Models for Mapping Potential Habitat at Landscape Scales: An Example Using Northern Spotted Owls

William C. McComb, Michael T. McGrath, Thomas A. Spies, and David Vesely

ABSTRACT. We are assessing the potential for current and alternative policies in the Oregon Coast Range to affect habitat capability for a suite of forest resources. We provide an example of a spatially explicit habitat capability model for northern spotted owls (*Strix occidentalis caurina)* to illustrate the approach we are taking to assess potential changes in habitat capability for vertebrates across the Coast Range. The model was based on vegetation structure at five spatial scales: the potential nest tree, a 0.5 ha potential nest patch, 28 ha around a potential nest patch, 212 ha around a potential nest patch, and a 1,810 ha home range area around a potential nest patch. Sensitivity analyses indicated that the proportion of the 28 ha patch in large trees around a potential nest patch, and the number of potential nest trees per ha in the nest patch, had the greatest influence on habitat capability estimates. The model was verified using georeferenced locations of spotted owl nests from systematically surveyed areas. Logistic regression analysis indicated that habitat capability scores were significantly associated with the probability of a site having a nest. Alternative model structures were tested during verification to test assumptions associated with four variables. The final model allowed development of a map of habitat capability for spotted owl nesting. The model will be linked to a model of forest dynamics to project changes in habitat capability under alternative land management policies. FOR. SCI. 48(2):203–216.

Key Words: Wildlife habitat relationships, forest habitat, forest planning.

THE DEVELOPMENT OF NEW FOREST POLICIES to meet biological diversity goals while providing for other social and economic values of forestlands is a major challenge for policymakers and managers (Wiersum 1995). In the Pacific Northwest, conflicts over attaining ecological, economic, and social goals for forests during the late 1980s and early 1990s paralyzed forest management on federal lands and led to considerable uncertainty in management of private lands (FEMAT 1993, p. 1–3). These controversies resulted in new forest polices in the region for federal and state lands and modified forest polices for private forestlands (FEMAT 1993, p. 1–3, Spies et al. 2002). In Oregon's Coast Range, separate policies for federal, state, and private lands were initiated in the 1990s. The President's Forest Plan (FEMAT 1993, p. 1–2) brought dramatic changes to federal forestland management, reducing timber sales from federal

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lands by almost 90% compared to the 1980s. New plans for state forests are based on structure-based management that explicitly considers wildlife habitat and forest health while managing for timber production (McAllister et al. 1999). State Forest Practices policies apply to private lands and are designed to protect some aspects of wildlife habitat.

In response to the controversies about sustainability of forest resources, scientists have become more involved in forest planning and management with the expectation that a strong scientific basis will improve our ability to sustain multiple forest values (Spies et al. 2002). Assessments such as FEMAT (1993, p. I–1) brought scientists into the policy arena. However, these past assessments were limited because: (1) they were restricted to federal lands; (2) they did not have the capacity to spatially project landscape changes under the policy alternatives; and (3) they had little opportunity to examine issues that lay outside the current policy crisis. In an attempt to address these limitations, we are developing a mechanism for understanding the potential implications of policy change on a suite of forest values, including habitat availability for selected wildlife species found in the Oregon Coast Range (Spies et al. 2002). We provide an example of a theoretical model building approach to estimate the capability of the Oregon Coast Range to provide nesting habitat for northern spotted owls.

Estimating Habitat Capability

Many studies have characterized habitat availability for species based on predefined land cover types that represent vegetation composition and/or seral stages (Ripple et al. 1991, 1997; Block et al. 1994; Karl et al. 2000; O'Neil et al. 2001). Although useful for large-scale assessments on static landscapes (Csuti 1996), the approach assumes that certain fine-scale features of vegetation (tree sizes, species, dead wood) and the physical environment (e.g., soils, moisture, talus) are represented within each class. Further, this approach does not provide the ability to portray dynamic landscapes (Flather et al. 1997).

Empirical models based on linear and logistic regression analysis (Morrison et al. 1987, Pausas et al. 1995), discriminant analysis (Livingston et al. 1990), and classification and regression tree analysis (O'Connor et al. 1996, Dettmers and Bart 1999) have also been used to identify potential habitat. Empirical models can be constrained when considering conditions that are beyond the bounds of the data that were used to develop the relationships. Habitat relationships data that span a range of spatial scales and vegetative conditions would be needed to develop entirely empirical habitat relationships models, but these data are generally unavailable, even for the most well-studied species. Despite the lack of adequate information to build empirical models that would be responsive to novel land management approaches, managers often are required to ensure that habitat is available over the foreseeable future for federally or state threatened or endangered species. Estimates of habitat availability and population viability are often sought by policy makers and planners (Thomas et al. 1990, FEMAT 1993, p. 11–13) or required by law (USDI 1990) when considering policy alternatives.

A theoretical model structure is more flexible than empirical models, can include conditions that might be represented in future conditions, and provides the opportunity to link structural characteristics of habitat with output from models of vegetation dynamics (Pausas et al. 1997, Hansen et al. 1999, Curnutt et al. 2000, Roloff et al. 2001). The results of this process allow managers and planners the opportunity to assess habitat area and pattern over space and time (Pausas et al. 1997).

Habitat Suitability Index (HSI) models were developed to facilitate the consideration of wildlife in multidisciplinary natural resource assessments (Schamberger and O'Neil 1986). Roloff and Kernohan (1999) found that most HSI models were deficient in consideration of input parameter variability, application of the models to inappropriate spatial scales, and verification on a narrow range of HSI values. Roloff and Kernohan (1999) offered criteria for improving the utility of HSI models and evaluating the model verification process using the aforementioned criteria. This process results in an index of model quality that ranges from 0 to 7, with 7 being optimal model verification. The maximum score achieved by studies evaluated by Roloff and Kernohan (1999) was 4.05, indicating the potential for significant improvements in development and testing of these types of models.

Inconsistencies in empirical relationships between animal occurrence or abundance and habitat conditions are quite common. Any model structure could be altered in a number of ways to reflect the uncertainty associated with these inconsistencies. Alternative model structures that reflect these uncertainties can be tested as alternative hypotheses against the original model design (Burnham and Anderson 1998:65). Selection of the best model from among the alternatives is based on the data available to test the models. Although no model structure will be optimum, this process does allow improvements to model structure based on independent data.

Habitat Selection by Northern Spotted Owls

Nesting habitat for northern spotted owls includes the presence of nesting structures within nest patches and an adequate area surrounding the nest patch to provide foraging sites, roost sites, and protection from predators (Forsman et al. 1984, p. 30, USDI 1992, p. 19). Platform and cavity nest trees averaged 75 and 91 cm diameter at breast height (dbh), respectively, in California (LaHaye et al. 1997), 106 and 135 cm in Oregon (Forsman et al. 1984:32), and 89 and 142 cm in Washington (Forsman and Geise 1997). Hershey et al. (1998) identified three factors associated with spotted owl nest patches around nest trees: number of trees 10–25 cm dbh/ha, number of trees 25–50 cm dbh/ha, and canopy heterogeneity. Finally, prey abundance and availability may influence nest site selection or nest success. Spotted owl prey often are associated with elements of conifer forests typically found in old stands (Rosenberg and Anthony 1992, Carey et al. 1992, 1999, p. 41). Northern spotted owl nests tend to be centered in clumps of old forest (e.g., suitable foraging or roosting habitat) more often than expected by chance with the area of

old forest decreasing as distance from the nest increases (Ripple et al. 1991, 1997, Lehmkuhl and Raphael 1993, Meyer et al. 1998, p. 26, Swindle et al. 1999).

