AN ABSTRACT OF THE THESIS OF

John P. Perkins for the degree of Master of Science in Forest Resources presented on May 25, 2000. Title: Land Cover At Northern Spotted Owl Nest and Non-nest Sites, East-central Coast Ranges, Oregon.

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William J. Ripple

This study examined the differences, at various scales, between northern spotted owl (*Strix occidentalis caurina*) nest sites and non-nest sites, i.e., sites where no nests were found during surveys, in the Coast Ranges of Oregon. I compared land cover around 41 owl nest sites (ONS) and 41 non-nest sites (NNS) at 5 different landscape scales (0.6-, 1.2-, 1.8-, 2.4-, and 3.0-km-radius circles). I also compared characteristics of 29 old-growth (overstory trees >86-cm diameter-at-breast-height [dbh]) patches where owl nest were found (ONP) with characteristics of 29 old-growth patches where no nest were found (NNP). All sites were in the Eugene District, Bureau of Land Management.

Land cover was classified into 8 categories and typed from aerial photographs. I quantified land-cover indices using a geographic information system and used logistic regression for binary responses to make statistical inferences.

At the 0.6-km-radius circle, percentages of old-growth and old-remnant (young conifer stands with some large-diameter trees) forests were the best predictors of

difference between ONS and NNS, being greater at ONS. The even distribution of forest cover types, as calculated using Simpson's Evenness Index, was also a good predictor of this difference, being more even at ONS. At the 1.2-km-radius circle, GISfrag, i.e., the mean distance among old-growth patches, was the best predictor of difference between ONS and NNS, being greater at NNS. At 1.8-, 2.4-, and 3.0-km-radius circles, the percentage of pole-young ("even-aged" conifer stands; trees 13-53-cm dbh) forests was the best predictor of difference between ONS and NNS, being greater at NNS. However, differences in all of these landscape indices between ONS and NNS, including GISfrag and percentage of pole-young forests, were greatest at the smallest circle size, and differences decreased as circle size increased.

At the old-growth patch scale, the ratio of core area (interior patch area >100 m from the outer patch edge) to patch size and complexity of patch shape were the best predictors of difference between ONP and NNP, being greater at ONP. Furthermore, spotted owls tend to nest in old-growth patches, particularly those ≥40-50 ha in size and with a ratio of core area to patch size ≥0.20-0.30.

This study supports assertions that spotted owl nest sites are associated with old-growth forests. Nest sites were also associated with old-remnant forests. Spotted owls avoid pole-young forests for nest sites.

Land Cover At Northern Spotted Owl Nest and Non-nest Sites,

East-central Coast Ranges, Oregon

by

John P. Perkins

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LIST OF ACRONYMS AND ABBREVIATIONS

BLM - Bureau of Land Management
OCFWRU- Oregon Cooperative Fish and Wildlife Research Unit

UTM - Universal Transverse Mercator
GIS - Geographic Information System
POS - Probability of Selection
AIC - Akaike's Information Criterion

ONS - owl nest sites
NNS - non-nest sites
ONP - old-growth nest patches
NNP - old-growth non-nest patches

NF - Non-forest (or percentage of)
OS - Open-sapling forest (or percentage of)
BM - Broadleaf-mix forest (or percentage of)
PY - Pole-young forest (or percentage of)
MY - Mature-young forest (or percentage of)
MA - Mature forest (or percentage of)
OR - Old-remnant forest (or percentage of)
OG - Old-growth forest (or percentage of)

RPR - Relative patch richness
SIEI - Simpson's evenness index
EDHC - Edge density high contrast
EDOG - Edge density old-growth
PDOG - Patch density old-growth
MINOG - Minimum sized old-growth patch
MAXOG - Maximum sized old-growth patch
MPSOG - Mean patch size old-growth
LCAOG - Landscape core area old-growth
GISfrag - Mean distance among old-growth patches

OGPS - Old-growth patch size
OGCA - Old-growth patch core area
RATIO - Ratio of core area to old-growth patch size
SHAPE - Old-growth patch shape

LAND COVER AT NORTHERN SPOTTED OWL NEST AND NON-NEST SITES, EAST-CENTRAL COAST RANGES, OREGON

INTRODUCTION

Loss and fragmentation of forest communities is the prevailing trend of landscape change in human-dominated regions of the world, and a major cause of declining bio-diversity (Whitcomb et al. 1981, Terborgh 1989, Groombridge 1992). Loss of forests is a landscape-level process in which forest area decreases, and forest stands (patches) become more isolated. Forest fragmentation is a landscape-level process in which forest patches are progressively sub-divided into more and smaller fragments (Fahrig 1997). Loss and fragmentation of late-successional forest (>80 years) produces a series of remnant late-successional patches surrounded by a matrix of early-successional vegetation (<80 years). Three primary effects of forest loss and fragmentation are decreased remnant patch size, increased isolation of remnant patches from other remnants, and an alteration of microclimates within and surrounding the remnant patch (Saunders et al. 1991, Chen et al. 1995, Fahrig 1997). Thus, in a landscape where forest loss and fragmentation occur, there are physical and biological changes in the environment (Saunders et al. 1991).

In the decades of the 1940s through the 1980s forest cutting in western Oregon focused on clear-cut harvest and establishment of Douglas-fir plantations (Swanson and Franklin 1992). Forest stands were mostly harvested in clear-cut units of <100 ac (45 ha, Smith et al. 1997). By the 1960s, cable logging in old-growth forests (>200 years) made it desirable to clear-cut larger areas (Smith et al. 1997), especially on private land (Spies et al. 1994). As a result, large tracts of late-successional forests in the Pacific Northwest were clear-cut and fragmented into smaller isolated patches (Spies et al. 1994, Ripple 1994).

Studies of forest use in this region indicate that northern spotted owls (*Strix occidentalis caurina*) generally select late-successional forest and particularly old-growth forest equal to or more than expected, and early-successional forests less than expected (Forsman 1980, Forsman et al. 1984, Solis and Gutiérrez 1990, Carey et al. 1992). Because of its association with late-successional forests and the rapid decline of these forests, the northern spotted owl was listed as a federally threatened species by the U.S. Fish and Wildlife Service effective July 23, 1990 (Federal Register 55 [123]: 26114-26194).

Most forest association studies for the northern spotted owl have been conducted where the owls were known to occur, deriving positive correlations for owl presence and some habitat features (Forsman et al. 1984; Carey et al. 1990; Solis and Gutiérrez 1990; Ripple et al. 1991, 1997; Blakesley et al. 1992; Lehmkuhl and Raphael 1993; Buchanan et al. 1993; Hunter et al. 1995; Meyer et al. 1998). While these studies provide information to predict where owls can occur, the owl-forest correlation is incomplete. To verify forest correlates to the presence of owls, documentation is required in areas where owls do not occur. Comparisons made between used and non-used sites, as opposed to use-versus-availability, determine those features that are both positively and negatively correlated with the observed patterns of selection. In this way, used and non-used sites can be described and predictions of occurrence can be calculated and applied directly to explicit binary response outcomes, i.e., used-versus-non-used sites.

The main goal of this study was to meet the needs of conservation managers by identifying, on landscape and patch scales, those features most associated with areas of high and low use potential for spotted owl breeding sites in the Coast Ranges of Oregon. In this way, features associated with used sites can be validated, and features associated with non-used sites can be targeted for management to increase the odds of use as breeding sites.

Specific objectives are presented below.

Objective 1: To identify landscape features, at several scales, that best discriminate between spotted owl nest sites and non-nest sites in the Coast Ranges of Oregon. Landscape features include composition (amount of land cover types) and pattern. Non-nest sites are sites where nests were not found during surveys.

Objective 2: To identify features that best discriminate between old-growth nest patches and old-growth non-nest patches. The term "patch", as used here, describes a forest stand, i.e., a distinguishable unit (Smith et al. 1997:11). Non-nest old-growth patches are old-growth patches where nests were not found during surveys.

STUDY AREA

The 1,978 km^2 study area was located in the east-central Coast Ranges of Oregon (43 47'-44 17' N, 123 08'-123 44'; Fig. 1). This area included the Coast Range Resource Area and western portions of the South Valley Resource Area on the Eugene District, BLM, and some adjacent lands including portions of the Siuslaw National Forest, Roseburg District, BLM, and rural areas adjacent to the southern Willamette Valley. The landscape of this study area is mostly a checkerboard pattern of alternating square mile (1.6 km^2) sections comprised of BLM (33%) and private (60%, mostly industrial timber companies). State of Oregon (4%), and national forest (3%) lands comprise the rest of the area (Fig. 1).

The topography is steep with narrow ridges and deeply incised drainage; elevation ranges from 120 to 870 m above MSL. The climate is maritime with mild, wet and cloudy winters, and relatively dry summers. Precipitation typically ranges from 1,700 to 3,000 mm, approximately 80% of which occurs between October 1 and March 31 (Franklin and Dyrness 1988).

Vegetation is dominated by conifers, primarily Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*; Franklin and Dyrness 1988). Red alder (*Alnus rubra*) often pioneers on disturbed sites or is associated with bigleaf maple (*Acer macrophyllum*) on riparian areas.

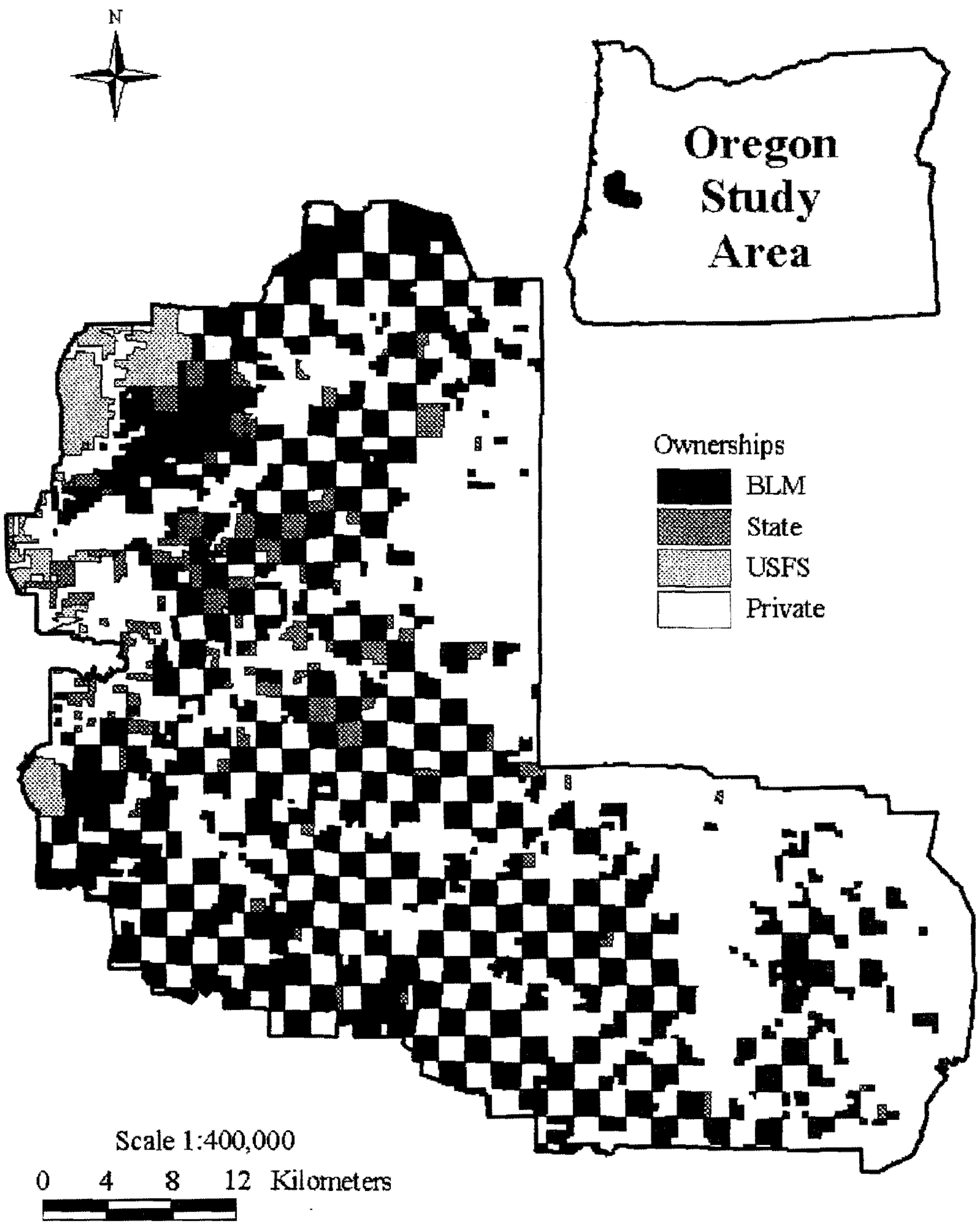

Figure 1. Map of the study area (1,978 km2) in the east-central Coast Ranges of Oregon.

METHODS

I proceeded with this study in the following 5 steps:

1. Nest surveys—survey methods were used as part of a completed demographic study; spotted owl nest-site locations were collected by biologists from Oregon State University (OSU).

2. Landscape mapping—the mosaic of land cover types for the whole study area was mapped from interpretation of aerial photos. Ground visits to a sample of forest patches were used to assess mapping accuracy.

3. Selection of study sites—41 owl nest sites (ONS) were selected from the list provided by OSU biologists, and 41 non-nest sites (NNS) were selected based on survey information. In addition, 29 old-growth nest patches (ONP) were selected from the lists provided by OSU biologists, and 29 old-growth non-nest patches (NNP) were selected based on survey information.

4. Calculation of land-cover indices—using the map of forest cover types generated in step 3, indices of landscape features were calculated at each ONS and NNS for each of 5 successively larger circular plots (0.6, 1.2, 1.8, 2.4, and 3.0-km-radii). Indices of old-growth patch features were calculated for each ONP and NNP.

5. Statistical analyses—I compared landscape indices between ONS and NNS, and compared old-growth patch indices between ONP and NNP to determine which indices best discriminated between nest and non-nest sites.

The following subsections describe, in detail, the methods used in those 5 steps.

Nest Surveys

The entire western portion of the Eugene District, BLM, including non-BLM sections, was surveyed annually for spotted owls between 1 April and 30 August 1990 through 1995. These surveys were conducted as part of a spotted owl demography and habitat study conducted by the Oregon Cooperative Fish and Wildlife Research Unit, OSU (Thrailkill et al. 1998). Locations of spotted owl nest trees were plotted on topographic maps in the field and Universal Transverse Mercator (UTM) locations for nest sites were recorded. A total of 63 nest trees were located in 43 owl-breeding territories (Thrailkill et al. 1998).

Landscape Mapping

I used natural color aerial photos (scale 1:12,000) taken in 1990 to produce a land-cover map of the study area. A stereoscope was used for interpretation of 7 forest cover-types and non-forest (Table 1). I designed the classification scheme to encompass the broadest range of forest-successional stages and structural features interpretable from aerial photos. Only patches estimated to be ≥1 ha in size were delineated. Mapped landscapes on aerial photos were transferred by hand onto acetate overlays on 7.5-min. quadrangle base maps (scale 1:24,000) and digitized for analysis (Fig. 2).

Table 1. Classification scheme for cover types in the east-central Coast Ranges of Oregon. Landscape mapping was based on interpretation of 1:12,000 scale aerial photos taken in 1990.

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1. Non-forest (NF) -- All areas not producing a stand of trees. These include agricultural lands, open water, rock outcrops, permanent brush fields and developed areas.

2. Open-sapling (OS) -- All areas, other than non-forest, with <40% canopy closure. Open patches might range from mostly devoid of vegetation to mostly covered by herbaceous species or heavily thinned forest. All sapling patches (<13-cm diameter-at-breast-height [dbh]) were included, regardless of canopy closure. Sapling patches were usually replanted conifers, but hardwood sprouts and shrubs might be in greater cover proportion than conifers.

