

**Regional-scale predictive models
of the distribution of the California spotted owl:
an exploratory analysis**

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INTRODUCTION

Until recently, conservation planning in the United States has been species-based, due to the prevalent interpretation of the Endangered Species Act and other legal mandates. Because knowledge and resources are insufficient to manage for all species individually, land-management agencies increasingly have advocated ecosystem-level regional planning, for example in the Northwest Forest Plan (USDA and USDI 1994). Viability analysis of well-selected focal species, however, can complement ecosystem-level conservation planning by revealing subtle thresholds in habitat area and landscape connectivity. This allows us to evaluate the effectiveness of conservation strategies in a way not possible with composite indicators of ecosystem function.

Although the concept of management indicator species, as often applied, has been discredited (Landres et al. 1988, Noss 1990), the broader notion that the population status of a species can be used to assess ecological integrity in conjunction with more integrative metrics remains useful. Lambeck (1997) suggested linking species and ecosystem-based efforts by focusing on a few focal species that are most sensitive to changes in key landscape processes. In the Sierra Nevada region, as in the Pacific Northwest, the spotted owl (*Strix occidentalis*) and other species associated with older forest have been the main foci of species-based conservation planning (e.g. Verner et al. 1992). The California spotted owl (*S. occidentalis occidentalis*) falls into three of Lambeck's four categories of focal species: it is area-limited, with a mean home range size of 20-50 km², dispersal-limited across open habitat, and resource-limited by its association with large trees (Verner et al. 1992).

Many potential focal species occur at low densities due to their high trophic position and are secretive or nocturnal. This makes collecting accurate census data difficult and expensive. Although planning for the owl benefits from the availability of long-term demographic data, population indices from intensive demographic studies may provide ambiguous information on declining viability without information on regional-scale trends in habitat (Doak 1995).

Coordinated planning across multiple ownerships is necessary for insuring viability of area-limited or wide-ranging species. However, although legal mandates have resulted in a database on spotted owl distribution that is more complete than for most rare species, data collection is primarily focused on federal lands with timber or other development activities. Our knowledge of owl distribution and abundance in Forest Service roadless areas, national parks, and private lands is still relatively poor. Empirical distribution models such as those developed here are an important initial stage in development of a multi-ownership monitoring program that can place habitat changes within the context of the regional metapopulation and form the basis for multi-species conservation planning (Carroll et al. 1999b). However, initial models must be seen as map-based hypotheses to be rigorously validated and refined with new field data (Murphy and Noon 1992, Carroll et al. 1999a). Analysis of regional-scale constraints should be followed by incorporation of progressively finer-scale factors. No one scale of analysis is likely to be sufficient (Noss 1990, Holling 1992, Peterson et al. 1998).

To build models of species distribution that are generalizable across the entire study region, a geographically-extensive data set of species occurrences is required. Ideally, such data are collected through standardized systematic surveys. Nevertheless, such efforts only have recently begun as part of agency monitoring efforts. "Found" distributional data sets, such as sightings data, are less useful for modeling because of bias in sampling effort and lack of verifiability. The owl distribution data used here, although greatly superior to most sightings or occurrence data sets, nevertheless show strong sampling bias that must be evaluated during the

analysis process. The GIS habitat data are also inconsistent in quality and format across management categories. Despite these problems, regional habitat models can provide initial estimates of species distribution and abundance as averaged over coarse spatial (watershed) and temporal (decadal) scales.

A lack of accurate maps of habitat quality often limits more complex dynamic modeling approaches, such as individual-based models. The use of a simple binary (suitable/non-suitable) habitat classification obscures the effects on connectivity of the landscape mosaic as a whole (Wiens 1997). Regional-scale empirical models often suggest habitat factors not evident from intensive field studies and can provide such data as habitat patch size or potential dispersal frequency for parameterizing dynamic models. Although the models reported here do not directly address area and connectivity factors, they can form the foundation for development of dynamic species viability models (e.g. Noon and McKelvey 1996a,b, Akçakaya and Raphael 1998, Schumaker 1998).

METHODS

STUDY AREA

The study area covers 93,000 km² in the Sierra Nevada mountains of California (figure 4). Its southern, western, and eastern boundaries were defined by those of the Sierra Nevada Ecosystem Project study boundary (SNEP 1996), while the northern boundary was defined by the boundary between the northern spotted owl (*Strix occidentalis caurina*) and California spotted owl subspecies as defined in the owl location database (California Dept. of Fish and Game, unpublished data). Mean elevation is 1600 m, ranging from sea level to over 4000 m. Climate is mediterranean, with most precipitation occurring in the winter months. Major vegetation types include oak woodlands, mixed coniferous forest, and alpine vegetation (Rundel et al. 1995). Land ownership is approximately 59% federal (51% Forest Service and 8% National Park Service) and 41% private.

SPECIES DISTRIBUTION DATA

Data on the locations of territories of California spotted owls were provided by the California Department of Fish and Game, which maintains a database of records submitted by agencies and private landowners. Department biologists classified 23,870 reported locations of owl observations into 2141 owl territory locations, of which 1707 fell within the Sierra Nevada study area boundary. Territories were reported primarily on Forest Service lands (81.2%), as well as in national parks (7.6%), and private land (9.8%). Occupancy status of locations was classified as by an owl pair (61.0%), territorial single (19.0%), or single owl (20.0%). Data on reproductive status by year is also given. Observations are primarily from the period 1991-1996 (74.1%), with 20.1% dating from 1987-1990, and 5.7% from before 1987.

HABITAT DATA

The habitat variables were developed in a GIS format (Table 1). They can be grouped into the five categories of vegetation, satellite imagery metrics, topography, climate, and human-impact related variables.

Vegetation variables were derived from GIS vegetation layers developed from supervised classification of Landsat Thematic imagery by the Remote Sensing Laboratory of USDA Forest Service Region 5 (USDA Forest Service, unpublished data). These included percent tree canopy closure, and tree size class as defined by the California Wildlife Habitat Relationships (CWHR) system (Mayer and Laudenslayer 1988). CWHR vegetation cover type classes were given approximate habitat values for the owl based on the average CWHR habitat index value for all size and closure classes of that cover type. This simplification of the CWHR system was used to take advantage of seamless cover type data developed for the study area from Forest Service, California Dept. of Forestry, and USGS BRD Gap Analysis Project data (L. Levien, unpublished data).