Methods

We used a theoretical modeling approach that included use of both existing literature and empirical relationships. This allowed us to link models to vegetation dynamics models to estimate change in habitat capability resulting from changes in land management policies. We differentiate our approach from traditional HSI modeling by including spatially explicit assessments of nesting and foraging conditions using moving windows to assess regions of a landscape capable of meeting reproduction and foraging requirements over biologically meaningful scales. The size of the moving windows represented various spatial scales related to the specific resources that each species requires for survival and reproduction, the characteristics of patches in which the resources occur, the distribution of resource patches throughout potential home ranges, and the geographic range of the species that occurs in the area of assessment (Johnson 1980, McComb 2001).

The models were developed and tested based on information from the Oregon Coast Range. The area was chosen because of its complex land ownership pattern and associated policies that interact to produce a complex landscape mosaic (Spies et al. 2002). Further, past management practices have led to listing of the northern spotted owl and other species as threatened under the Endangered Species Act (USDI 1990), and the draft recovery plan for the species relied heavily on increasing habitat area and connectivity throughout its range (USDI 1992, p. 100–103).

Vegetation Data

In order to develop habitat capability models representing a range of spatial scales, we needed estimates of vegetation composition and structure that ranged in detail from nest sites to home ranges over the Coast Range. We based our analysis on a vegetation map derived from information integrated from regional grids of ground-based vegetation sampling (n = 629 plots), mapped environmental data, and 1988 Landsat Thematic Mapper imagery using the Gradient Nearest Neighbor method (Ohmann and Gregory, in press). The approach applies direct gradient analysis and nearest neighbor imputation to ascribe detailed ground attributes (e.g., tree species and size) of vegetation to each 25 × 25 m pixel in a digital landscape of the Oregon Coast Range (Figure 1). Mapped predictions maintain the covariance structure among multiple response variables, represent the range of variability in the plot data, and portray spatial heterogeneity in an ecologically realistic way. Model performance was excellent at the regional scale (Ohmann and Gregory, in press), and results of habitat mapping based on these data should reasonably reflect regional patterns in habitat for the northern spotted owl. We do not know how well this approach might be useful for characterizing habitat elements such as soils or dead wood availability that might be important to other species. At the stand level, prediction accuracy varied from good to poor depending on the vegetation attribute under consideration (Ohmann and Gregory, in press). Habitat capability maps derived from these vegetation maps are appropriately used for regional-level planning and policy analysis, but would not be suitable for guiding local management decisions.

Habitat Modeling

We developed a modeling approach that would allow us to perform the following functions:

1. Quantify capability of sites across the Oregon Coast Range to provide habitat for northern spotted owls in the present landscape.
2. Provide spatially explicit estimates of habitat capability for northern spotted owls required for mapping habitat distribution across current and possible future landscapes. Landscape-scale habitat capability information is a prerequisite to understanding the effects of land management on animal survival, reproduction, and dispersal among metapopulations (Lindenmayer et al. 2000).
3. Assess the effects of alternative land policy scenarios on habitat pattern and area using landscape-scale estimates of habitat capability.

The method was designed to be adaptable to goals, constraints, and future conditions not currently represented on landscapes but that might result from new approaches imposed by land managers. Further, it allows comparisons among future forest landscape patterns to estimate if any are likely to produce better conditions than others for spotted owls.

Models represented multiple spatial scales, empirical relationships were considered, and if empirical relationships were not available, then the literature and expert opinion were used to refine the model structure. We also conducted both sensitivity analyses and verification using known locations to test alternative model structures.

Each model predicts a Habitat Capability Index (HCI) that includes a set of Capability Indices (CI) associated with the capability of a landscape patch and its surrounding neighborhood to provide conditions important to survival and reproduction. Capability Indices are scaled from 0 to 1, where 0 indicates that conditions are not suitable to satisfy one or more requirements and 1 represents theoretical optimum conditions. The value for a CI at a given location was calculated based on estimates of vegetation and physical conditions over a range of scales on the landscape. The selection of vegetation and physical variables to include in the HCI models depended on four factors. First, we used variables for which the relationship to reproduction or survival could be supported by empirical evidence. Second, variables were necessarily restricted to those that could be estimated from existing GIS layers, including the vegetation data layer that was based on satellite imagery, environmental data, and field data (Ohmann and Gregory, in press). Third, we selected variables that could be projected into the future using models of forest dynamics (Spies et al. 2002). Finally, we only retained variables that had a noticeable influence on HCI values as a result of sensitivity analysis.

