3 km ($P < 0.05$). Beyond 0.6 km, the amount of old forest in rings around nest sites and old-forest random points was similar (Figs. 3A,B).

The probability that a particular point in old forest was a nest site was positively associated with the percentage of old forest within 0.2 km of the site, even after accounting for the percentage of old forest in the circular area closer to the site (Fig. 4). Conversely, the estimated odds decrease with increasing percentage of old forest in rings beyond 0.2 km (after accounting for the percentage of old forest in the closer circle). The coefficients for this negative association were significant ($P \leq 0.10$) at 1.5–1.7 km (Fig. 4). Beyond 2.6 km the coefficients oscillate between negative and positive.

In summary, spotted owl nests differed on average from old-forest random points by having more old forest in rings immediately surrounding them and less old forest in outer rings surrounding them. Thus, spotted owl nests tended to be centered in clumps of old forest, which differed from the average distribution of old forests on the general landscape (Fig. 5).

The amount of old forest around the 126 nest sites (summarized to 70 territories) versus 14 activity centers of spotted owls that did not nest during the study indicated the percentage of old forest around nests was greater ($P \leq 0.10$ in several plots; Figs. 6A,B). The odds that a pair nested during the study increased by as much as 50% with a 10% increase in the amount of old forest within 1.2 km (Fig. 6B).

DISCUSSION

Unlike previous studies addressing spotted owl habitat association, this study allowed us to

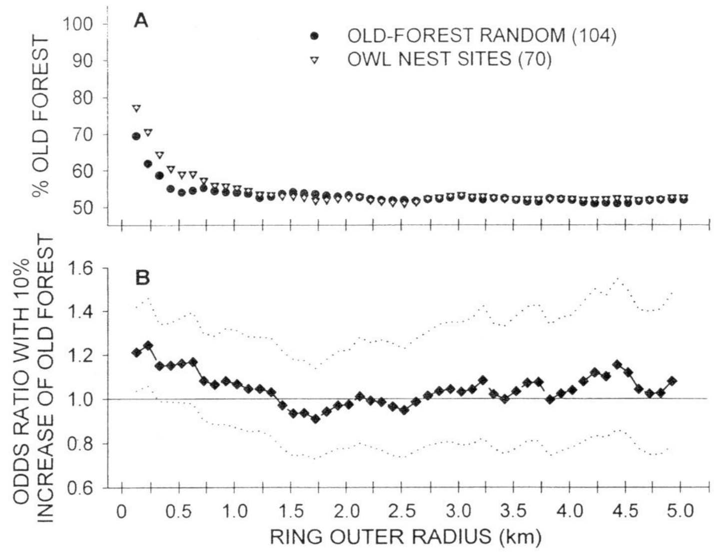

Fig. 3. Old forest in 50 concentric 100-m-wide ring-plots around northern spotted owl nest sites and old-forest random points in the central Cascade Mountains, Oregon, 1987–95. (A) Percentage of old forest, and (B) odds associated with a 10% increase of old forest in ring $x + 1 = e^{(10)\beta}$. The dotted lines in (B) indicate 95% confidence intervals.

assess association between spotted owl nests and habitat distribution. We considered habitat or forest distribution to mean the arrangement of forest relative to each analyzed point, and we used 3 approaches to analyze our data. Concentric circle-plot analyses are useful to land managers, are commonly used (Ripple et al. 1991*b*, Hunter et al. 1995, Ripple et al. 1997, Meyer et al. 1998), and are most analogous to owl home ranges. The technique, however, has been criticized for lacking independence across scales because a circle of given size includes all circles of smaller size (Ramsey et al. 1994). Because of this plot arrangement, a habitat difference detected at large plot sizes might be an artifact of differences occurring in smaller plots

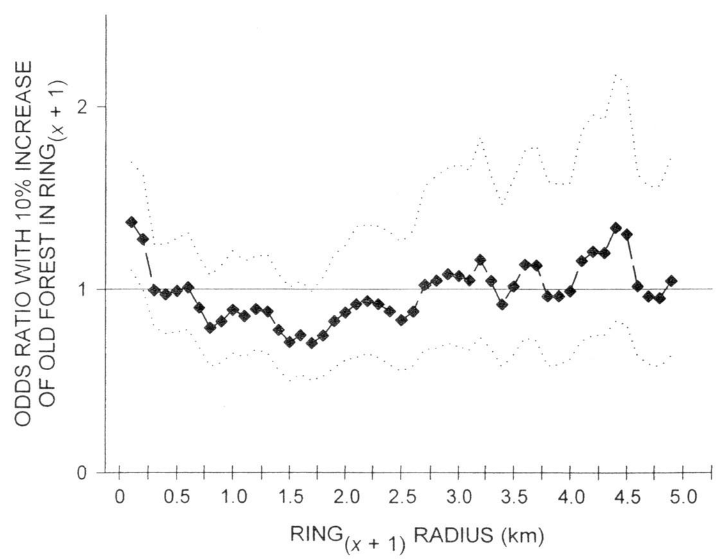

Fig. 4. Odds associated with a 10% increase of old forest in Ring $x + 1 = e^{(10)\beta}$ in 50 circle + ring plots around northern spotted owl nest sites and old-forest random points in the central Cascade Mountains, Oregon, 1987–95. The dotted lines indicate 95% confidence intervals.