Imagery-derived vegetation mapping with attributes other than cover type is not yet available for non-Forest Service portions of the study area. I used imagery-based metrics to develop models that were not limited by the extent of the vegetation data, but that could be

applied to the entire study area. "Pseudo-habitat" variables derived directly from unclassified satellite imagery are correlated to varying degrees with ecological factors such as net primary productivity and green phytomass (Cihlar et al. 1991, Merrill et al. 1993, White et al. 1997) and have proved useful in modeling wildlife distributions (Mace et al. 1999). Vegetation variables and imagery metrics such as tasseled-cap greenness may be expected to be correlated with abundance of prey species through their relationships to primary productivity. However the relationship between such variables and productivity is weakened by phenological variation between years and spatial variation in percent bare ground and percent dry biomass (Merrill et al. 1993).

I acquired Landsat TM imagery spanning a seasonal range of 20 June to 3 September for the years 1989 to 1991. Images for 1996 were also available, but were less contemporaneous with the majority of owl locations. I derived from TM imagery the tasseled-cap indices of brightness, greenness, and wetness (Crist and Cicone 1984), and the modified Normalized Difference Vegetation Index (NDVI) (Nemani et al. 1993). The second source of imagery, the Advanced Very High Resolution Radiometer (AVHRR) sensor, has low spatial and spectral resolution compared with the Landsat TM sensor (Eidenshink 1992). Its daily temporal resolution, however, may allow improved estimation of ecological factors that show seasonal variation. Maximum daily NDVI values from the AVHRR sensor were acquired for the entire study area for each month in 1995 (James and Kalluri 1993).

I derived topographic variables from a digital elevation model assembled at 90 m resolution (USGS, unpublished data). A topographic complexity variable was derived by combining the values for aspect curvature and slope (ESRI, Inc. 1998). High values of this variable indicate steep or irregular terrain. A cosine transformation was used to convert aspect to a variable that ranged from zero on most-exposed (SW) aspects to 2.0 on least-exposed (NE) aspects (Beers et al. 1966).

I acquired climatic data for mean annual precipitation and mean annual snowfall (1961-1990) at approximately 2-km resolution (Daly et al. 1994). These climatic data were derived from meteorological records and elevation data by means of the PRISM model (Daly et al. 1994).

Variables that may serve as surrogates for the effects of humans on wildlife at the regional scale include road density and human population density (Mladenoff et al. 1995, Merrill et al. 1999). GIS data on roads, trails, and railroads were assembled for the study area and grouped into classes based on degree of expected use. Road density calculations, performed at a 1-km resolution, incorporated weights based on this classification, with highways weighted two to three times the weight of unpaved roads. I rated trails and other routes at 0.35 that of unpaved roads (Merrill et al. 1999). Road data, which was available for the entire study area at the 1:100,000 scale, is conservative in that it underestimates road density by approximately 30% when compared with 1:24,000 scale data (C. Carroll, unpublished data).

I acquired data on human population at the scale of census blocks. The average area of a census block in this region is 400 ha. A data layer representing all population centers as points was interpolated using an inverse distance weighting algorithm (ESRI, Inc. 1998). This provides an approximation of the effects of population centers over distance, for example as it might affect levels of recreational use of public lands (Merrill et al. 1999).

Table 1. Data layers evaluated in the development of the California spotted owl distribution models for the Sierra Nevada.

Data Layer	Resolution	Source
<u>Vegetation variables</u>		
Tree canopy closure	100 m	USDA R5 Remote Sensing Lab
Tree size class	100 m	"
CWHR owl habitat value	≥100 m	"
<u>Satellite imagery metrics</u>		
Average daily NDVI	1 km	EROS Data Center
Modified NDVI	30 m	USDA R5 Remote Sensing Lab
Brightness	30 m	"
Greenness	30 m	"
Wetness	30m	"
<u>Topographic variables</u>		
Elevation	90m	SNEP, USGS
Slope	90m	"
Transformed macroaspect	90m	"
Topographic complexity	90m	"
<u>Climatic variables</u>		
Average annual precipitation	2 km	OCS
Average annual snowfall	2 km	OCS
<u>Human-impact associated variables</u>		
Human population density	2 km	CIESIN
Interpolated human population density	1:100,000	USGS
Road density	1:100,00	USGS

Source abbreviations:

CIESIN - Center for International Earth Science Information Network

OCS - Oregon Climate Survey

SNEP - Sierra Nevada Ecosystem Project

USGS - US Geological Survey

MODEL DEVELOPMENT

I used multiple logistic regression to compare habitat variables at territory locations with those at random points (Hosmer and Lemeshow 1989). Before building the multivariate models, I conducted exploratory analysis of univariate relationships between potential predictor variables and the occurrence data using non-parametric significance tests and generalized additive modeling (Hastie 1993). Generalized additive modeling plots were used to assess curvature and thresholds in the univariate models. A large set of alternate multivariate models was constructed and evaluated with the Bayesian Information Criterion (BIC), a diagnostic statistic that penalizes for overfitting (Schwarz 1978). I allowed models to contain variables that did not appear highly significant in univariate tests if this resulted in lower BIC values. I also considered interpretability and field knowledge of the species when choosing among competing models that had similar BIC values. The percentage of variance explained by the model was assessed with Somers' Dxy and R² values (Harrell et al. 1996). Because many candidate models were considered, the multivariate analysis should be considered exploratory.

The spatial correlation structure of wildlife distribution data can be modeled as a combination of coarse-scale trend and mesoscale variation (Bailey and Gatrell 1995). Trend surface variables derived from geographic coordinates were incorporated into the models. However, since the standard north-south and east-west coordinate axes are arbitrary in orientation when compared with the orientation of distribution trends, I rotated coordinate axes by 30 degrees so that they became parallel (rotated UTM northing) and perpendicular (rotated UTM easting) to the Sierra range. I modeled mesoscale environmental covariates with a moving-average function that assigns to each cell the mean value of the attributes within a surrounding circular moving window (Haining 1990, ESRI, Inc. 1998). Models including attributes at a resolution of 0.1 km², and with attributes derived from moving windows of 1 km², 3 km², and 30 km² were compared to assess the relative predictive power of habitat associations at different scales.

Potential variables were also assessed with resampling validation of the candidate logistic regression models using backward step-down variable deletion and 100 bootstrap replications. The fit of the final model was assessed with calibration (ROC) curves.

I used the coefficients from the final multivariate model to calculate a resource selection function (RSF) $w(x)$ for used (occurrences) and available (random) resources (Manly et al. 1993, Boyce and McDonald 1999), using the equation:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i)$$

Because the number of used versus unused resource units is not known, the RSFs represent only a relative probability of occurrence of a species at a location (Manly 1993). I therefore map the resulting RSF values as quantiles (e.g., most suitable decile of study area) rather than actual values.