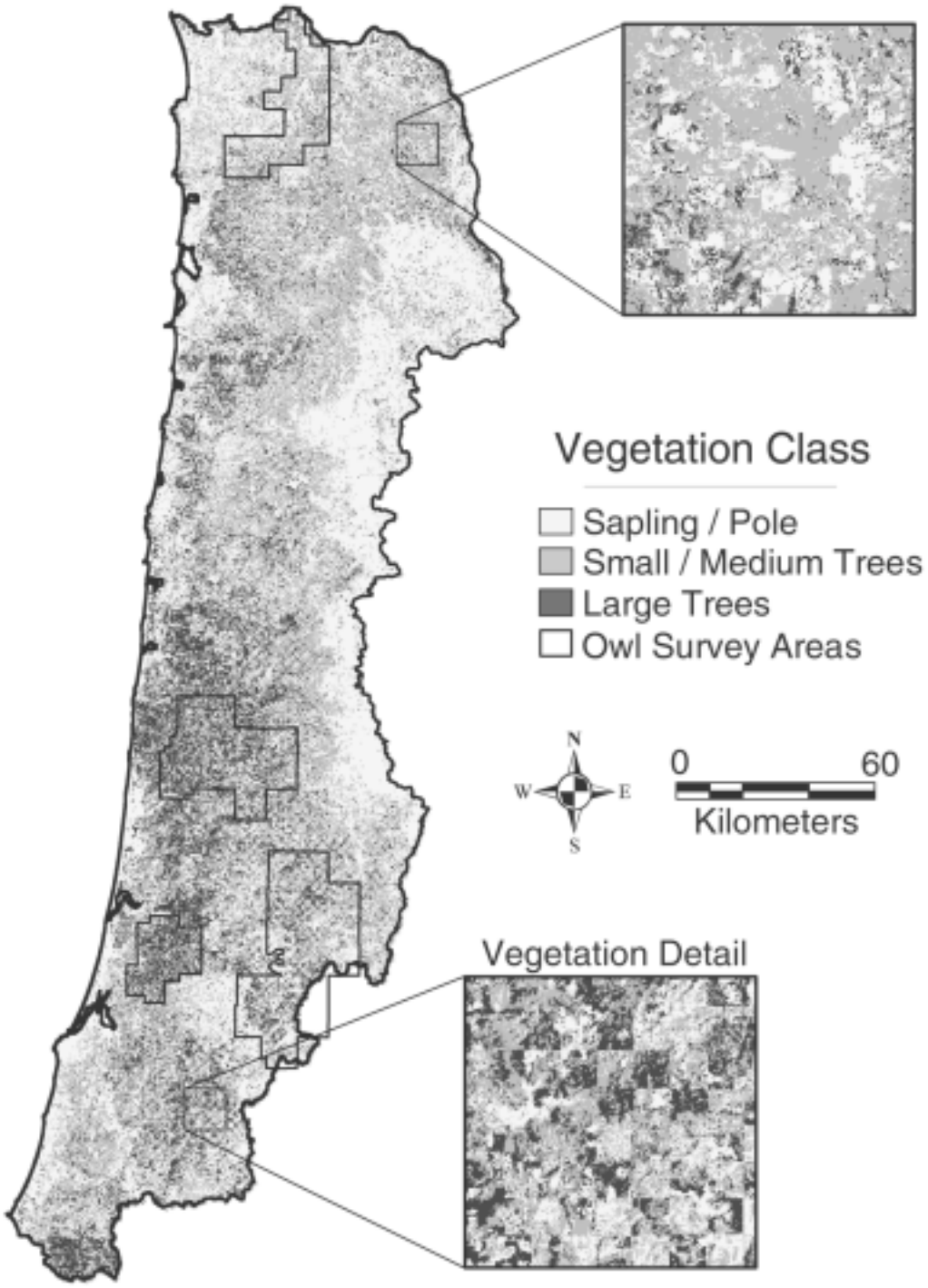

Figure 1. Vegetation patterns in the Oregon Coast Range based on the Gradient Nearest Neighbor method (Ohmann and Gregory, in press), used as a basis for estimating habitat capability index classifications and spotted owl survey areas in which model accuracy was assessed. Sapling/pole patches were defined as forested pixels with <1.5 m^2/ha of basal area or ≥1.5 m^2/ha of basal area and with dominant and codominant trees having a quadratic mean diameter (QMD) <25 cm. Small/medium tree patches were defined as forested pixels with ≥1.5 m^2/ha of basal area with dominant and codominant trees having a QMD between 25–50 cm. Large tree patches were defined as forested pixels with ≥1.5 m^2/ha of basal area with dominant and codominant trees having a QMD>50 cm dbh.

An assumption underlying the modeling approach is that the optimum value of a measured variable for satisfying survival or reproduction requirements is known. The specification of an optimum value for any measured variable is complicated by conflicting definitions of "optimum" and lack of empirical data to support such a specification (Van Horne 1991). Because we will use the model only to compare among landscapes relative to one another (rather than to determine the absolute distance from the optimum habitat condition), we assumed that a comparison of habitat capability among alternative land management policies would be robust in spite of errors in assigning an optimum value to a measured variable. Optimum values of measured variables were estimated by examining the range of variation among

observations made in relatively unmanaged Oregon Coast Range forests (Landres et al. 1999) and selecting the mean (for normally distributed data) or median (for nonnormal data) for the variable estimated in the vegetation types used by the species.

We assumed that habitat selection by species such as spotted owls occurs at different scales extending from a central place (Rosenberg and McKelvey 1999). For our HCI models, each 25 × 25 m pixel was evaluated relative to its potential to provide a nest site during the breeding season, based on the estimates of fine-scale features within the focal pixel and conditions around it. To evaluate potential nesting sites and nesting patches (a 9 pixel window of 0.56 ha surrounding the focal pixel), variables were selected that described the density of potential nest trees within the focal pixel and factors that have been shown to discriminate owl nest patches from available habitat (Hershey et al. 1998).

Each focal pixel was further evaluated relative to the conditions in the broader landscape surrounding it. We measured the availability of habitat components needed for reproduction in a focal pixel (i.e., the pixel to which the habitat capability score is applied) and measured conditions in an "analytical window" centered on the focal pixel. Habitat that could be used for foraging, roosting, and/or cover was assessed within three radii (0.3, 0.8, and 2.4 km) from the focal pixel based on past research (Meyer et al. 1998:18, Swindle et al. 1999). The vegetation structure and composition of pixels in the patches around each focal pixel was evaluated and influenced the capability score assigned to the focal pixel. This process was repeated for all pixels in the landscape.

The model incorporated comments to the degree possible from experts on spotted owl biology and habitat modeling: Robert G. Anthony, Larry Irwin, Craig Loehle, William Ripple, and Gary Roloff. These are reflected in the following parameters and functions.

Habitat Capability Index

The HCI attributes greater weight to nesting conditions associated with a potential nest site than to conditions in the landscape surrounding the nest site. We assumed that without conditions for nesting, reproduction would be unlikely and that populations could not persist. We attempted to account for desirable landscape conditions, which are assumed to provide adequate conditions for prey and other survival needs, based on landscape attributes associated with spotted owl nest sites (Meyer et al. 1998, p. 39–41, Swindle et al. 1999).

$$HCI_f = \sqrt[3]{NCI_f^2 * LCI} \qquad (1)$$

where

HCI = habitat capability index

f = the focal pixel

NCI = nest stand capability index [Equation (2)]

LCI = landscape capability index [Equation (3)]

Nest Stand Capability Index.—*NCI* was calculated for a focal pixel at the center of a 3 × 3 "moving window." This moving window of pixels averages conditions for the 0.56 ha surrounding and including the "focal" pixel (i.e., 3 × 3 pixels). Averaging is done to: (1) smooth interpixel variation; (2) reduce effects of georeferencing and model error in validation analysis; and (3) provide a "patch" level summary consistent with the scale of the stand inventory data collected to describe vegetation in previous studies (Hershey et al. 1998, Ohmann and Gregory, in press).

The subcomponents of *NCI* are assumed to be largely compensatory [the numerator is additive; Equation (2)], although the density of trees >75 cm dbh, is given additional weight in this equation (i.e., by being squared) because it is a surrogate for nest tree availability. Thus, if no nest trees are available, then nesting is not as likely to occur.

$$NCI_f = \frac{\sum_{i=1}^{9} \frac{D1 + D2 + D3^2 + D4}{4}}{9} \qquad (2)$$

where

NCI = nesting capability index

f = focal pixel

i = pixel

$D1$ = index to density of trees 10–25 cm dbh (Figure 2a)

$D2$ = index to density of trees 25–50 cm dbh (Figure 2b)

$D3$ = index to density of trees > 75 cm dbh (Figure 2c)

$D4$ = diameter diversity index (Figure 2d, Appendix 1)

Diameter Class Density Indices Hershey et al. (1998) found tree densities for the *D*1 and *D*2 size classes aided in differentiating spotted owl nest stands from other mature to old-growth stands. The functions relating tree densities to habitat suitability are based on the upper 95% CI values reported by Hershey et al. (1998) as representing optimal conditions (Figure 2a and 2b).