3. Broadleaf-mix (BM) -- Red alder and big-leaf maple compose 40% of the over-story canopy. Patches with >60% broadleaf species are often associated with roadsides and riparian zones. Patches with 40-60% broadleaf species were often transition zones between riparian zones and upland areas.

4. Pole-young (PY) – Over-story trees were mostly conifers 13-53-cm dbh. These "even-aged" patches were <80-yrs old.

5. Mature-young (MY) -- These patches were mostly conifers 13-53-cm dbh with 10-60 conifers/ha that were 53-86-cm dbh. A small element of conifers >86-cm dbh might be present.

6. Mature (MA) -- Patches with >60 conifers/ha that were 53-86-cm dbh. Some conifers >86-cm dbh might be present.

7. Old-remnant (OR) -- These patches were mostly conifers 13-53-cm dbh with 2-22 conifers/ha that were >86-cm dbh. A small element of conifers 53-86-cm dbh might be present. These stands were produced by fire and selective timber harvest that left some large remnant trees intact while new forest replaced most of the previous patch.

8. Old-growth (OG) -- Patches with >22 conifers/ha that were >86-cm dbh. These stands typically have multi-layered and multi-species canopies, large trees and snags, and large down woody debris.

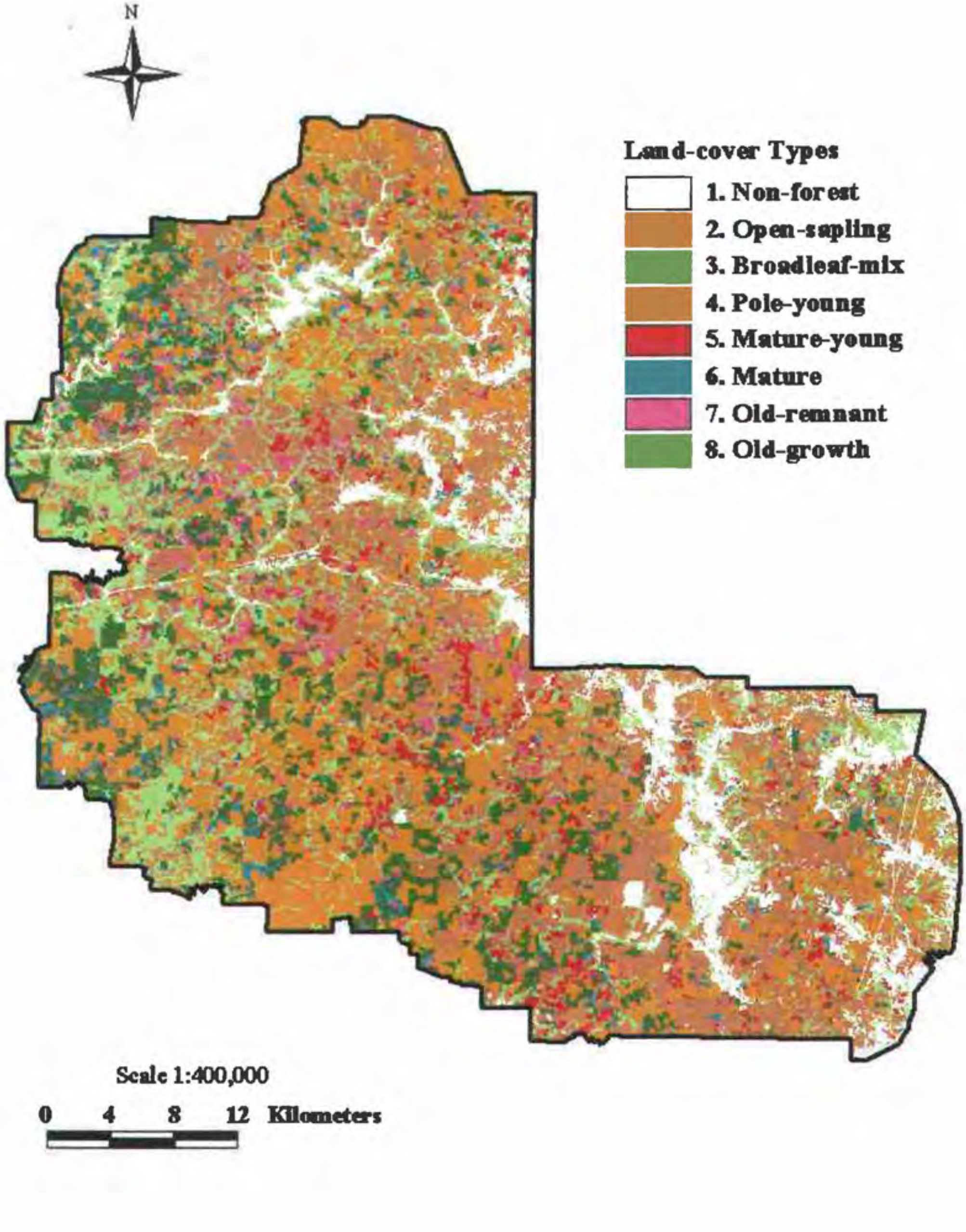

Figure 2. Land-cover map of the 1,978 km^2 study area in the Coast Ranges of Oregon; based on interpretation of aerial photos taken in 1990.

I visited 33 randomly selected areas on the study area, each approximately 4 km^2 in size. Within each 4 km^2 area, I randomly selected one patch of each cover type that was present and visited that patch to determine if it was correctly classified. The random sample of patches I visited were restricted to patches that were within 200 m of a road, i.e., that were easily accessible.

Overall map classification accuracy for the total 131 polygons sampled was 86% (Table 2). The Kappa statistic is an indicator of the percentage correct values in an accuracy evaluation due to actual agreement versus chance agreement (Lillesand and Kiefer 1994:616). Based on this small sample, the Kappa statistic was 84%.

Table 2. Error matrix for the cover-type map, east-central Coast Ranges, Oregon. Landscape mapping was based on interpretation of 1:12,000 scale aerial photos taken in 1990. Column totals represent the number of times sample patches were accurately classified (producer's accuracy). Row totals represent the number of times sample patches actually represented that type on the ground (user's accuracy).

Cover Types[a]	OS	BM	PY	MY	MA	OR	OG	Total
OS	4	0	0	0	0	0	0	4
BM	0	26	1	0	0	0	0	27
PY	0	1	24	0	0	0	0	25
MY	0	0	0	11	2	4	0	17
MA	0	1	0	1	11	0	1	14
OR	0	0	0	3	3	16	1	23
OG	0	0	0	0	0	0	21	21
Total	4	28	25	15	16	20	23	131
Producer's Accuracy	100%	93%	96%	73%	69%	80%	91%	
User's Accuracy	100%	96%	96%	65%	79%	70%	100%	

Overall accuracy = (4 + 26 + 24 + 11 + 11 + 16 + 21) / 131 = 86%

[a]OS = open-sapling; BM = broadleaf-mix; PY = pole-young; MY = mature-young; MA = mature; OR = old-remnant; OG = old-growth. Non-forest patches were not visited.

Selection of Study Sites

Selection of owl nest sites.—I selected 41 of the 43 territories in which owl pairs nested in 1990-1995. The 2 territories not included in my sample were dropped because they were not completely mapped. Spotted owl pairs often use several nest sites in the same breeding territory during different years (Forsman et al. 1984, Forsman and Giese 1997). I, therefore, selected the nest site with the greatest number of recorded nesting attempts to use as plot center for 7 owl territories with multiple nests. I randomly selected 1 nest location to use as plot center for 7 other territories with multiple nests, each with the same number of recorded nesting attempts. The remaining 27 owl territories had 1 known nest site each.

Selection of non-nest sites.—It is important to have a balanced study to optimize the precision for treatment comparisons, and because the sampling distribution for binomial data is nearly normal for small sample sizes if the proportional mean (π) is near one-half (Ramsey and Schafer 1997). I, therefore, randomly selected, without replacement, 41 NNS for comparison. I restricted selection of NNS to cover types where spotted owls were likely to nest, which included all types represented except open-sapling and non-forest. In addition, I used a simple inhibition process (Diggle et al. 1976) to spatially separate NNS from ONS and other NNS by 1,260 m (nearest distance between nest sites of different pairs in the same year). This inhibition process spatially distinguished landscapes around ONS from that at NNS and served to distribute NNS over the landscape similar to that of ONS (Fig. 3).

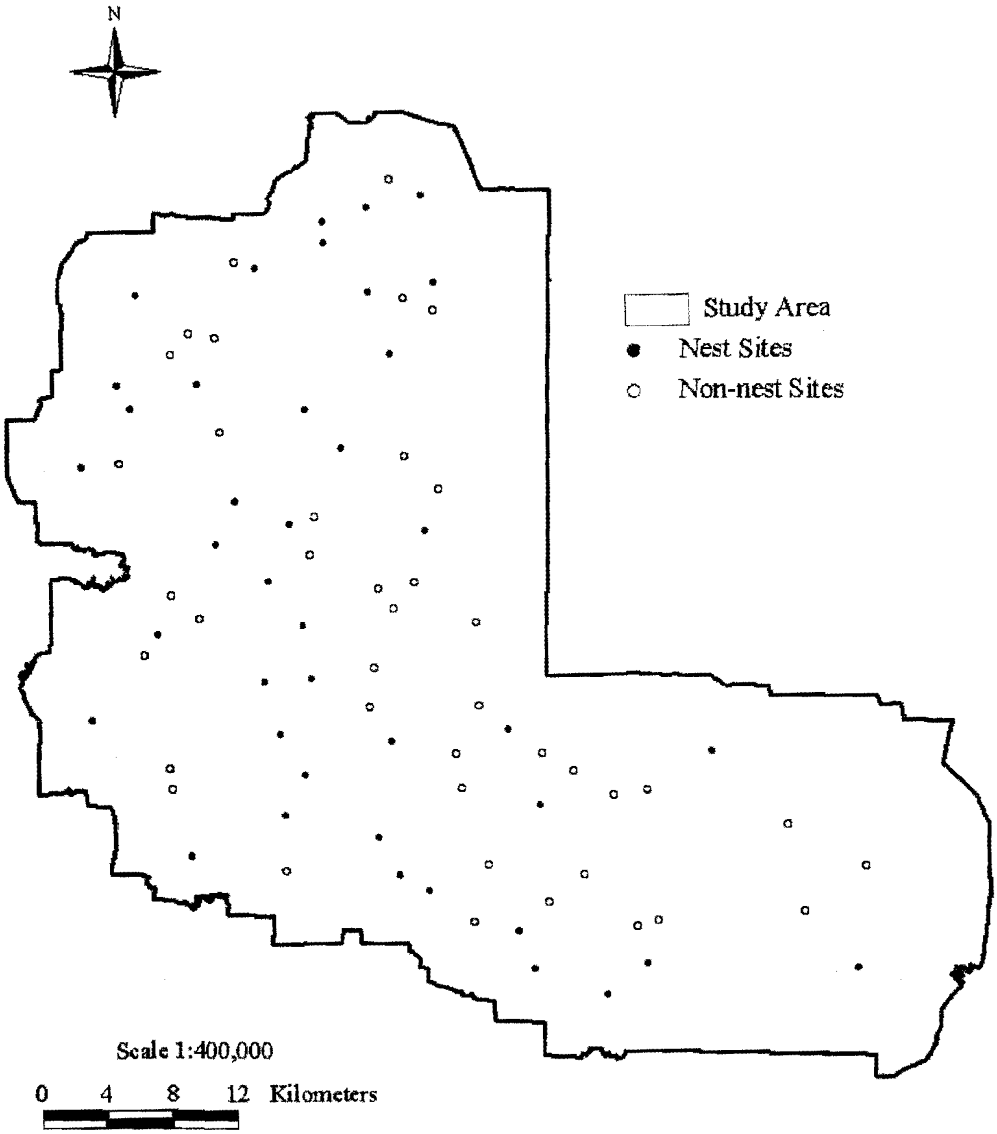

Figure 3. Black circles represent owl nest sites and open circles represent non-nest sites. All nest and non-nest sites were spatially separated by at least 1,260m; all sites were located within the Eugene BLM boundary; and sites were located in all but non-forest and open-sapling cover types. Spotted owl surveys were conducted from 1990 through 1995 in the east-central Coast Ranges of Oregon.

Selection of old-growth nest patches.—Over the period of study, 30 of 41 known owl pairs attempted to nest in 33 different old-growth patches. One owl pair nested in 2 old-growth patches, and another pair nested in 4 old-growth patches during the survey period from 1990 to 1995. Two other owl pairs nested in the same large old-growth patch. I selected 29 ONP from the 33 old-growth patches in which owl pairs nested. I randomly selected one ONP for each of the 2 owl pairs that nested in >1 old-growth patch. The old-growth patch where two different pairs nested was represented only once in the data set (Fig. 4).

Selection of old-growth non-nest patches.—I selected 29 NNP from 690 old-growth patches that were completely mapped and where no nests were found during the survey period (Fig. 4). The size range of non-nest old-growth patches was large. I, therefore, sorted non-nest old-growth patches by patch size and used stratified sampling to capture the variability of non-nest patch size while maintaining a balanced study (Krebs 1989). There were 24 patches per strata, i.e., 690 patches ÷ 29 strata = 24 patches per strata. I randomly selected a number between 1 and 24 to select a patch from the smallest strata of patch sizes. I, then, systematically, added 24 to that random number to select a patch from the next patch-size strata and proceeded in that systematic fashion to sequentially select a patch from each of the 29 patch-size strata.

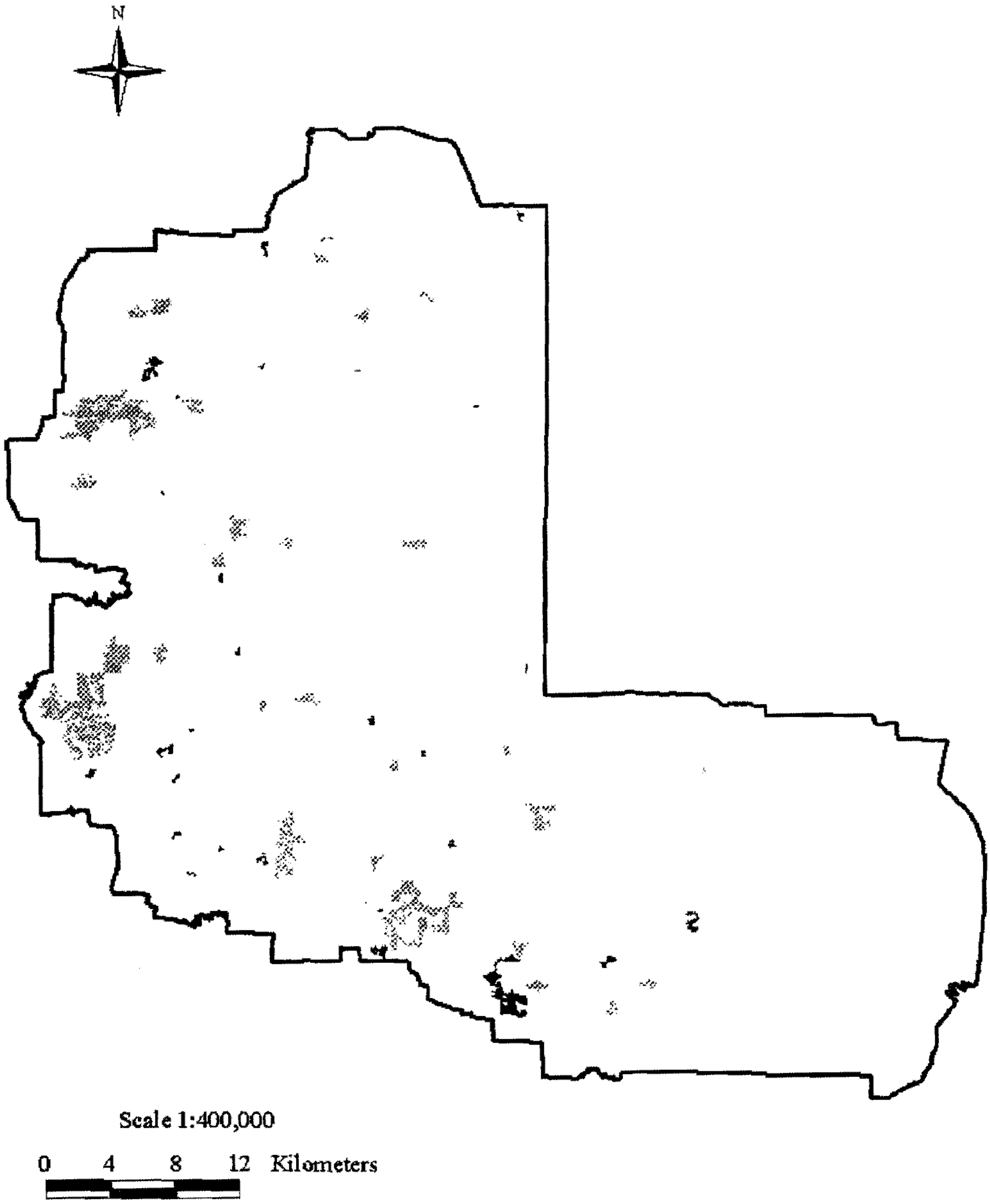

Figure 4. Locations of old-growth patches used by spotted owls (gray patches) as nest sites and old-growth patches where nests were not found during spotted owl surveys (black patches). The surveys were conducted from 1990 through 1995 in the east-central Coast Ranges of Oregon.

