Habitat Selection by a California Spotted Owl Population: A Landscape Scale Analysis Using Resource Selection Functions

By

Andrea Heather Chatfield
Department of Fisheries, Wildlife, and Conservation Biology
University of Minnesota
St. Paul, Minnesota

A Thesis submitted to:

Dr. R. J. Gutiérrez (advisor)
Department of Fisheries, Wildlife and Conservation Biology
University of Minnesota

Dr. Todd W. Arnold
Department of Fisheries, Wildlife and Conservation Biology
University of Minnesota

Dr. Paul V. Bolstad
Department of Forest Resources
University of Minnesota

In partial fulfillment of the requirements for the degree of Master of Science in Wildlife Conservation

December 2005
ACKNOWLEDGEMENTS

Funding for this project was provided by the U. S. Forest Service, Region 5.

I thank my committee members, Dr. Todd Arnold and Dr. Paul Bolstad, for their insightful comments and guidance throughout the process. I also thank the members of the Gutiérrez lab, Mark Seamans, Guthrie Zimmerman, Jeremy Rockweit, Michelle Crozier, and Dave Grandmaison for their support, friendship, suggestions, brainstorming sessions, and numerous lengthy discussions on habitat selection, experimental design, and statistical analysis. As project supervisor of the Eldorado Spotted Owl Demography Study, Mark, has been a tremendous source of information, guidance, and support throughout my 6 years working for the project. Jeremy, who has unfortunately borne the brunt of my frustrations, has been an endless source of love and encouragement.

I am also grateful to Jeff Corcoran and Angela Rex for their assistance with data collection, and for their continued friendship.

Finally, and foremost, I would like to thank my advisor, Dr. Rocky Gutiérrez, for his guidance and patience. Rocky has been a wonderful mentor and role model, and I feel privileged to have been a part of his research lab.
ABSTRACT

I examined habitat selection by California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, California from 1998 to 2003. I assessed habitat selection at three spatial scales (40, 121, and 473 ha circular plots), which were scales relevant to an owl’s nest/roost patch, protected activity center (PAC), and territory. I developed a set of a priori models based on landscape metrics (habitat amount, average patch size, patch density, amount of edge between habitat and non-habitat, and habitat diversity) that I hypothesized could explain the spatial pattern of spotted owl habitat use at each scale. I used an information-theoretic approach based on Akaike’s Information Criterion (AIC) within a logistic regression framework to model habitat selection, and calculated resource selection functions (RSF) to characterize the relative probability of occupancy using parameter estimates generated from the logistic regression models. I developed a GIS-based vegetation cover-class map from which I calculated habitat metrics. At each of the two finer scales (PAC scale and nest/roost patch scale), I compared either 37 plots centered on actual independent nest locations, or 64 plots centered on actual independent roost locations with equal numbers of randomly placed plots within owl home ranges. At these finer scales my goal was to describe nest and roost habitat selection within a home range, given that an owl has already made an initial selection of a particular territory. At the territory scale, I compared habitat metrics within 51 known owl territories to habitat metrics within 51 plots selected at random from within the entire 355 km² study area.
The amount of habitat had the largest influence on spotted owl site occupancy, and was positively correlated with the probability of owl presence at all spatial scales. At the patch scale, nesting and roosting habitat was most strongly correlated with the amount of late-seral forest having at least 30% canopy cover and mid-seral forest having high canopy cover (≥70%). In addition, roosting habitat was negatively correlated with the amount of habitat diversity. At the PAC scale, nest habitat selection was most strongly influenced by the amount of core habitat (forest > 100 m from an edge) which consisted of late-seral mixed-conifer forests having at least 30% canopy cover and mid-seral mixed-conifer forests having high canopy cover (≥70%). For roost site selection at the PAC scale, the amount of late-seral forest having at least 30% canopy cover was an important predictor of roosting habitat. At the territory scale selection was strongest for mid- to late-seral mixed-conifer forests having high canopy cover (≥70%). None of the other habitat metrics (edge, patch size, patch density) appeared to be strongly related to spotted owl site-occupancy.

I calculated RSFs to develop maps of habitat capability for my study area using my top models. These maps represented the conditional probability that a pixel (i.e., 30 x 30 m block of habitat) was used as a nest or roost site by a spotted owl given that the pixel had a prior probability of use at the territory scale. Based on these results, managers can maintain spotted owl habitat through retention of late-seral stands, retention of mid-seral stands with high canopy cover, and retention of medium-sized trees that serve as recruits to replace older trees.
# TABLE OF CONTENTS

Acknowledgements ................................................................. i

Abstract .................................................................................. ii

Table of Contents ...................................................................... iv

List of Tables ........................................................................... v

List of Figures ........................................................................... v

Introduction ................................................................................ 1

Study Area and Methods .......................................................... 2
  Study Area ............................................................................... 2
  Location of Owls ..................................................................... 3
  Landscape Mapping ................................................................. 3
  Study Design ........................................................................... 8

Habitat Metrics .......................................................................... 10

Model Development .................................................................... 11

Statistical Analysis ..................................................................... 17

Model Validation ......................................................................... 22

Results ........................................................................................ 29
  Nest/Roost Patch Scale ............................................................ 29

Protected Activity Scale (PAC) Scale (121 ha) ......................... 34

Territory Scale (473 ha) ............................................................... 38

Habitat Suitability Map ............................................................... 41

Discussion .................................................................................. 46
LIST OF TABLES

1. Error matrix for accuracy assessment of cover-class map ............................. 6
2. Abbreviations and descriptions of landscape variables ................................. 7
3. Set of a priori models used to evaluate the relationship between habitat variables and spotted owl site occupancy ......................................................... 13
4. Predicted Effects of a priori hypothesized models ......................................... 20
5. Information-theoretic ranking of competing models ...................................... 26
6. Evaluation of model performance for reduced set of competing models .......... 31

LIST OF FIGURES

1. GIS-based cover-class map of the Eldorado study area ................................. 5
2. Functional relationships depicted by the top-fitting regression model at the patch scale (40 ha) ................................................................. 33
3. Functional relationships depicted by the top-fitting regression model at the PAC scale (121 ha) ................................................................. 37
4. Functional relationship depicted by the top-fitting regression model at the territory scale (473 ha) ................................................................. 41
5. Map of predicted probability of nest site selection at the patch scale ............ 43
6. Map of predicted probability of roost site selection at the patch scale .......... 44
7. Map of predicted probability of occupancy at the territory scale ................. 45
INTRODUCTION

Few natural resource issues have been as controversial in the past 15 years as the conservation of the spotted owl (*Strix occidentalis*). This matter is not likely to be resolved in the near future (Courtney et al. 2004). Studies consistently provide evidence for the species’ close association with economically valuable late-seral stage forests (Gutiérrez 1985, Meyer et al. 1998, Zabel et al. 2003). These associations have resulted in timber harvest restrictions in many western states (U.S. Forest Service 1992; Toppinen et al. 2001). Both the northern spotted owl (*Strix occidentalis caurina*) and the Mexican spotted owl (*Strix o. lucida*) are threatened species (U.S. Fish and Wildlife Service 1990, 1993). In contrast, even though several demographic studies of the California spotted owl (*S. o. occidentalis*) suggest that populations may be declining, this subspecies has been denied listing (U.S. Fish and Wildlife Service 2003).

While habitat requirements of the California spotted owl are often assumed to be similar to those of the northern spotted owl, studies have shown that California spotted owls use a broader range of habitats than northern spotted owls (Call et al. 1992; Gutiérrez et al. 1992). Because reliable knowledge about habitat use is fundamental to the conservation of the species, I investigated landscape-scale habitat selection by California spotted owls in the central Sierra Nevada. I developed GIS-based statistical habitat suitability models at multiple spatial scales, corresponding to the scales of nest/roost patch, protected activity center (a “PAC” is a land allocation within the range of this subspecies which is intended to protect habitat near an owl, Verner et al. 1992b), and territory. I also used resource selection functions (RSF) to quantify the relative
probability that a particular area would be used by owls given their selection for specific habitat characteristics. RSFs are thought to be more biologically meaningful, and more relevant to management than previous techniques used to evaluate habitat selection (Manly et al. 2002). RSFs have practical application for predicting habitat selection by California spotted owls, and can serve as important tools for predicting the effects of future land-use alterations and forestry practices on spotted owl populations, particularly in the Sierra Nevada where a major adaptive management program has been proposed for the spotted owl (U.S. Forest Service 2004).

The main objectives of my study were to: 1) estimate if California spotted owl habitat use was non-random with respect to habitat characteristics at the territory scale, 2) estimate if habitat use within home ranges was non-random, given that a spotted owl had selected a particular territory, 3) estimate what parameters of landscape pattern were correlated with habitat use at each scale, and 4) estimate whether or not these important habitat parameters could be used to distinguish used from available habitat in a predictable manner.

STUDY AREA AND METHODS

Study Area

I conducted my study at the site of the long-term Eldorado California spotted owl demography study located in the central Sierra Nevada of California (latitude: 39°, 00'). The study area encompassed 355 km² of mountainous topography in the Eldorado and Tahoe National Forests, which ranged in elevation from 366 to 2,257 m. Land ownership
was 62.7% public and 37.3% private that was arranged in a checkerboard pattern.

Vegetation was typical of Sierran mixed conifer montane forests. Elevations above 2,000 m were dominated by red fir (Abies magnifica), while forests at lower elevations were dominated by ponderosa pine (Pinus ponderosa), white fir (Abies concolor), Douglas-fir (Pseudotsuga menziesii), sugar pine (Pinus lambertiana), incense cedar (Calocedrus decurrens), and black oak (Quercus kellogii) (Küchler 1977; Bias and Gutiérrez 1992; Moen and Gutiérrez 1997).

**Location of Owls**

Territorial owls were located annually between April and August, 1998 to 2002, and their reproductive status was assessed using methods outlined by Forsman (1983). Once located, owls were banded with a U. S. Fish and Wildlife Service locking band on one leg, and a unique combination of color band and color tab on the other leg. Sex of the owls was distinguished by calls and nesting behavior. Locations of owl roosts and nests were recorded using a global positioning system (GPS).

**Landscape Mapping**

Because existing USFS vegetation maps were less than 60% accurate (M. Bond, unpublished data), I created an entirely new vegetation classification map of the Eldorado study area primarily using 1-m scale digital ortho-photo quarter quads (DOQQs) created in 1998, which I supplemented with 1:15,840 color aerial photographs taken in 2000 (Figure 1). I subjected my resulting classification map to extensive site-verification and accuracy assessment (Table 1). I defined eight land-cover classes that were consistent with the California Wildlife Habitat Relationships (CWRH) system that assigns a habitat
type, size class, and canopy cover to habitat classes (Mayer and Laudenslayer 1988), and
that I felt could be reliably identified on the DOQQs (Table 2). I digitized these land-
cover class polygons using ArcView, version 3.2 (Environmental Systems Research
Institute 1999), with a minimum mapping unit (resolution) of 900m².

Map Accuracy Assessment. I assessed the accuracy of my map by randomly
selecting 160 locations across the study area, and then directly sampling vegetation at the
location. Without prior knowledge of the site’s map classification, I located random
locations in the field using a GPS, and visually estimated the stand’s dominant species
composition, dominant size class (DBH), and average % canopy closure. I then classified
each location into a single cover class (water was excluded from the accuracy
assessment), and estimated classification accuracy from agreement (%) between the
cover class map and the on-site vegetation classification and measurements. Overall map
classification accuracy averaged 83% with user’s and producer’s accuracy ranging from
68% to 89% and from 47% to 97% for individual cover classes, respectively. User’s
accuracy, or reliability, is a measure of how well the map represents the true vegetation
class, while producer’s accuracy is a measure of how well a specific geographic region
can be mapped (Story and Congalton 1986; see Table 1 for an error matrix of class
accuracies).
**Figure 1.** GIS-based land-cover class map of the Eldorado study area in the central Sierra Nevada, California. Cover class polygons were delineated from 1998 1-m digital ortho-photo quarter quads, and 2000 color 1:15840 scale aerial photographs.
Table 1. Error matrix for accuracy assessment of GIS-based land-cover class map of the Eldorado study area in the central Sierra Nevada, California. Accuracy was based on agreement between map and ground measurements taken at 160 random locations across the study area.