The function relating habitat suitability to density of trees >75 cm dbh was based on data from unmanaged Douglas-fir stands in the region (Figure 2c). We assumed that unmanaged stands would more likely fall within the range of natural variability for acceptable conditions (Landres et al. 1999) than managed stands, and that many of the features selected by spotted owls more frequently occur in old stands (Forsman et al. 1984, p. 31–32). Densities of 47 trees/ha >75 cm dbh represent the lower 95% confidence limit for an 80-yr-old stand, and 58 and 65 trees/ha represent the mean and upper 95% confidence limit, respectively, for >75 cm dbh trees in a >200-yr-old stand (T.A. Spies, unpublished data).

Diameter Diversity Index Spotted owl nest stands often have a high level of canopy heterogeneity (Hershey et al. 1998). We used a diameter diversity index (DDI) as an index to canopy heterogeneity (Figure 2d; Appendix 1). We based the relationship between habitat suitability and DDI on esti-

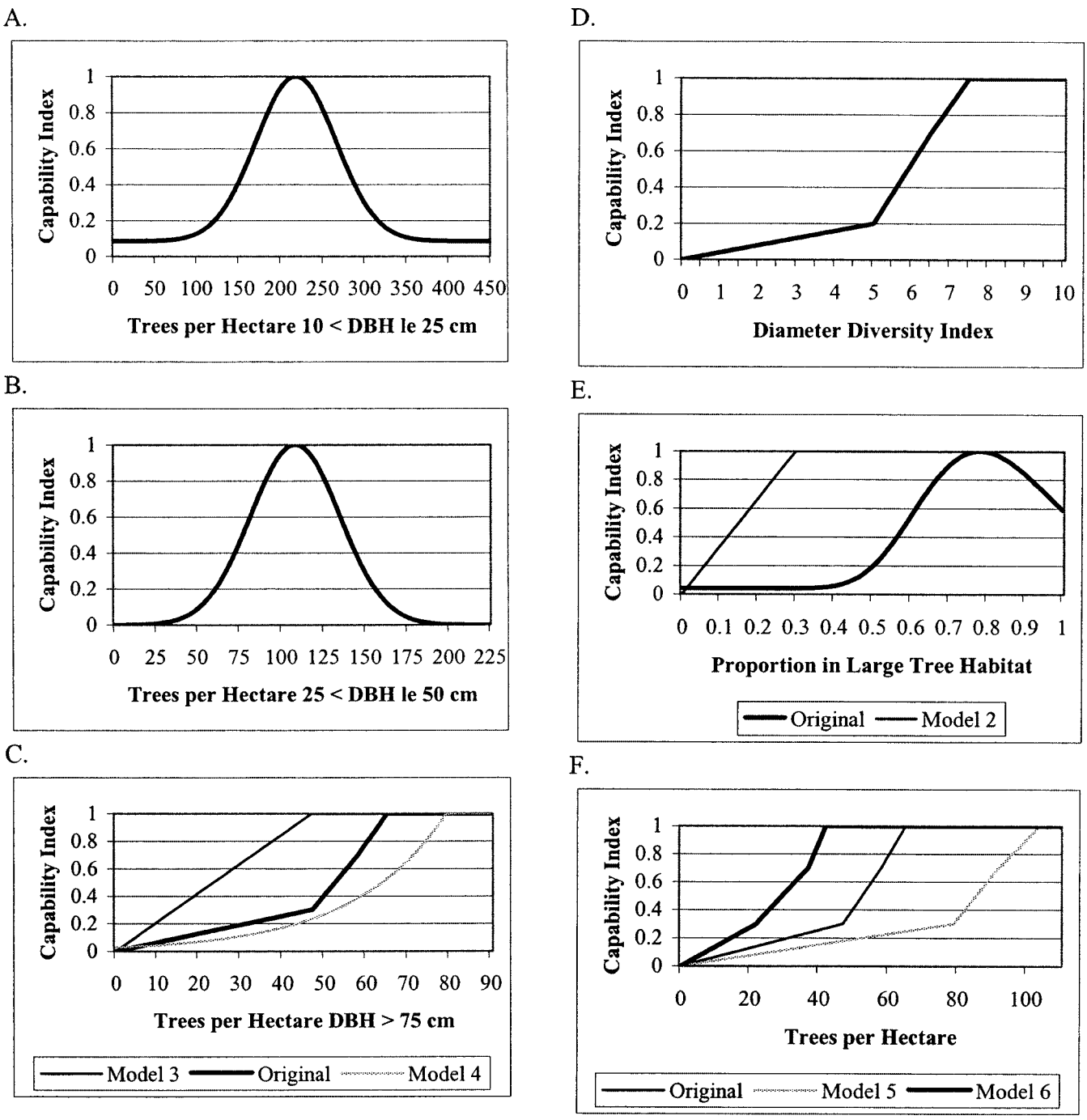

Figure 2. Habitat capability functions for each of the subindices used in the Habitat Capability Model and alternative model structures for northern spotted owls in the Oregon Coast Range. Figures represent the index to density of trees 10–25 cm dbh (a); index to density of trees 25–50 cm dbh (b); the index to density of trees >75 cm dbh and alternative models 3 and 4, which suggest habitat capability increases more rapidly or more slowly, respectively, with more trees >75 cm dbh (c); the diameter diversity index (d); a habitat index for 28 ha surrounding the focal pixel and its alternative (model 2), that habitat capability increases more rapidly with increasing area of large tree stands within 28 ha (e); an index for potential nest trees (density of trees dbh >75 cm) and alternative models 5 and 6, suggesting a potential nest tree index is best represented by the density of trees dbh >50 cm or >100 cm, respectively (f).

mates for unmanaged stands in the Coast Range. Stands <40 yr old have a DDI <5.0; stands 40–80 yr old have DDI ranging between 5.0 and 6.5; stands 80–120 yr old have DDI ranging between 6.5 and 7.5; and stands >120 yr have DDI >7.5 (T.A. Spies, unpublished data).

Landscape Capability Index.—Metrics for LCI were calculated within three radii surrounding the focal pixel (0.3, 0.8, and 2.4 km) representing patches of 28, 212, and 1,810 ha. We estimated the proportion of each patch in three vegetation development classes based on estimates of tree size and species in each pixel: sapling/pole, small/medium tree, and large tree (O'Neil et al. 2001). Sapling/pole patches were defined as forested pixels with <1.5 m^2/ha of basal area or ≥1.5 m^2/ha of basal area and with dominant and codominant trees having a quadratic mean diameter (QMD) <25 cm. Small/medium tree patches were defined as forested pixels

with ≥1.5 m^2/ha of basal area with dominant and codominant trees having a QMD between 25–50 cm. Large tree patches were defined as forested pixels with ≥1.5 m^2/ha of basal area with dominant and codominant trees having a QMD > 50 cm dbh. The 28 ha patch size was selected because owl nests tend to be located in clumps of large trees at this scale (Swindle et al. 1999). The 212 ha patch size was selected because it represents the scale beyond which the amount of large-tree conditions surrounding owl nests is similar to what is randomly available and may be the scale at which owls may select nest sites (Meyer et al. 1998, p. 34, Swindle et al. 1999). The 1,810 ha patch represents an estimate of the extent of an average spotted owl home range (G. S. Miller and E.C. Meslow, Oregon State University, unpublished data).

$$LCI_f = \sqrt[6]{S_1^3 * S_2^2 * S_3} \quad (3)$$

where

LCI_f = landscape capability index for the focal pixel

S_1 = habitat index for 28 ha surrounding the focal pixel (Figure 2e)

S_2 = habitat index for 212 ha surrounding the focal pixel [Equation (4)].