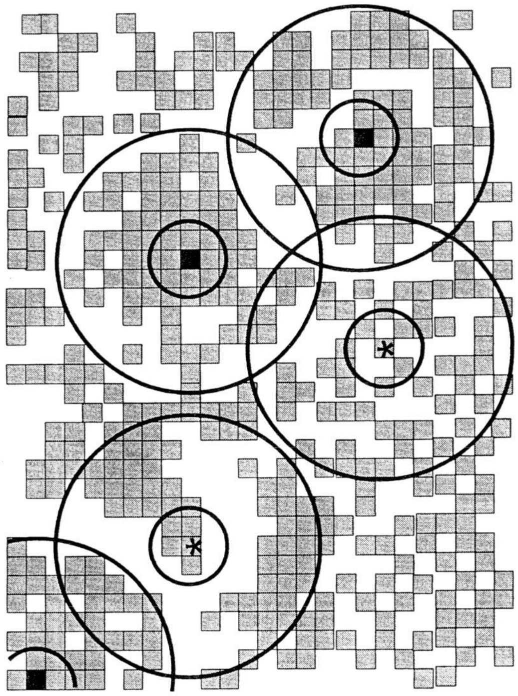

Fig. 5. Hypothetical landscape with 50% old-forest cover depicting forest distribution relative to northern spotted owl nests where shaded squares represent old-forest habitat, blackened squares represent typical northern spotted owl nests, and asterisks depict typical old-forest random points. In contrast to circles around old-forest random points, inner circles around owl nests encounter more old-forest squares along their perimeters and fewer old-forest squares along outer circles.

(Ramsey et al. 1994). Therefore, nonoverlapping ring-plots can provide additional information because they are more spatially independent. Nevertheless, circular plots may elucidate the amount of old forest typically found in spotted owl home ranges.

The ring-plot analyses were instructive because they indicated that the amount of old forest differed most in rings of a smaller maximum size than was detected in circle-plots. Thus, they elucidated the scales contributing most to the observed differences in the circle approach and indicated old forests were relatively clumped in distribution around spotted owl nests. However, concentric rings can also lack independence due to spatial autocorrelation with adjacent rings.

The circle + ring analyses mathematically accounted for the correlation problems of the other analyses by treating the amount of old forest in the inner area of a plot (Circle x) and the outer area of a plot (Ring $x + 1$) as separate variables (Ramsey et al. 1994). The circle + ring model set identified the scales contributing most toward distinguishing spotted owl nests from old-forest random points and may indicate the landscape scale most important to spotted owls for nest-site positioning. Because each set of analyses provided unique insights and inferences, we believe they were biologically most

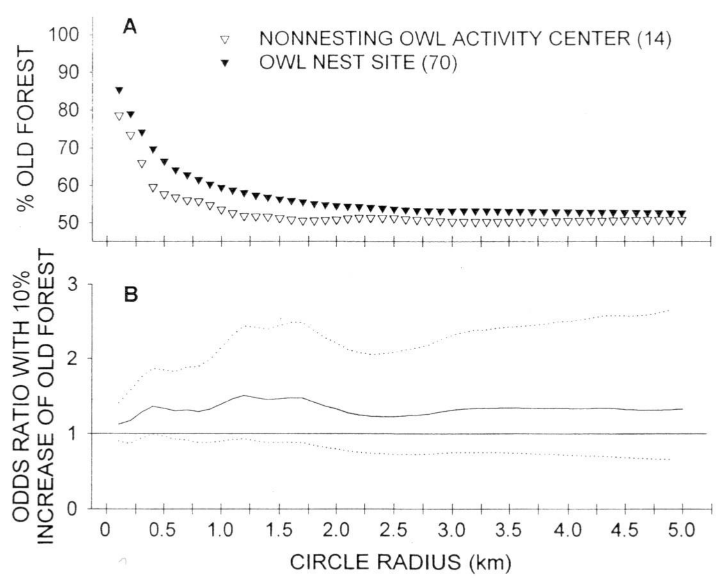

Fig. 6. Old forest in 50 concentric circle-plots around 14 nonnesting northern spotted owl activity centers compared to 70 activity centers with nest sites, central Cascade Mountains, Oregon, 1987–95. (A) Percentage of old forest, and (B) odds of nesting associated with a 10% increase of old-forest = $e^{(10)\beta}$. The dotted lines in (B) indicate 95% confidence intervals.

useful and interpretable when viewed in combination.

Our analyses suggest spotted owl nests were associated with clumped distributions of old forest and indicated the influence of old forest on nest-site selection was greatest near the nest. These findings agree with other studies where nests were consistently positioned in forest patches that were larger, on average, than were generally available (Ripple et al. 1997).