<table>
<thead>
<tr>
<th>Reference Data (Field Plots)*</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>13</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>16</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>17</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>19</td>
</tr>
<tr>
<td>Classified Data (Cover-class map)*</td>
<td>3</td>
<td>12</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>14</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td></td>
<td>36</td>
<td>2</td>
<td>3</td>
<td></td>
<td></td>
<td>41</td>
</tr>
<tr>
<td>5</td>
<td></td>
<td>2</td>
<td></td>
<td></td>
<td>9</td>
<td>1</td>
<td></td>
<td>12</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td></td>
<td>2</td>
<td>4</td>
<td>17</td>
<td>1</td>
<td></td>
<td>25</td>
</tr>
<tr>
<td>7</td>
<td></td>
<td></td>
<td></td>
<td>4</td>
<td>1</td>
<td>28</td>
<td>33</td>
<td>160</td>
</tr>
</tbody>
</table>

| 1 | 17 | 20 | 13 | 40 | 19 | 22 | 29 | 160 |

<table>
<thead>
<tr>
<th>Producer's Accuracy</th>
<th>User's Accuracy</th>
<th>Overall Accuracy</th>
</tr>
</thead>
<tbody>
<tr>
<td>Class 1 = 13/17 = 76%</td>
<td>Class 1 = 13/16 = 81%</td>
<td>132/160 = 83%</td>
</tr>
<tr>
<td>Class 2 = 17/20 = 85%</td>
<td>Class 2 = 17/19 = 89%</td>
<td></td>
</tr>
<tr>
<td>Class 3 = 12/13 = 92%</td>
<td>Class 3 = 12/14 = 86%</td>
<td></td>
</tr>
<tr>
<td>Class 4 = 36/40 = 90%</td>
<td>Class 4 = 36/41 = 88%</td>
<td></td>
</tr>
<tr>
<td>Class 5 = 9/19 = 47%</td>
<td>Class 5 = 9/12 = 75%</td>
<td></td>
</tr>
<tr>
<td>Class 6 = 17/22 = 77%</td>
<td>Class 6 = 17/25 = 68%</td>
<td></td>
</tr>
<tr>
<td>Class 7 = 28/29 = 97%</td>
<td>Class 7 = 28/33 = 85%</td>
<td></td>
</tr>
</tbody>
</table>

* See Table 2 for definitions of numbered habitat classes.
Table 2. Abbreviations and descriptions for the landscape variables used to predict spotted owl occupancy within the Eldorado study area.

<table>
<thead>
<tr>
<th>Landscape Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Habitat Type:</strong></td>
<td></td>
</tr>
<tr>
<td>8   Water</td>
<td></td>
</tr>
<tr>
<td>7   Mature (≥24&quot; DBH) conifer/mixed-conifer forest with high canopy closure (≥70%).</td>
<td></td>
</tr>
<tr>
<td>6   Mature (≥24&quot; DBH) conifer/mixed-conifer forest with low to medium canopy closure (30-69%).</td>
<td></td>
</tr>
<tr>
<td>5   Medium (11-23.9&quot; DBH) conifer/mixed-conifer forest with high canopy closure (≥70%).</td>
<td></td>
</tr>
<tr>
<td>4   Medium (11-23.9&quot; DBH) conifer/mixed-conifer forest with low to medium canopy closure (30-69%).</td>
<td></td>
</tr>
<tr>
<td>3   Pole (6-10.9&quot; DBH) forest.</td>
<td></td>
</tr>
<tr>
<td>2   Clearcut or small tree (&lt; 6&quot; DBH)/shrub.</td>
<td></td>
</tr>
<tr>
<td>1   Hardwood forest (&gt; 10% hardwood canopy closure and &lt; 10% conifer canopy closure).</td>
<td></td>
</tr>
<tr>
<td><strong>Habitat Pattern:</strong></td>
<td></td>
</tr>
<tr>
<td>AMT   The total amount of area occupied by a particular habitat type within a circular plot.</td>
<td></td>
</tr>
<tr>
<td>CORE  The total amount of core habitat occupied by a particular habitat type. Core habitat is defined as habitat ≥ 100 m from a polygon edge.</td>
<td></td>
</tr>
<tr>
<td>SIZE  The mean size of habitat patches of a particular type within a circular plot.</td>
<td></td>
</tr>
<tr>
<td>DEN   The number of patches of a particular habitat type within a circular plot.</td>
<td></td>
</tr>
<tr>
<td>DIV   The relative habitat diversity within a circular plot as influenced by habitat richness and evenness.</td>
<td></td>
</tr>
<tr>
<td>EDGE  The amount of edge between a particular type of habitat patch and all other habitat types within a circular plot.</td>
<td></td>
</tr>
<tr>
<td>ELEV  The elevation at the center of the circular plot.</td>
<td></td>
</tr>
</tbody>
</table>


**Study Design**

My study design consisted of two segments in which I examined habitat selection at 3 different spatial scales: 40, 121, and 473 ha circular plots centered on owl nest and/or roost locations, which were spatial scales consistent with Johnson’s (1980) hierarchy of selection. My first design segment involved the broadest spatial scale (473 ha), which represented 1/2 the mean nearest neighbor distance among owl territories in my study area. This scale was equivalent to Johnson’s second-order selection. At this territory scale I examined the selection of habitat types and configurations by spotted owls based on their availability within the study area. Manly et al. (2002) stated that this was an example of a Design I, Sampling Protocol A because available habitat was measured by sampling potential territory plots over the entire study area, and there was the implicit assumption that the probability of a potential site being used was approximately the same for all spotted owls. In order to examine selection at the territory scale, I quantified habitat characteristics within circular plots of 473 ha centered on the geometric mean of all nest and roost locations within a territory from 1998 to 2002. Roost and nest locations at individual territories were generally tightly clustered, supporting my use of the geometric mean of these locations as a territory center. I used standard logistic regression within a model selection framework (see below) to compare habitat characteristics estimated at 51 owl territories with 51 areas that were randomly distributed throughout the study area. Therefore, this was a comparison of used vs. available habitat within my entire study area. I minimized the amount of overlap
between used and available plots by restricting my random points to areas outside of known owl territories.

The second aspect of my study design involved the two finer spatial scales, 40 and 121 ha. The 40 ha scale represented the estimated average size of nest stands used by California spotted owls (Gutiérrez et al. 1992). This scale corresponded to Johnson’s (1980) fourth order selection that has been hypothesized to relate to the actual procurement of resources from an area, in this case the actual nest or roost stand. The 121 ha scale represented the protected activity center (PAC; see Verner et al. 1992b), which is the current management standard used to protect owl habitat by the Forest Service. This scale corresponded to Johnson’s (1980) third order selection that is related to the use of specific habitat components within a home range. In my study this included activity areas surrounding nest and roost locations. I addressed these two levels of selection with respect to: 1) habitat types and patterns selected by owls for nesting, and 2) habitat types and patterns selected by owls for roosting, both of which were based on what was available to them within their home ranges. Therefore, in this segment of my study design, I evaluated the habitat types and configurations spotted owls selected as nest and roost sites given what was available to them within their chosen home range.

To examine nest and roost site selection, I selected one random roost location and one random nest location (from those territories where an actual nest location had been located) from among those recorded during the entire study period (\( n = 37 \) nest sites; \( n = 64 \) roost sites). I then selected a random “available” site situated within the owl’s theoretical home range (\( n = 37 \) “available” nest sites; \( n = 64 \) “available” roost sites). I
selected a different set of random points for each of the two spatial scales. Selecting random “available” sites from within owl home ranges ensured that these sites were sufficiently close to used sites such that owls could have selected them as possible alternative nest or roost sites. Laymon (1988) estimated the average home range size for this population of California spotted owls to be 1,660 ha, which corresponds to a circle having a radius of 2,300 m. Therefore, for the 40 ha scale, I sampled random points between 720 m and 2,300 m from the nest or roost to ensure the plot fell outside of the sampled nest or roost area but within the owl’s estimated home range area. For the 121 ha scale, I only selected random points that were between 1,242 m and 2,300 m from the owl nest or roost location. To place these random points, I randomly selected a direction and distance from the nest or roost location. Because spotted owls are habitat specialists (Gutiérrez et al.1992), and there are large areas of unsuitable habitat within my study area, I excluded random locations that fell entirely within unsuitable habitat (e.g., extensive brush fields or water). This restriction allowed me to avoid trivial comparisons of selection patterns (Johnson 1980).

**Habitat Metrics**

I measured 6 different landscape metrics to characterize the amount, configuration, and heterogeneity of habitat across the landscape (Table 2). I used a geographic information system (GIS) to facilitate estimation of these metrics. I first created a map layer of all UTM coordinates for occupied and random plot centers at all three spatial scales, which I overlaid on my vector-based cover class map. I then created circular plots centered on these UTM coordinates (i.e., plot centers) having radii of 357,
621 or 1,226 m, depending on the scale of analysis. Using the cover class GIS layer, I estimated habitat metrics associated with each circular plot using the ArcView extension, Patch Analyst (Elkie et al. 1999). To avoid overestimating the amount of edge by including the edge of the circular analysis area, I converted the cover class map to raster format, and used the raster-based spatial analysis program, Fragstats (McGarigal and Marks 1995) to estimate the amount of edge within plots. Fragstats allowed calculation of a contrast-weighted edge measurement by assigning areas outside of the analysis area a value of zero, so that the outer edge of the circular plot was not included in the calculation of total edge. This weighted-edge calculation option was not available with the vector-based Patch Analyst program. I manually checked a random subset of habitat measurements within each spatial scale to ensure accurate calculation of landscape variables by the spatial analysis software. The elevation variable, used only at the territory scale, was the elevation at the plot center and was estimated from a digital elevation model (DEM) with a resolution of 5 m isopleths. In order to avoid very large parameter estimates, I rescaled the elevation and edge measurements by dividing them each by 100.

**Model Development**

Prior to analysis, I reviewed the literature to estimate ways in which habitat type and configuration might influence spotted owl habitat selection. I then developed a set of *a priori* models using my landscape metrics that represented hypotheses about potential relationships between habitat pattern and spotted owl occupancy. I developed these models with strong consideration for their management relevance. I was particularly
interested in how the amounts and configurations of different types of forested habitat affected the probability of owl occupancy. My final set of hypothesized candidate models consisted of 24 habitat models (Table 3). These were grouped into the following five categories: (1) habitat amount models, (2) habitat patch size and density models, (3) canopy cover models, (4) edge effect models, and (5) habitat diversity models.

The habitat amount models reflected hypotheses that spotted owls selected areas based on the amount of a particular habitat type or types. Most studies of spotted owl habitat selection have suggested a strong association with late-seral stage forests. These studies have consistently indicated that greater amounts of late-seral stage forest surround nest and roost sites than random sites. Carey et al. (1992) found that northern spotted owls consistently selected old forest at landscape, home range, and foraging/roosting site scales. Call et al. (1992) found that California spotted owls used forest dominated by large trees, as well as forest dominated by medium trees with high canopy cover more than expected given their availability. At a finer spatial scale, Hunter et al. (1995) found that nest and roost areas had significantly greater amounts of mature and old growth forest. Ripple et al. (1997) found nest sites contained more old conifer forest at a variety of scales, and Meyer et al. (1998) found that the amount of suitable habitat was the dominant covariate in their resource selection functions for northern spotted owls. Therefore, I included several definitions of suitable habitat that were consistent with the findings of the above studies. In addition, I included a model that hypothesized a negative effect of amount of non-habitat (non-forested land) on spotted owl occupancy (model 2c, Table 3).
Table 3. Suite of models hypothesized *a priori* to the analysis to evaluate the relationship between resource selection (i.e., landscape characteristic association) and the probability of site use by California spotted owls in the central Sierra Nevada. The response variable is the resource selection probability function and the model structure displayed is the logit of the logistic regression model.