S_3 = home range index for 1,810 ha surrounding the focal pixel [Equation (4)].

Greater weight was applied to areas closest to the focal pixel (through exponentiation) because habitat in close proximity to potential nest sites is most influential on occupancy, productivity, and foraging behavior (Meyer et al. 1998, Rosenberg and McKelvey 1999, Swindle et al. 1999). By having the index be multiplicative, we assumed that the habitat conditions contribute to overall habitat quality, but that S_1, S_2, and S_3 cannot entirely compensate for each other (van Horne and Wiens 1991). Vegetation included in one patch size also was included in the area assessed at the next larger patch size (the 28 ha patch is a portion of the 212 ha patch which is a portion of 1810 ha patch) to reflect the overall contribution of each scale to habitat around the focal pixel.

Habitat Index for the 28 ha patch The capability index increases logarithmically with the proportion of the 28 ha patch in large-tree condition and declines once the area of large trees drops below 80% (Figure 2e). This distribution has been suggested from relationships observed around spotted owl nests in Oregon (R. G. Anthony, pers. comm.). Owl nest sites averaged approximately 70% old forest (i.e., large trees) at this scale in the central Cascades of Oregon (Swindle et al. 1999).

Habitat Index for the 212 ha patch The proportion of large-tree stands is associated with spotted owl nests at this scale (Ripple et al. 1991, 1997, Meyer et al. 1998, Swindle et al. 1999). However, small/medium-tree stands may provide resources for the owl by serving as source habitat for certain prey species (Eric Forsman, USDA Forest Service, pers. comm.). Small/medium-tree stands in western Oregon tend to be used in proportion to availability by foraging owls (Forsman et al. 1984, Table 4). Thus, the index for the 212 ha patch is responsive to availability of both large-tree and small/medium-tree stands to owls and recognizes that small/medium-tree stands can be partially compensatory for large-tree stands (van Horne and Wiens 1991). Nonetheless, we hypothesize that large-tree stands provide higher quality habitat than small/medium stands, and reflect this hypothesis with the coefficients of a 3:1 ratio, in favor of large-tree conditions. The denominator standardizes the equation as a proportion.

$$S_{2_f} = \frac{\frac{3}{4}P_{ml} + \frac{1}{4}P_y}{0.75} \quad (4)$$

where

S_2 = capability index for the 212 ha patch surrounding the focal pixel

f = focal pixel

P_{ml} = proportion of large-tree stands within 0.8 km of the focal pixel

P_y = proportion of small/medium-tree stands within 0.8 km of the focal pixel

Habitat Index for the 1,810 ha patch The capability of the landscape at the 1,810 ha patch size (home range extent) to contribute habitat to a focal pixel was identical to the 212 ha size, except that it was weighted less heavily in the *LCI* (no exponentiation).

Sensitivity Analysis

We conducted a sensitivity analysis to identify variables that had the greatest effect on HCI scores in the Oregon Coast Range. The results of a sensitivity analysis are specific to the landscape under assessment. Variables that may appear to be unrelated to HCI estimates in one landscape may be associated with HCI scores in other landscapes that have different forest patterns. Unfortunately, conducting this analysis using the range of conditions on the current landscape may not accurately represent conditions that might occur in the future under new management approaches. Consequently we conducted assessments across a range of current conditions to consider variability in landscape patterns as much as possible. The range of variability and moments of each variable in the model were obtained from three watersheds in the Coast Range: Nehalem (177,825 ha), Alsea (220,365 ha), and Umpqua (264,125 ha), to allow evaluation in northern, central, and southern watersheds, respectively.

To fit a probability function to each parameter we conducted 1,000 Monte Carlo iterations using the Latin hypercube sampling method applied to the probability distribution of each variable (Rose et al. 1991, Palisade Corporation 1997, p. 15–34). HCI scores were computed for each simulation. Simulations were performed using @Risk (Palisade Corporation 1997, p. 15–34).

After each simulation, we calculated the Spearman rank correlation coefficient between each of the habitat variables and the predicted HCI scores and then used the squared correlation coefficients (r^2) as an index to the percentage of

the total variation in HCI explained by each habitat variable. Based on the r^2 values, we assessed how uncertainties associated with estimates of vegetation or physical variables were likely to influence model predictions.

Verification

We assessed model performance using georeferenced locations of spotted owl nests provided by Dr. Eric Forsman, Janice Reid, and the Oregon Department of Forestry that are based on annual systematic surveys for owl nests from four areas in the Oregon Coast Range (Figure 1). Nests found between 1990–1999 were used to test the model. Individual owls were marked throughout this period. During this period, 502 nests were reported within 155 distinct owl territories based on marked individuals. For those territories where >1 nest was reported, we averaged HCI scores for nests within distinct territories. We could therefore ensure that the 155 nest sites used to verify the model represented nests of 155 marked nesting pairs. We also randomly selected 155 locations within the systematically surveyed areas where no nests were found during the sample period. Random unused sites were selected to fall at least 1,600 m (2 800 m radii) from a known nest. This allowed us to independently test all parameters in the model except the contribution of the 1,810 ha home range patch size. Given the density of owls in the intensively surveyed areas, it was not possible to find unused sites >4,800 m from a nest site.

By comparing the original model against six alternative models for four subindices, we evaluated individual variable response functions and the necessity of subindices. HCI scores were calculated for the georeferenced nest and random unused locations based on the original and alternative hypotheses. We then used logistic regression to evaluate which model performed best. When evaluating the HCI scores of known nest occurrences ($y = 1$) and absences ($y = 0$), the logistic regression slope parameter was used to indicate how well the HCI score separated the two groups for each hypothesis. A slope parameter that was statistically significant indicated that the HCI model did reasonably well at predicting group membership.

Subsequent to determining the efficacy of each model hypothesis to separate known absences from known occurrences, the best performing model hypothesis was determined based on Akaike's information criterion (AIC) value. The model hypothesis with the lowest AIC value was identified as the "best" model, and models with ΔAIC <5 were viewed as competing, or equal, models (Burnham and Anderson 1998:63).

The following alternative model structures were tested to identify the best model structure based on AIC values:

M_1: The surrounding landscape is not related to habitat capability for nesting by spotted owls. [Alternative Equation (1)]

$$HCI = NCI$$

M_2: Habitat capability increases more rapidly with increasing area of large-tree stands within 0.3 km of spotted owl nests than in the original model (Figure 2e).