GIS maps derived from extrapolation of the final multivariate models were compared with maps of land ownership and management categories, late-successional/old-growth (LSOG) rankings developed during the SNEP study (Franklin and Fites-Kauffman 1996), and Areas of Late-Successional Emphasis (ALSE) developed from LSOG rankings and conservation planning principles (Franklin et al. 1996).

RESULTS

UNIVARIATE ANALYSIS

The univariate generalized additive models for rotated UTM easting, rotated UTM northing, slope, and snowfall suggested quadratic curvatures in these variables. GAM results suggested that probability of occurrences was reduced for below a road density threshold of approximately 0.6 km/km². High levels of rank correlation (greater than 0.80) were evident between several potential predictor variables at the 1 km² scale: elevation and snow ($r_s = 0.82$), the satellite imagery metrics of brightness, greenness, wetness, and modified NDVI (r_s absolute values of 0.76 to 0.90), and especially tree canopy closure and tree size class ($r_s = 0.94$). GAM plots for road density, CWHR value, tree canopy closure, and tree size class are shown in figure 1.

MULTIVARIATE MODELS

Coefficients, standard errors, and significance values for the selected model are reported in Table 2. Cross-validation results generally provided clear support for selection of one of a pair of strongly correlated variables (e.g., snow over elevation, modified NDVI over greenness). However, transformed aspect as a quadratic function was included in some alternate models with BIC values similar to the final model. The final model for all land ownerships included variables representing rotated UTM easting, rotated UTM northing, slope, and snowfall as quadratic functions, brightness, wetness, modified NDVI, and CWHR owl habitat value as linear functions, a variable for the low road density threshold (< 0.6 km/km²), and an interaction term for CWHR owl habitat value with wetness ($n = 8025$ [1705 nest sites, 6320 random], $-2LL = 5141.37$, $\chi^2 = 3159.68$, $df = 14$, $p = 0.000$, $D_{xy} = 0.763$, $R^2 = 0.485$).

Inclusion of variables only available for Forest Service lands, with resultant reduction in sample size, resulted in a model with the addition of tree canopy closure as a linear function, and the removal of brightness and modified NDVI ($n = 4621$ [1571 nest sites, 3050 random], $-2LL = 4491.62$, $\chi^2 = 1432.64$, $df = 13$, $p = 0.000$, $D_{xy} = 0.595$, $R^2 = 0.348$). This model was a slight improvement upon a model for points on Forest Service lands that contained only the variables included in the general model ($-2LL = 4529.15$, $\chi^2 = 1395.12$, $df = 14$, $p = 0.000$, $D_{xy} = 0.584$, $R^2 = 0.341$). Despite the significant positive univariate association between owl locations and tree size class, ($r_s = 0.33$, $p < 0.001$), the high correlation of size class with tree canopy closure resulted in its exclusion from parsimonious multivariate models.

A comparison of models across scales suggest that the model with highest predictive power incorporates variables averaged over a “landscape” of approximately 1 km² (figure 2). Models without the trend surface variables showed BIC values that were poorer by 85 to 154, depending on scale, with finer-scale models showing the largest discrepancy (figure 2). The calibration curve shows the final model to be well-calibrated at most probability levels, with some over prediction at the highest probability levels (figure 3).

Comparisons of model predictions with land management categories are shown in table 3. RSF values were derived here without including the effects of the road density threshold, which was judged to be an artifact of reduced observer effort in non-roaded areas, a common bias in sightings and other “found” data that obscures potential relationships between species

distribution and lower levels of road density (Carroll et al. 1999b). Non-reserved Forest service lands have the highest mean quantile of predicted habitat value (65.57), followed by national parks (55.77), Forest Service wilderness (46.58), and non-federal lands (35.65). Areas of Late-Successional Emphasis (ALSE) show higher mean quantiles (81.87) than non-ALSE's (54.66) or areas not considered in the ALSE planning process (35.72). Predicted habitat value at random points is highly correlated with SNEP late-successional/old-growth (LSOG) ratings ($n = 3974$, $r_s = 0.565$, $p < 0.001$)(table 3).

Table 2. Variables contained in multiple logistic regression model showing coefficients, standard errors, and significance values from the Wald test.

<u>Variable</u>	<u>Coefficient</u>	<u>Standard error</u>	<u>t value</u>	<u>p</u>
Intercept	-7.0835	0.6923	-10.2317	<0.0001
Rotated UTME	9.3041*10 ⁻⁵	1.0906*10 ⁻⁵	8.5310	<0.0001
Rotated UTME(quadratic)	-5.2367*10 ⁻¹⁰	6.1151*10 ⁻¹¹	-8.5635	<0.0001
Rotated UTMN	2.4177*10 ⁻⁶	8.9637*10 ⁻⁷	2.6972	0.0070
Rotated UTMN(quadratic)	-5.6902*10 ⁻¹²	1.1288*10 ⁻¹²	-5.0410	<0.0001
Slope	0.3384	0.0287	11.7998	<0.0001
Slope(quadratic)	-0.0106	9.4837*10 ⁻⁴	-11.2188	<0.0001
Snowfall(mm)	2.5356*10 ⁻⁴	7.5932*10 ⁻⁵		3.3393 0.0008
Snow(quadratic)	-5.2587*10 ⁻⁸	1.1001*10 ⁻⁸	-4.7803	<0.0001
Low road density threshold	-1.3374	0.1597	-8.3748	<0.0001
Brightness	-0.0195	3.2218*10 ⁻³	-6.0454	<0.0001
Wetness	0.1505	0.0129	11.6825	<0.0001
CWHR value	1.4112	0.1130	12.4931	<0.0001
Modified NDVI	1.0156*10 ⁻³	3.3121*10 ⁻⁴	3.0663	0.0022
Wetness*CWHR value	-0.0808	9.5578*10 ⁻³	-8.4582	<0.0001

Table 3. Comparison of mean quantiles of owl distribution model output with categories of land management and SNEP late-successional/old-growth classification and Area of Late-Successional Emphasis (ALSE) status..