<table>
<thead>
<tr>
<th>Verbal Hypothesis</th>
<th>Model Structure</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1. Null hypothesis:</strong> (No effect due to landscape variables) $\beta_0$</td>
<td></td>
</tr>
<tr>
<td><strong>2. Habitat amount models:</strong> (Spotted owls select areas based on the amount of a particular habitat type or types)</td>
<td></td>
</tr>
<tr>
<td>a) Positive effect of amount of spotted owl habitat: $\beta_0 + \beta_1\text{AMT}(7)$  $\beta_0 + \beta_1\text{AMT}(6+7)$  $\beta_0 + \beta_1\text{AMT}(5+6+7)$</td>
<td></td>
</tr>
<tr>
<td>b) Positive effect of amount of core spotted owl habitat: $\beta_0 + \beta_1\text{CORE}(5+6+7)$</td>
<td></td>
</tr>
<tr>
<td>c) Negative effect of amount of non-habitat: $\beta_0 + \beta_1\text{AMT}(2+3)$</td>
<td></td>
</tr>
<tr>
<td><strong>3. Patch size and patch density models</strong> (Spotted owls select areas based on the size and number of suitable habitat patches)</td>
<td></td>
</tr>
<tr>
<td>a) Positive effect of amount habitat and positive effect of patch size: $\beta_0 + \beta_1\text{AMT}(6+7) + \beta_2\text{SIZE}(6+7)$  $\beta_0 + \beta_1\text{AMT}(5+6+7) + \beta_2\text{SIZE}(5+6+7)$</td>
<td></td>
</tr>
<tr>
<td>b) Positive effect of amount of mature forest and positive effect of patch density: $\beta_0 + \beta_1\text{AMT}(6+7) + \beta_2\text{DEN}(6+7)$  $\beta_0 + \beta_1\text{AMT}(5+6+7) + \beta_2\text{DEN}(5+6+7)$</td>
<td></td>
</tr>
<tr>
<td><strong>4. Canopy cover models:</strong> (Spotted owls select areas with a greater proportion of habitat with $&gt;70%$ canopy cover)</td>
<td></td>
</tr>
<tr>
<td>a) Positive effect of amount of habitat having high canopy cover: $\beta_0 + \beta_1\text{AMT}(5+7)$</td>
<td></td>
</tr>
<tr>
<td>b) Positive effect of high canopy cover core habitat and positive effect of patch size: $\beta_0 + \beta_1\text{CORE}(5+7) + \beta_2\text{SIZE}(5+7)$</td>
<td></td>
</tr>
<tr>
<td>c) Positive effect of core high canopy cover habitat and negative effect of patch density: $\beta_0 + \beta_1\text{CORE}(5+7) + \beta_2\text{DEN}(5+7)$</td>
<td></td>
</tr>
<tr>
<td>d) Positive effect of increasing ratio of amount of high/medium canopy cover habitat: $\beta_0 + \beta_1(\text{AMT}(5+7)/\text{AMT}(4+6))$</td>
<td></td>
</tr>
</tbody>
</table>
5. **Edge effect models:** (Spotted owls select areas with large amounts of core habitat and large amounts of edge between habitat and non-habitat)

   a) Positive effect of amount of core habitat and positive effect of edge:
   \[ \beta_0 + \beta_1 \text{CORE}(7) + \beta_2 \text{EDGE}(4+5+6+7) \]
   \[ \beta_0 + \beta_1 \text{CORE}(5+6+7) + \beta_2 \text{EDGE}(4+5+6+7) \]

   b) Positive effect of amount of habitat and positive effect of edge:
   \[ \beta_0 + \beta_1 \text{AMT}(5+6+7) + \beta_2 \text{EDGE}(4+5+6+7) \]

   c) Positive effect of amount of core habitat, positive effect of habitat patch size, and positive effect of edge:
   \[ \beta_0 + \beta_1 \text{CORE}(7) + \beta_2 \text{SIZE}(7) + \beta_3 \text{EDGE}(4+5+6+7) \]
   \[ \beta_0 + \beta_1 \text{CORE}(5+6+7) + \beta_2 \text{SIZE}(5+6+7) + \beta_3 \text{EDGE}(4+5+6+7) \]

   d) Positive effect of amount of habitat, positive effect of edge, and negative effect of edge interacting with elevation (473-ha scale only):
   \[ \beta_0 + \beta_1 \text{AMT}(7) + \beta_2 \text{EDGE}(7) + \beta_3 \text{ELEV} + \beta_4 \text{EDGE}(7) \times \text{ELEV} \]
   \[ \beta_0 + \beta_1 \text{AMT}(5+6+7) + \beta_2 \text{EDGE}(4+5+6+7) + \beta_3 \text{ELEV} + \beta_4 \text{EDGE}(5+6+7) \times \text{ELEV} \]

6. **Habitat diversity models:** (Spotted owls select areas of high habitat heterogeneity)

   a) Negative effect of habitat diversity:
   \[ \beta_0 + \beta_1 \text{DIV} \]

   b) Positive effect of amount of habitat and negative effect of habitat diversity:
   \[ \beta_0 + \beta_1 \text{AMT}(7) + \beta_2 \text{DIV} \]
   \[ \beta_0 + \beta_1 \text{AMT}(5+6+7) + \beta_2 \text{DIV} \]
My patch size and density models reflected hypotheses that spotted owls selected areas based on the size and number of suitable habitat patches. Several studies suggested that habitat patch size and density, in addition to total amount of habitat, were important in spotted owl habitat selection. Lehmkuhl and Raphael (1993) found a greater average habitat patch size and lower patch density within owl plots than within random plots. Similarly, Meyer et al. (1998) found that northern spotted owl sites contained larger old growth patches than did random sites. Ripple et al. (1997) found that nest habitat patches were larger than the largest old forest patch within random sites. My patch size and density models reflected these findings.

My canopy cover models reflected hypotheses that spotted owls selected areas with a greater proportion of habitat with high (≥70%) canopy cover. Numerous studies have suggested that canopy cover was an important factor in spotted owl habitat selection. In studies of the California spotted owl, Bias and Gutiérrez (1992) found that nest sites were in habitat with >69% canopy closure, and LaHaye et al. (1997) found that nest sites contained a greater average percent canopy closure than random locations. Similarly, Moen and Gutiérrez (1997) found that habitat dominated by medium trees with high canopy cover was more abundant in owl territories than within random sites, and Call et al. (1992) found that owl home ranges contained more forest with >69% canopy cover than what was available within the study area. My canopy cover models incorporated the amounts and patterns of habitat classes 5 and 7 (high canopy cover habitat dominated by medium and large trees, respectively). These models were particularly important because of the recent changes made to the Sierra Nevada Forest Plan (U.S. Forest Service 2004), which is a proposed management plan for the Sierra
Nevada where the potential importance of high canopy closure to owls seemingly has been neglected.

My edge effect models reflected hypotheses that spotted owls selected areas with large amounts of suitable habitat or suitable core habitat, and large amounts of edge between habitat and non-habitat. While numerous studies have suggested that there were potential negative effects of forest fragmentation on spotted owls, others have found a potential positive effect of some degree of spatial heterogeneity. Ward et al. (1998) found that northern spotted owls foraged in ecotones between late- and early-seral stage mixed conifer forest where woodrats (Neotoma fuscipes) were most abundant. This finding was supported by Franklin et al. (2000) who found that both the amount of interior mature coniferous forest and the amount of edge between these forests and other habitat types had a strong influence on northern spotted owl survival and reproduction. I incorporated the findings of these two studies into my models (models 5a and 5b, Table 3). In addition, I included a model with a predicted interaction between the amount of edge and elevation, with the influence of edge decreasing with increasing elevation. In the Sierra Nevada, woodrats were associated with foothill riparian/hardwood forests (Neal et al. 1990; Verner et al. 1992a), and were most likely the dominant prey for owls inhabiting lower elevation territories (Laymon 1988). Conversely, at higher elevations northern flying squirrels (Glaucomys sabrinus), which are an interior, conifer forest species, were most likely the dominant prey item (Laymon 1988; Verner et al 1992a) on my study area. Therefore, it seemed reasonable to expect edges between conifer forest and other habitat types to be more beneficial to owls at lower elevation territories, and
interior forest with fewer edges to be more beneficial at higher elevation territories. I represented this hypothesis with model 5d (Table 3), but I only examined it at the territory scale because it was a hypothesis that was relevant primarily at this broader scale.

Finally, my habitat diversity models reflected hypotheses that spotted owls selected areas that had low habitat heterogeneity. Several studies have suggested that spotted owls inhabited sites with lower levels of habitat heterogeneity than random areas (Bias and Gutiérrez 1992; Hunter et al. 1995; Moen and Gutiérrez 1997). My three habitat diversity models reflected these previous findings.

I expected considerable correlation between certain habitat variables. However, I did not examine correlation between model variables until after formulation of my a priori models in order to avoid subjective bias in model development.

**Statistical Analysis**

To examine habitat selection, I used a model selection approach based on information-theory (Akaike 1973). Given a set of carefully constructed a priori candidate models, information-theoretic methods provide a quantitative assessment of the “strength of evidence” in the data regarding the plausibility of each model relative to the entire set (Burnham and Anderson 1998). I used Akaike’s Information Criterion (AIC; Akaike 1973) as an objective criterion to select the model which best explained the data. Because my sample sizes were modest relative to the total number of candidate models, I used AIC<sub>c</sub>, which is a modification of AIC adjusted for small sample size (Burnham and Anderson 1998). AIC<sub>c</sub> takes the following form:
AIC_c = -2 log(L(\theta)) + 2K + (2K(K + 1)/(n - K - 1))

Where \( \theta \) is the response variable (probability of use, in this case), log(L(\theta)) is the value of the log-likelihood function at its maximum, K is the total number of estimable parameters in the particular model, and n is sample size. There was no evidence of overdispersion in the data so I did not use the quasi-corrected QAIC_c (Burnham and Anderson 1998).

Burnham and Anderson (1998) suggested that models within 2 AIC of one another were competing. Therefore, I considered models within 2 AIC_c units of the top model as my competing model set, and it was this set of reduced models that was examined in greater detail. I used 95% confidence intervals on the parameter estimates to assess the degree to which the signs of the estimated slope parameters in the reduced model set were reliably estimated.

For each scale of analysis, I used standard logistic regression within the model selection framework to analyze my set of a priori hypothesized models. I used logistic regression in PROC LOGISTIC in program SAS (SAS Institute Inc.1999) for my analyses because logistic regression describes how a binary response variable is associated with a set of exploratory variables (Hosmer and Lemeshow 2000). I fitted each a priori model to a logistic model that took the following form:

\[
\pi = \exp(\beta_0 + \beta_1x_1 + \beta_2x_2 + \ldots + \beta_kx_k) / [1 + \exp(\beta_0 + \beta_1x_1 + \beta_2x_2 + \ldots + \beta_kx_k)]
\]

where \( \beta_1 \) to \( \beta_k \) are coefficients to be estimated from the available data, and \( x_1 \) to \( x_k \) are the independent habitat variables, and the dependent data are 1 for used units and 0 for available units. I examined 3 different statistical forms for each of my a priori
hypotheses: a linear, a quadratic, and a logistic form. A linear structure predicted that the effect of the habitat covariates would change at some constant rate as the probability of occupancy increased. A quadratic form predicted that the greatest effect would occur at some intermediate value of the habitat covariate, while lower effects would occur at either extreme. A quadratic structure can also fit an exponential relationship if both coefficients are positive (or negative). The logistic form predicted a change in effect at a constant rate until the effect approached an asymptote. I predicted model effects for each form of the base model (Table 4). I added 0.1 to covariate values to account for values of zero when I used logarithmic transformations when modeling pseudothreshold forms (Franklin et al. 2000). To test for redundancy in explanatory power among habitat variables, I completed a correlation analysis to identify variables with moderate to high correlation \((r \geq 0.60)\) within each of my hypothesized models.
Table 4. Predicted effects of *a priori* hypothesized models used to relate the effects of landscape habitat characteristics with probability of California spotted owl presence in the Eldorado study area, central Sierra Nevada Mountains, California. \( \theta \) represents the probability of owl presence.