M_3: Habitat capability increases more rapidly with more trees >75 cm dbh (Figure 2c).

M_4: Habitat capability increases more slowly with more trees >75 cm dbh (Figure 2c).

M_5: Potential nest trees are represented by the density of trees >50 cm dbh (Figure 2f).

M_6: Potential nest trees are represented by the density of trees >100 cm dbh (Figure 2f).

Results

Based on the criteria described by Roloff and Kernohan (1999), our verification process for the northern spotted owl model received a score of 5.5, with demerits attributed to a narrow range of HCI scores (8 out of 10 habitat classes), and using presence–absence data for model verification. Nonetheless, our modeling approach seems to be an improvement over other theoretical models reviewed by Roloff and Kernohan (1999).

Sensitivity Analysis

Of the components of the nest stand index, canopy heterogeneity typically explained the most variation in the HCI score (Figure 3A through F). Among the LCI components, the 28 ha patch size (300 m radius) explained the most variation in the HCI score for all scales in the LCI (Figure 3A through F), with canopy heterogeneity and the density of trees ≥75 cm dbh also having high explanatory power in the HCI model. The density of trees in the 10 to 25 cm and 25 to 50 cm diameter classes within the nest stand index, and the 1,810 ha patch size (2,400 m radius) explained the least amount of variation in the resulting HCI score. Among the three basins in which the sensitivity analysis was performed, model sensitivity was generally similar (Figure 3).

Model Verification

The seven model structures adequately discriminated known spotted owl nest sites from known absences (Table 1). Alternate HCI model 2 (i.e., habitat capability increases more rapidly as a function of the proportion of large-tree stands within 28 ha around a nest) was selected as the "best" model, based on ΔAIC scores (Table 1), but model 5 was viewed as a competing model. The original model ranked as the fourth best HCI model. HCI model 2 explained more information among spotted owl nests and unused sites than the original model. Using an HCI score of 0.37, overall classification accuracy was optimized at 76% and misclassified nest sites (Type II error) were minimized at 10% for model 2 (Table 1). Model 2 was applied to a representative area of the Coast Range to provide a visual assessment of performance. Generally, as HCI scores increased, the proportion of nest sites increased and random sites decreased (Figure 4). Consequently we selected HCI model 2 to depict categories of habitat capability for the spotted owl in the Oregon Coast Range (Figure 5).

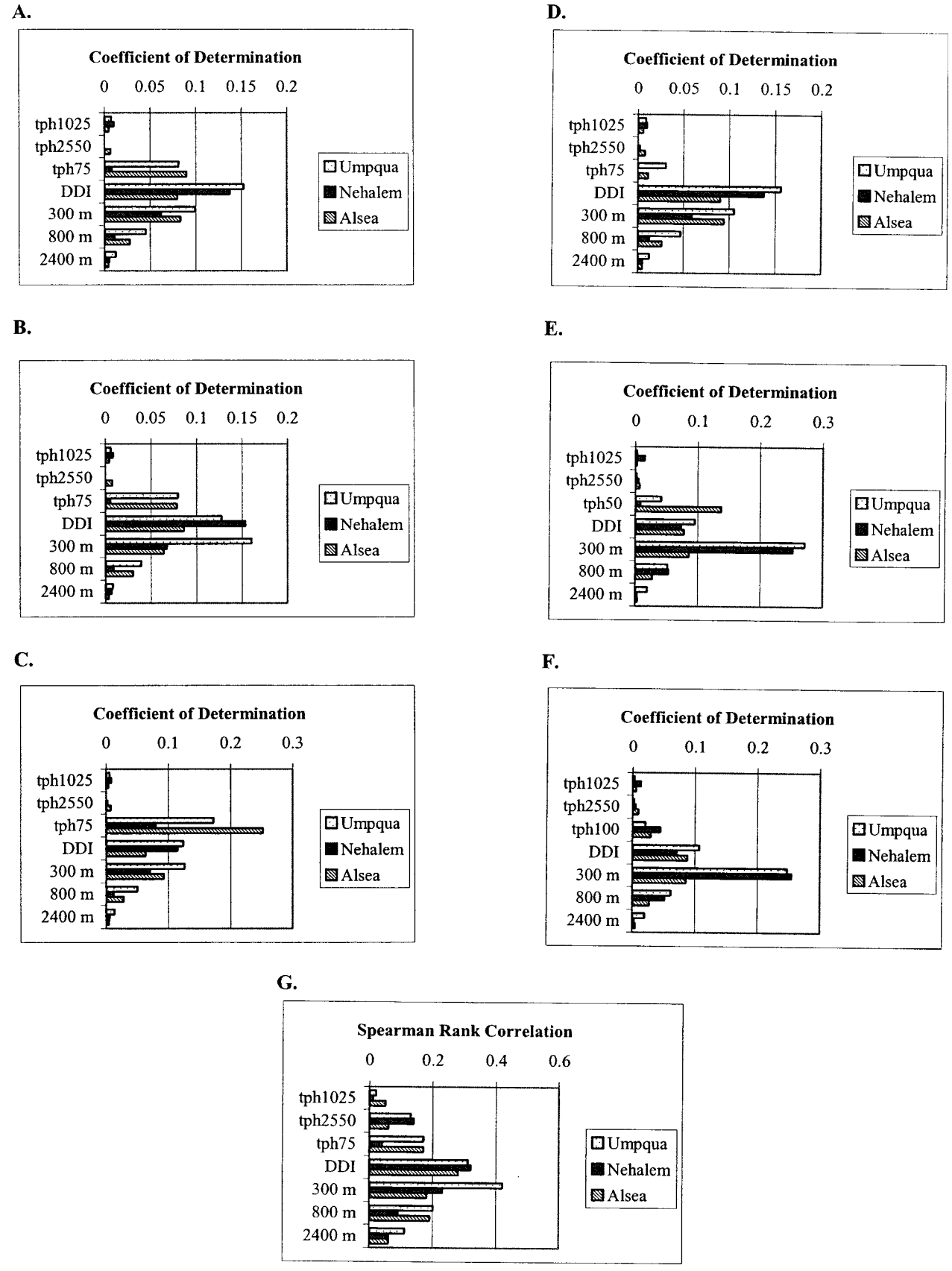

Figure 3. Results of Monte Carlo simulations for determination of resulting HCI sensitivity to component variables in three Oregon Coast Range basins. Partial residuals (R^2) are presented for component variables in the original (a), and second through sixth alternate hypotheses (b through f, respectively). Spearman rank correlation coefficients are presented for each component variable's correlation with the resulting HCI score for the second alternate hypothesis (g). Indices included in the analysis were the density of trees 10–25 cm dbh (tph 1,025), density of trees 25–50 cm dbh (tph 2,550), density of trees >75 cm dbh (tph 75), diameter diversity index (DDI), habitat index for 28 ha surrounding the focal pixel (300 m), habitat index for 212 ha surrounding the focal pixel (800 m), and the home range index for 1,810 ha surrounding the focal pixel (2,400 m).