Within the range of an organism, the absence of that organism from a particular site cannot be determined, but it can be inferred based on repeated surveys during appropriate seasons and conditions. For this study, non-nest sites represent sites where nest were not found during surveys.

Confidence in non-used sites is essential when making used-versus-non-used comparisons. To evaluate the minimum amount of cover-type area surveyed on the study area, GIS was used to delineate a 0.5-mile-radius 'calling area' centered on all survey stations. The encompassed proportions of cover types within calling areas were then compared to the total amount of cover types available on the study area. Survey experience indicated that the 0.5-mile radius is reasonable and is probably the minimum limit of an effective calling radius, especially when call stations are located on prominent points such as log-landings, where the majority of survey stations were placed.

I believe there was extensive coverage of the total survey area based on 3 facts: (1) across the mapped study area and as calculated by the 0.5-mile radii, approximately 95% of OG, OR, MA, and MY and 70% of OS, BM, PY, and NF was surveyed; (2) all nest and non-nest sites were located within the Eugene District, BLM boundaries, but a large portion of OS, BM, PY, and NF on the mapped study area was located outside those boundaries; and (3) roadless areas, not included in the calling area analysis, were also surveyed. In addition, the proportion of nest trees found during surveys increased with each successive visit to the sites and equaled 0.923 after the minimum 6 visits (Table 3). Furthermore, the best demographic survival models, as reported by

Thrailkill et al. (1998), did not indicate any time effects on re-sighting probabilities for sub-adult and adult birds, suggesting broadcast surveys were consistent each year.

Table 3. The proportion of nest trees found per number of survey efforts (visits), or the probability[a] of finding a nest tree per number of visits in all areas where no nest sites were previously found. These data are based on all known owl sites, demography study of the northern spotted owl, Eugene District, Bureau of Land Management, Oregon, 1990-1995.

Number of Visits	**1**	**2**	**3**	**4**	**5**	**6**	**>6**
Proportion of Nest Trees Found	0.10	0.44	0.62	0.74	0.90	0.92	1.00

[a]The probability of finding a nest tree is based on the assumption that all spotted owl nest sites were located on the study area each of the 6 years surveyed.

Calculation of Land-cover Indices

Calculation of Landscape Indices.— I compared landscape structure between 41 ONS and 41 NNS at 5 concentric circle sizes, including 0.6-km radius (112 ha); 1.2-km radius (456 ha); 1.8-km radius (1,037 ha); 2.4-km radius (1,844 ha); and 3.0-km radius (2,815 ha; Fig. 5). Minor differences between total area per plot size as presented here and πr^2 calculations are due to use of raster-based images and the 25-m grid cell size.

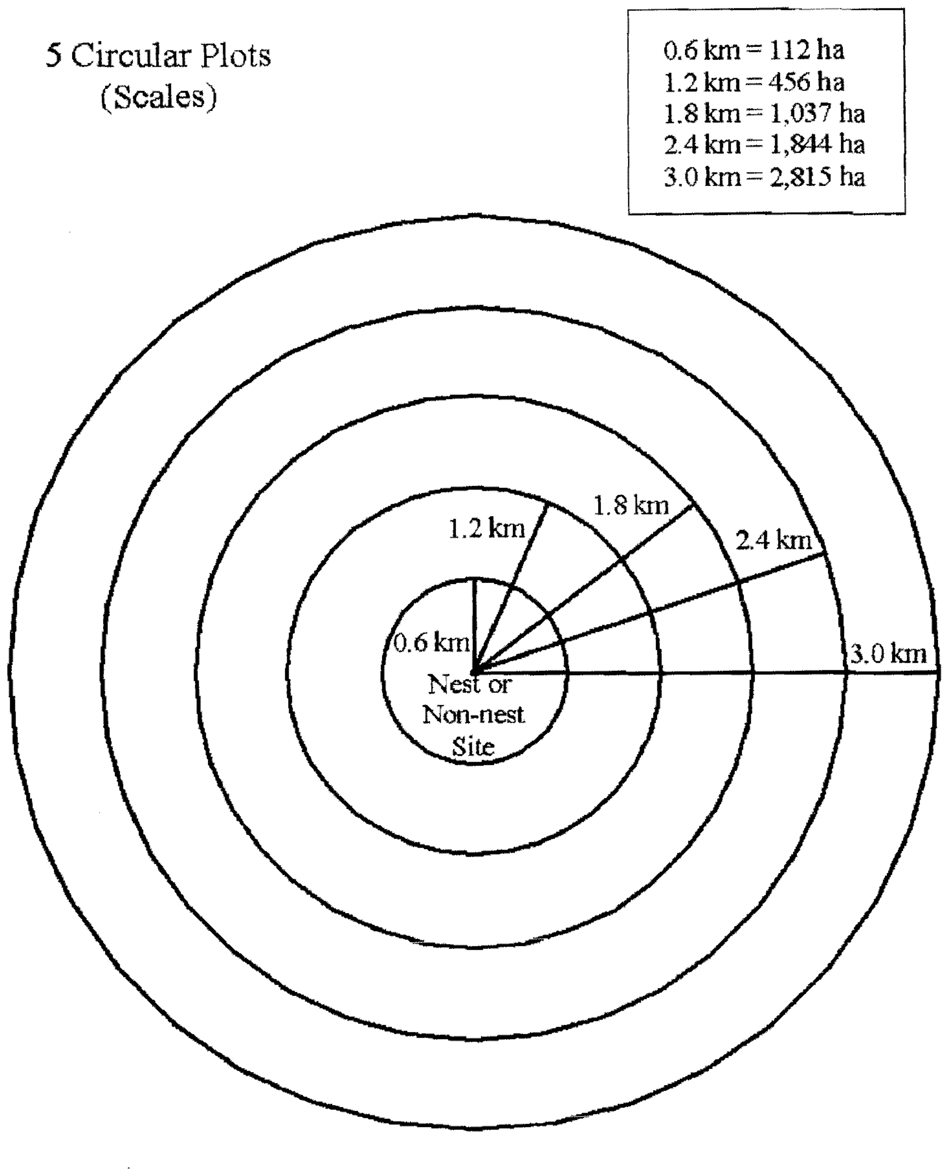

Figure 5. Illustration of the 5 concentric circular plots (scales) used for landscape analyses. Landscape features were compared between spotted owl nest and non-nest sites. Surveys were conducted from 1990 through 1995 in the east-central Coast Ranges of Oregon.

Many landscape indices are computable, represent different scales and effects of landscape structure, and might be more or less difficult for land managers to interpret and manipulate. Within each of the 5 circular plots, I analyzed 18 different indices of landscape pattern that I hypothesized to be ecologically meaningful to the owls while being of interpretive value to biologist and forest managers. (Table 4).

Table 4. Abbreviations and brief descriptions for the 18 landscape indices, divided into the following 5 categories: cover types, composition diversity, edge density, old-growth patches, and old-growth loss and fragmentation.

Index	**Description**
Cover types:	
NF	% of non-forest.
OS	% of open-sapling forest.
BM	% of broadleaf-mix forest.
PY	% of pole-young forest.
MY	% of mature-young forest.
MA	% of mature forest.
OR	% of old-remnant forest.
OG	% of old-growth forest.
Composition diversity:	
RPR	Relative patch richness of patch types (% of cover types represented).
SIEI	Simpson's evenness index of the distribution of area among cover types (range of values = 0-1).
Edge density:	
EDHC	Edge density high contrast (range of values ≥0).
EDOG	Edge density old-growth (range of values ≥0).
Old-growth patches:	
PDOG	Patch density old-growth (range of values ≥0).
MINOG	Smallest sized old-growth patch (range of values >0).
MAXOG	Largest sized old-growth patch (range of values >0).
MPSOG	Mean patch size old-growth (range of values >0).
LCAOG	Landscape core area old-growth (% landscape in core area, where core is defined as interior patch area >100 m from the outer patch edge).
Old-growth loss and fragmentation:	
GISfrag	Mean distance among old-growth patches (range of values >0).

To calculate all landscape indices, I first used ERDAS IMAGINE (version 8.2) and the original cover-type image to produce 5 GIS layers covering the entire study area: (1) old-growth patches, (2) old-growth patch interior, (3) high-contrast perimeter, (4) old-growth perimeter, and (5) GISfrag, i.e., mean distance among old-growth patches. I used the RECODE model in IMAGINE to produce the old-growth patch layer. I used the RECODE and SEARCH (into old-growth patches) models on the old-growth patch layer to produce the layer representing old-growth patch interior. I used the RECODE and NON-DIRECTIONAL EDGE (Derivative Filter) models to produce the layers representing high-contrast and old-growth perimeter densities. Finally, I used the SEARCH (away from old-growth forests) model on the old-growth patch layer to produce the GISfrag layer. I, then, used the MASK model in IMAGINE to overlay circular plots produced in ESRI ARCINFO (version 3.5.1) on each GIS layer. All landscape indices were directly calculated in IMAGINE or by spreadsheet manipulation of those calculations.

For any given patch type (1-8), I calculated the amount (AREA) represented within a landscape boundary. AREA equals the sum area (ha) of a given patch type, divided by the total landscape area (ha) and multiplied by 100 to convert it to a %. Because northern spotted owls tend to be associated with late-successional forest (Forsman et al. 1984, Swindle 1998), the amount of these forests might be a good indicator of spotted owl breeding sites within home-range-size landscapes (Lehmkuhl and Raphael 1993). I would, therefore, expect some late-successional patch types to be a good predictor of nest-site selection and some early-successional or non-forest types to be associated with non-nest sites.

Patch richness measures the compositional component of cover-type diversity. Relative patch richness (RPR) equals the number of cover types present within a landscape, divided by the total number of cover types in the classification scheme, i.e., 8, and multiplied by 100 to convert it to a percentage. The RPR value approaches 0% with fewer cover types represented; it equals 100% when all cover types in the classification scheme are represented.

Northern flying squirrels (*Glaucomys sabrinus*) comprised 43.9% of the diet of spotted owls on my study area (Thrailkill et al. 1998:A-6). However, a wide variety of other species were, also, prey items (Thrailkill et al. 1998:A-6). Prey species might be widely distributed in several cover types, and some prey species might disperse into old-growth stands from younger forest (Sakai and Noon 1997). If cover-type diversity is important to prey availability, I would expect the value of RPR to be higher at ONS compared to NNS. If, however, spotted owls depend mostly on old-growth forest, I would expect lower RPR values near ONS compared to NNS. There is usually greater landscape heterogeneity over larger areas compared to smaller ones. I would, therefore, expect the value of RPR to increase as scale increased at both ONS and NNS.

Evenness measures the distribution of area among cover (patch) types. Simpson's Evenness Index (SIEI) "equals 1 minus the sum, across all patch types, of the proportional abundance of each patch type squared, divided by 1 minus 1 divided by the number of patch types" (McGarigal and Marks 1993:C52). SIEI equals zero when the landscape contains only 1 patch and approaches zero when patch types are disproportionately represented. SIEI equals 1 when all patch types in the landscape are equally represented (McGarigal and Marks 1993:C52). If homogenous landscapes of old-growth forest are important to nesting spotted owls, I would expect lower SIEI values at ONS compared to NNS, especially at smaller scales. If, however, owls prefer to nest in landscapes with several cover types, each well represented, I would expect higher SIEI values at ONS compared to NNS. Regardless of owl nesting preferences, highly fragmented landscapes at nest sites and monotypic landscapes at non-nest sites could produce higher SIEI values at ONS compared to NNS.

The amount of edge in a landscape might be important to wildlife-edge relationships. The more extreme the structural difference across edges, the more dramatic the effects on some species (Harris 1984). For example, the ecological processes (edge effects), such as light and wind intensity that effect changes in disturbance affects and microclimates, are greatly influenced by the degree of structural contrast between a patch and its neighbor (Chen and Franklin 1990). Brood parasites and avian nest predators are often associated with edges between forests and fields. Forest fragmentation increases the amount of edge, resulting in decreased reproductive success for some birds in remaining forest patches (Wilcove 1985). Some species, e.g., great horned owls (*Bubo virginianus*), seem to prefer edges with high contrast (Dunning et al. 1992). Great-horned owls are a predator on spotted owls and might compete with spotted owls for space (Thomas et al. 1990).

Edge density of high contrast (EDHC) equals the sum of the lengths (km) of all edge segments corresponding between forest patches of all types and open areas, i.e., NF or OS types, divided by the total landscape area (km^2). If amount of high contrast edge negatively affects spotted owl survival and reproduction, I would expect EDHC values to be lower around ONS compared to NNS, especially at smaller scales. If high contrast edge is important foraging habitat, I would expect EDHC values to be higher around ONS compared to NNS.

Edge density of old-growth (EDOG) equals the sum of the lengths (km) of all edge segments corresponding between old-growth patches and all other cover types combined, divided by the total landscape area (km^2). In northwest California, reproductive output was positively associated with the amount of old-growth edge (Franklin 1997). I would, therefore, expect EDOG values to be greater at ONS compared to NNS.

Patch density measures the number of patches for a given type per unit area. Patch density of old-growth (PDOG) equals the number of old-growth patches represented per km^2. A landscape with a greater density of old-growth patches would be considered more fragmented than one with a lower density of old-growth patches (Fahrig 1997). Interpretation of PDOG might be difficult, however, if few old-growth patches are represented at NNS or if remaining old-growth forests are highly fragmented. PDOG could serve as a good fragmentation index, but interpretation of PDOG should be considered with other indices of old-growth pattern (McGarigal and

Marks 1993). If large contiguous blocks of old-growth are important to spotted owls, I would expect lower PDOG values around ONS compared to NNS.

I calculated 3 indices of old-growth pattern that are directly related to patch size. Minimum old-growth patch (MINOG) is the smallest old-growth patch in each circular plot. Maximum old-growth patch (MAXOG) is the largest old-growth patch in each circular plot. Mean patch size of old-growth (MPSOG) equals the sum area (ha) of all old-growth patches represented, divided by the number of old-growth patches within a circle plot.