<table>
<thead>
<tr>
<th>Hypothesized Base Model</th>
<th>Linear Form</th>
<th>Pseudothreshold Form</th>
<th>Quadratic Form</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) ( \theta )</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2) ( \theta_{amt(7)} )</td>
<td>( \beta_{amt(7)} &gt; 0 )</td>
<td>( \beta_{ln(amt(7))} &gt; 0 )</td>
<td>( \beta_{amt(7)} &gt; 0, \beta_{(amt(7))^2} &lt; 0 )</td>
</tr>
<tr>
<td>3) ( \theta_{amt(6+7)} )</td>
<td>( \beta_{amt(6+7)} &gt; 0 )</td>
<td>( \beta_{ln(amt(6+7))} &gt; 0 )</td>
<td>( \beta_{amt(6+7)} &gt; 0, \beta_{(amt(6+7))^2} &lt; 0 )</td>
</tr>
<tr>
<td>4) ( \theta_{amt(5+6+7)} )</td>
<td>( \beta_{amt(5+6+7)} &gt; 0 )</td>
<td>( \beta_{ln(amt(5+6+7))} &gt; 0 )</td>
<td>( \beta_{amt(5+6+7)} &gt; 0, \beta_{(amt(5+6+7))^2} &lt; 0 )</td>
</tr>
<tr>
<td>5) ( \theta_{core(5+6+7)} )</td>
<td>( \beta_{core(5+6+7)} &gt; 0 )</td>
<td>( \beta_{ln(core(5+6+7))} &gt; 0 )</td>
<td>( \beta_{core(5+6+7)} &gt; 0, \beta_{(core(5+6+7))^2} &lt; 0 )</td>
</tr>
<tr>
<td>6) ( \theta_{amt(2+3)} )</td>
<td>( \beta_{amt(2+3)} &lt; 0 )</td>
<td>( \beta_{ln(amt(2+3))} &lt; 0 )</td>
<td>( \beta_{amt(2+3)} &gt; 0, \beta_{(amt(2+3))^2} &lt; 0 )</td>
</tr>
<tr>
<td>7) ( \theta_{amt(6+7) + size(6+7)} )</td>
<td>( \beta_{amt(6+7)} &gt; 0, \beta_{size(6+7)} &gt; 0 )</td>
<td>( \beta_{ln(amt(6+7))} &gt; 0, \beta_{ln(size(6+7))} &gt; 0 )</td>
<td>( \beta_{amt(6+7)} &gt; 0, \beta_{(amt(6+7))^2} &lt; 0, \beta_{size(6+7)} &gt; 0, \beta_{(size(6+7))^2} &lt; 0 )</td>
</tr>
<tr>
<td>8) ( \theta_{amt(5+6+7) + size(5+6+7)} )</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9) ( \theta_{amt(6+7) + den(6+7)} )</td>
<td>( \beta_{amt(6+7)} &gt; 0, \beta_{den(6+7)} &lt; 0 )</td>
<td>( \beta_{ln(amt(6+7))} &gt; 0, \beta_{ln(den(6+7))} &lt; 0 )</td>
<td>( \beta_{amt(6+7)} &gt; 0, \beta_{(amt(6+7))^2} &lt; 0, \beta_{den(6+7)} &gt; 0, \beta_{(den(6+7))^2} &lt; 0 )</td>
</tr>
<tr>
<td>10) ( \theta_{amt(5+6+7) + den(5+6+7)} )</td>
<td>( \beta_{amt(5+6+7)} &gt; 0, \beta_{den(5+6+7)} &lt; 0 )</td>
<td>( \beta_{ln(amt(5+6+7))} &gt; 0, \beta_{ln(den(5+6+7))} &lt; 0 )</td>
<td>( \beta_{amt(5+6+7)} &gt; 0, \beta_{(amt(5+6+7))^2} &lt; 0, \beta_{den(5+6+7)} &gt; 0, \beta_{(den(5+6+7))^2} &lt; 0 )</td>
</tr>
<tr>
<td>11) ( \theta_{amt(5+7)} )</td>
<td>( \beta_{amt(5+7)} &gt; 0 )</td>
<td>( \beta_{ln(amt(5+7))} &gt; 0 )</td>
<td>( \beta_{amt(5+7)} &gt; 0, \beta_{(amt(5+7))^2} &lt; 0 )</td>
</tr>
<tr>
<td>12) ( \theta_{core(5+7) + size(5+7)} )</td>
<td>( \beta_{core(5+7)} &gt; 0, \beta_{size(5+7)} &gt; 0 )</td>
<td>( \beta_{ln(core(5+7))} &gt; 0, \beta_{ln(size(5+7))} &gt; 0 )</td>
<td>( \beta_{core(5+7)} &gt; 0, \beta_{(core(5+7))^2} &lt; 0, \beta_{size(5+7)} &gt; 0, \beta_{(size(5+7))^2} &lt; 0 )</td>
</tr>
<tr>
<td>13) ( \theta_{core(5+7) + den(5+7)} )</td>
<td>( \beta_{core(5+7)} &gt; 0, \beta_{den(5+7)} &lt; 0 )</td>
<td>( \beta_{ln(core(5+7))} &gt; 0, \beta_{ln(den(5+7))} &lt; 0 )</td>
<td>( \beta_{core(5+7)} &gt; 0, \beta_{(core(5+7))^2} &lt; 0, \beta_{den(5+7)} &gt; 0, \beta_{(den(5+7))^2} &lt; 0 )</td>
</tr>
<tr>
<td>14) ( \theta_{(amt(5+7)/amt(4+6))} )</td>
<td>( \beta_{(amt(5+7)/amt(4+6))} &gt; 0 )</td>
<td>( \beta_{ln(amt(5+7)/amt(4+6)))} &gt; 0 )</td>
<td>( \beta_{amt(5+7)/amt(4+6))} &gt; 0, \beta_{(amt(5+7)/amt(4+6)))^2} &lt; 0 )</td>
</tr>
<tr>
<td>15) ( \theta_{core(7) + edge(4+5+6+7)} )</td>
<td>( \beta_{core(7)} &gt; 0, \beta_{edge(4+5+6+7)} &lt; 0 )</td>
<td>( \beta_{ln(core(7))} &gt; 0, \beta_{ln(edge(4+5+6+7))} &lt; 0 )</td>
<td>( \beta_{core(7)} &gt; 0, \beta_{edge(4+5+6+7)}^2 &lt; 0, \beta_{edge(4+5+6+7)} &gt; 0, \beta_{edge(4+5+6+7))^2} &lt; 0 )</td>
</tr>
<tr>
<td>16) ( \theta_{core(5+6+7) + edge(4+5+6+7)} )</td>
<td>( \beta_{core(5+6+7)} &gt; 0, \beta_{edge(4+5+6+7)} &lt; 0 )</td>
<td>( \beta_{ln(core(5+6+7))} &gt; 0, \beta_{ln(edge(4+5+6+7))} &lt; 0 )</td>
<td>( \beta_{core(5+6+7)} &gt; 0, \beta_{edge(4+5+6+7)^2} &lt; 0, \beta_{edge(4+5+6+7)} &gt; 0, \beta_{edge(4+5+6+7))^2} &lt; 0 )</td>
</tr>
</tbody>
</table>
### Predicted Effects

<table>
<thead>
<tr>
<th>Hypothesized Base Model</th>
<th>Linear Form</th>
<th>Pseudothreshold Form</th>
<th>Quadratic Form</th>
</tr>
</thead>
<tbody>
<tr>
<td>17) ( \theta_{\text{amt}(5+6+7) + \text{edge}(4+5+6+7)} )</td>
<td>( \beta_{\text{amt}(5+6+7)} &gt; 0, \beta_{\text{edge}(4+5+6+7)} &gt; 0 )</td>
<td>( \beta_{\ln(\text{amt}(5+6+7))} &gt; 0, \beta_{\text{edge}(4+5+6+7)} &gt; 0 )</td>
<td>( \beta_{\text{amt}(5+6+7)} &gt; 0, \beta_{\text{amt}(5+6+7)^2} &lt; 0 )</td>
</tr>
<tr>
<td>18) ( \theta_{\text{core}(7) + \text{size}(7) + \text{edge}(4+5+6+7)} )</td>
<td>( \beta_{\text{core}(7)} &gt; 0, \beta_{\text{size}(7)} &gt; 0, \beta_{\text{edge}(4+5+6+7)} &gt; 0 )</td>
<td>( \beta_{\ln(\text{core}(7))} &gt; 0, \beta_{\text{size}(7)} &gt; 0, \beta_{\text{edge}(4+5+6+7)} &gt; 0 )</td>
<td>( \beta_{\text{core}(7)} &gt; 0, \beta_{\text{core}(7)^2} &lt; 0, \beta_{\text{size}(7)} &gt; 0, \beta_{\text{edge}(4+5+6+7)} &gt; 0 )</td>
</tr>
<tr>
<td>19) ( \theta_{\text{core}(5+6+7) + \text{size}(5+6+7) + \text{edge}(4+5+6+7)} )</td>
<td>( \beta_{\text{core}(5+6+7)} &gt; 0, \beta_{\text{size}(5+6+7)} &gt; 0, \beta_{\text{edge}(4+5+6+7)} &gt; 0 )</td>
<td>( \beta_{\ln(\text{core}(5+6+7))} &gt; 0, \beta_{\text{size}(5+6+7)} &gt; 0, \beta_{\text{edge}(4+5+6+7)} &gt; 0 )</td>
<td>( \beta_{\text{core}(5+6+7)} &gt; 0, \beta_{\text{core}(5+6+7)^2} &lt; 0, \beta_{\text{size}(5+6+7)} &gt; 0, \beta_{\text{edge}(4+5+6+7)^2} &lt; 0 )</td>
</tr>
<tr>
<td>20) ( \theta_{\text{amt}(7) + \text{edge}(7) + \text{elev} + \text{edge}(7)^{\text{elev}}} )</td>
<td>( \beta_{\text{amt}(7)} &gt; 0, \beta_{\text{edge}(7)} &gt; 0, \beta_{\text{edge}(7)^{\text{elev}}} &gt; 0 )</td>
<td>( \beta_{\ln(\text{amt}(7))} &gt; 0, \beta_{\text{edge}(7)^{\text{elev}}} &gt; 0 )</td>
<td>( \beta_{\text{amt}(7)} &gt; 0, \beta_{\text{edge}(7)^{\text{elev}}} &gt; 0 )</td>
</tr>
<tr>
<td>21) ( \theta_{\text{amt}(5+6+7) + \text{div} + \text{edge}(4+5+6+7) + \text{elev} + \text{edge}(4+5+6+7)^{\text{elev}}} )</td>
<td>( \beta_{\text{amt}(5+6+7)} &gt; 0, \beta_{\text{edge}(4+5+6+7)} &gt; 0, \beta_{\text{edge}(4+5+6+7)^{\text{elev}}} &gt; 0 )</td>
<td>( \beta_{\ln(\text{amt}(5+6+7))} &gt; 0, \beta_{\text{edge}(4+5+6+7)^{\text{elev}}} &gt; 0 )</td>
<td>( \beta_{\text{amt}(5+6+7)} &gt; 0, \beta_{\text{amt}(5+6+7)^2} &lt; 0, \beta_{\text{div}} &gt; 0, \beta_{\ln(\text{div})} &gt; 0 )</td>
</tr>
<tr>
<td>22) ( \theta_{\text{div}} )</td>
<td>( \beta_{\text{div}} &gt; 0 )</td>
<td>( \beta_{\ln(\text{div})} &gt; 0 )</td>
<td>( \beta_{\text{div}} &gt; 0, \beta_{\ln(\text{div})}^2 &lt; 0 )</td>
</tr>
<tr>
<td>23) ( \theta_{\text{amt}(7) + \text{div}} )</td>
<td>( \beta_{\text{amt}(7)} &gt; 0, \beta_{\text{div}} &gt; 0 )</td>
<td>( \beta_{\ln(\text{amt}(7))} &gt; 0, \beta_{\text{div}} &gt; 0 )</td>
<td>( \beta_{\text{amt}(7)} &gt; 0, \beta_{\text{amt}(7)^2} &lt; 0, \beta_{\text{div}} &gt; 0, \beta_{\ln(\text{div})} &gt; 0 )</td>
</tr>
<tr>
<td>24) ( \theta_{\text{amt}(5+6+7) + \text{div}} )</td>
<td>( \beta_{\text{amt}(5+6+7)} &gt; 0, \beta_{\text{div}} &gt; 0 )</td>
<td>( \beta_{\ln(\text{amt}(5+6+7))} &gt; 0, \beta_{\ln(\text{div})} &gt; 0 )</td>
<td>( \beta_{\text{amt}(5+6+7)} &gt; 0, \beta_{\text{amt}(5+6+7)^2} &lt; 0, \beta_{\text{div}} &gt; 0, \beta_{\ln(\text{div})} &lt; 0 )</td>
</tr>
</tbody>
</table>
I ranked my *a priori* hypothesized models using AIC\(_c\) values and calculated Akaike weights, \(w_i\), for each model. Akaike weights provided a measure of the likelihood of each model given the data and model set (Burnham and Anderson 1998) and were expressed as:

\[
w_i = \frac{\exp(-\frac{1}{2} \Delta_i)}{\sum \exp(-\frac{1}{2} \Delta_i)}
\]

I then used the logistic regression coefficients to estimate the selection coefficients, \(\beta_i\), in the log-linear function below to obtain the relative probability of use (i.e., the RSF):

\[
\text{RSF} = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k)
\]

This function estimated the relative probability of a particular habitat being used by a spotted owl. Because I did not know the sampling probabilities of used and available habitat, I was unable to calculate an intercept, \(\beta_0\), which would have allowed calculation of the actual probability of use of a particular area, rather than the relative probability of use (Manly et al. 2002).

**Model Validation**

The ultimate goal of resource selection models is reliable prediction of resource use (Pearce and Ferrier 2000; Rushton et al. 2004). While AIC is a useful technique for choosing the “best” model from a set of alternative models, being the “best” among a set of poor or unreliable models does not make it a “good” model (Burnham and Anderson 2002). Therefore, measures of model performance and uncertainty are needed. Validation is a critical component of model development because it provides such a measure of overall model performance (i.e. can habitat parameters be used to discriminate between used and available habitat?).
The performance of wildlife habitat models derived from logistic regression is often assessed by cross-validation (i.e., examining the agreement between model predictions and actual observations). A species is predicted to be present or absent at a site based on whether the predicted probability for the site is higher or lower than a specified probability value (Pearce and Ferrier 2000). However, there is an element of circularity when evaluating a model with data from which it was developed (Boyce et al. 2002). This often leads to overly optimistic measures of classification accuracy (Boyce et al. 2002). A jackknife approach can alleviate this problem. In jackknife cross-validation a single observation is removed from the data set and the remaining data are used to estimate the model parameters. However, this method also has limitations. Such threshold-based cross-validation methods of accuracy assessment can be misleading because its interpretation depends on knowledge of the prior probability of occurrence of the species in question (Pearce and Ferrier 2000). In addition, traditional measures of discrimination capacity depend on the arbitrary choice of a decision threshold, which further complicates the interpretation of the classification statistics because they dichotomize an inherently continuous variable (Altman et al. 1994).

Another method for evaluating the predictive performance of wildlife habitat models is the receiver operating characteristic (ROC) technique. ROC analysis evaluates the proportion of correctly and incorrectly classified predictions over a continuous range of threshold probability cut-off levels (Hosmer and Lemeshow 2000). It is therefore, independent of both species prevalence and decision threshold effects (Pearce and Ferrier 2000). ROC analysis is often found in the medical literature and has recently emerged in
ecological studies (Cummings 2000; Pearce and Ferrier 2000; Boyce et al. 2002). The ROC curve, originating from signal detection theory, shows how the receiver operates the existence of signal in the presence of noise. It plots the probability of detecting true signals (sensitivity) and false signals (1-specificity) for an entire range of possible cutpoints (Hosmer and Lemeshow 2000). In my case, sensitivity is defined as the probability that a model yields a positive prediction where an animal actually occurs at a location. Specificity is the probability that a low score is predicted where no animal is observed. Plotting sensitivity as a function of 1-specificity for each threshold yields a ROC curve. The area under the curve (AUC) provides a measure of the model’s discrimination ability. A model with no predictive power has an AUC of 0.5 (random discrimination ability), while a perfect model corresponds to an AUC of 1.0 (perfect discrimination ability).

I evaluated my competing models using the following three methods: 1) jackknife cross-validation, 2) receiver operator characteristic (ROC) curves, and 3) comparison with an independent data set (territory scale only). Using the CTABLE option in the PROC LOGISTIC model statement in program SAS (SAS Institute Inc. 1999), I calculated the predictive accuracy that approximates an unbiased jackknifing method for the competing models at each scale of analysis. I used a probability threshold of 0.5 to distinguish between predictions of used and available. I performed ROC analyses using program SAS (SAS Institute Inc. 1999), which calculates AUC values and their standard errors using a non-parametric approach.
Many ecological modelers agree that model evaluation should include a comparison with an independent data set (e.g., Guisan and Zimmerman 2000; Pearce and Ferrier 2000; Boyce et al. 2002). While time and costs generally preclude collection of independent data in ecological studies, I was able to conduct a limited test of the predictive capabilities of my competing models at the territory scale. In addition to the 355 km² density study area that has been intensively monitored since 1986, 12 spotted owl territories within a larger region surrounding the Eldorado spotted owl demography project have been monitored since 1996. I mapped cover classes and calculated habitat metrics within these 12 regional territories. I then applied my top candidate models to the landscape configuration within these owl territories and assessed the models’ ability to accurately reflect owl occupancy using the same cross-validation technique described above. I realize that this was not a complete test of the predictive capability of the model because I only tested the model with sites of known spotted owl occupancy. A full test of the model would have entailed randomly selecting locations outside of the density study area and assessing the model’s ability to predict spotted owl use through landscape analysis and field survey of those sites, but this was not logistically feasible.
Table 5. Information-theoretic ranking of competing models (models within 2 AICc units of “top” model) describing California spotted owl habitat selection at each of three spatial scales.

<table>
<thead>
<tr>
<th>Model no.</th>
<th>Model terms</th>
<th>K&lt;sup&gt;a&lt;/sup&gt;</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt; &lt;sup&gt;b&lt;/sup&gt;</th>
<th>Δ AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>w&lt;sub&gt;i&lt;/sub&gt; &lt;sup&gt;c&lt;/sup&gt;</th>
<th>Estimated slope parameters (95% C.I.)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Patch Scale (Nests):</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>( \ln[\text{AMT}(5+6+7)] )</td>
<td>2</td>
<td>57.93</td>
<td>0</td>
<td>0.178</td>
<td>( \beta_0 = -13.570 ) (-20.836, -6.305) ( \beta_1 = 4.718 ) (2.275, 7.161)</td>
</tr>
<tr>
<td>5</td>
<td>( \ln[\text{CORE}(5+6+7)] )</td>
<td>2</td>
<td>59.05</td>
<td>1.12</td>
<td>0.102</td>
<td>( \beta_0 = -0.080 ) (-0.762, 0.602) ( \beta_1 = 1.232 ) (0.737, 1.727)</td>
</tr>
<tr>
<td>6</td>
<td>(\text{AMT}(5+6+7))</td>
<td>2</td>
<td>59.11</td>
<td>1.17</td>
<td>0.099</td>
<td>( \beta_0 = -4.733 ) (-7.058, -2.408) ( \beta_1 = 0.257 ) (0.138, 0.376)</td>
</tr>
<tr>
<td>8</td>
<td>(\ln[\text{AMT}(5+6+7)]+\ln[\text{SIZE}(5+6+7)])</td>
<td>3</td>
<td>59.31</td>
<td>1.38</td>
<td>0.089</td>
<td>( \beta_0 = -12.761 ) (-20.142, -5.380) ( \beta_1 = 3.927 ) (1.0046, 6.849) ( \beta_2 = 0.657 ) (-0.802, 2.116)</td>
</tr>
<tr>
<td>10</td>
<td>(\ln[\text{AMT}(5+6+7)]+\ln[\text{DEN}(5+6+7)])</td>
<td>3</td>
<td>59.32</td>
<td>1.38</td>
<td>0.089</td>
<td>( \beta_0 = -12.688 ) (-20.097, -5.279) ( \beta_1 = 4.579 ) (2.126, 7.0322) ( \beta_2 = -0.683 ) (-2.204, 0.839)</td>
</tr>
<tr>
<td>19</td>
<td>(\ln[\text{AMT}(5+6+7)]+\ln[\text{EDGE}(4+5+6+7)])</td>
<td>3</td>
<td>59.37</td>
<td>1.78</td>
<td>0.073</td>
<td>( \beta_0 = -12.289 ) (-20.382, -4.195) ( \beta_1 = 4.472 ) (1.953, 6.990) ( \beta_2 = -0.214 ) (-0.911, 0.483)</td>
</tr>
<tr>
<td><strong>Patch Scale (Roosts):</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>(\text{DIV}+\text{AMT}(5+6+7))</td>
<td>3</td>
<td>125.59</td>
<td>0</td>
<td>0.294</td>
<td>( \beta_0 = -0.420 ) (-2.886, 2.046) ( \beta_1 = -2.159 ) (-4.206, -0.111) ( \beta_2 = 0.192 ) (0.125, 0.259)</td>
</tr>
<tr>
<td>7</td>
<td>(\text{AMT}(6+7)+\text{SIZE}(6+7))</td>
<td>3</td>
<td>127.28</td>
<td>1.69</td>
<td>0.126</td>
<td>( \beta_0 = -2.497 ) (-3.437, -1.557) ( \beta_1 = 0.247 ) (0.138, 0.355) ( \beta_2 = -0.0796 ) (-0.184, 0.0251)</td>
</tr>
<tr>
<td>3</td>
<td>(\text{AMT}(6+7))</td>
<td>2</td>
<td>127.42</td>
<td>1.83</td>
<td>0.118</td>
<td>( \beta_0 = -2.349 ) (-3.243, -1.454) ( \beta_1 = 0.184 ) (0.121, 0.247)</td>
</tr>
</tbody>
</table>