Table 1. Validation regression and classification accuracy results for the original and six alternative northern spotted owl HCI models.

Model[1]	ΔAIC	Parameter estimate[2]	HCI breakpoint[3]	Classification accuracy[4]	Type II error[5]
				(%)	
M_2	0.0	5.37	0.37	75.5	10.0
M_5	4.75	5.32	0.28	75.5	11.6
M_6	8.12	5.46	0.29	75.8	12.3
M_4	8.26	5.51	0.28	75.8	11.9
Original	8.56	5.44	0.29	75.5	12.4
M_3	10.27	4.69	0.24	76.1	8.4
M_1	11.56	5.79	0.33	72.6	13.6

[1] M_1: The surrounding landscape is not related to nesting habitat; M_2: Habitat capability increases more rapidly with increasing area of large-tree stands within 0.3 km of spotted owl nests than in the original model; M_3: Habitat capability increases more rapidly with more trees >75 cm dbh; M_4: Habitat capability increases more slowly with more trees >75 cm dbh; M_5: Potential nest trees are represented by the density of trees >50 cm dbh; and M_6: Potential nest trees are represented by the density of trees >100 cm dbh.

[2] Maximum likelihood estimate derived from a logistic regression analysis of habitat suitability index score on occurrence data ($y = 1$ for spotted owl nest sites and $y = 0$ for unused sites). All parameter estimates were significant at $P < 0.0001$.

[3] The HCI score, on a scale of 0.00 to 1.00, that best discriminates between spotted owl nests and unused sites.

[4] The number of correctly predicted spotted owl nests and unused sites, at the reported HCI breakpoint, divided by the total number of sites classified ($n = 310$) and multiplied by 100.

[5] The number of known spotted owl nest sites misclassified as unused sites, at the reported HCI breakpoint, divided by the total number of known spotted owl nest sites ($n = 155$) and multiplied by 100.

Discussion

The results of our model development process indicate that prediction of habitat conditions associated with spotted owl nests could be conducted with reasonable accuracy under current conditions (90% of nest sites were classified correctly). Thus, it is encouraging that similar models could be developed for other species of interest or concern within the region. However, habitat capability modeling represents only the first step in identifying the potential for a landscape to allow persistence of a species over an area over time. For instance, in our example, providing habitat structure and composition over landscapes that would lead to high HCI values should provide owls with areas in which they could nest, but our model does not address issues associated with nest success, intraspecific interactions (e.g., competition, dispersal), or inter-specific interactions (predation or competition). Providing adequate opportunities to nest across a landscape is a prerequisite to long-term persistence, but it does not ensure persistence. With long-lived species such as spotted owls, nest success, mortality, and dispersal may be highly variable from year to year. Climatic conditions, natural disturbances, and interactions with other species [e.g., barred owls (*Strix varia*)] may cause populations to change despite high levels of habitat capability across the landscape. Nonetheless, until these demographic parameters can be predicted with more certainty, the approach that we outlined could be used to predict general patterns of nest habitat availability over large areas over time. For instance, at the very least it would be prudent for forest management policies and management actions to ensure that habitat capability for the species is not reduced. Indeed, if high quality habitat for a species drops below 30–40% of the landscape, then lack of connectivity can isolate habitat patches, especially for species with low gap-crossing ability (With 1999). Although spotted owls disperse widely (Miller 1989), high quality nesting habitat (HCI > 0.5) in the Oregon Coast Range represents only 5.4% of the region (Figure 5). If other species such as mammals and amphibians with reduced dispersal capabilities are similarly affected, then they may experience reduced genetic variability or other population effects (Mills and Tallmon 1999).

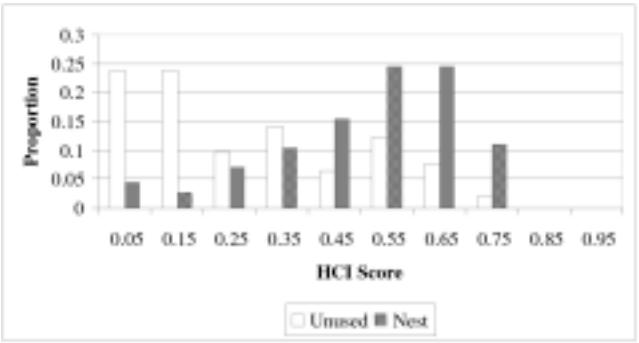

Figure 4. Proportion of northern spotted owl nest sites and unused sites as a function of habitat capability index scores in the Oregon Coast Range.

Because our model structure allows us to predict habitat capability from vegetation dynamics models, we can estimate the rate and distribution of habitat recovery across complex landscapes. For instance, the approach could be used to identify disconnected patches of potential nesting habitat that could be used as the basis for developing regional management strategies that could improve connectivity as quickly as possible among patches over time (With 1999). Clearly an adaptive management approach including population monitoring for this or any other species of concern would be a key component to any planning or management strategy.

Within the Oregon Coast Range, conditions of the landscape immediately surrounding a potential nest patch seemed to influence HCI estimates more than other variables. Given the presence of a potential nest site in a 28 ha patch, central place foragers such as spotted owls may be selecting locations to nest based on the local patch conditions. Such selection may lead to a reproductive advantage for the species, but there also may be landscape effects that are not clear from available data. Reproductive success