The trend of increased association of old forest with decreased distance from the nest is biologically intuitive, from an energetics standpoint, for central-place foraging species like spotted owls. Additionally, use of large areas of old-forest habitat is understandable for a species that tends to specialize on medium-sized prey items that occur at low densities (Forsman et al. 1984; Carey et al. 1991, 1992; Rosenberg and Anthony 1992, Carey 1993), especially on a landscape that primarily consists of either unmanaged older forests or young plantations.

The relation between fitness parameters and the amount and arrangement of old forest remains unclear (Noon and Biles 1990, Murphy and Noon 1992). However, our comparison of nests versus activity centers of spotted owls that did not nest during the study indicates that a relation may exist between spotted owl productivity and the amount of old forest. This finding was consistent with Ripple et al. (1997) who suggested a relation may exist between spotted owl reproductive performance and proportion of old conifer forest within 1,826-ha (2.4-km) plots in southwestern Oregon. Meyer et al. (1998) found that sites occupied by spotted owls differed from random landscape locations by having more old growth, larger than average old-growth patches, and larger maximum size of old-growth patches in all plot sizes investigated (0.8-, 1.6-, 2.4-, and 3.4-km radii). However, they failed to identify relations between the amounts of old-forest classes and reproduction. In northern California, Franklin (1997) found that annual survival of spotted owls on territories was positively associated with both amounts of interior old-growth forest and length of edge between those forests and other vegetation types. Contrary to our results, however, he found reproductive output to be negatively associated with interior forest but positively associated with edge. His findings may differ solely because of the markedly different habitat, climatic conditions, and prey ecology of his study area. Nevertheless, the relation between amount of structurally complex forest and spotted owl reproduction warrants further inquiry.

The observational design of this study disallowed exclusion of alternative explanations for the patterns observed. For example, foresters may have avoided spotted owl nest areas when harvesting trees. We doubt this explanation, however, because many of the spotted owl pairs in our study were not known prior to 1988, when data for our habitat map were collected. Also, there was little reason for foresters to follow specific guidelines regarding spotted owl nests and harvest units prior to that time.

For several reasons, our results may be conservative in terms of spatial scale. First, while typical of federal lands (excluding wilderness) in the Oregon Cascades, the studied landscape had few or no unfragmented areas; thus, in a fairly uniformly fragmented landscape, spotted owls were associated with more old forest than was generally available. Second, habitat classification was based on satellite imagery, which was arguably less accurate than aerial photo interpretation and appeared to yield lower estimates of old-forest habitat. Third, because spotted owls exhibit high affinity and tenacity to home ranges and favored nest locations, they may continue to reside and nest in specific locations in spite of adjacent habitat alterations subsequent to original selection of the site. In other words, spotted owl pairs may select a particular nest site prior to habitat alteration and then continue using it even if conditions affecting their survival and reproductive potentials (or those of their young) have changed.

The findings discussed here, both in terms of habitat association and habitat distribution, depended on the dichotomous nature of the habitat conditions in the study area: forests tending to be either very young (nonhabitat) or very old (structurally and biologically complex) and relatively uniform within patches. These associations will likely prove more difficult to demonstrate in regions where there are more intermediate-aged forests, or where uneven-aged forests are common because of human or natural disturbance regimes.

Circular plots inadequately describe actual spotted owl home ranges. However, researchers have demonstrated the feasibility of using them in place of radiotelemetry for habitat-related inquiry (Lehmkuhl and Raphael 1993). One way to account for the added variability caused by using circles is to use large samples.

MANAGEMENT IMPLICATIONS

The common assumptions that a core area is important for spotted owls, and sensitivity to habitat loss is greater closer to the nest site, are supported by this study. On our study area, the landscape scales of most pertinence to spotted owl nest-site location when considering the proportion of old forest seem to be (in descending order) (1) the surrounding 10–15 ha (approx 200-m radius; results from circle + ring analysis), (2) the surrounding 30–115 ha (approx 300–600-m radius; results from ring-plot analysis), (3) the surrounding 200 ha (800-m radius; results from circle-plot analysis), and (4) possibly the surrounding 700 ha (1,500-m radius; results from circle + ring analysis). Because individual spotted owl pairs in our 9-year study used as many as 5 different nest trees (within a 10-ha area), it seems important to provide core areas large enough for multiple nest sites. The exact spatial results reported above are specific to spotted owls in this study area and are likely to be different for other parts of the spotted owls' range. However, the general trend of higher amounts of structurally complex habitat nearer to the nest likely applies to other portions of the subspecies' range.

These results do not indicate that old-forest habitat beyond 800 m from a nest site is unimportant to spotted owls. In this study area, mean home range size was nearly 1,800 ha (G. S. Miller and E. C. Meslow, Oregon State Universty, unpublished data), which is approximated by a circular area of 2,400 m in radius. Thus, spotted owls in this area use old-forest habitat >800 m from the nest. The degree to which old-forest habitat beyond this distance is important or is offset by greater amounts of old-forest habitat ≤800 m from the nest is unknown. However, our comparison of landscapes surrounding nesting spotted owls versus landscapes surrounding nonreproductively active spotted owls indicated the odds of nesting increased by 50% for every 10% increase of old forest within a 1,200-m-radius circle.

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