If amount of old-growth forest is important to breeding owls, I would expect values for all 3 patch-size indices to be larger at ONS compared to NNS at all scales. Because smaller plots often truncate large patches, I would expect MAXOG and MPSOG to increase at ONS and NNS as scale increased.

Core area, the interior area of a patch, is related to the edge effects and is affected by patch shape (McGarigal and Marks 1993). Landscape core area of old-growth (LCAOG) equals the sum of the core areas (ha) of each old-growth patch, divided by the total landscape area (ha) and multiplied by 100 to convert to a percentage; it is the percentage of the landscape comprised of old-growth core area. Core area was defined as the interior patch area >100 m (4 pixels x 25 m) from the outer edge of each old-growth patch. This edge buffer distance encompasses most of the clear-cut edge influence on ambient air temperature and humidity of old-growth forests (Chen et al. 1995).

Spotted owls might be associated with interior forest of late-successional patch types (Thomas et al. 1990). If the amount of interior old-growth forest is important to nesting spotted owls, I would expect LCAOG values to be greater at ONS compared to NNS, especially at smaller scales.

Nearest-neighbor distance is the distance from the outer edge of a patch to the nearest patch of the same type; it represents an edge-to-edge proximity (McGarigal and Marks 1993). GISfrag, an index used to quantify fragmentation and loss of old-growth forest, was calculated by taking the mean nearest-neighbor distance (m) among old-growth patches in a circle plot (Ripple et al. 1997). High GISfrag values indicate high fragmentation and loss; minimum fragmentation and loss occurs as GISfrag values approach zero. If close juxtaposition of old-growth patches is important to foraging owls, I would expect lower GISfrag values at ONS compared with NNS, especially at smaller scales.

Calculation of Old-forest Patch Indices.— I calculated 4 patch indices related to patch size, amount of core area, and patch shape that I hypothesized to be ecologically meaningful to the owls while being of interpretive value to biologist and forest managers (Table 5). I used the CLUMP model in IMAGINE on the following 3 GIS layers to calculate specific old-growth patch indices: (1) old-growth patches, (2) old-growth patch interior, and (3) old-growth perimeter. Production of these 3 images was described in the previous section.

Table 5. Abbreviations and brief descriptions for the 4 old-growth patch indices.

Index	Description
OGPS	Old-growth patch size (ha; range of values >0).
OGCA	Old-growth patch core area (ha; range of values ≥0).
RATIO	Ratio of core area (ha) to old-growth patch size (ha; 0 ≤ Ratio < 1).
SHAPE	Old-growth patch shape (shape = 1 when the patch is square and increases without limit as patch shape becomes more irregular).

I calculated the area (ha) of each old-growth nest and non-nest patch (OGPS). Evidence shows that spotted owls nest in larger old-growth patches than are randomly available (Ripple et al. 1997, Meyer et al. 1998). I would, therefore, expect ONP to be significantly larger than NNP.

Core area (OGCA) equals the size (ha) of the interior of each old-growth patch as defined above for LCAOG. If the amount of core area in an old-forest nest patch is important to breeding spotted owls, I would expect OGCA values to be greater at ONP compared to NNP.

RATIO equals core area (OGCA) divided by patch area (OGPS), giving the proportion of an old-growth patch that is occupied by interior forest. If the proportion of core area in an ONP is important to breeding spotted owls, I would expect RATIO values to be greater at ONP compared to NNP.

Patch shape is based on a perimeter-area relationship. Shape measures the complexity of patch shape compared to some standard. For raster images, patch shape is evaluated with a square standard. SHAPE equals patch perimeter (m) divided by the square root of patch area (m^2) and multiplied by 0.25 to adjust for the square standard (McGarigal and Marks 1993:C5).

Patch shape has been shown to influence inter-patch migration of small mammals (Buechner 1989), and might influence animal foraging strategies (Forman and Godron 1986). If spotted owls require complex shapes to maximize the amount of edge of old-growth nest patches for foraging, I would expect SHAPE values to be greater at ONP compared to NNP. If, however, spotted owls require simple shapes to minimize the amount of edge due to adverse edge effects, I would expect SHAPE values to be lesser at ONP compared to NNP.

Statistical Analyses

Observed-versus-expected.—To determine the observed and expected number of nest and non-nest sites in each cover type for the landscape data set, I calculated the associated Chi-squared statistic and *p*-value for each proportional occurrence. The number of expected sites is based on the availability of cover types and was calculated by multiplying the proportion of each available cover type (AREA of each cover type ÷ AREA of all used cover types combined) x n (41). The Chi-squared test ($X^2 = \sum(O_i - E_i)^2/E_i$) show differences between availability and usage. P represents the probability that the number of observed sites per cover type is in proportion to availability of each cover type (Byers et al. 1984).

Statistical Design.—In this observational study, I made binary comparisons between landscape features around (a) ONS versus (b) NNS, and between patch features at (a) ONP versus (b) NNP. Each binary group was defined by its' level of response. Nest sites were selected by owls (response level = 1 or yes); non-nest sites were not selected by owls (response level = 0 or no). The sampling design was retrospective because sampling was carried out for each level of the response variable (Ramsey and Schafer 1997:530). Based on map coverage and available survey data, sample sizes representing ONS and ONP used by individual owl-pairs were the maximum possible.

I used logistic regression for binary responses (Ramsey and Schafer 1997) to select the combination of variables that best separated ONS from NNS, and ONP from NNP (SAS Institute 1997). The first set of analyses, using circular plots, compared land cover at 5 different home-range landscape scales between ONS and NNS. The second set of analysis compared patch features between ONP and NNP, which represented ecological processes and selection order different from landscapes scales (Johnson 1980).

Probability of Selection.— Regression assumes every point has the same importance in determining the solution, i.e., in calculating parameter estimates (Ramsey and Schafer 1997). Unequal variance estimates result when sampling without replacement from a finite population because the number of available sites diminishes with each prior selection (Levy and Lemeshow 1981). Weighted regression can account for unequal variance regardless of its source (Draper and Smith 1981). Thus, by including a variable for probability of selection (POS) as a weighted difference among site selection, the unequal variance in POS between nest and non-nest sites and that among non-nest sites is then accounted for in the regression modeling (Draper and Smith 1981, Kmenta 1986).

POS, Landscape Data Set.—Since each ONS was selected by an individual owl pair, i.e., not selected from a diminishing pool of possibilities by the researcher, the probability of selection was constant. Therefore, I used POS (ONS) = A ÷ A = 1, where A represented the total number of UTMs (871,130,000 m^2) available for breeding, i.e., the total number of UTMs available in all cover types combined, except OS and NF, within the area 3,000 m from the map edge. OS and NF cover types were not considered available for nest or non-nest site selection, and no nest or non-nest sites were located <3,000 m from any map edge to accommodate the largest circle-plot radius.

Since each NNS was selected from a diminishing pool of possibilities, I used POS (NNS) = (A - number of UTMs available sequentially) ÷ A (Levy and Lemeshow 1981:119). The number of UTMs available sequentially were re-estimated for each succeeding NNS selected after accounting for: (1) area available for nesting within a 1,260-m radius of selected sites became unavailable for subsequent selection (spatial restriction placed on selection of all sites); (2) to accommodate the largest circle-plot radius, area within a 3,000-m radius of the map edge was not considered available for all sites; and (3) any overlap of (1) and (2) was counted only once.

For the old-growth patch data set, each ONP was selected by an individual owl pair, i.e., not selected from a diminishing pool of possibilities, and a stratified selection process was used to select NNP. Therefore, POS was constant for ONP and NNP and not used as a weighted variable in the regression modeling.

Model Selection.—The goal in multivariate analysis is to select variables that result in models that are both biologically meaningful and useful within the scientific context of the problem. The most parsimonious model that still explains the data is preferred (Hosmer and Lemeshow 1989, Burnham et al. 1995). Minimizing the number of variables in the model is more likely to produce a model that is numerically stable, and easily generalized (Hosmer and Lemeshow 1989).

The selection process began with the development of hypotheses for the selection of measures based on current knowledge about spotted owls. Considerations for landscape indices included both the mechanism and predictions for each variable relative to spotted owl nest site selection.

To reduce the number of variables for multivariate analyses, I first used Pearson's correlation matrices to examine correlations among variables for each of the 5 circular landscape scales and the old-growth patch scale. Variables with correlation coefficients (r) > 0.70 or < -0.70 were considered highly correlated.

To further reduce the number of variables for multivariate analyses, I ran a univariate logistic regression analysis for each variable to determine which of the remaining explanatory variables seemed more important. To be conservative, those variables with a univariate p-value ≤ 0.25 were still considered for multivariate analysis because more restrictive levels might fail to identify important variables (Hosmer and

Lemeshow 1989:86). I explored polynomial terms and all possible interactive effects of these important explanatory variables on the logit scale (Ramsey and Schafer 1997).

For multivariate analysis, I evaluated all possible subset models of the remaining variables using a p-value ≤ 0.25 as the criteria for variable entry and retention (Hosmer and Lemeshow 1989). I used Akaike's Information Criterion (AIC) as the basis for objectively ranking models to select a "best" model (Burnham et al. 1995). The best model for each scale was selected based on minimum AIC values. Models within 2 AIC units of the best model were considered to be competing models.

Interpretation of Coefficients.—In logistic regression, the natural link for a binary response variable is the logit; exponentiating the logit yields the odds of a yes response (Ramsey and Schafer 1997:570). Where appropriate, I estimated odds ratios for each main-effect variable in each best and competing models. The odds ratio shows the factor by which the odds on nest-site selection increased when the corresponding variable changed from its mean at non-nest sites to its mean at nest sites using the formula:

$$\exp\left[\beta_i\left(\bar{x} \text{ of } X_i \text{ at nest sites } - \bar{x} \text{ of } X_i \text{ at non-nest sites}\right)\right],$$

where $\bar{x}$ of X_i represents the mean of each variable and β_i represents the parameter estimate (Ramsey et al. 1994).

RESULTS

Landscapes at Nest and Non-nest Sites

Spotted owls mostly used old-growth ($n = 30$) and old-remnant forests ($n = 8$) for nest sites (93%). Non-nest sites were located in cover types more in proportion to availability (Table 6).

Table 6. The number of observed (Ob.) and expected (Ex.) spotted owl nest and non-nest sites located in each cover type, and the associated Chi-squared statistic and *p*-value for each proportional occurrence, east-central Coast Ranges, Oregon.

Cover Type[a]	Nest Sites (ob.)	Nest Sites[b] (ex.)	Chi^2 Stat.	*p*-value[c]	Non-Nest Sites (ob.)	Non-Nest Sites (ex.)	Chi^2 Stat.	*p*-value
Old-growth	30	6	96.0	0.000	4	6	0.7	0.414
Old-remnant	8	2	18.0	0.000	4	2	2.0	0.157
Mature	0	2	2.0	0.157	3	2	0.5	0.480
Mature-young	1	2	0.5	0.480	4	2	2.0	0.157
Pole-young	1	17	15.0	0.000	17	17	0.0	1.000
Broadleaf-mix	1	12	10.1	0.001	9	12	0.7	0.386
Sites Total	41	41			41	41		

[a]Open-sapling and non-forest types were not considered available for nest sites.

[b]Calculated by multiplying the proportion of each available cover type (AREA of each cover type ÷ AREA of old-growth, old-remnant, mature, mature-young, pole-young, and broadleaf-mix combined) x n (41).

[c]Represents probability that the number of observed sites per cover type is in proportion to availability of each cover type (Z-stat. = 2.65, df = 5).

Univariate Analysis.—Logistic model: logit (Y) = β_0 + $\beta_1 X_1$ (in Circle $_X$), where, Y = 1 for nest sites and Y = 0 for non-nest sites, β_0 = the intercept, β_1 is the regression coefficient for the independent variable, and X_1 is the independent variable. Using a *p*-value <0.01 with relevant terms to suggest statistical significance in univariate comparisons, OG was significantly greater ($P = 0.0096$) at ONS than at NNS for the 0.6-km-radius circle (Table 7). However, OR was not significantly greater ($P = 0.2259$) at ONS than at NNS for the 0.6-km-radius circle (Table 7). PY was significantly less ($P = 0.0084$) at ONS than at NNS for the 0.6-km-radius circle, but only moderately to marginally less ($P = 0.1092$) for the 4 largest circles (Table 7). SIEI was only marginally greater ($P = 0.0555$) at ONS than at NNS for the 0.6-km-radius circle (Table 7). GISfrag was moderately less ($P = 0.0133$) at ONS than at NNS for the 0.6-km-radius circle (Table 7). Additionally, EDOG was significantly greater ($P = 0.0090$), MAXOG and MPSOG were moderately greater ($P = 0.0419$), and LCAOG was only marginally greater ($P = 0.1084$) at ONS than at NNS at the 0.6-km-radius circle (Table 7). All other landscape indices had *p*-values ≥0.1352 at all scales (Table 7). All interaction terms had *p*-values >0.25 at all scales. In univariate analyses, most non-linear terms had *p*-values >0.25, and no non-linear terms were retained in multivariate models at any scale. At all 5 landscape scales, MAXOG, MPSOG, EDOG, and LCAOG were highly correlated with OG ($r \geq 0.715$), and GISfrag was highly correlated ($r \leq -0.740$) with OG for 1.8-, 2.4-, and 3.0-km-radius circles.

Table 7. Means, standard errors (SE), and probability values from univariate logistic regression analysis for landscape indices in 0.6-, 1.2-, 1.8-, 2.4-, and 3.0-km-radius circles around ONS[a] and NNS, east-central Coast Ranges, Oregon.

		ONS (n = 41)		NNS (n = 41)		
Index	**Radius (km)**	**Mean**	**SE[b]**	**Mean**	**SE**	***p*-value[c]**
NF (**% Non-forest**)	0.6	2.6	1.2	4.0	1.3	0.7039
	1.2	3.2	1.0	4.7	1.4	0.5913
	1.8	3.8	1.0	4.6	1.1	0.7803
	2.4	4.2	1.2	4.6	1.0	0.8852
	3.0	4.5	1.2	4.9	1.0	0.8601
OS (**% Open-sapling**)	0.6	17.8	2.2	17.6	2.5	0.8973
	1.2	22.2	2.2	22.8	2.1	0.8661
	1.8	24.4	2.1	23.0	1.9	0.8100
	2.4	25.8	2.1	24.1	1.8	0.7804
	3.0	26.5	2.1	24.9	1.5	0.7919
BM (**% Broadleaf-mix**)	0.6	15.0	1.9	17.4	2.9	0.7120
	1.2	19.7	2.0	17.7	2.0	0.5778
	1.8	20.3	1.9	18.2	1.7	0.5669
	2.4	20.3	1.7	18.7	1.6	0.6434
	3.0	20.2	1.5	18.7	1.5	0.6242
PY (**% Pole-young**)	0.6	15.4	1.9	36.0	4.1	0.0084
	1.2	22.2	2.0	33.7	3.1	0.0488
	1.8	24.1	2.1	33.8	2.7	0.0826
	2.4	23.6	1.9	32.4	2.3	0.0869
	3.0	23.7	1.8	31.4	2.1	0.1092
MY (**% Mature-young**)	0.6	3.3	0.7	5.0	1.3	0.4866
	1.2	4.7	0.8	3.6	0.6	0.5186
	1.8	4.7	0.8	3.6	0.5	0.5552
	2.4	4.3	0.6	3.7	0.4	0.6950
	3.0	3.9	0.5	3.7	0.4	0.8908
MA (**% Mature**)	0.6	4.8	1.4	4.1	1.1	0.7709
	1.2	3.3	0.8	2.9	0.6	0.7641
	1.8	3.0	0.6	2.8	0.5	0.7978
	2.4	2.9	0.5	2.8	0.5	0.8025
	3.0	2.9	0.4	2.4	0.4	0.5503

Table 7. Continued.