Row 26
<table>
<thead>
<tr>
<th>Model no.</th>
<th>Model terms</th>
<th>$K^a$</th>
<th>$\Delta AIC_c$</th>
<th>$w_i^c$</th>
<th>Estimated slope parameters (95% C.I.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>PAC Scale (Nests):</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
| 5 | $ln[\text{CORE}(5+6+7)]$ | 2 | 76.7 | 0 | 0.169 | $\beta_0 = -1.341 (-2.292, -0.390)$  
| | | | | | | $\beta_1 = 0.883 (0.454, 1.312)$  
| 16 | $ln[\text{CORE}(5+6+7)]+ln[\text{EDGE}(4+5+6+7)]$ | 3 | 76.86 | 0.16 | 0.157 | $\beta_0 = -2.557 (-4.636, -0.478)$  
| | | | | | | $\beta_1 = 0.953 (0.494, 1.413)$  
| | | | | | | $\beta_2 = 0.304 (-0.146, 0.753)$  
| 18 | $ln[\text{CORE}(5+6+7)]+ln[\text{SIZE}(5+6+7)]+ln[\text{EDGE}(4+5+6+7)]$ | 4 | 77.11 | 0.4 | 0.138 | $\beta_0 = -2.557 (-4.636, -0.478)$  
| | | | | | | $\beta_1 = 0.953 (0.494, 1.413)$  
| | | | | | | $\beta_2 = 0.304 (-0.146, 0.753)$  
| | | | | | | $\beta_3 = 0.288 (-0.142, 0.718)$  
| 7 | $\text{AMT}(6+7)+\text{SIZE}(6+7)$ | 3 | 78.26 | 1.56 | 0.078 | $\beta_0 = -3.216 (-4.786, -1.645)$  
| | | | | | | $\beta_1 = 0.101 (0.0525, 0.149)$  
| | | | | | | $\beta_2 = -0.0408 (-0.0806, -0.00105)$  
| PAC Scale (Roosts): | | | | | |
| 3 | $ln[\text{AMT}(6+7)]$ | 2 | 141.77 | 0 | 0.381 | $\beta_0 = -5.751 (-8.417, -3.085)$  
| | | | | | | $\beta_1 = 1.695 (0.949, 2.442)$  
| 9 | $ln[\text{AMT}(6+7)]+ln[\text{DEN}(6+7)]$ | 3 | 143.36 | 1.59 | 0.172 | $\beta_0 = -6.115 (-9.058, -3.171)$  
| | | | | | | $\beta_1 = 1.701 (0.937, 2.464)$  
| | | | | | | $\beta_2 = 0.291 (-0.514, 1.0966)$  
| 7 | $ln[\text{AMT}(6+7)]+ln[\text{SIZE}(6+7)]$ | 3 | 143.38 | 1.61 | 0.17 | $\beta_0 = -6.079 (-8.992, -3.166)$  
| | | | | | | $\beta_1 = 1.976 (0.858, 3.0944)$  
| | | | | | | $\beta_2 = -0.278 (-1.0595, 0.504)$  

---

27
<table>
<thead>
<tr>
<th>Model no.</th>
<th>Model terms</th>
<th>K&lt;sup&gt;a&lt;/sup&gt;</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Δ AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>w&lt;sub&gt;i&lt;/sub&gt;&lt;sup&gt;c&lt;/sup&gt;</th>
<th>Estimated slope parameters (95% C.I.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>17</td>
<td>AMT(5+6+7)+EDGE(4+5+6+7)+ELEV+EDGE(4+5+6+7)*ELEV</td>
<td>5</td>
<td>119.67</td>
<td>0</td>
<td>0.155</td>
<td>$\beta_0 = 4.212 (-8.326, 16.749)$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\beta_1 = 0.0236 (0.0133, 0.339)$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\beta_2 = -0.0463 (-0.105, 0.0124)$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\beta_3 = -0.174 (-0.439, 0.0913)$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\beta_4 = 0.00104 (-0.00017, 0.00225)$</td>
</tr>
<tr>
<td>11</td>
<td>AMT(5+7)</td>
<td>2</td>
<td>120.83</td>
<td>1.16</td>
<td>0.086</td>
<td>$\beta_0 = -1.732 (-2.636, -0.828)$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\beta_1 = 0.0239 (0.0122, 0.0357)$</td>
</tr>
<tr>
<td>4</td>
<td>AMT(5+6+7)</td>
<td>2</td>
<td>121.09</td>
<td>1.43</td>
<td>0.076</td>
<td>$\beta_0 = -2.802 (-4.144, -1.461)$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\beta_1 = 0.0200 (0.0108, 0.0292)$</td>
</tr>
<tr>
<td>19</td>
<td>AMT(5+6+7)+EDGE(4+5+6+7)</td>
<td>3</td>
<td>121.38</td>
<td>1.71</td>
<td>0.066</td>
<td>$\beta_0 = -4.0135 (-6.311, -1.717)$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\beta_1 = 0.0211 (0.0115, 0.0306)$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\beta_2 = 0.00500 (-0.00235, 0.0123)$</td>
</tr>
<tr>
<td>24</td>
<td>DIV+AMT(5+6+7)</td>
<td>3</td>
<td>121.58</td>
<td>1.91</td>
<td>0.059</td>
<td>$\beta_0 = -6.452 (-12.412, -0.491)$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\beta_1 = 2.587 (-1.483, 6.658)$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\beta_2 = 0.0159 (0.00489, 0.0268)$</td>
</tr>
</tbody>
</table>

<sup>a</sup>Number of estimable parameters in model  
<sup>b</sup>Akaike’s information criterion adjusted for small sample size  
<sup>c</sup>Akaike’s weight
RESULTS

For each spatial scale of analysis I developed 21 base models, each with the three different model forms (linear, pseudothreshold, and quadratic), and a null model of no effect due to habitat variables (model 1, Table 4). In addition, at the territory scale I included 2 elevation effect models (models 20 and 21, Table 4), which predicted an interaction between edge and elevation. At each scale I selected a reduced set of models from this full set using 2 AICc units as the criterion for determining the top competing models (Burnham and Anderson 1998). I also used AICc values, Akaike weights (w_i), and slope parameter estimates with 95% confidence intervals for each a priori hypothesized model in the reduced set as a basis for inference (see Table 5).

Nest/Roost Patch Scale (40 ha)

Nest Site Selection: At the patch scale, nest site selection was most influenced by the amount of mid-seral forest having high canopy cover (≥70%), and late-seral forest having at least 30% canopy cover. This top model (lnAMT(5+6+7); pseudothreshold form of model 4 in Table 4) for predicting spotted owl presence was 1.75 times more likely than the second competing model and 1.80 times more likely than the third. The competing model set consisted of 6 models having a cumulative Akaike weight of 0.641. The variable, AMT(5+6+7), was present in each of the 6 competing models, and appeared consistently throughout the complete set of 64 a priori models. The cumulative Akaike weight for all models in the a priori set containing the variable AMT(5+6+7) was 0.83, and if models having either AMT(5+6+7) or CORE(5+6+7) were considered, the cumulative Akaike weight was 0.99. The variable, CORE(5+6+7), was present in the second competing model, but all other models contained the habitat variable
AMT(5+6+7). This suggested that the amount of suitable habitat was a more important predictor of spotted owl occupancy than the amount of suitable core habitat at this scale of analysis. The size, density, and edge covariates (SIZE(5+6+7), DEN(5+6+7), and EDGE(4+5+6+7)) were also present in the competing model set, but appeared to have little predictive power because the 95% confidence intervals on their estimated slope parameters all included zero (Table 5).

My jackknife cross-validation resulted in classification accuracies ranging from 78.4 to 81.1% (Table 6). My AUC values for the ROC curve analysis ranged from 0.91 to 0.92 (Table 6).

I retained the top model (lnAMT(5+6+7); pseudothreshold form of model 4, Table 4) as my “best-fitting” model for use in making inferences regarding spotted owl nest site selection at the patch scale. This model had the lowest AICc value and slightly outperformed the other models in the model validation stage. The RSF took the following form:

\[
\text{RSF} = \exp(4.718 \times \ln(0.1 + \text{AMT}(5+6+7)))
\]

This model suggested that, at the patch scale, as the amount of mid-seral forests having high canopy cover, and late-seral forest having at least 30% canopy cover increased, the relative probability of spotted owl nest site occupancy increased up to a point, beyond which the probability of occupancy approached an asymptote (Figure 2a).
Table 6. Evaluation of model performance for reduced set of competing \textit{a priori} models that describe habitat selection at each of three spatial scales. Validation methods included cross-validation using a jackknife approach, receiver operator characteristic curves, and comparison with an independent data set (territory scale only).

<table>
<thead>
<tr>
<th>Model no.</th>
<th>Model terms</th>
<th>A.U.C.\textsuperscript{a}</th>
<th>%CC\textsubscript{j} \textsuperscript{b}</th>
<th>%CC\textsubscript{i} \textsuperscript{c}</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Patch Scale (Nests):</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>ln[AMT(5+6+7)]</td>
<td>0.910</td>
<td>81.1</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>ln[CORE(5+6+7)]</td>
<td>0.912</td>
<td>81.1</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>AMT(5+6+7)</td>
<td>0.908</td>
<td>79.7</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>ln[AMT(5+6+7)]+ln[SIZE(5+6+7)]</td>
<td>0.915</td>
<td>78.4</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>ln[AMT(5+6+7)]+ln[DEN(5+6+7)]</td>
<td>0.916</td>
<td>78.4</td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>ln[AMT(5+6+7)]+ln[EDGE(4+5+6+7)]</td>
<td>0.907</td>
<td>78.4</td>
<td></td>
</tr>
<tr>
<td><strong>Patch Scale (Roosts):</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>DIV+AMT(5+6+7)</td>
<td>0.864</td>
<td>78.1</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>AMT(6+7)+SIZE(6+7)</td>
<td>0.857</td>
<td>78.9</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>AMT(6+7)</td>
<td>0.851</td>
<td>78.1</td>
<td></td>
</tr>
<tr>
<td><strong>PAC Scale (Nests):</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>ln[CORE(5+6+7)]</td>
<td>0.830</td>
<td>71.6</td>
<td></td>
</tr>
<tr>
<td>18</td>
<td>ln[CORE(5+6+7)]+ln[SIZE(5+6+7)]+ln[EDGE(4+5+6+7)]</td>
<td>0.836</td>
<td>74.3</td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>ln[CORE(5+6+7)]+ln[EDGE(4+5+6+7)]</td>
<td>0.852</td>
<td>74.3</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>AMT(6+7)+SIZE(6+7)</td>
<td>0.843</td>
<td>73.0</td>
<td></td>
</tr>
<tr>
<td><strong>PAC Scale (Roosts):</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>ln[AMT(6+7)]</td>
<td>0.789</td>
<td>69.5</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>ln[AMT(6+7)]+ln[DEN(6+7)]</td>
<td>0.791</td>
<td>69.5</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>ln[AMT(6+7)]+ln[SIZE(6+7)]</td>
<td>0.790</td>
<td>69.5</td>
<td></td>
</tr>
<tr>
<td><strong>Territory Scale:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>AMT(5+6+7)+EDGE(4+5+6+7)+ELEV+EDGE(4+5+6+7)*ELEV</td>
<td>0.800</td>
<td>70.6</td>
<td>41.7</td>
</tr>
<tr>
<td>11</td>
<td>AMT(5+7)</td>
<td>0.755</td>
<td>66.7</td>
<td>83.3</td>
</tr>
<tr>
<td>4</td>
<td>AMT(5+6+7)</td>
<td>0.760</td>
<td>67.6</td>
<td>58.3</td>
</tr>
<tr>
<td>19</td>
<td>AMT(5+6+7)+EDGE(4+5+6+7)</td>
<td>0.766</td>
<td>71.6</td>
<td>66.7</td>
</tr>
<tr>
<td>24</td>
<td>DIV+AMT(5+6+7)</td>
<td>0.773</td>
<td>69.6</td>
<td>66.7</td>
</tr>
</tbody>
</table>

\textsuperscript{a}Area under curve measurement of the receiver operator characteristic curve  
\textsuperscript{b}Percent correct classification using jackknife cross-validation (p=0.5 cut-off level)  
\textsuperscript{c}Percent correct classification of an independent data set (473 ha scale only)
Roost Site Selection: At the patch scale, roost site selection was positively correlated with the amount of mid-seral forest having high canopy cover and late-seral forest having at least 30% canopy cover, and negatively correlated with the amount of habitat diversity. This relationship was represented by the best approximating a priori model, DIV + AMT(5+6+7) (linear form of model 24, Table 4), which was 2.33 times more likely than the second competing model and 2.48 times more likely than the third competing model. There were 3 models in the competing model set and the cumulative Akaike weight of these models was 0.537. The variables AMT(6+7) and SIZE(6+7) were also present in the competing model set, however, these two variables were somewhat correlated (r=0.74), and the covariate SIZE(6+7) had a 95% confidence interval on the slope parameter that included zero, suggesting that it was relatively uninformative in this model set.