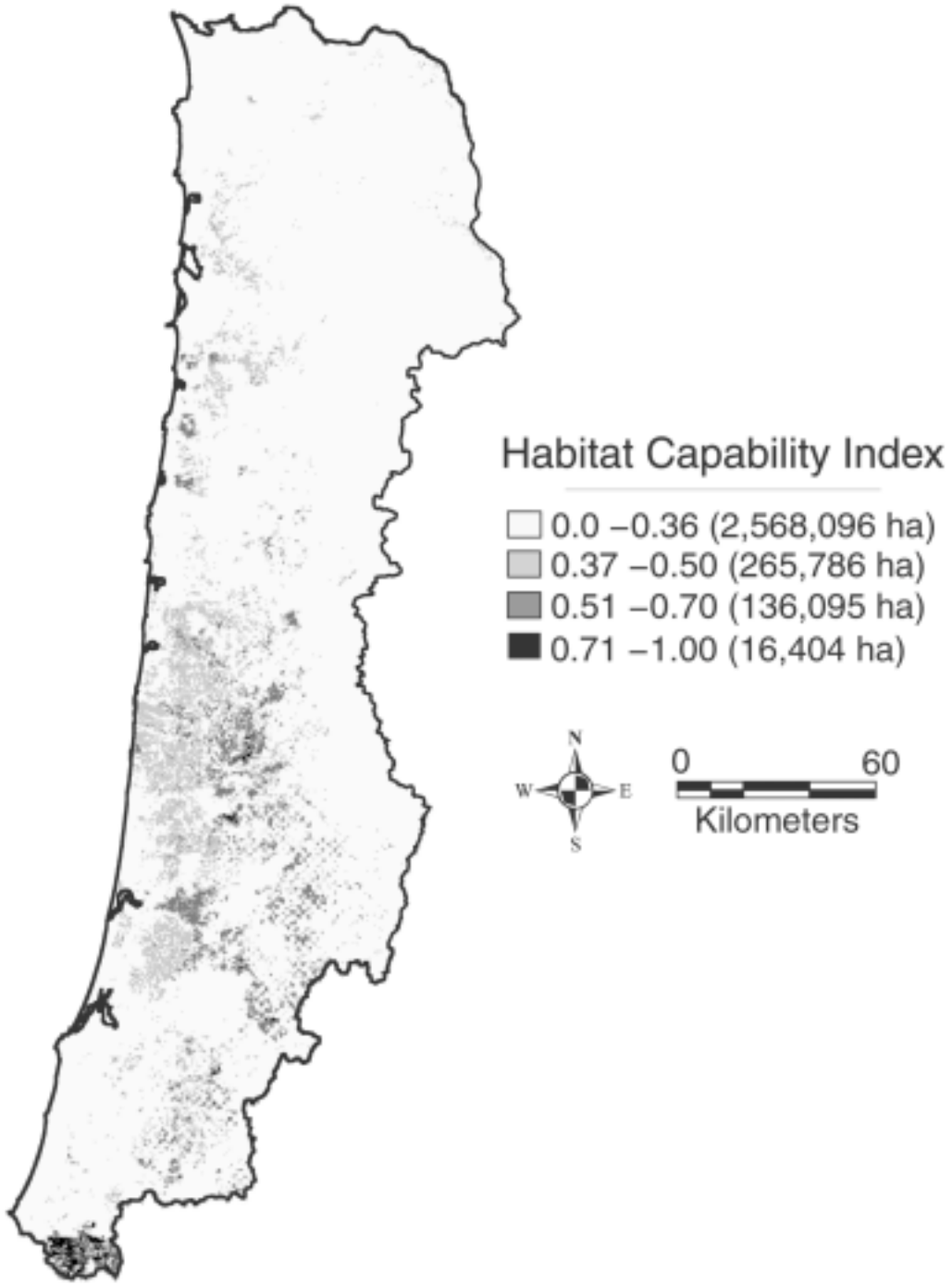

Figure 5. Habitat capability for the northern spotted owl over the Oregon Coast Range under 1988 conditions. An HCI score of 0.37 equates with the demarcation between northern spotted owl nesting habitat and unused habitat.

may be highly affected by annual climatic conditions, natural disturbances, prey availability, and mate choice over the reproductive life of females. Each of these factors may fluctuate markedly from year to year, and net reproductive success may relate to the probability of a favorable combination of these factors occurring in any single nesting season. For a female to contribute to population growth, infrequent nest success may be the norm and may be related to availability of high quality habitat throughout its home range. Testing associations between landscape conditions and reproductive success would require information on lifetime reproductive success of many females over a range of landscape conditions.

We used logistic regression analyses and ΔAIC to test a number of alternative model structures and variable weightings. Although we considered simply developing empirical models using logistic regression to predict the probability of a nest site at a pixel, the data available to build the models are constrained by current conditions on the systematically surveyed landscapes. Predicting habitat quality under future novel conditions not represented in the current landscape would force predictions beyond the

bounds of the data used to develop the model. The HCI approach is more adaptable to a range of future conditions, and alternative model structures can be evaluated. Based on available habitat relationships information for the species, we chose alternative models that seemed most likely to influence relationships with reproductive or foraging success, but there are many alternative model structures and weightings that could have been tested. We have not identified an optimal model, but using the process of testing six alternative model structures, we identified an improvement over our original model for the Oregon Coast Range. Clearly this approach provides the opportunity to continue to improve models. Additional improvements can be made through external peer review of the models and field-testing. Finally, these sorts of habitat models may lend themselves well to improvements made through open-source model development (similar in many respects to open source programming used in the computer industry). In this instance, the users of the model simply have the obligation of making available to all other users documentation of the improvements made and evidence for improvement based on additional testing.

Scope and Limitations

In our example, the HCI models are limited in a few important ways. First, they were developed and tested on current conditions in the Oregon Coast Range and may not perform similarly in other conditions. Also, we only evaluated nest site selection and not other aspects of the species biology. Further, systematic survey data were not available on nonfederal lands where populations may be lowest and where the LCI estimates may be quite different from those on federal lands due to past land management practices. The model should be used cautiously on large landscapes dominated by nonfederal lands.

The model that we developed is dependent on the underlying vegetation model (Ohmann and Gregory, in press). The vegetation data probably provide reasonable estimates of structure and composition over large areas (>1,000 ha), but may perform poorly at small spatial scales (1–10 ha). Results from the models should be used for strategic planning but not site-specific management.

Finally, we developed models for the nesting season, but did not consider habitat requirements during the nonbreeding season. If overwinter survival represents a key demographic process to long-term persistence of the species, then an additional HCI component would have to be developed.

Conclusions

Our modeling approach, when applied to spotted owl nest sites, performed well in identifying used sites. The model provides the basis for understanding the potential rate of habitat recovery over time under current policies and land ownership, and can be used to assist in assessment of alternative policies. Development of these types of models for a suite of species can allow managers not only to quantify changes in nesting quality for selected species, but also provide estimates of changes in many other resources. Policy makers and managers would then be capable of making more informed decisions when considering plans where impacts on many resources must be considered over complex, multiowner landscapes.

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APPENDIX 1

Derivation of the Diameter Diversity Index

The diameter diversity index is based on tree densities in different diameter (dbh) classes and is the sum of weighted individual indices for each diameter class. These classes include 5–24 cm, 25–49 cm, 50–99 cm, and ≥100 cm. Two steps are involved in determining the individual indices. First, an index value from 0 to 1 is determined for each class using coefficients from a straight-line regression equation in which tree density is the independent variable. The index value reflects tree density relative to the median density found in old forest stands (T.A. Spies, unpubl. data). The regression line runs from the origin to a point where X (i.e., density expressed as trees per hectare) equals the median from the old stands, and Y (the individual index) equals 1. A tree density equal to or greater than the median value within a dbh class results in an individual index value of 1.

The second step involves applying a weight to the individual index values. The weights for each dbh class are approximately equal to the relative height differences between "average" trees in the four dbh classes. Average trees

were defined as those with dbh's equal to the midpoints of the first three dbh categories, and the mean dbh of trees of the >100 cm class in the old-growth data set. Heights were determined with asymptotic equations that predict height from dbh (Garman et al. 1995, p. 13–22). Tree heights were determined from several equations representing different locations in the Coast Range. These heights were then averaged to arrive at a mean height for each dbh class. The relative differences in height among the dbh classes were approximately 1, 2, 3, and 4 (i.e., a tree of average diameter in the ≥100 cm class is about four times taller than a tree of average diameter in the 5–24 cm category). The individual index is weighted by multiplying the individual index value for a dbh class by the weight for that class. The four weighted individual index values are then summed to arrive at the DDI, which has a maximum value of 10.