		ONS (n = 41)		NNS (n = 41)		
Index	**Radius (km)**	**Mean**	**SE**	**Mean**	**SE**	***p*-value**
OR (% Old-remnant)	0.6	9.5	1.6	4.7	0.9	0.2259
	1.2	5.8	0.9	4.2	0.6	0.4827
	1.8	5.2	0.8	3.9	0.5	0.4783
	2.4	4.9	0.7	3.7	0.4	0.4555
	3.0	4.8	0.6	3.8	0.4	0.4639
OG (% Old-growth)	0.6	31.6	2.8	11.1	2.2	0.0096
	1.2	18.9	2.3	10.5	1.7	0.1464
	1.8	14.6	1.8	10.1	1.4	0.3406
	2.4	14.0	1.7	10.0	1.2	0.3259
	3.0	13.5	1.5	10.2	1.1	0.3576
RPR (Relative patch richness; %)	0.6	69.8	2.4	66.8	2.8	0.8795
	1.2	85.9	1.8	85.0	1.5	0.8795
	1.8	93.6	1.4	94.2	1.2	0.7595
	2.4	95.7	1.0	97.6	0.8	0.4119
	3.0	97.4	0.8	97.7	0.8	0.8608
SIEI (Simpson's evenness index)	0.6	0.859	0.018	0.774	0.027	0.0555
	1.2	0.861	0.012	0.810	0.017	0.1352
	1.8	0.853	0.010	0.824	0.012	0.2648
	2.4	0.859	0.009	0.836	0.010	0.3543
	3.0	0.860	0.008	0.845	0.009	0.4855
EDHC (Edge density high contrast; km/km^2)	0.6	2.90	0.31	2.75	0.27	0.8598
	1.2	3.06	0.24	2.93	0.19	0.8249
	1.8	3.07	0.19	2.95	0.15	0.7831
	2.4	3.14	0.17	3.02	0.13	0.7790
	3.0	3.24	0.17	3.22	0.13	0.9975
EDOG (Edge density old-growth; km/km^2)	0.6	3.90	0.30	1.71	0.32	0.0090
	1.2	2.55	0.25	1.65	0.25	0.1726
	1.8	2.02	0.22	1.57	0.21	0.4227
	2.4	1.93	0.19	1.54	0.18	0.4135
	3.0	1.90	0.18	1.57	0.16	0.4455

Table 7. Continued.

Index	Radius (km)	ONS (*n* = 41) Mean	ONS SE	NNS (*n* = 41) Mean	NNS SE	*p*-value
PDOG (Patch density old-growth; n/km²)	0.6	1.83	0.15	1.33	0.23	0.2723
	1.2	0.90	0.07	0.78	0.11	0.5529
	1.8	0.69	0.05	0.60	0.05	0.5076
	2.4	0.69	0.04	0.65	0.06	0.7024
	3.0	0.62	0.04	0.56	0.05	0.5258
MINOG[d] (Minimum sized old-growth patch; ha)	0.6	13.8	3.3	3.7	1.4	0.2325
	1.2	4.0	1.2	4.3	2.5	0.7645
	1.8	3.0	1.3	1.4	0.3	0.6464
	2.4	0.9	0.2	1.0	0.2	0.8800
	3.0	0.8	0.1	1.0	0.2	0.4992
MAXOG (Maximum sized old-growth patch; ha)	0.6	30.7	3.2	9.5	2.0	0.0117
	1.2	59.2	9.6	26.2	4.3	0.1691
	1.8	85.2	16.2	43.5	6.1	0.3037
	2.4	112.2	22.6	61.1	9.1	0.3037
	3.0	138.8	27.6	83.6	12.0	0.4186
MPSOG (Mean patch size old-growth; ha)	0.6	21.2	2.9	6.1	1.5	0.0419
	1.2	23.2	2.9	12.2	2.7	0.1888
	1.8	23.2	3.4	14.4	1.5	0.2903
	2.4	19.4	2.0	14.1	1.4	0.3182
	3.0	21.3	2.1	17.6	1.6	0.5250
LCAOG (Landscape core area old-growth; %)	0.6	6.9	1.3	1.8	0.6	0.1084
	1.2	4.2	0.9	1.5	0.4	0.2325
	1.8	3.0	0.6	1.5	0.3	0.3056
	2.4	2.8	0.5	1.6	0.3	0.3113
	3.0	2.8	0.4	1.8	0.3	0.3418
GISfrag (Mean distance among old-growth patches; m)	0.6	189	21.4	593	82.1	0.0133
	1.2	331	28.5	574	66.0	0.0462
	1.8	417	33.0	574	57.0	0.1406
	2.4	459	35.8	578	49.1	0.2278
	3.0	491	38.3	585	44.0	0.3279

[a]ONS = owl nest sites; NNS = non-nest sites.

[b]Standard errors (SE) are descriptive.

[c] Probability values were derived from univariate logistic regression analysis of landscape indices.

[d]MINOG, MAXOG and MPSOG sometimes represent incomplete patches due to truncation at plot boundaries.

As circle radius increased, OG decreased at ONS from a mean of 31.6 to 13.5%, whereas it remained approximately constant at NNS (10.0-11.1%; Fig. 6H). As circle radius increased, OR decreased at ONS from a mean of 9.5 to 4.8%, whereas it remained approximately constant at NNS (4.7-3.8%; Fig. 6G). Conversely, the amount of pole-young increased at ONS as circle radius increased from a mean of 15.4 to 23.7%, and remained approximately constant at NNS (36.0-31.4%; Fig. 6D). With exceptions in the 0.6-km-radius circle, percentages of all other cover types, i.e., NF, OS, BM, MY and MA, remained approximately constant at ONS and NNS as circle radius increased, and ONS did not differ significantly from NNS for those types (Fig. 6A, 6B, 6C, 6E, and 6F).

SIEI remained relatively constant at ONS but increased as circle radius increased at NNS (Fig. 6J). GISfrag increased considerably at ONS as circle radius increased but remained relatively constant across scales at NNS (Fig. 6R). EDOG and LCAOG were highly correlated with OG at all scales and mimicked the pattern of OG across scales (Fig. 6L and 6Q). MAXOG and MPSOG were also highly correlated with OG at all scales, but those indices did not mimic the pattern of OG across scales. MAXOG increased linearly in ONS and NNS as circle radius increased; largely because smaller radius circles measured smaller portions of large old-growth patches (Fig. 6O). MPSOG remained relatively constant at ONS but increased as circle radius increased at NNS, with the exception of a slight decrease in MPSOG between the 1.8- and 2.4-km-radius circles (Fig. 6P). PDOG decreased at ONS and NNS as circle radius increased (Fig. 6M).

With the exception of MINOG, which decreased sharply from the 0.6-km-radius circle to the 1.2-km-radius circle at ONS, there was little difference in RPR, EDHC or MINOG between ONS and NNS, or change across scales (Fig. 6I, 6K and 6N).

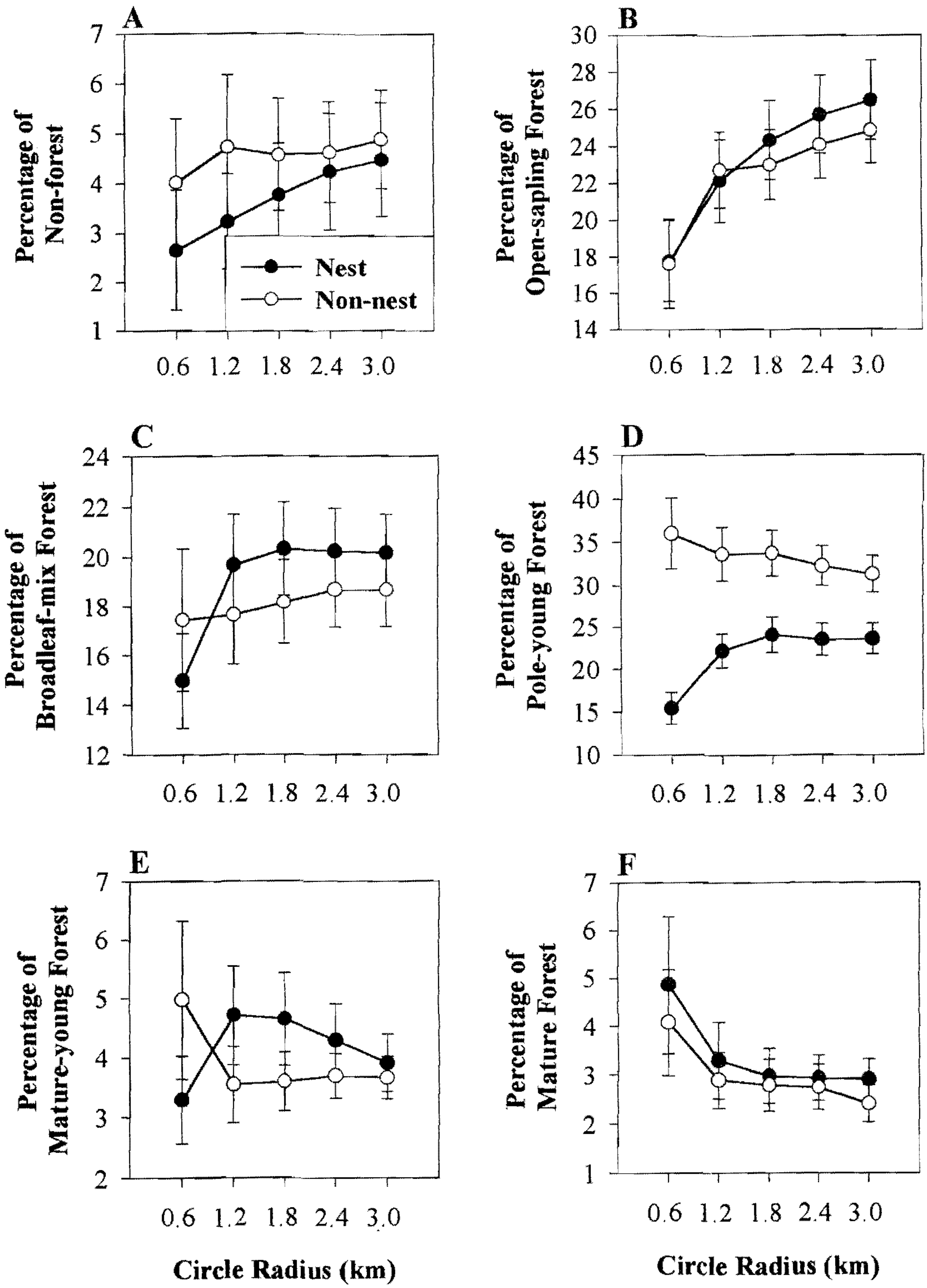

Figure 6. Average values (±1 SE) of landscape indices in 0.6, 1.2, 1.8, 2.4, and 3.0-km-radius circles around 41 owl nest sites (NNS●) and 41 non-nest sites (NNS○), east-central Coast Ranges, Oregon.

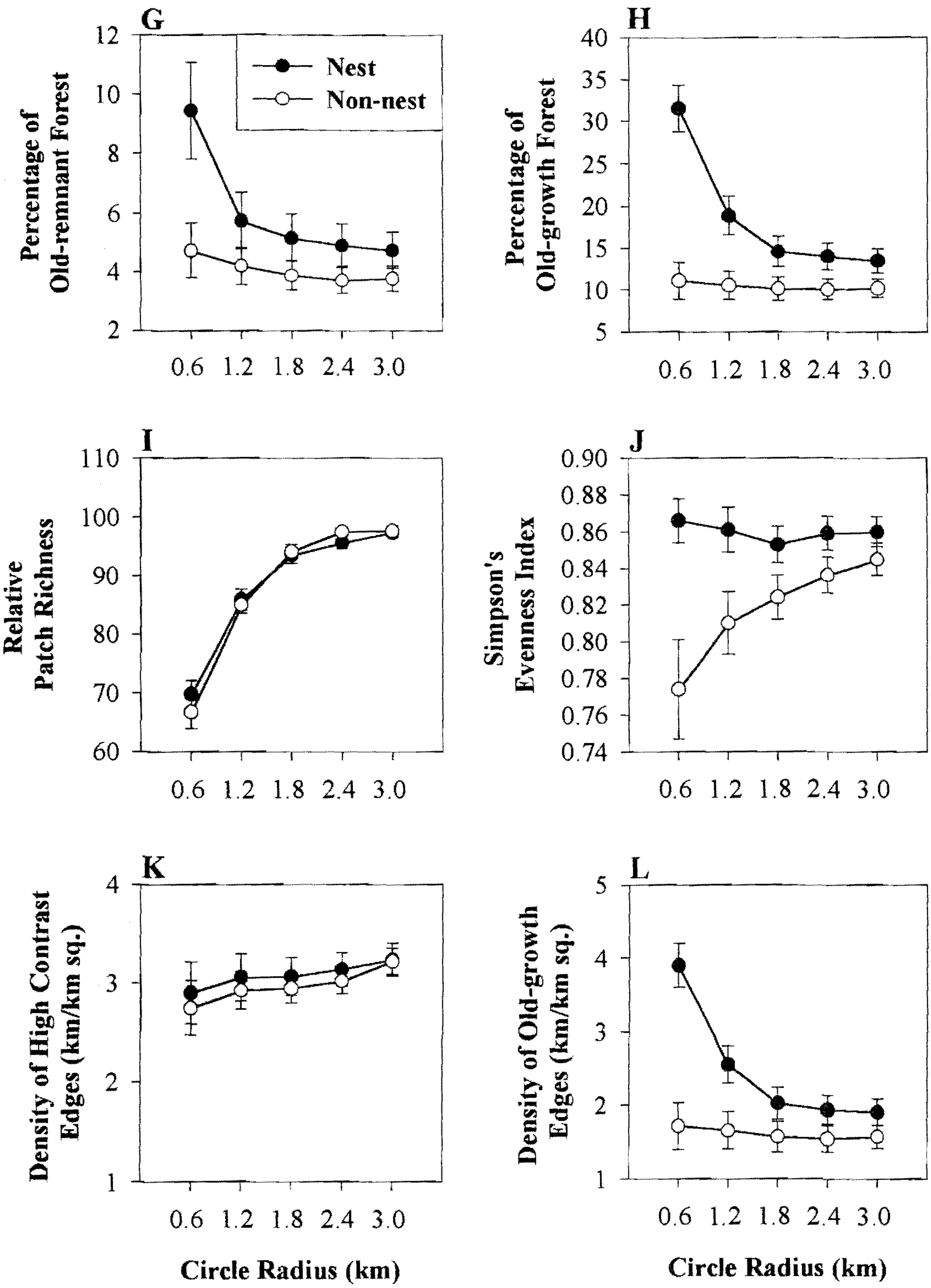

Figure 6. Continued.