<u>Land management category</u>	<u>Percent area</u>	<u>Mean quantile</u>
Non-federal	40.62	35.65
Non-reserved Forest Service	40.02	65.57
Forest Service wilderness	11.15	46.58
National Parks	8.21	55.77
<u>SNEP LSOG ranking</u>		
0	22.99	37.94
1	19.70	49.97
2	28.76	66.82
3	20.30	74.30
4	6.11	81.89
5	2.14	88.26
<u>ALSE status</u>		
Not mapped	39.61	35.72
Non-ALSE	49.07	54.66
ALSE	11.32	81.87

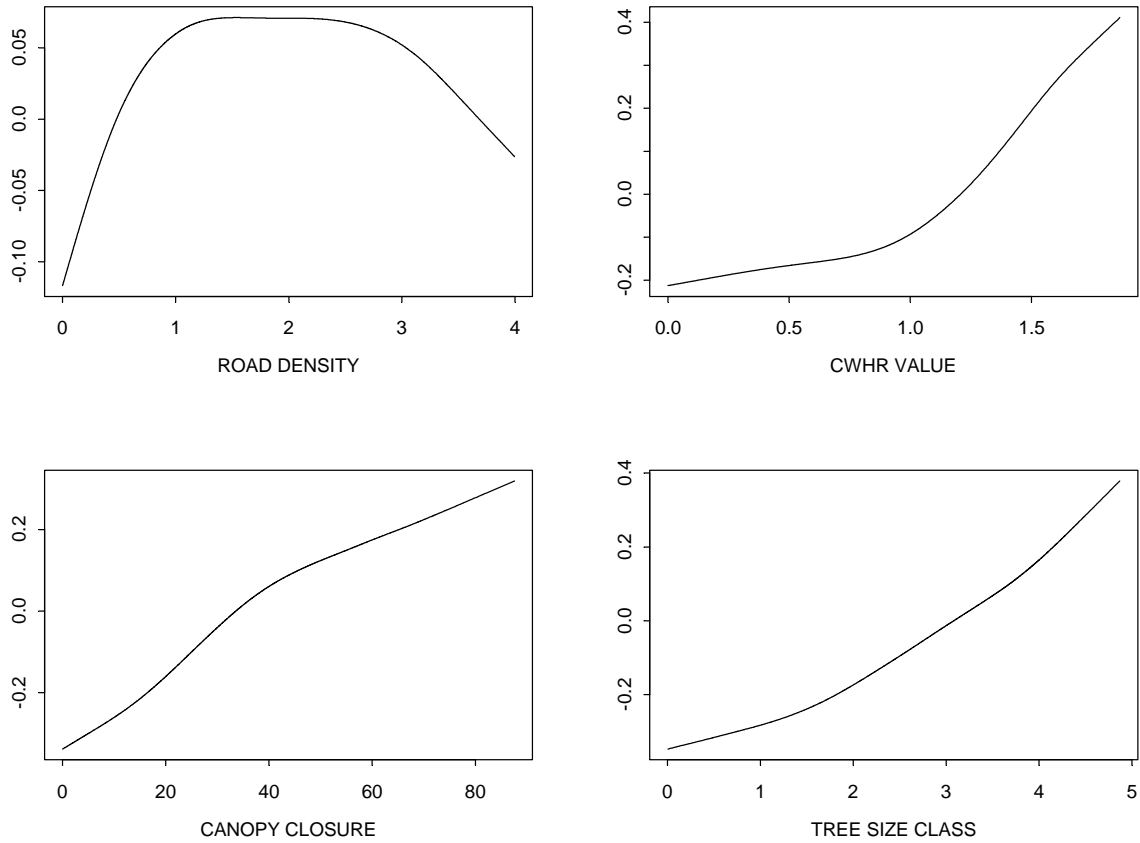


Figure 1. Generalized additive modeling (GAM) plots showing the univariate relationship between owl distribution and the four variables of road density, CWHR owl habitat value, canopy closure, and tree size class.

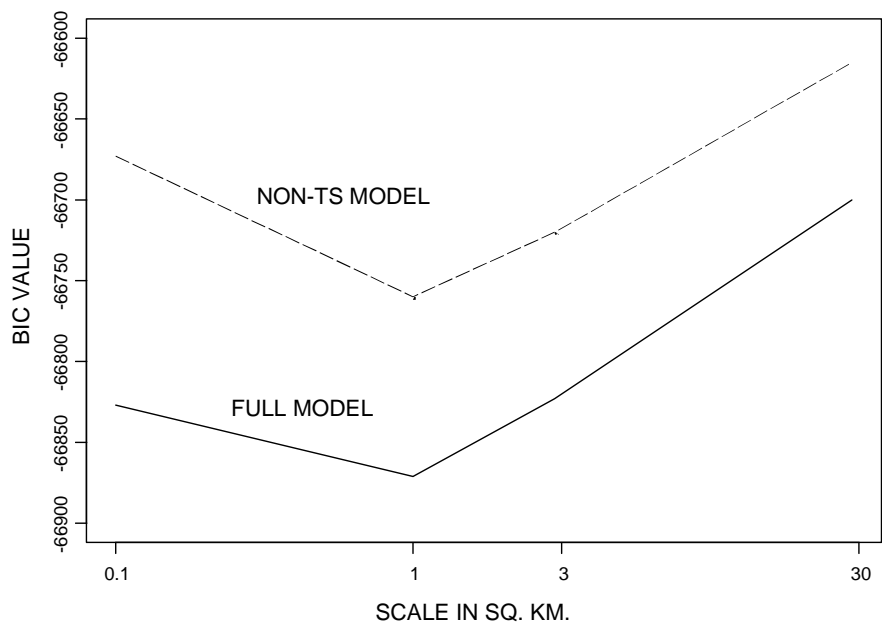


Figure 2. Plot of scale of moving window used in developing multivariate owl distribution model versus BIC value, a model statistic for which the lower values indicate better model fit.