My model validation using a jackknife approach resulted in classification accuracies ranging from 78.1% to 78.9% (Table 6). My AUC values based on the ROC technique ranged from 0.85 to 0.86 (Table 6).

The top competing model (DIV + AMT(5+6+7)) was retained as the “best” approximating model for use in making inferences regarding roost site selection at the patch scale. The equation for the RSF was as follows:

$$RSF = \exp(-2.159*\text{RICH} + 0.192*\text{AMT}(5+6+7))$$

This model suggested that the relative probability of spotted owl roost site selection increased with decreasing habitat heterogeneity and increasing amounts of mid-seral forest having high canopy cover and late-seral forest having at least 30% canopy cover (Figure 2b).
Figure 2. Resource selection functions depicting the relationship between landscape variables and the probability of spotted owl occupancy described by the top fitting regression models for a) nest, and b) roost sites at the patch scale (40 ha).

a) Nest-site selection at the patch scale

![Nest-site selection graph]

b) Roost-site selection at the patch scale

![Roost-site selection graph]
Protected Activity Center (PAC) Scale (121 ha)

Nest Site Selection: At the PAC scale, nest site selection was most influenced by the amount of interior habitat (forest >100 m from an edge) characterized by mid-seral forests having high (≥70%) canopy cover, and late-seral forest having at least 30% canopy cover. The relationship was best represented by a pseudothreshold form (\(\ln\text{CORE}(5+6+7)\); model 5, Table 4), which suggested that as the amount of suitable habitat increased, the probability of spotted owl occupancy increased at a constant rate until it approached an asymptote. This top model had an Akaike weight of only 0.187 and was only 1.08 times more likely than the second competing model, suggesting substantial model selection uncertainty. This model uncertainty was supported by the fact that the cumulative Akaike weights of the 4 models in the competing model set was 0.560. However, the variable that represented the amount of interior forest, CORE(5+6+7), appeared in 3 of the 4 competing models and appeared consistently throughout the complete set of 64 a priori models. Cumulative Akaike weights for all models in the a priori model set containing this variable was 0.71. The edge and patch size covariates (EDGE(4+5+6+7) and SIZE(5+6+7)) appeared in 2 of the 4 competing models but had 95% confidence intervals on the slope parameter estimates that overlapped zero in all instances suggesting these covariates were relatively uninformative in the models.

My model validation using a jackknife procedure yielded accuracy measurements of 74.3% to 77.0% (Table 6). My ROC analysis resulted in AUC values ranging from 0.830 to 0.852 (Table 6).
I used the model with the lowest $\text{AIC}_c$ value ($\text{lnCORE}(5+6+7)$) as the “best” approximating model for use in making inferences concerning the effects of habitat types and configurations on the probability of spotted owl nest site selection. Using this model the RSF was as follows:

$$\text{RSF} = \exp(0.883 \times \text{ln}(0.1+\text{CORE}(5+6+7)))$$

This model suggested that, at the PAC scale, as the amount of interior mid-seral forests having high canopy cover and as the amount of interior late-seral forest having at least 30% canopy cover increased, the relative probability of spotted owl nest site occupancy increased up to a point, beyond which the probability of occupancy approached an asymptote (Figure 3a).

**Roost Site Selection:** At the PAC scale, the landscape characteristic that most influenced roost site selection was the amount of late-seral forest having at least 30% canopy cover. This relationship was represented by the top *a priori* model, lnAMT(6+7) (pseudothreshold form of model 3, Table 4), which had an Akaike weight of 0.396 and was 2.22 times more likely than the second competing model. The competing model set consisted of 3 models which had a cumulative Akaike weight of 0.738. The variable AMT(6+7) appeared in all 3 competing models in the pseudothreshold form and had 95% confidence intervals on parameter estimates that did not overlap zero. Furthermore, the variable AMT(6+7) appeared consistently throughout the complete set of 64 *a priori* models, and cumulative Akaike weights for all models in the *a priori* model set containing this variable was 0.99.
The patch size and patch density variables (SIZE(6+7) and DEN(6+7)) were also present in the competing model set. However, slope parameter estimates for both covariates had 95% confidence intervals that overlapped zero, suggesting that they were relatively uninformative in these models. In addition, the variables SIZE(6+7) and AMT(6+7) in model 7 (Table 5) were somewhat correlated (r=0.77).

Jackknife cross-validation estimated model accuracy to be between 69.5% and 71.1% (Table 6). The ROC curve technique yielded model accuracies of 0.79 (Table 6).

I used the top competing model (lnAMT(6+7)) as my “best” model for making inferences regarding spotted owl roost site selection at the PAC scale. The equation for the RSF was as follows:

\[ \text{RSF} = \exp(1.695 \times \ln(0.1 + \text{AMT}(6+7))) \]

This model suggested that as the amount of late-seral forest having at least 30% canopy cover increased, the relative probability of spotted owl roost site occupancy increased up to a point, beyond which the probability of occupancy approached an asymptote (Figure 3b).
Figure 3. Resource selection functions depicting the relationship between landscape variables and the probability of spotted owl occupancy described by the top fitting regression models for a) nest, and b) roost sites at the PAC scale (121 ha).

a) Nest-site selection at the PAC scale

b) Roost-site selection at the PAC scale
**Territory Scale (473 ha)**

At the territory scale, California spotted owls selected habitats that were characterized by late-seral forests having at least 30% canopy closure, and mid-seral forests having high canopy cover (≥70%). In addition, elevation and the amount of edge habitat were both negatively correlated with the probability of spotted owl occupancy, and there was an interaction between edge and elevation with edge becoming more important as elevation increased. These relationships were represented by the best approximating *a priori* model for this scale (AMT(5+6+7) + EDGE(4+5+6+7) + ELEV + EDGE(4+5+6+7)*ELEV; model 21, Table 4). This top model was complex and had an Akaike weight of only 0.155, which suggested substantial model selection uncertainty. My inference of model uncertainty was supported by the fact that there were 5 competing models, of which the top model was only 1.80 times more likely than the second model, and only 2.04 times more likely than the third. Further, the cumulative Akaike weights for these 5 models was only 0.414 (cumulative Akaike weights of all 65 models in the *a priori* set was 1.0). Thus, no model substantially outperformed any other model.

However, the variable that depicted the amount of mid- to late-seral forest with high canopy cover (AMT(5+7)) at a site was present either as a covariate or nested within a covariate in each of the top 5 competing models. This habitat type variable also appeared in many models within the complete set of 65 *a priori* models and cumulative Akaike weights for all models in the set containing this variable was 0.92. This suggested that the low individual weights of the top models were the result of the Akaike weight being distributed among the numerous models within the *a priori* model set that contained this important habitat covariate. The linear form of this variable best represented the
relationship between amount of suitable habitat and the probability of territory occupancy.

The models containing the covariate that represented the amount of forest in habitat class 5 and 7 (AMT(5+7)) or habitat class 5, 6 and 7 (AMT(5+6+7)) as the sole predictor variable in a model performed almost identically. This suggested that habitat classes 5 and 7 (mid- and late-seral forest having high canopy cover) were more important in predicting owl presence than class 6 (late-seral forest having at least 30% canopy cover).

The parameter estimates for the top five candidate models (Table 5) also suggested that the habitat amount variables (i.e. AMT(5+7) and AMT(5+6+7)) were both important predictor variables, with 95% confidence intervals for coefficient estimates that did not include zero. Conversely, the Edge, Elevation, and Diversity variables (EDGE(4+5+6+7), ELEV, DIV and EDGE*ELEV) all had 95% confidence intervals on the slope parameters that included zero suggesting that they were relatively uninformative in these models.

My jackknife cross-validation estimated model accuracy to be between 68.6% and 71.6% for the reduced set of models (Table 6). ROC analysis yielded similar results with AUC values ranging from 0.755 to 0.800 (Table 6). At this territory scale analysis, I evaluated the predictive accuracy of all 5 competing models using my small independent data set. The second competing model (AMT(5+7); model 11, Table 5) had a predictive accuracy of 83.3% which was substantially better than the performance of the other models (41.7% - 66.7%; Table 6).
Given the very small differences in AICc values between the top two competing models, and their similar performances in jackknife cross-validation and ROC analysis, it appeared that either structure might be appropriate. However, the top model in the competing set (AMT(5+6+7) + EDGE(4+5+6+7) + ELEV + EDGE(4+5+6+7)*ELEV; model 21, Table 5) performed poorly (41.7%) when applied to owl territories outside of the main study area, and had 95% confidence intervals on the slope parameter estimates that substantially overlapped zero for 3 of the 4 covariates. In contrast, the second model (AMT(5+7); model 11, Table 5) performed relatively well (83.3%) when applied to owl territories outside of the main study area, and had fewer parameters than the more complex top model. Therefore, I used the second, more parsimonious model as my “best” model for use in making inferences concerning the effects of habitat types and patterns on the probability of spotted owl territory occupancy. The equation for the RSF was as follows:

\[ \text{RSF} = \exp(0.0239\times\text{AMT}(5+7)) \]

This model suggested that the relative probability of spotted owl territory occupancy increased with increasing amounts of mid- to late-seral forests having high canopy cover (Figure 4).
**Figure 4.** Resource selection function depicting the relationship between amount of habitat and the probability of spotted owl occupancy described by the top fitting regression model at the territory scale (473 ha).

![Graph showing the relationship between AMT(5+7) (ha) and Relative Probability of Occupancy.]

**HABITAT SUITABILITY MAP**

To create a map depicting the probability of spotted owl occupancy, I applied the RSFs generated from my top models (patch and territory scales) to the 355 km² Eldorado study area (Figures 5-7). I developed three separate maps: 1) relative probability of nest-site selection (40 ha scale), 2) relative probability of roost-site selection (40 ha scale), and 3) relative probability of territory selection (473 ha scale). To create these maps I used ArcView, version 8.0 (Environmental Systems Research Institute 2002) to automate the RSFs in a GIS by implementing systematic circular moving windows that estimated the relative probability of use for each pixel (i.e., 30 x 30 m block of land) in the landscape (see McGrath et al. 2003 and Niemuth 2003 for previous applications). These moving windows corresponded to the territory scale and the nest/roost patch scale, with the sizes...
of the moving windows equal to the scale of analysis (i.e., 40 and 473 ha). Using the neighborhood statistics function in ArcView Spatial Analyst, and the cover-class GIS layer, an automated moving window calculated the habitat metrics specific to my top models. I then used the map calculator function in Spatial Analyst to estimate RSFs for every pixel in the study area. For the nest-site selection and roost-site selection maps I used the 40 ha scale because this seemed more relevant for making inference regarding nest and roost patch selection, whereas 121 ha may be more representative of the core area of an owls territory (i.e. the highest use portion of an owl’s home range; Kaufman 1962). In addition, at the 40 ha scale I was better able to distinguish between used and available habitat as reflected in the overall fit of my habitat models (Table 6).