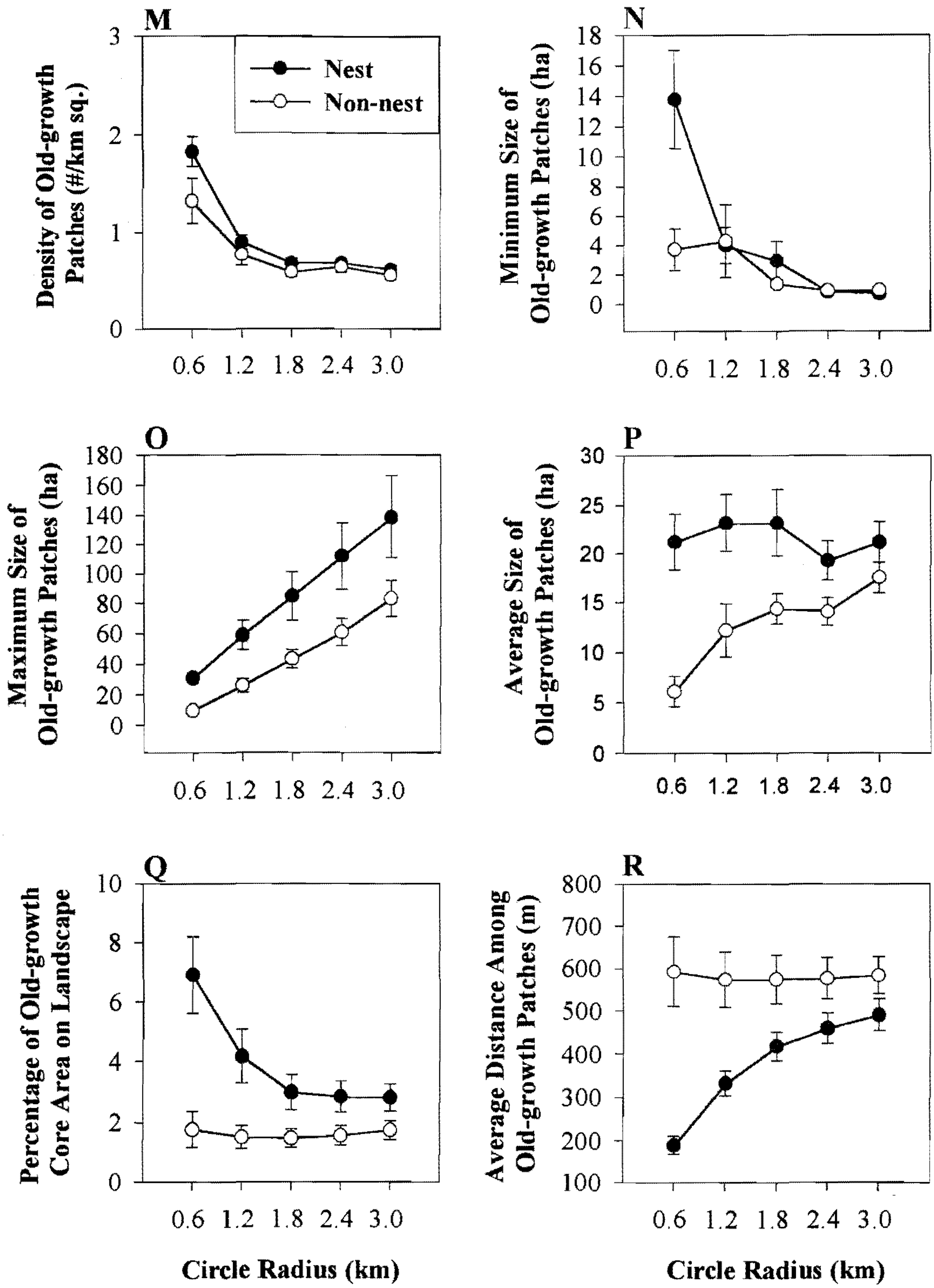

Figure 6. Continued.

Multivariate Analyses.—Logistic model: logit (Y) = $\beta_0 + \beta_1 X_1 + \beta_2 X_2$ (in Circle $_X$), where, Y = 1 for nest sites and Y = 0 for non-nest sites, β_0 = the intercept, β_1 and β_2 are the regression coefficients for the independent variables, and X_1 and X_2 are the independent variables. For all 5 circle sizes, 1- to 3-variable logistic functions comparing ONS versus NNS were most correlated with the observed patterns of nest site selection ($P \leq 0.1196$). The highest levels of statistical significance were associated with 0.6-km-radius circles ($P = 0.0054$), suggesting that landscape characteristics at that scale might be most influential in determining nest site selection. For the smallest circle of 0.6-km-radius, OR, OG and SIEI were the best predictors of the difference between ONS and NNS, being higher at ONS than at NNS. ONS had nearly 3 times the amount of old-growth forests compared with NNS and >2 times the amount of old-remnant forests. Based on Simpson's Evenness Index, ONS had a more even distribution of cover types compared with NNS within 0.6-km-radius circles.

For the second smallest circle-size of 1.2-km-radius, GISfrag was the best predictor of the difference between ONS and NNS, being lower at ONS (331m) compared to NNS (574m). At all 3 of the largest circles, PY was the best predictor of the difference between ONS and NNS, being lower at ONS than at NNS.

One competing model was within 2 AIC units of the best model for the 0.6-km-radius circle size, but no models were within 2 AIC units of the best model for any of the 4 larger circle sizes (Table 8). Odds ratios indicate the factors by which the odds on selection increased when the corresponding variable changed from its mean at non-nest sites to its mean at nest sites (Table 8).

Table 8. Multivariate logistic regression models[a], including variables, parameter estimates (β), Standard Errors of estimate [SE(β)], and probability values, that best (lowest Akaike's Information Criterion [AIC]) distinguished ONS[b] from NNS within 0.6-, 1.2-, 1.8-, 2.4-, and 3.0-km-radius circles around nest and non-nest sites in the east-central Coast Ranges of Oregon. Odds ratios indicate the factors by which the odds on selection increased when the corresponding variable changed from its mean at non-nest sites to its mean at nest sites.

Scale, Model Ranking and AIC-value	Variable[b]	β	SE (β)	p-value	Odds Ratios[c]
0.6-km-radius					
Model 1 (AIC = 36.186)	Intercept	-12.4121	7.4408	0.0953	
	OR	0.1051	0.0582	0.0710	1.6:1
	OG	0.1105	0.0409	0.0069	9.6:1
	SIEI	12.5051	8.0343	0.1196	3.2:1
Model 2 (AIC = 37.875)	Intercept	-1.5519	0.9453	0.1006	
	OR	0.1131	0.0571	0.0477	1.7:1
	OG	0.1075	0.0387	0.0054	9.1:1
1.2-km-radius					
Model 1 (AIC = 47.222)	Intercept	2.7111	0.7536	0.0003	
	GISfrag	-0.0029	0.0015	0.0462	2.1:1
1.8-km-radius					
Model 1 (AIC = 48.657)	Intercept	2.8129	0.9142	0.0021	
	PY	-0.0459	0.0264	0.0826	1.6:1
2.4-km-radius					
Model 1 (AIC = 48.698)	Intercept	2.9246	0.9861	0.0030	
	PY	-0.0515	0.0301	0.0869	1.6:1
3.0-km-radius					
Model 1 (AIC = 49.100)	Intercept	2.9182	1.0321	0.0047	
	PY	-0.0521	0.0325	0.1092	1.5:1

[a]Logistic model: Logit(Y) = $\beta_0 + \beta_1 X_1 + \beta_2 X_2$ (in Circle $_x$), where, $Y = 1$ for nest sites and $Y = 0$ for non-nest sites, β_0 = the intercept, β_1 and β_2 are the regression coefficients for the independent variables, and X_1 and X_2 are the independent variables.

[b]ONS = owl nest sites, NNS = non-nest sites, OF = percentage of old forest, OR = percentage of old-remnant forest, GISfrag = fragmentation and loss of old-growth, and PY = percentage of pole-young forest.

[c]Odds ratio for this variable was based on the following formula: exp [β_i ($\bar{x}$ of X_i at nest sites - $\bar{x}$ of X_i at non-nest sites)], where $\bar{x}$ of X_i represents the mean of each variable and β_i represents the parameter estimate. See Table 7 for the mean values of main-effect variables.

Nest and Non-nest Old-growth Patches

Univariate Analysis.—Logistic model: logit $(Y) = \beta_0 + \beta_1 X_1$, where, $Y = 1$ for nest patches and $Y = 0$ for non-nest patches, β_0 = the intercept, β_1 is the regression coefficient for the independent variable, and X_1 is the independent variable. Using a *p*-value <0.01 with relevant terms to suggest statistical significance in univariate comparisons, RATIO was significantly greater at ONP than at NNP ($P = 0.0004$; Table 9). SHAPE was moderately greater ($P = 0.0295$) and OGPS was marginally greater ($P = 0.1062$) at ONP compared with NNP (Table 9). The difference in OGCA between ONP and NNP was not significant ($P = 0.2364$; Table 9). All interaction terms had *p*-values >0.25 at all scales. In univariate analyses, most non-linear terms had *p*-values >0.25, and no non-linear terms were retained in the multivariate model.

Table 9. Means, standard errors (SE), and probability values from univariate logistic regression analysis for old-growth patch indices at ONP[a] and NNP in the east-central Coast Ranges of Oregon.

	ONP (n = 29)		(NNP (n =29)		
Index	**Means**	**SE[b]**	**Means**	**SE**	***p*-value[c]**
OGPS	132.7	47.9	25.7	10.3	0.1062
OGCA	36.5	15.4	5.1	3.8	0.2364
RATIO	0.184	0.025	0.048	0.016	0.0004
SHAPE	2.838	0.370	1.783	0.108	0.0295

[a]ONP = owl nest-patch ; NNP = non-nest patch.
[b]Standard errors (SE) are descriptive.
[c]Probability values were derived from univariate logistic regression analysis of old-growth patch indices.

CAOG was highly correlated with PSOG (r = 0.983), indicating that larger old-growth patches have greater amounts of interior forest. SHAPE was also highly correlated with PSOG (r = 0.908), indicating that larger old-growth patches have a more complex shape compared to smaller patches.

Multivariate Analysis.—Logistic model: logit (Y) = $\beta_0 + \beta_1 X_1 + \beta_2 X_2$, where, Y = 1 for nest patches and Y = 0 for non-nest patches, β_0 = the intercept, β_1 and β_2 are the regression coefficients for the independent variables, and X_1 and X_2 are the independent variables. For old-growth patches, 1- to 2-variable logistic functions comparing ONP versus NNP were most correlated with the observed patterns of old-growth patch selection ($P \leq 0.1803$; Table 10). For the old-growth patch scale, RATIO and SHAPE were the best predictors of the difference between ONP and NNP, being greater at ONP (Table 10). ONP had nearly 4 times the average ratio of core area to patch size compared with NNP. Based on the Shape index, ONP had more complex shapes compared with NNP.

Table 10. The multivariate logistic regression model[a], including the variable, parameter estimate (β), Standard Error of estimate [SE(β)], and the probability value, that best (lowest Akaike's Information Criterion [AIC]) distinguished ONP[b] from NNP in the east-central Coast Ranges of Oregon. The odds ratio indicates the factor by which the odds on selection increased when the corresponding variable changed from its mean at non-nest patches to its mean at nest patches.

AIC-value	Variable[b]	β	SE (β)	p-value	Odds Ratio[c]
AIC = 65.855	Intercept	-2.0678	0.8418	0.0140	
	RATIO	8.8872	3.0289	0.0033	3.3:1
	SHAPE	0.5292	0.3950	0.1803	1.7:1
AIC = 66.440	Intercept	-1.0882	0.4020	0.0068	
	RATIO	10.3209	2.9202	0.0004	4.1:1

[a]Logistic model: Logit (Y) = β_0 + $\beta_1 X_1$, where, Y = 1 for nest patches and Y = 0 for non-nest patches, β_0 = the intercept, β_1 is the regression coefficient for the independent variable, and X_1 is the independent variable.

[b]ONP = owl nest patches, NNP = non-nest patches. RATIO = patch core area divided by patch area, giving the proportion of an old-growth patch that is occupied by interior forest. SHAPE = patch perimeter (m) divided by the square root of patch area (m^2) and multiplied by 0.25 to adjust for the square standard.

[c]Odds ratio for this variable was based on the following formula: exp [β_i ($\bar{x}$ of X_i at nest sites - $\bar{x}$ of X_i at non-nest sites)], where $\bar{x}$ of X_i represents the mean of each variable and β_i represents the parameter estimate. See Table 9 for the mean values of main-effect variables.

Old-growth nest patches consisted of nearly 20% core area on average compared to <5% for old-growth non-nest patches. Also, as ratio of core area to patch size increased, the proportion of old-growth patches used as nest sites increased dramatically, becoming asymptotic at the proportion of ~0.90 for patches with a RATIO value ~0.20-0.30 or greater (Figure 7A).

The SHAPE index is based on the perimeter-to-area ratio and, consequently, is insensitive to specific patch shape. Therefore, the SHAPE index is not useful as a measure of patch morphology, but is best considered as a measure of overall shape complexity (McGarigal and Marks 1993:39). At the old-growth patch scale, however, SHAPE and CAOG indices were highly correlated with old-growth patch size ($r \geq 0.908$).

The average old-growth nest patch was >5 times larger than the average old-growth non-nest patch. Furthermore, as old-growth patch size increased, the proportion of old-growth patches used as nest sites also increased dramatically, becoming asymptotic at the proportion of ~0.80 for patches ~40-50 ha in size or greater (Figure 7B). Old-growth patch size is the simplest patch index to comprehend and manage for and is, therefore, considered the most biologically interpretable of these correlated indices.

Figure 7A. Proportion of Old-growth Patches Used As Nest Sites per Ratio of Core Area to Patch Size

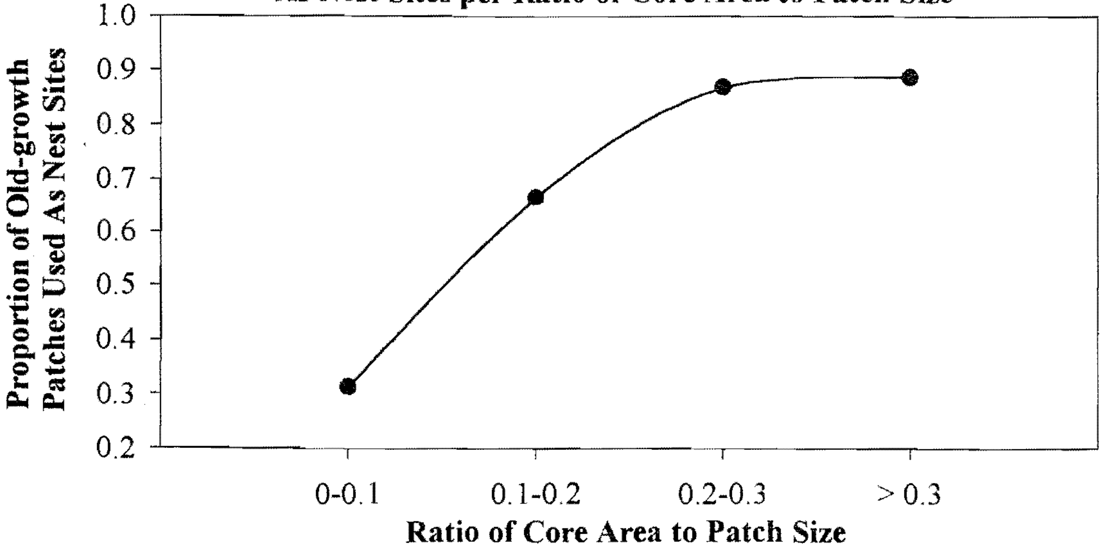

Figure 7B. Proportion of Old-growth Patches Used As Nest Sites per Patch Size

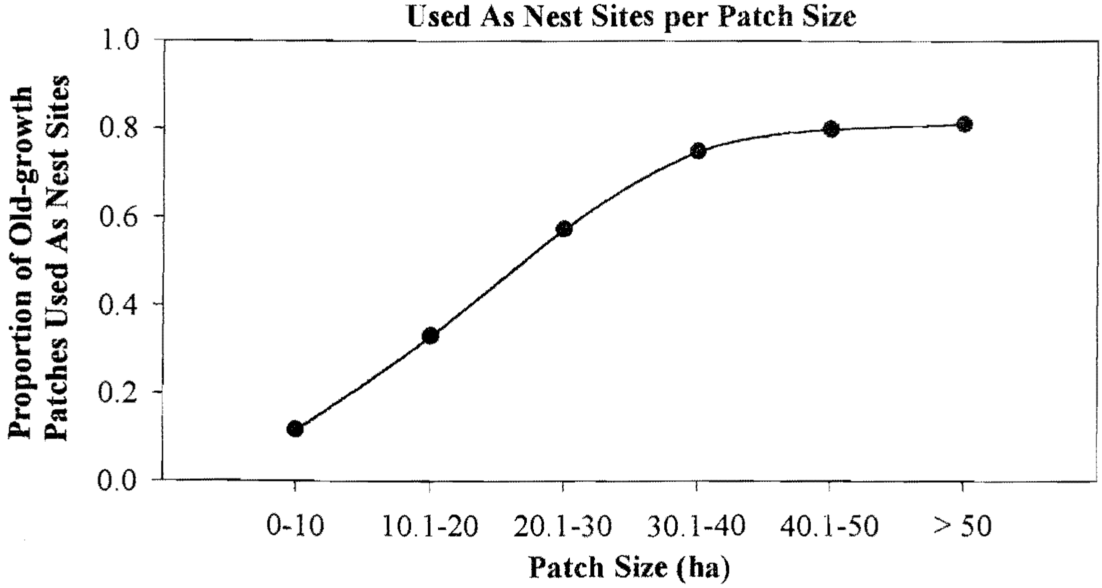

Figure 7. Figure 7A shows the relationship between ratio of core area to patch size (RATIO) and the proportion of old-growth patches used as nest sites. Figure 7B shows the relationship between old-growth patch size (OGPS) and the proportion of old-growth patches used as nest sites; east-central Coast Ranges, Oregon.