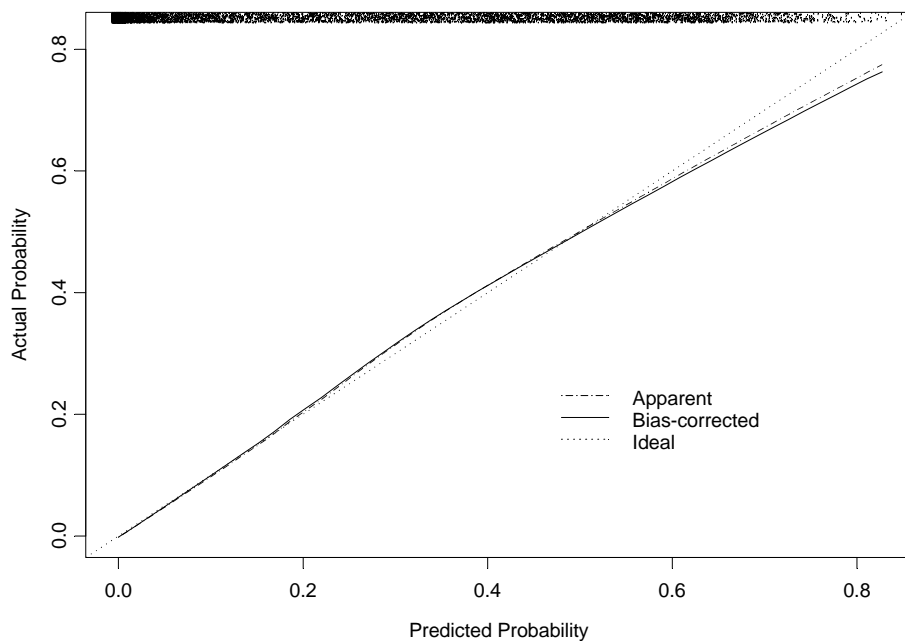


Figure 3. Calibration (ROC) curve for owl distribution model derived from 100 bootstrap replications.

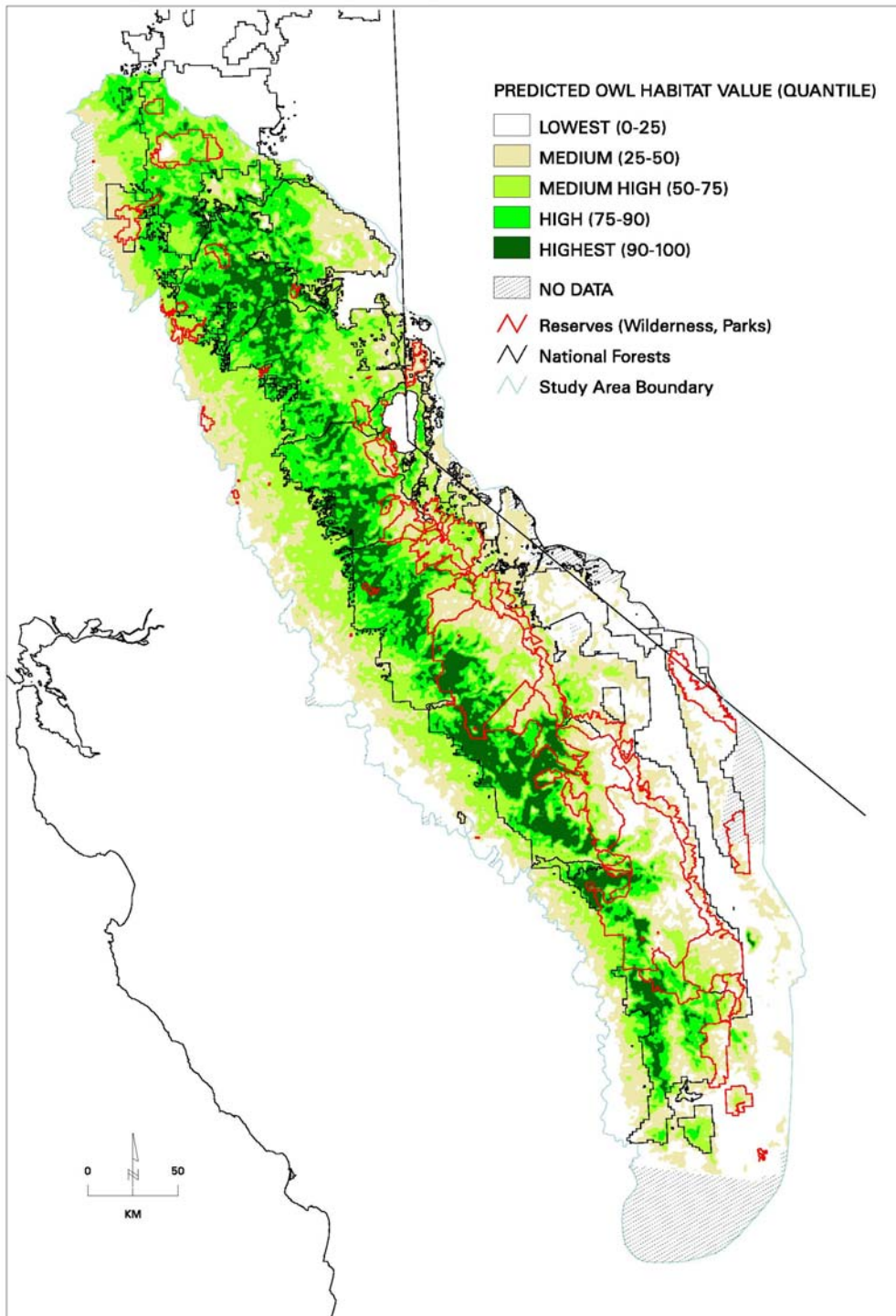


Figure 4. Distribution of the California spotted owl as predicted by a resource selection function (RSF).