I scaled RSF scores for each scale of analysis such that the maximum relative predicted probability of use assumed a value of 1. For ease of interpretation and application, I considered five broad categories of selection probability: very low (0-20th percentile), low (20-40th percentile), moderate (40-60th percentile), high (60-80th percentile), and very high (80-100th percentile), with percentiles based on all pixels within the study area.
Figure 5. Predicted probability of nest site selection (40 ha scale) by California spotted owls across the Eldorado study area in the central Sierra Nevada Mountains, California.
Figure 6. Predicted probability of roost site selection (40 ha scale) by California spotted owls across the Eldorado study area in the central Sierra Nevada Mountains, California.
Figure 7. Predicted probability of occurrence of California spotted owls across the Eldorado study area in the central Sierra Nevada Mountains, California at the territory (473 ha) scale.
DISCUSSION

The amount, distribution, and type of habitat have been central considerations when evaluating conservation strategies of the California spotted owl. Current management plans for the species have been predicated on hypothesized relationships of owl habitat selection (Verner et al. 1992b). A conundrum faced by the California spotted owl technical team (hereafter CASPO) was the fact that California spotted owls were widely distributed across the Sierra Nevada, and the history of vegetation change across this range was exceedingly complex. Thus, they created an interim conservation strategy that largely reflected the uncertainty about the precise habitat relationships of the owl. My results appeared to be consistent with their inferences and supported this uncertainty.

In each of my analyses the amount of mid- to late-seral stage habitat had the greatest correlation with spotted owl occupancy. However, the habitat classes that were most correlated with spotted owls presence varied somewhat among the different scales, and between nesting and roosting habitat. At the patch scale, nest-site selection had the greatest correlation with the amount of high canopy cover mid-seral forest, and mature and old growth forest having at least 30% canopy cover, while roost sites were characterized by these same forest types in addition to low habitat diversity. Similarly, at the scale of a protected activity center (PAC), interior (>100 m from an edge) mid-seral forest having high canopy cover, and interior mature and old growth forest having at least 30% canopy cover had the greatest correlation with spotted owl nest site selection. Roost site selection at the PAC scale was most influenced by the amount of mature and old growth forest having at least 30% canopy cover. However, most of these relationships were characterized by models having a pseudothreshold form, which suggested some
uncertainty about the relationship of canopy cover amounts or total amounts of habitat found within this size of area around a nest or roost site. But it does suggest the basis for future experiments.

At the territory scale, the habitat characteristic most influential in California spotted owl site selection was the amount of mid- to late-seral forest characterized by high (≥70%) canopy cover, which is consistent with other spotted owl studies (Bias and Gutiérrez 1992; Call et al. 1992; LaHaye et al. 1997; Moen and Gutiérrez 1997; Ward et al. 1998; Swindle et al. 1999; Thome et al. 1999; May and Gutiérrez 2002; Hunsaker et al. 2002). Late-seral forests with low to medium canopy cover (30-69%) did not seem to be as important in spotted owl habitat selection at the territory scale. These habitats are more abundant across the study area than high canopy cover forests. While spotted owls most likely used this habitat type, it probably was not a limiting factor within the study area, at the territory scale. The importance of my study, relative to other California spotted owl habitat studies was my use of model selection based on hypotheses derived from the results of all previous spotted owl studies. This allowed me to objectively evaluate the importance of specific habitat conditions in a comprehensive manner.

Individual Akaike weights for my top models were relatively low and, thus, appeared poor with respect to model uncertainty. However, this was most likely due to the fact that the amount of suitable habitat was such a strong predictor of spotted owl occupancy. Further, this important variable was present in many of my \textit{a priori} hypothesized models. As a result model weights were distributed among the models within the full set that contained this habitat amount variable. I conducted a \textit{post hoc}
analysis in which I examined a model set consisting only of the top habitat amount model and all other models not containing a habitat amount covariate. When the habitat amount variables were removed from the \textit{a priori} model set, Akaike weights for the top model were much higher (0.782 to 0.999 depending on the scale of analysis). This \textit{post hoc} modeling effort helped to reconcile the discrepancy between my apparent model uncertainty and the strong predictive capability of my top models.

While amount of suitable habitat was clearly the most influential habitat covariate at each spatial scale, several additional metrics appeared in the competing model sets. However, none of these landscape metrics (i.e., edge, patch size, patch density, and habitat diversity) appeared to be strongly correlated with spotted owl habitat selection. While the amount of edge habitat was found to be important in several studies of habitat selection in northern spotted owls (Carey and Peeler 1995; Ripple et al. 1997; Ward et al. 1998; Folliard et al. 2000; Franklin et al. 2000; Zabel et al. 2003) this variable was relatively uninformative in my models. Of interest was the fact that all these studies which found such a relationship were conducted on the northern spotted owl where the primary logging method of the past was clear-cutting. Verner et al. (1992b) suggested that the wide array of past logging methods and land uses in the Sierra Nevada led to a highly diverse vegetation environment, which made it difficult to understand current California spotted owl habitat use and distributions.

One reason I might not have detected the more subtle effects of habitat heterogeneity on site selection is because the amount of habitat had such a large influence on the distribution of spotted owls, which may have overshadowed the secondary effects
of habitat patterns. It is also possible that the complexity of patterns precluded identification of patterns that would be associated with owls. These could explain why habitat indices such as patch size, patch density, amount of edge, and habitat diversity were only slightly related to site occupancy. Habitat studies for the northern spotted owl (Carey et al. 1992; Meyer et al. 1998) have reported similar results. In addition, for the habitat edge metric, I only considered the amount of edge between mixed-conifer forest and all other cover classes (clearcut, brush, pole, and hardwood) following Franklin et al. (2000). If additional ecotones (e.g., edge between mid- and late-seral forests, or edge between hardwood and mixed-conifer forests) were considered, a relationship might have become evident, but the analyses would then be constrained by a large number of models and relatively small sample sizes. Nevertheless, due to the large amount of hardwood forest (mainly black oak and live oak) on my study area, the influence of hardwood forests on spotted owl habitat selection deserves further consideration.

A general guiding principle in ecology is that preferences for particular environmental characteristics should co-evolve with the qualities of those environments. As a result, organisms should respond positively to those environments in which survival and reproduction are high (Orians and Wittenberger 1991). This forms the basis for the theory of habitat selection. However, habitat selection by spotted owls in disturbed areas, like the central Sierra Nevada, may represent patterns of selection that evolved in earlier times. This may be the case in many parts of the Sierra Nevada where mixed-conifer forests have a history of intensive logging (Verner et al. 1992b). Such a time-lagged population response to habitat loss in a long-lived species with high site fidelity may only
become evident with examination of variability in reproductive success among owls across my study area (i.e., across a range of habitat conditions). If there is indeed a time lag in response to habitat loss, we might expect the amount of old growth required by spotted owls to be underestimated by my habitat models. This may have been the case with selection of models having mid-seral forest with high canopy cover and late-seral forest with low canopy cover in my study. Owls may have used these habitats only because their preferred habitat (e.g., old-growth forest with high canopy cover) was relatively scarce. The observed selection of a particular habitat type, that is not necessarily a preferred habitat, could have been an artifact of pre-logging distributions rather than a reflection of present habitat selection. Alternatively, it could mean that there is a range of variability in habitats that owls will select even if there is differential reproductive success of survival attributable to those habitats.

Finally, it was critical to my analysis to develop an accurate vegetation classification map of the Eldorado study area, which was nonexistent at the time. I succeeded in creating a GIS-based cover-class map with an overall classification accuracy of 83%. However, one potentially important habitat component that was lacking in my GIS cover class map was the residual tree component. Residual trees (>30” DBH) have been found to be associated with spotted owls in the central Sierra Nevada (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997). Residual trees may be an especially important component of mid-seral stage forests by providing potential nest sites and by contributing to the structural diversity and thermal properties of a stand. They may have also influenced the importance of late seral stage forests having canopy
cover as low as 30% because residuals often provide nest sites or they ameliorate temperatures of stands. My inability to map forest structural characteristics (e.g., the number of vegetative strata and residual trees) at such a broad spatial scale limited my ability to detect preferences for these more subtle habitat characteristics.

CASPO concluded that California spotted owls were habitat specialists, particularly for nesting and roosting habitat. However, it also appeared that they used a broader range of forested habitats than the northern subspecies. While researchers have inferred that mature and old forest having high canopy cover were primary habitats of the California spotted owl, they have been less certain about the extent to which other forested habitats were used. My results were consistent with those inferences. CASPO concluded that a reserve design conservation strategy like that recommended by the Interagency Scientific Committee’s (ISC) for the northern spotted owl (Thomas et al. 1990) was not appropriate for the California subspecies. Some of my ambiguous results regarding the effects of habitat configuration and heterogeneity supported that conclusion as well. My results were consistent with the greater variability in forest condition in the Sierra Nevada, especially with respect to past timber harvest, than with the general dichotomy of habitat/no habitat typical of the Pacific Northwest owl habitat where clear-felling was the dominant harvest method. The diverse array of stand age and structure increases uncertainty about characterization of suitable owl habitat in the Sierra Nevada. The extreme habitat heterogeneity that resulted from decades of extensive selection logging, high grading, individual tree harvest, clear-felling, mining, grazing, wildfire, and land clearing also makes mapping vegetation classes very difficult. While achieving a
high degree of accuracy, I categorized only 8 very broad classes for my cover-
classification map. In reality, each cover class had a considerable degree of variability.
In addition, the habitat heterogeneity and inter-gradation of habitat (ecotones) in the
Sierra Nevada makes defining and identifying edge habitat much more difficult,
particularly identifying edges with biological relevance to spotted owls. While habitat
metrics such as edge, maximum patch size, patch density, and habitat diversity may be
appropriate for characterizing habitat for the northern spotted owl, they may not be the
most suitable metrics for describing habitat characteristics important to the California
spotted owl.

Management Implications

Despite the long history of intensive logging across most of its range, the
California spotted owl continues to be widely distributed throughout the mixed-conifer
zone of the Sierra Nevada (Verner et al. 1992b; Franklin et al. 2004). Because the
amount of suitable habitat had such a prominent influence on habitat selection in each of
the top models across all three spatial scales, managers can have direct effects on this
population of spotted owls. The CASPO report recommendations, and the findings from
this study, support a management strategy that maintains the current distribution of
California spotted owls through retention of all old growth habitat, retention of mid-seral
stands with high canopy cover, retention of all large trees and snags, retention of most
medium trees which serve as recruits to replace older trees, and by thinning small trees to
reduce the risk of catastrophic fire. Fire is of particular concern in the central Sierra
Nevada because forests having dense canopy and a high density of small trees can
potentially increase the risk of catastrophic fire. A response by managers is to substantially thin many forest stands. If this response includes substantial reduction in canopy cover and removal of medium and large trees, as proposed by the Sierra Nevada Forest Management Plan amendments (U.S. Forest Service 2004), it could greatly affect the habitat valued for spotted owls. However, it is not known if there is a lower threshold in canopy cover beyond which owls will abandon the site or have reduced fitness. Such a threshold can only be assessed through experimental manipulation of canopy cover.

The monitoring of regional and national population distributions, fitness, and survival through field surveys cannot realistically keep pace with the rate of habitat alteration through logging, fire suppression, and human development in the Sierra Nevada. As a result, it is becoming more important to map species at large spatial scales with reduced field effort. The development of scientifically-based modeling processes for the creation and evaluation of maps used for identifying preferred habitats for species is essential if wildlife scientists and managers are to compile successful conservation management plans that will ensure the continued existence of a growing number of threatened species (Osborne et al. 2001). RSF models developed for habitat specialists such as the spotted owl are often fairly straightforward and robust because the models are strongly influenced by the amount of old growth forests. The generally high predictive accuracy of my habitat selection models indicate that resource selection functions (RSF) generated from the data for territory (473 ha) and nest/roost patch (40 ha) scales can be used to predict the relative probability that a given landscape mosaic will be suitable for
spotted owl occupancy. Thus, spatially explicit RSFs are a useful tool for assessing habitat capability over large areas when interfaced with a GIS.

REFERENCES


McGargial K, Marks BJ. 1994 FRAGSTATS—spatial pattern analysis program for quantifying landscape structure. Version 2.0. Forest Science Department, Oregon State University, Corvallis, Oregon, USA.