DISCUSSION

I used logistic regression for binary responses to compare features between ONS and NNS and between ONP and NNP. Logistic regression analysis describes how a binary (1 or 0) response variable, such as the presence or absence of a nest tree, is associated with a set of explanatory variables, such as the percent landscape covered with old-growth and old-remnant forests; the model describes a population probability or proportion as a function of explanatory variables (Ramsey and Schafer 1997). The application of logistic regression analysis to use-versus-non-use data is very straightforward in structure and context of this problem, and interpretation is particularly useful when distinguishing between used and non-used groups.

Landscapes at Nest and Non-nest Sites

0.6-km-radius Circles.—Larger amounts of late-successional forest associated with spotted owl nest sites in my study area supports the conclusions of other studies that compared owl sites to available sites (Ripple et al. 1991, 1997; Lehmkuhl and Raphael 1993; Hunter et al. 1995; Meyer et al. 1997; Swindle et al. 1999). On BLM lands in western Oregon there was a greater mean percentage of old-growth forests within 0.8-km-radius circles at random owl locations (sites in which an owl pair was observed) compared with random landscape locations (31.5 vs. 10.4%; Meyer et al. 1997). Hunter et al. (1995) reported greater mean amounts of mature and old-growth forests combined in 0.8-km-radius circles around spotted owl nest sites compared with random landscape locations in northern California (94.1ha vs. 71.8 ha or 46.8% vs. 35.7%). Ripple et al. (1991) also reported greater mean amounts of percent mature and old-growth forest combined within 0.91-km-radius circles at spotted owl nest sites compared with random sites (78.2 vs. 63.2%) in the west-central Cascades of Oregon. Swindle et al. (1999) demonstrated that spotted owl nests in the central Cascade Mountains of Oregon were associated with clumped arrangements of old forest (mature and old-growth combined) out to 0.6 km, beyond which random old-forest sites were similar.

The percentage of late-successional forest around owl sites in my study area was less than in most other study areas (Swindle et al. 1998:39). Historically, wildfires were responsible for landscape patterns of forest vegetation in the Oregon Coast Ranges (Franklin and Dyrness 1988). These fires were either started by lightning or deliberately set by native Americans. Subsequent to the implementation of modern methods of fire suppression in the 20th century (Smith et al. 1997), landscape vegetation patterns in the Oregon Coast Ranges are mostly influenced by clear-cuts, even-aged plantations, and the checkerboard ownership pattern. In non-federal ownerships, the landscape is dominated by early-successional forest. Federally owned lands consist of forest in a wide range of successional stages including most of the remaining old-growth which covered 9.7% of the study area in 1990 (Fig. 8). Rapid loss of late-successional forest and the pattern of checkerboard ownership make it difficult to manage for species like the spotted owl that have very large home-ranges and use large tracts of late-successional forest.

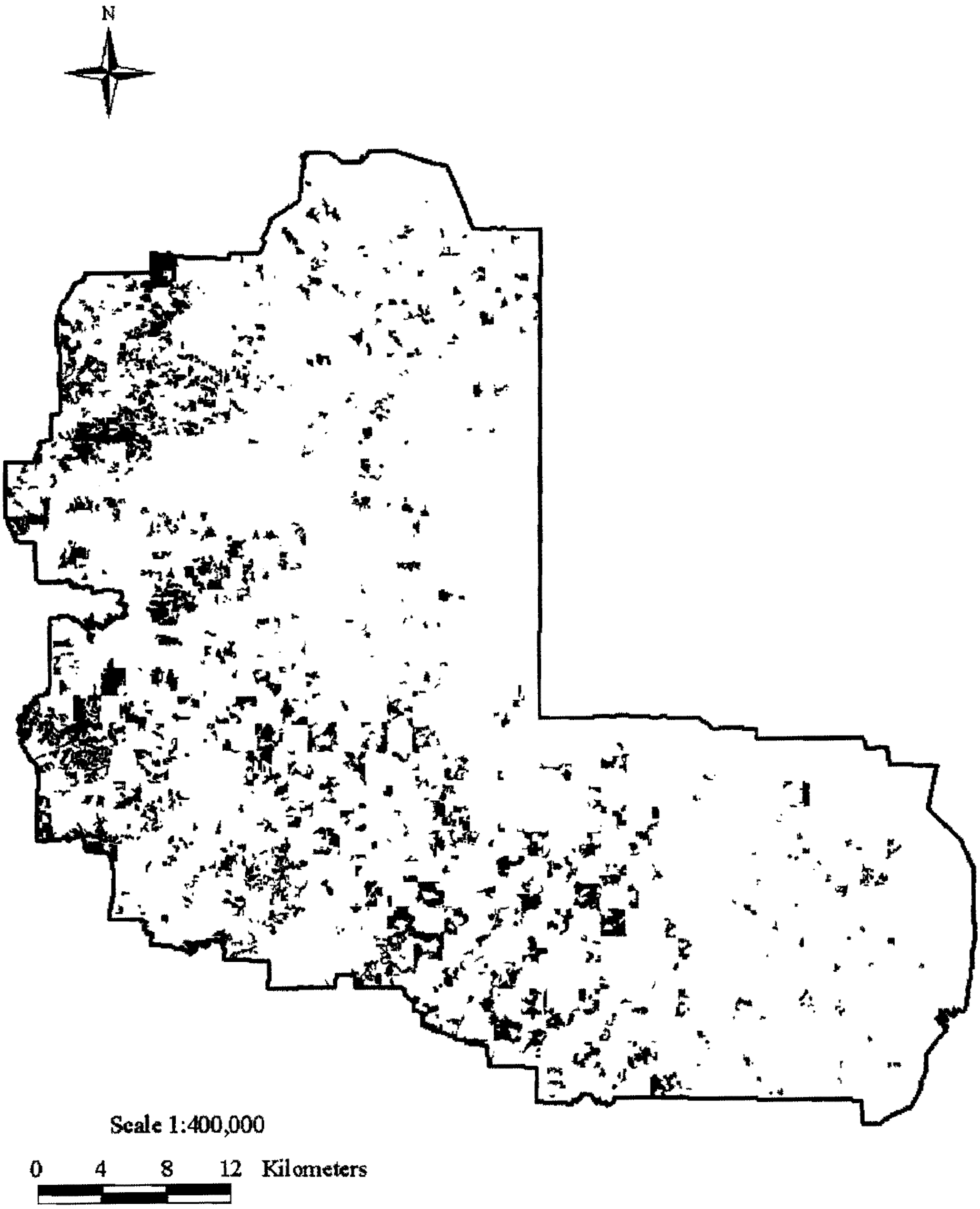

Figure 8. Map of the study area, east-central Coast Ranges, Oregon. Based on interpretation of 1990 aerial photos, black areas show old-growth (overstory trees >86-cm dbh) patches, and demonstrate the influence of checkerboard ownership on old-growth patterns, the isolation of old-growth patches, and the uneven distribution of old-growth patches on the landscape.

Nearly 20% (8) of the nest sites were in old-remnant forests and there was more of this forest type in the 0.6-km radius circle around ONS compared to NNS. In 1995, we collected history information on forest stands in conjunction with the spotted owl demography and habitat associations study on the Eugene District, BLM. Based on retrospective analysis of sample patches on this study area, old-remnant stands were produced by a variety of factors including fire, salvage logging after fire or wind-throw, seed tree harvests with some retention, and selective logging of merchantable trees that left some large remnant structures intact while new forest replaced most of the previous patch (OCFWRU Unpubl. Data). Carey et al. (1992) reported a cover type similar to old-remnant, ("mixed-old forest"), was used by owls for foraging in the southern Oregon Coast Ranges. They also reported that 4 of 8 owls that used old forest in proportion to availability selected for mixed-old forest. On the Olympic Peninsula, Lehmkuhl and Raphael (1993) also reported use by spotted owls of a similar forest type, "atypical habitat", which they lumped with old forest for their analysis.

In 1992, we measured attributes of forest stands in conjunction with the spotted owl demography and habitat associations study on the Eugene District, BLM (Thrailkill et al. 1998). Data from random old-growth and old-remnant stands on this study area show that old-remnant forest structure is similar to that of old-growth in many ways, including density of snags ≥25-cm dbh, number of vegetation layers, percent canopy cover, and percent ground covered by woody debris. However, there were also distinguishable differences in forest structure between these two forest types. For example, old-growth stands had nearly twice the mean density of large trees ≥53-cm dbh compared to old-remnant stands, but less than half the mean density of trees 13-53-cm dbh (OCFWRU Unpubl. Data).

Cover types were more evenly distributed within 0.6-km-radius circles at ONS compared to NNS, implying greater landscape diversity at ONS. In northwest California, Folliard (1993) also noted greater stand diversity in managed forest where owls were found compared with randomly selected landscapes. A diversity of forest-successional stages might offer advantages to foraging spotted owls because some rodent species might be produced in early-successional forests and disperse into old-growth forests used by owls (Sakai and Noon 1997). In northwestern California, for example, dusky-footed woodrats (*Neotoma fuscipes*), the primary prey item for northern spotted owls in that area (Ward et al. 1998), reach their highest densities in "sapling/poletimber" and "shrubfields" resulting from past clear-cut timber harvest (Sakai and Noon 1997). During evening, dusky-footed woodrats moved short distances into adjacent old-growth forests occupied by spotted owls (Sakai and Noon 1997). Although woodrats (*Neotoma spp.*) are prey items for spotted owls in western Oregon, northern flying squirrels (*Glaucomys sabrinus*) are the main prey item in my study area, and flying squirrels are generally absent from clear-cuts and very young forests (Gashwiler 1970).

There is less old-growth forest in the Oregon Coast Ranges compared to most areas within the range of the northern spotted owl (Thomas et al. 1990). Old-remnant forests were well represented at ONS at this scale and had some affect on higher SIEI values at ONS compared with NNS. Old-remnant forests have some characteristics associated with old-growth forests and might be used by owls as a surrogate for old-growth forests in areas where old-growth is lacking. For example, the 8 nest sites in old-remnant patches had a mean of 20.1% old-remnant forest compared with an overall mean of 9.5% for all ONS in 0.6-km-radius circles. In addition, those 8 nest sites had a mean of 14.1% old-growth forest compared with an overall mean of 31.6% for that circle size. As a possible surrogate for old-growth, old-remnant forests might be associated with population "sinks", i.e., within-habitat reproduction is insufficient to balance local mortality (Pulliam 1988). The role of old-remnant forests as a component of spotted ow habitat and the ability of these forests to meet the life needs of owls has, yet, to be determined.

Regardless of owl nest site preferences, the condition of this altered landscape affects the distribution of cover types. Less old-growth forests and more old-remnant forest at ONS compared to other areas, and monotypic landscapes at NNS, dominated by even-aged pole-young forests, would produce higher SIEI values at ONS compared to NNS.

1.2-km-radius circles.—The average GISfrag value, i.e., the mean distance among old-growth patches, at non-nest sites in the 1.2-km-radius circle was nearly twice as great as that at nest sites. Descriptive statistics show the difference in GISfrag between nest and non-nest sites was, in fact, greatest at the smallest circle size. The average GISfrag value in the 0.6-km-radius circle at non-nest sites was >3 times greater than that at nest sites. Ramsey et al. (1994) demonstrated that differences in the amount of old forest (mature and old-growth combined) in 3.4-km radius circles around owl nest sites versus available sites in the west-central Cascades of Oregon was due to real differences in smaller circular plots contained within. That is, there was a lack of independence among concentric circular plots due to spatial autocorrelation because larger circles incorporate proportions of forest types in the smaller concentric circles. In this study, GISfrag was highly correlated between the 0.6- and 1.2-km-radius circles ($r = 0.955$).

Descriptive statistics and logistic regressions comparing ONS to NNS were strongest for 0.6-km-radius circles, suggesting that spotted owls select nest sites based on landscape features near the nest. Because differences were detected for larger-radius circles, nest site selection by owls might be influenced by landscape features in areas larger than 112 ha. Average annual home-range size and forage/roost locations based on telemetry data suggest that area and specific locations outside the 0.6-km-radius range are important to spotted owls (Forsman et al. 1984, Thomas et al. 1990, Carey et al. 1990, 1992).

Forest fragmentation is a process in which forest patches are progressively sub-divided into more and smaller fragments. Studies have found that fragmentation of late-successional forest is less in landscapes around spotted owl sites compared to available sites (Lehmkuhl and Raphael 1993, Hunter et al. 1995, Ripple et al. 1997). On the Olympic Peninsula, the habitat isolation index was lower around owl locations than random locations at all 3 circle sizes (Lehmkuhl and Raphael 1993). In northwestern California, fragmentation of mature and old-growth forests combined was lower around spotted owl nest sites compared to random sites ($P < 0.01$) out to 1,200 m (Hunter et al. (1995). In southwestern Oregon, GISfrag was lower for nest sites compared with random sites ($P = 0.002$) within a 2.4-km-radius circle (Ripple et al. 1997). Meyer et al. (1998), however, found that none of the six fragmentation indices used for comparison differed significantly between random owl sites and random landscape locations on BLM lands in western Oregon. Chavez-Leon (1989) also found that configuration of late-successional forest was similar between owl sites and surrounding areas in northwestern California.

Northern spotted owls might exhibit negative response behaviors to heavily fragmented landscapes. In a southwestern Oregon study, home range overlap between spotted owl pairs and separation of paired individuals increased with fragmentation of late-successional forest (Carey et al. 1992). They also provided anecdotal evidence that instances of adult nomadism and the proportion of adult-subadult pairs increased in the most heavily fragmented landscape.

There is some evidence that individual owls tend to increase their home-range size in response to fragmentation of late-successional forest (Forsman et al. 1984, Carey et al. 1990). An increase in home range size would probably increase energy demands on foraging owls and might increase the risk of predation (Thomas et al. 1990). Telemetry studies conducted in Oregon and Washington showed that old-growth was the only cover type used consistently more than expected by spotted owls for roosting and foraging (Thomas et al. 1990:149).