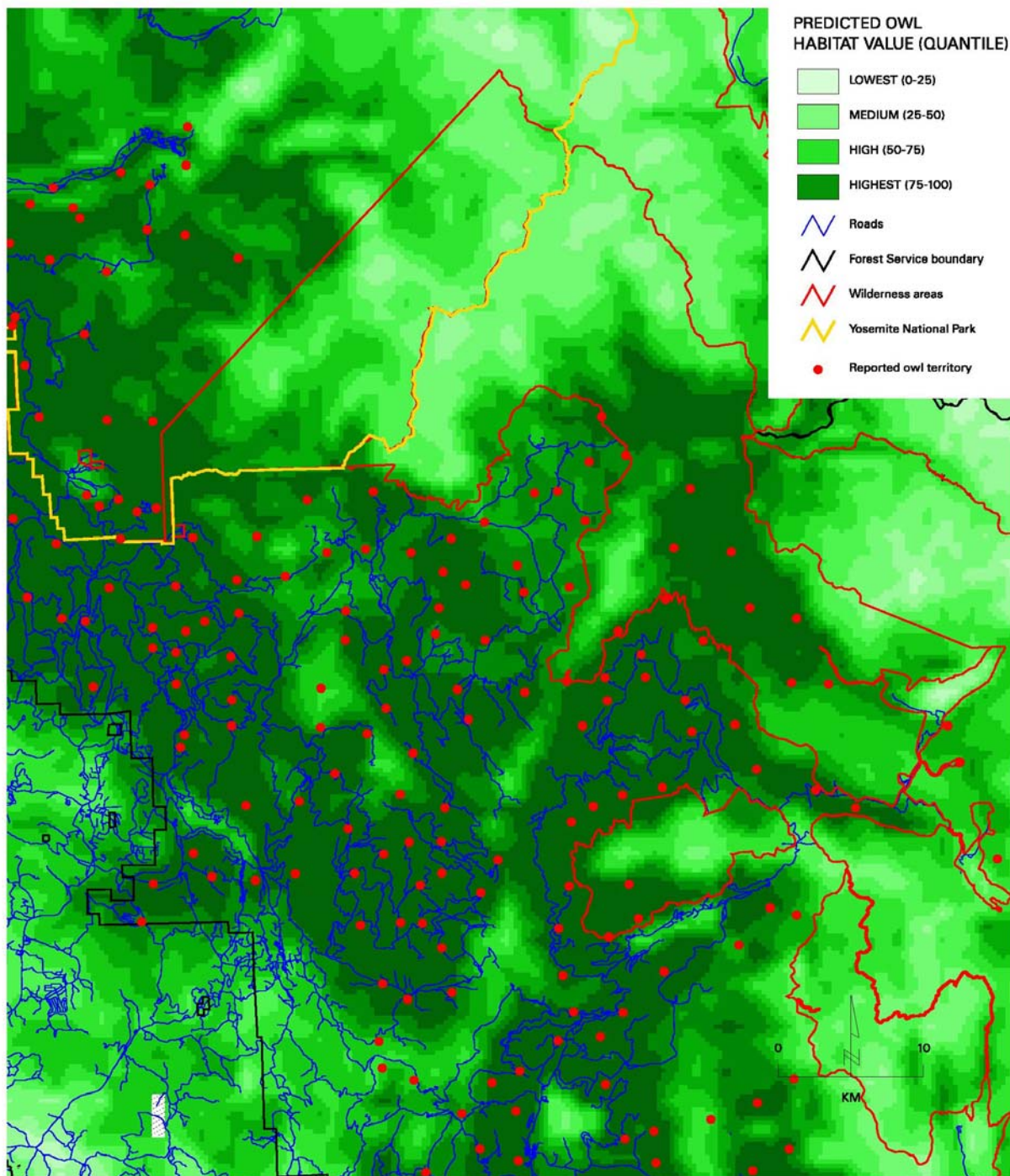


Figure 5. Detail of predicted owl habitat for area southeast of Yosemite National Park. Note sampling bias against national park, private, and unroaded habitat.

DISCUSSION

The high level of significance shown by the model suggests that regional-scale empirical models can reveal important factors associated with the distribution of the California spotted owl. Interpretation of model results contributes to constructing new hypotheses regarding specific limiting factors governing distributional patterns. Equally important, model predictions allow map-based conservation planning at a spatial scale relevant to the population processes of wide-ranging species and allow initial plans to be iteratively refined as new data become available. The large amount of unexplained variance in our analysis suggests that regional-scale models alone are not sufficient for the development of detailed conservation plans. Conversely, the models reveal factors not evident at finer scales. Given the sampling bias inherent in found data sets, a large proportion of unexplained variance is probably unavoidable. Historical effects and stochastic variability in habitat occupancy unrelated to the current habitat pattern will determine some proportion of the variation in the distribution and abundance of a species. Our analysis also does not attempt to quantify the relationships between probability of occurrence and population density or between density and individual survival and reproduction (Van Horne 1983).

The degree of model fit as measured by Somer's D_{xy} (0.763), is higher than that reported for a grizzly bear model (Merrill et al. 1999) and fisher (*Martes pennanti*), lynx (*Lynx canadensis*), and wolverine (*Gulo gulo*) models derived from sightings data (Carroll et al. 1999b), and for a fisher model derived from presence-absence survey data (Carroll et al. 1999a). The significance of the low road density threshold and visual examination of patterns of predicted habitat and reported territories suggest that survey effort is biased both by jurisdiction and by access constraints (figure 5). However, it does not appear that the model's significance arises primarily from predicting where survey effort has occurred rather than where owls are located. A model developed using only data from Forest Service lands was similar to that developed for all ownerships, although of lower predictive power ($D_{xy} = 0.584$). Sampling bias weakens the power to detect species/habitat associations, but initial models can help inform the development of more rigorous monitoring programs.

INTERPRETATION OF MODEL ATTRIBUTES

The tasseled-cap index of brightness and wetness appear to be important correlates of owl distribution. Interpretation of changes in tasseled-cap indices is complex due to variation between cover types classes (e.g., forest versus grassland) and topography. Forest stands may first increase and then decrease along the tasseled-cap axes as they age. Brightness often corresponds to the amount and reflectivity of exposed soil. The closed-conifer cover type as a whole generally has higher wetness values than non-forested cover types. Within the closed-conifer type, wetness is often highest in young conifer stands, with hardwoods and older conifers having lower wetness (Cohen et al. 1995). Wetness was the single best predictor of forest age in Pacific Northwest conifer forests (Cohen et al. 1995). The positive main effect of wetness in our model, combined with the negative interaction term with CWHR value, is consistent with these earlier findings, because CWHR value is high in conifer and mixed-conifer/hardwood types.

The replacement of brightness and modified NDVI by tree canopy closure in the alternate model is consistent with the relationship between brightness and exposed soil, as well as the

correlation between canopy closure and forest productivity as measured by metrics such as NDVI. Low to mid-elevation forest with high levels of canopy closure have been found to be valuable habitat for many species of concern such as the fisher (Carroll et al. 1999a). Although the interpretability of models containing variables such as canopy closure and tree size class is higher than for those using tasseled-cap attributes, it is encouraging that the general model, when applied to Forest Service lands only, has predictive power close to that of the model using detailed vegetation attributes (Dxy of 0.584 versus 0.595).

The significance of snowfall may be related to direct climatic effects on owl survival and fecundity or to its value as a surrogate for climatically-induced gradients in vegetation and prey communities. Temporal trends in climate variables affect demographic rates in the northern (Franklin et al. in press) and Mexican spotted owl (*Strix occidentalis lucida*) (Seamans et al. 1999), and spatial trends in climate variables likely play an equally important role. The significance of slope may be due to correlations between topography and site productivity or microclimatic conditions.

Significance of trend surface variables, such as the rotated UTM coordinates used here, has been attributed to barriers to dispersal (Gates et al. 1994) or intraspecific interactions (Periera & Itami 1991). Population-level processes such as source-sink dynamics may confound effects of local habitat selection (Pulliam 1988). This significance may also be due to the effect of unmeasured coarse-scale covariates such as changes in prey community composition. Strong regional-scale trends have been evident in previous studies of other wide-ranging focal species such as the fisher (Carroll et al. 1999a) and American marten (*Martes americana*) (Chapin et al. 1998).