1.8-, 2.4- and 3.0-km-radius circles.— Lower percentages of pole-young forest in each of the three largest circles was strongly associated with nest site selection.

Conversely, non-nest sites at these scales had much higher amounts of this cover type by comparison.

In this study, the amount of pole-young was highly correlated among concentric circular plots ($r \geq 0.671$). Difference in the amount of pole-young between nest and non-nest sites was, in fact, greatest at the smallest circle size, and this difference decreased as circle size increased. At the smallest landscape scales, non-nest sites were most associated with large amounts of pole-young forest and areas where old-growth forest were highly fragmented. The accumulated amount of pole-young forest around non-nest sites as circle size increased and the lack of old-growth forest in the larger circles around nest sites was responsible for producing a negative PY coefficient as the only main-effect variable for each of the three largest circle sizes.

Stand attribute data from random pole-young stands on this study area show this cover type usually lacked large diameter trees and snags, and multi-layered canopies (OCFWRU, Unpubl. Data). These important structures are typically used for nesting, roosting and foraging by spotted owls (Thomas et al. 1990). In addition, pole-young stands are typically in the stem-exclusion stage (Smith et al. 1997). During this stage, the dense even-aged trees compete for resources, suppressing sunlight and soil moisture (Smith et al. 1997). This effectively prevents the establishment of shrubs that provide important cover and food sources for small mammals (Carey and Peeler 1995); prey items for spotted owls (Thomas et al. 1990).

Prior harvest restrictions around known spotted owl sites might have contributed to observations of greater amounts of old-growth forest at nest sites and greater amounts of pole-young forest at non-nest sites. BLM districts in western Oregon began to protect late-successional forests within a 2.4-km radius around 90 known spotted owl territories in 1983 (Unpubl. Memorandum of Understanding between BLM and the Oregon Department of fish and Wildlife [ODFW]), increasing that number to 110 territories in 1987. Six (15%) of the 41 nest sites used in these analyses were listed for protection under those "agreements" prior to 1990. Difference in amount of old-growth between nest and non-nest sites were moderate at the 2.4-km-radius circle ($T_{80} = 1.94$, $P = 0.058$). When the 6 nest sites representing restricted harvest areas were removed from this data set, differences in amount of old-growth forest between nest and non-nest sites deceased at the 2.4-km-radius circle ($T_{74} = 1.42$, $P = 0.159$). However, there were still greater amounts of old-growth forest at nest sites in the 2 smallest circles when harvest restrictions were accounted for ($P \leq 0.005$). This management strategy demonstrates the influence and probable benefits of harvest restrictions around known owl sites. However, the harvest restrictions around earlier known owl sites on BLM lands probably increased the amount of timber harvest elsewhere on the landscape because of harvest quotas, removing important habitat components around unknown owl sites.

Unfortunately, I was unable to distinguish older broadleaf patches from younger, even-aged patches on the aerial photos. Older broadleaf-mix forests in this area are structurally diverse, well developed and consist largely of big-leaf maple trees associated with large-diameter conifers. These older forests are often found along stream corridors. Conversely, young broadleaf-mix forests, like pole-young forests, were often clear-cut areas prior to about 1975, and are often associated with riparian areas, upland transition zones and roadsides. Like pole-young forests, young broadleaf-mix forests are relatively simple in structure and provide few nesting structures. Based on my observations, I would consider older broadleaf-mix forest an important component of spotted owl habitat, but young even-aged broadleaf-mix forests should be considered marginal.

Landscape Patterns.—Pattern relates to the spatial arrangement of cover types. On BLM lands in western Oregon, none of the complex pattern variables associated with old-growth forest appeared to affect site selection by spotted owls (Meyer et al. 1997). However, the methods used by Meyer et al. to determine vegetation pattern might have been inappropriate. Carey et al. (1992) reported that landscape pattern variables in southwest Oregon had less predictive ability for spotted owl use than the amount of old forest associated with owl ranges. In the Oregon Coast Ranges one study found that variation in abundance of bird species, with the exception of a few 'edge' species, was more related to area than forest pattern (McGarigal and McComb 1995). Moreover, results of recent modeling efforts to determine the relative effects of loss (amount) and spatial pattern of "habitat" on population extinction, showed that effects of habitat loss far outweighed the effects of spatial pattern (Fahrig 1997).

Most of the old-growth pattern variables were highly correlated with the amount of old-growth forest. Ripple et al. (1997) also found that, with the exception of patch density, most pattern variables associated with old-conifer forest were highly correlated with the amount of that forest type in southwest Oregon (r = 0.60-0.91). Some old-growth patterns might be important to spotted owls. Managing for large amounts of old-growth also produces large amounts of core area, edges, complex shapes and clumped distributions of old-growth patches.

Nest and Non-nest Old-growth Patches

Core area has been found to be a better predictor of site quality than total patch area for some forest interior species (Temple 1986). Evidence suggests that changes in vegetation, competition, brood parasitism, and predation along forest edges has resulted in the population decline of some bird species associated with forest interior (Brittingham and Temple 1983, Wilcove 1985, Temple 1986, Yahner and Scott 1988).

Based on straight-line distance from nest sites to the nearest edge of another cover type, on average, nest sites in old-growth patches were inside the old-growth core area when the closest cover type was an opening, but outside the old-growth core area when the closest cover type was forested ($\bar{x}$ = 107m [n = 9] versus $\bar{x}$ = 69m [n = 20]). Distance from openings is, apparently, important for nesting spotted owls, where a core area of interior forest, buffered around a nest site, might provide important microclimates and protection from predators.

Patch shape is a function of edge-to-area ratio. The more complex the patch shape, the larger the edge-to-area ratio. The SHAPE index, including non-nest patches, was, highly correlated with patch size. However, inspection of mapped old-growth-nest patches on this study area revealed that patch shape is, in part, influenced by the distribution of adjacent clear-cut harvest units, i.e., harvest units that often removed part of the larger old-growth patches that previously existed. In addition, most of the old-growth nest patches are adjacent to riparian zones, and the convoluted shape of nest patches are, in part, influenced by the narrow and meandering shape of adjacent broadleaf-mix patches that are associated with riparian zones.

Patch shape might influence inter-patch migration of small mammals (Buechner 1989) and animal foraging behavior (Forman and Godron 1986). Larger old-growth-nest patches with convoluted edges are tangent to a greater number of patches and a greater number of cover types compared to non-nest patches ($\bar{x}$ number of patches tangent to nest patches = 14 versus 5 at non-nest patches; $\bar{x}$ number of cover types tangent to nest patches = 5 versus 3 at non-nest patches). Although pellet analysis from this study area show northern flying squirrels are the owl's primary prey in terms of percent biomass and composition ($\bar{x}$ of 46.1% biomass over the period of study), much of the owl's diet consisted of other prey species (Thrailkill et al. 1998:A-6). Those prey species are associated with a variety of cover types. A greater variety of cover types tangent to old-growth nest patches might provide access to a variety of prey species. In areas where old-growth forests have been reduced, foraging in a variety of cover types might be implemented as an alternative strategy to foraging behavior on dichotomous landscapes, e.g., the central Cascades of Oregon that largely consists of unmanaged older forests and young plantation forests (mostly unused by spotted owls). Results of more even distributions of cover types around owl nest sites compared with non-nest sites in the 0.6-km-radius circles might support this concept.

For a central-place foraging species like spotted owls (Carey and Peeler 1995), however, particularly during breeding season, foraging in a wide range of cover types distributed across the landscape would, probably, require more energy than foraging in preferred cover types closer to the nest site, thereby, reducing owl fitness (Thomas et al. 1990).

Larger old-growth patches associated with spotted owl sites supports the conclusions of other studies that compared owl sites to available sites (Lehmkuhl and Raphael 1993; Ripple et al. 1997; Meyer et al. 1997). Lehmkuhl and Raphael's (1993) study on the Olympic Peninsula showed that spotted owl sites were associated with larger "habitat" patches. In southwest Oregon, nest patch size was much larger than the largest available patches in random available plots (Ripple et al. 1997). Meyer et al.'s (1997) study on BLM lands in western Oregon also showed that spotted owls were associated with larger old-growth patches. The contrasting differences between those previous studies and this study are: (1) they compared used sites to available sites as opposed to non-used sites; (2) they often used other statistical methods to analyze their data; (3) in those studies, patch size was often truncated by fixed plot boundaries, thereby, underestimating actual patch size; and (4) in those studies, only areas within fixed plot radii were mapped as opposed to the complete study area, so variability of patch size outside plot areas was not accounted for during sample selection. Despite these differences, however, larger old-growth patch size appears to be strongly associated with spotted owl sites and particularly nest locations.

Late-successional forest occupied approximately 63% of the landscape in a recent pre-logging time frame (Ripple et al. 2000). As of 1990, old-growth, old-remnant, mature and mature-young forests combined made up only 19% of the study area landscape; old-growth forests in this area made up only 9.7% of this landscape as of 1990. Nest-site preference by owls for particular old-growth patch characteristics might be relevant to available landscape conditions, i.e., preference based on ratio of core area to patch size, patch shape or patch size might differ in other areas.

Population

Thomas et al. (1990) identified the central Coast Ranges as an "area of concern" where harvesting of late-successional forest has threatened the viability of the subpopulation of spotted owls. Nesting spotted owls in this area select for old-growth forest, but proportions of this cover type around nest sites are extremely low relative to other areas. Less old-growth forest does not mean less is sufficient for successful breeding in this area of the Coast Ranges. There is just less old-growth forest available.

Ultimately, the most meaningful measure of habitat effectiveness should be demographic performance of spotted owls. The estimated annual rate of population change for this area from 1990-93 showed a population declining at 8.7% annually (Thrailkill et al. 1996). This was a short period of study, however, for a long-lived species. Also, this estimated annual rate of decline might be somewhat exaggerated because of negative bias in survival estimates resulting from undetected emigration (Burnham et al. 1996).

The question of whether the projected rate of decline is too fast to be averted by management actions cannot be answered at this time. Higher-quality sites in this area will likely remain occupied for some time. Under the Northwest Forest Plan (U.S. Dept. Agriculture and U.S. Dept. Interior 1994), efforts to reverse the trend of habitat reduction in Late-successional Reserves and Adaptive Management Areas could help reverse the declining population trend in this area.

Methods

In this type of study, it is imperative that used sites be spatially separated from non-used sites to distinguish spatial features associated with each. Criteria for spatial inhibition should be based on available biological information for the given area, e.g., nearest distance between nest sites of different pairs in the same year.

Circular plots are economical and easy to manage, but circles inadequately describe home-ranges, and spatial calculations within circles can be misleading. I do not recommend calculating descriptive patch indices, i.e., minimum, maximum or mean patch size, within confined plots that truncate patch features. Statistics should be generated for complete patches to avoid underestimating important features. Also, for nearest neighbor GIS calculations that implement SEARCH models, e.g., GISfrag, calculations will be biased if based on mapped areas only within plot boundaries. To yield accurate calculations, mapped portions should include all adjacent patches outside the plot boundary and appropriate GIS layers should be generated before applying circular plots.

Finally, manual calculations of land-cover indices is very time consuming and tends to produce data error due to data transfer mistakes. For landscape calculations, I recommend using automated map-analysis techniques which are available for analyzing spatial data. Land-cover features can be calculated for raster data with a moving window function. This function assigns a mathematical value to each pixel on the values of neighboring pixels in a raster-based image. For example, a 5x5 moving window that looks at majority values would assign to each pixel the most common value found in the window based on the 25 neighboring pixels around it. Moving windows can vary in shape (rectangle, circle, annulus, wedge, irregular, and weighted) and size. Upon completion of the moving window function, the pixels that represent points of interest need to be determined in the output product. The output pixel data will contain the information data. Programming languages, like Arc Macro Language (AML) and C, are also useful for automation. An AML will automate repetitive analysis in GIS, while C can be used for modifying Fragstats (McGarigal and Marks 1993), allowing an analyst to do multiple files at one time.

CONCLUSIONS

Research and Management Implications

These results indicate that old-growth forests and clumped dispersions of old-growth patches are associated with northern spotted owl nest sites in the east-central Coast Ranges of Oregon. Furthermore, spotted owls tend to nest in old-growth patches, particularly those ≥40-50 ha in size and with ≥20-30% core area, given a 100-m-edge buffer. Most patterns of old-growth forests are highly correlated with the amount of old-growth or patch size. Therefore, managing for large amounts or large patches of old-growth produces related old-growth patterns. Old-remnant forests are also associated with nest sites. Old-remnant forests might be used as a surrogate for old-growth in areas where old-growth is lacking. Even-aged pole-young forests represent a large percentage of the landscape (27.3%). My results indicate that spotted owls avoid this cover type for nest sites.

Until reliable demographic-habitat models become available, I suggest old-growth and old-remnant forests in this area, including small patches, be protected from further timber harvest. Small patches of these cover types might not be used for nest sites but could provide refugia and foraging areas for the owls while younger forests surrounding these patches develop structurally. Although these results show little use by owls of mature and mature-young forests for nesting, these cover types are important roosting and foraging cover (Forsman et al. 1984, Thrailkill and Meslow

1990), are currently developing complex forest structures, and, therefore, should be conserved in this area.

Land managers should not necessarily use current landscape conditions around nest sites as management goals. Given that a species might successfully reproduce in sink habitats, use of landscape parameters as goals for management that describe existing conditions, with evidence of a declining population, might lead to undesirable results. Efforts are currently underway to develop models relating demographic performance to landscape parameters across the range of the northern spotted owl (R. G. Anthony, personal communication).

Development of pole-young forests should be avoided in this area where management for spotted owl breeding sites is the goal. Pole-young forests in this area should , also, be targeted for management to increase the probability of use as owl nest sites. Stand-growth models should be developed soon to prescribe silvicultural treatments that will accelerate the development of old-growth structures in pole-young stands. Modeling efforts should consider treatment options for various land-use allocations under the Northwest Forest Plan (U.S. Dept. Agriculture and U.S. Dept. Interior 1994).

Land exchanges and purchases should be conducted wherever possible to consolidate federal ownership around lands allocated for management of late-successional forest. Also, an interconnected array of forest patches for owl movement and juvenile dispersal should be maintained in matrix allocations (U.S. Dept. Agriculture and U.S. Dept. Interior 1994). Finally, landscape data covering all ownerships should be used to monitor trends in the amount and distribution of forest cover types, and sample surveys should be conducted periodically to determine densities of spotted owls outside demography study areas.

Method of Comparison

Species-vegetation association studies provide important descriptions, addressing the "what" or proximate mechanisms questions. Addressing these observational questions are preliminary and necessary to "why" or questions about ultimate causes. In other words, one must first observe and verify a relationship before addressing why that relationship occurs.

A common method used to determine wildlife-vegetation associations is to compare structures at used sites to those at randomly selected sites within some predefined area. A limitation to use-versus-availability studies is the fact that used sites are a sub-population of available sites; they are not separate populations. Therefore, current methods of statistical analysis for multivariate data, including logistic regression, might be inappropriate for use-versus-availability studies. Also, the interpretation of models based on use-versus-availability data is difficult "because the relationship of the logistic regression coefficients to the selection process depends substantially on the total amount of the various resources that are used" (F. Ramsey, personal communication). Furthermore, use-versus-availability does not validate use or address the manager's dilemma of what to target for habitat improvements.

Effective wildlife management largely depends upon understanding and predicting habitat needs. Comparisons between used and non-used sites, as opposed to use-versus-availability, can be used to identify those features that are both positively and negatively correlated with the observed patterns of selection. Important features associated with non-used sites can then be targeted for habitat improvements. Management prescriptions, based on features associated with used sites, can be developed and applied to non-used sites to increase the odds of use. Plans to manage single species, however, should be considered within the context of ecosystem management plans to avoid negative impacts on other sensitive species within that system.

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