The strong correlation of predicted owl habitat with LSOG supports the use of empirical models as a complement to efforts such as the SNEP LSOG analysis. While the SNEP data provides detailed information on vegetation structural attributes, empirical species models can provide greater replicability over time and over multiple ownerships.

The large role that non-reserved forest lands play in insuring owl viability is highlighted by their higher habitat value in our analysis (table 3), even after partially accounting for lower survey effort in parks and wilderness. This is similar to results of a fisher distribution model for northwestern California that found habitat in late-seral reserves (LSR) to be of higher value than that in wilderness areas. However, significant owl habitat is present in the low to mid-elevation portions of Sierran parks and wilderness areas (figures 4 and 5), and model results may help prioritize survey effort in these areas. The map of predicted owl distribution (figure 4) provides a more detailed view of the range discontinuities or areas of concern noted in Beck and Gould (1992: figure 3A). Although habitat appears relatively continuous at the scale of the entire range (figure 4), discontinuities due to topography and timber extraction become more evident at finer scales (figure 5).

In contrast to previous work with the fisher, species/habitat associations for the owl appear to be strongest at the scale of the nest stand. Given the imprecision inherent in model comparisons, results reported here, which suggest greatest predictive power at the 1 km² level, are slightly smaller in scale but broadly consistent with earlier results from studies of the northern spotted owl (*Strix occidentalis caurina*) suggesting strong associations at the 3 km² (Meyer et al. 1998) and 6 km² level (Ramsey et al. 1994). Because the model structure used here includes trend surface variables, scale of selection would be biased downward. Scale of selection in the owl does appear significantly smaller than that found for the fisher in northwestern

California (10-30 km²). This may be due to the greater biological significance of nest sites as opposed to fisher foraging locations recorded at sooted track plates. It may also arise from differences in the processes, such as dispersal limitation, that influence spatial population structure in non-volant versus volant animals. This contrast in scale, even between species that share common associations with mid-elevation productive forest, highlights the challenges inherent in multi-species conservation planning.

FUTURE RESEARCH NEEDS

Due to funding limitations, this analysis has been limited to an exploration of the utility of an approach that combines found distributional data with regional-scale habitat attributes. Before these results can be used in planning for species viability, the owl location database should be subjected to a more extensive analysis of sampling bias and its effects on model predictions. The information on reproductive status by year contained in the database should be explored for potential correlations with habitat attributes. Habitat variables that affect reproductive status may differ from those associated with adult survival or distribution (Seamans et al. 1999, Franklin et al. in press). Cross-scale comparison of results with more detailed data from demographic study areas would provide further insights. Development of similar empirical models for other sympatric species of concern, such as the fisher, and use of model predictions in dynamic viability models may offer significant new insights to help create a comprehensive conservation strategy for the Sierra Nevada region.

LITERATURE CITED

- Akçakaya, H. R., and M. G. Raphael. 1998. Assessing human impact despite uncertainty: viability of the northern spotted owl metapopulation in the northwestern USA. *Biodiversity and Conservation* 7:875-894.
- Allen, T. F. H., and T. B. Starr. 1982. *Hierarchy: perspectives for ecological complexity*. University of Chicago Press, Chicago.
- Bailey, T. C. and A. C. Gatrell. 1995. *Interactive spatial data analysis*. Addison-Wesley, NY.
- Beck, T. W., and G. I. Gould, Jr. 1992. Background and current management situation for the California spotted owl. Pages 37-53 in J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutierrez, G. I. Gould, and T. W. Beck, eds. *The California spotted owl: a technical assessment of its current status*. Gen. Tech. Rep. PSW-GTR-133. USDA Forest Service PSW Research Station, Albany, CA.
- Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. *Journal of Forestry* 64:691-692.
- Boyce, M. S., and L. L. MacDonald. 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution* 14:268-272.
- Carroll, C., W. J. Zielinski, and R. F. Noss. 1999a. Using presence-absence data to build and test spatial habitat models for the fisher in the Klamath region, U. S. A. *Conservation Biology* 13:00-00.
- Carroll, C., R. F. Noss, and P. C. Paquet. 1999b. *Carnivores as focal species for conservation planning in the Rocky Mountain region*. World Wildlife Fund, Toronto, Ontario, Canada.
- Chapin, T. G., D. J. Harrison, and D. D. Katnik. 1998. Influence of landscape pattern on habitat use by American marten in an industrial forest. *Conservation Biology* 12:96-227.
- Cihlar, J., L. St.-Laurent, and J. A. Dyer. 1991. Relation between the normalized difference vegetation index and ecological variables. *Remote Sensing of the Environment* 35:279-298.
- Cohen, W. B., T. A. Spies, and M. Fiorella. 1995. Estimating the age and structure of forests in a multi-ownership landscape of western Oregon, U.S.A. *International Journal of Remote Sensing* 16:721-746.
- Crist, E. P., and R. C. Cicone. 1984. Application of the tasseled cap concept to simulated thematic mapper data. *Photogrammetric Engineering and Remote Sensing* 50:343-352.

- Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology* 33: 140-158.
- Doak, D. 1995. Source-sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. *Conservation Biology* 9:1370-1379.
- Eidenshink, J. C., 1992, The 1990 conterminous U.S. AVHRR data set. *Photogrammetric Engineering and Remote Sensing*, 58(6), 809-813.
- ESRI, Inc. 1998. Arc-Info Version 7.1. Environmental Systems Research Institute, Inc. Redlands, CA.
- Franklin, A. B., D. R. Anderson, R. J. Gutierrez, and K. P. Burnham. In press. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs*.
- Franklin, J. F., and J. A. Fites-Kaufmann. 1996. Assessment of late-successional forests of the Sierra Nevada. Pages 627-662 in *Sierra Nevada Ecosystem Project: Final report to Congress, Volume II*. Centers for Water and Wildland Resources, University of California, Davis, CA.
- Franklin, J. F., D. Graber, K. N. Johnson, J. A. Fites-Kaufmann, K. Menning, D. Parsons, J. Sessions, T. A. Spies, J. C. Tappeiner, D. A. Thornburgh. 1996. Alternative approaches to conservation of late successional forests in the Sierra Nevada and their evaluation. Pages 53-70 in *Sierra Nevada Ecosystem Project: Final report to Congress, Addendum*. Centers for Water and Wildland Resources, University of California, Davis, CA.
- Gates, S., D. W. Gibbons, P. C. Lack, and R. J. Fuller. 1994. Declining farmland bird species: modelling geographical patterns of abundance in Britain. Pages 153-177 in P. J. Edwards, R. M. May, and N. R. Webb, editors. *Large-scale ecology and conservation biology*. Blackwell Science, Cambridge.
- Haining, R. 1990. *Spatial data analysis in the social and environmental sciences*. Cambridge University Press, Cambridge, UK.
- Harrell, F. E., K. L. Lee, and D. B. Mark. 1996. Multivariable prognostic models: Issues in developing models, evaluating assumptions and adequacy, and measuring and reducing errors. *Statistics in Medicine* 15:361-387.
- Hastie, T. J. 1993. Generalized additive models. Pages 249-308 in J. M. Chambers and T. J. Hastie. *Statistical Models* in S. Chapman and Hall, New York, NY.
- Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs* 62:447-502.

- Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. Wiley, NY. 307 pp.
- James, M. E., and Kalluri, S., 1993, The Pathfinder AVHRR land data set: An improved coarse resolution data set for terrestrial monitoring: The International Journal of Remote Sensing, 15, 3347-3364.
- Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. Conservation Biology 11:849-856.
- Lamberson, R. H., R. McKelvey, B. R. Noon, and C. Voss. 1992. A dynamic analysis of northern spotted owl viability in a fragmented forest landscape. Conservation Biology 6:505-512.
- Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. Conservation Biology 2:316-328.
- Mace, R. D., J. S. Waller, T. L. Manley, K. Ake, and W. T. Wittinger. 1999. Landscape evaluation of grizzly bear habitat in western Montana. Conservation Biology 13:367-377.
- Manly, B. F. J. 1993. Resource selection by animals. Chapman and Hall, New York, NY.
- Mayer, K. E., and W. F. Laudenslayer, Jr. 1988. A guide to wildlife habitats of California. California Department of Forestry and Fire Protection, Sacramento.
- McGarigal, K., and W.C. McComb. 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. Ecological Monographs 65: 235-260.
- McKelvey, K., B. R. Noon, and R. H. Lamberson. 1993. Conservation planning for species occupying fragmented landscapes: the case of the northern spotted owl. pp. 424-450 in P.M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer, Sunderland, MA.
- Merrill, E. H., M. K. Bramble-Brodahl, R. W. Marris, and M. S. Boyce. 1993. Estimation of green herbaceous phytomass from Landsat MSS data in Yellowstone National Park. Journal of Range Management 46:151-157.
- Merrill, T., D. J. Mattson, R. G. Wright, and H. B. Quigley. 1999. Defining landscapes suitable for restoration of grizzly bears *Ursus arctos* in Idaho. Biological Conservation 87:231-248.
- Meyer, J. S., L. I. Irwin, and M. S. Boyce. 1998. Influence of habitat abundance and fragmentation on northern spotted owls in western Oregon. Wildlife Monographs 139:1-51.

- Mladenoff, D.J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conservation Biology* 9: 279-294.
- Murphy, D. D., and B. R. Noon. 1992. Integrating scientific methods with habitat planning: reserve design for northern spotted owls. *Ecological Applications* 2: 3-17.
- Nemani, R., L. Pierce, S. Running, and L. Band. 1993. Forest ecosystem processes at the watershed scale: sensitivity to remotely-sensed leaf-area index estimates. *Int. J. Remote Sensing* 14: 2519-2534.
- Noon, B. R. and K. S. McKelvey. 1996a. A common framework for conservation planning: linking individual and metapopulation models. Pages 139-165 in D. R. McCullough, editor. *Metapopulations and wildlife conservation*. Island Press, Washington, D.C.
- Noon, B. R. and K. S. McKelvey. 1996b. Management of the spotted owl: a case history in conservation biology. *Annual Review of Ecology and Systematics* 27:135-62.
- Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4:355-364.
- Noss, R. F., M. A. O'Connell, and D. D. Murphy. 1997. *The science of conservation planning: habitat conservation under the Endangered Species Act*. Island Press, Washington, DC.
- Periera, J. M., and R. M. Itami. 1991. GIS-based habitat modeling using logistic multiple regression - a study of the Mt. Graham red squirrel. *Photogrammetric Engineering and Remote Sensing* 57: 1475-1486.
- Peterson, G. C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6-18.
- Pulliam, R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652- 661.
- Ramsey, F. L., M. McCracken, J. A. Crawford, M. S. Drut, and W. J. Ripple. 1994. Habitat association studies of the northern spotted owl, sage grouse, and flammulated owl. Pages 189-209 in N. Lange, L. Ryan, and L. Billard, D. Brillinger, L. Conquest, and J. Greenhouse, editors. *Case studies in biometry*. John Wiley & Sons, New York.
- Ritchie, M.E., and H. Olff. 1999. Spatial laws yield a synthetic theory of biodiversity. *Nature* 400:557-560.
- Rundel, P. W., D. J. Parsons, and D. T. Gordon. 1995. Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. Pages 559-600 in M. G. Barbour and J. Major, editors. *Terrestrial vegetation of California*. California Native Plant Society Special Publication No. 9. Davis, California.

- Seamans, M. E., R. J. Gutierrez, C. A. May, and M. Z. Peery. 1999. Demography of two mexican spotted owl populations. *Conservation Biology* 13:744-754.
- Schumaker, N. H. 1998. A users guide to the PATCH model. EPA/600/R-98/135. U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, Oregon.
- Schwarz, G. 1978. Estimating the dimension of a model. *Annals of Statistics* 6:461-464.
- SNEP. 1996. Sierra Nevada Ecosystem Project: Final report to Congress. Centers for Water and Wildland Resources, University of California, Davis, CA.
- U.S.D.A. and U.S.D.I. 1994. Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. Portland, OR. 2 vol.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893-901.
- Verner, J., K. S. McKelvey, B. R. Noon, R. J. Gutierrez, G. I. Gould, and T. W. Beck. 1992. The California spotted owl: a technical assessment of its current status. Gen. Tech. Rep. PSW-GTR-133. USDA Forest Service PSW Research Station, Albany, CA.
- White, J. D., S. W. Running, R. Nemani, R. E. Keane, and K. C. Ryan. 1997. Measurement and remote sensing of LAI in Rocky Mountain montane ecosystems. *Canadian Journal of Forest Research* 27:1714-1727.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.
- Wiens, J. A. 1997. Metapopulation dynamics and landscape ecology. Pages 43-62 in I. Hanski and M. E. Gilpin, eds. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, CA.