Using Presence-Absence Data to Build and Test Spatial Habitat Models for the Fisher in the Klamath Region, U.S.A.

CARLOS CARROLL,*‡ WILLIAM J. ZIELINSKI,* AND REED F. NOSS†

*Pacific Southwest Research Station, USDA Forest Service, 1700 Bayview Drive, Arcata, CA 95521, U.S.A.

†Conservation Science, Inc., 7310 NW Acorn Ridge, Corvallis, OR 97330, U.S.A.

Abstract: *Forest carnivores such as the fisher* (Martes pennanti) *have frequently been the target of conservation concern because of their association in some regions with older forests and sensitivity to landscape-level habitat alteration. Although the fisher has been extirpated from most of its former range in the western United States, it is still found in northwestern California. Fisher distribution, however, is still poorly known in most of this region where surveys have not been conducted. To predict fisher distribution across the region, we created a multiple logistic regression model using data from 682 previously surveyed locations and a vegetation layer created from satellite imagery. A moving-window function in a geographic information system was used to derive landscape-level indices of canopy closure, tree size class, and percent conifer. The model was validated with new data from 468 survey locations. The correct classification rate of 78.6% with the new data was similar to that achieved with the original data set (80.4%). Whereas several fine-scale habitat attributes were significantly correlated with fisher presence, the multivariate model containing only landscape and regional-scale variables performed as well as one incorporating fine-scale data, suggesting that habitat selection by fishers may be dominated by factors operating at the home-range scale and above. Fisher distribution was strongly associated with landscapes with high levels of tree canopy closure. Regional gradients such as annual precipitation were also significant. At the plot level, the diameter of hardwoods was greater at sites with fisher detections. A comparison of regional fisher distribution with land-management categories suggests that increased emphasis on the protection of biologically productive, low- to mid-elevation forests is important to ensuring the long-term viability of fisher populations.*

Utilización de Datos de Presencia-Ausencia para Construir y Evaluar Modelos Espaciales de Hábitat para el Pescador de la Región Klamath, U.S.A.

Resumen: *Carnívoros del bosque como to es el pescador* (Martes pennanti) *ban silo frecuentemente el blanco de preocupaciones conservacionistas debido a su asociación en algunas regiones con bosque maduro y sensibilidad a alteraciones a nivel de paisaje. A pesar de que el pescador ha sido extirpado de la mayoria de su rango privio en el Oeste de los Estados Unidos, es aún encontrado en el Noroeste de California. La distribución del pescador, sin embargo, es aun pobremente conocida en la mayor parte de esta región donde los muestreos aún no ban sido realizados. Para predecir la distribución del pescador a to largo de la región, cremos un modelo de regrisión logística utilizando datos de 682 localidades previamente muestreadas y una capa de vegetacion creada a partir de imagenes de satélite. Una función de ventana en movimiento en un sistema de información geográfico fue utilizada para derivar índices de compactación del dosel, clases de tamaños de árboles y porcentaje de coniferas a nivel de paisaje. EL modelo se validó con datos nuevos de 468 localidades muestreadas. La tasa de clasificación correcta de un 78.6% con los datos nuevos fue similar a la obtenida con el juego de datos originales (80.4%). Mientras que diversos atributos a escala fina estuvieron significativamente correlacionados con la presencia del pescador, el modelo miltivariado conteniendo solo variables a nivel de paisaje y regional ejecutó tan bien como aquel que incorporo los datos de escala fina, su-*

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giriendo que la selección de hábitat por los pescadores puede estar dominada por factores que operan a escala de rango de hogar y por arriba de esta escala. La distribución de los pescadores estuvo fuertemente asociada con paisajes con niveles altos de compactación del dosel. Los gradientes regionales como la precipitación anual también fueron significativos. A nivel de sitio, el diámetro de las maderas duras fue mayor en sitios con detecciones de pescadores. Una comparación de la distribución regional de pescadores con categorias de manejo del suelo sugiere que un énfasis incrementado en la protección de bosques biológicamente productivos, con elevación baja a media es importante en el aseguramiento de la viabilidad de largo plazo de poblaciones de pescadores.

Introduction

Interaction across spatial scales has become a major topic in ecology as the increasing rate of habitat alteration and species extinction has forced researchers to broaden their scale of analysis (Wiens et al. 1993). The shift in focus from individual endangered species to species assemblages has led to a search for habitat attributes that can predict the status of multiple species at regional scales. New agency monitoring mandates have led to the increasing availability of regional-scale data on both species distributions and habitat attributes. As yet, however, there has been little integration of these data into predictive models of species occurrence at regional scales. We used presence-absence survey data and vegetation data created in a geographic information system (GIS) from satellite imagery to predict the distribution of the fisher (*Martes pennanti*) across the Klamath region of northwestern California and southwestern Oregon. We then validated our predictive model with new field data.

Forest carnivores such as the fisher have frequently been the target of conservation concern due to their association in the western United States with older forests and their assumed sensitivity to habitat fragmentation (Powell & Zielinski 1994). The fisher's large home-range size, low fecundity, and limited dispersal ability across open habitat make it sensitive to anthropogenic habitat alteration such as extensive logging (Powell & Zielinski 1994). These characteristics also make the fisher ideal for investigating the effects of landscape composition and pattern on dispersal dynamics and population viability.

The fisher, the largest member of the genus *Martes*, is a generalist predator, feeding on small to medium-sized mammals and birds, as well as carrion (Powell 1993). Fishers are sexually dimorphic and exhibit intrasexual territoriality. Home-range size, although varying among regions, averages about 15 km2 among females and 40 km2 among males in the western United States (Powell & Zielinski 1994). Historically, fishers were distributed across North America from Hudson's Bay southward to Virginia in the east and to Yellowstone and the southern Sierra Nevada in the west. By 1900, trapping and logging had led to extirpation of fishers from most of the eastern United States. Regrowth of forest and regulation of trapping in New England and the northern Great Lakes states have allowed the fisher to recolonize those areas. Populations in the western United States, however, have continued to decline (Powell & Zielinski 1994). In recent decades the scarcity of sightings in Washington, Oregon, and the northern Sierra Nevada point to the fisher's probable extirpation from much of this area (Aubry & Houston 1992; Zielinski et al. 1996; Aubry 1997). The population in the Klamath region may be the largest remaining in the western United States (Powell & Zielinski 1994).

Hierarchy theory provides a means of conceptualizing the linkages between processes operating at multiple scales (Allen & Starr 1982). Analysis at the spatial scale at which an organism most strongly responds to environmental variation may increase the generality of species-habitat correlations and provide more powerful insights about processes (Wiens 1989a). Most previous studies of fishers have used radiotelemetry data to examine habitat associations within the home range. Processes evident at this scale include selection of foraging, resting, and denning sites. Dispersing juvenile fishers, however, may make decisions on home-range establishment by integrating perceptions of landscape quality over a wide area, causing the effects of habitat selection to be most evident at scales above the home range (Powell & Zielinski 1994). In addition, regional-scale processes such as source-sink and metapopulation dynamics and regional land-use and floristic patterns may be important determinants of fisher distribution.

Evaluation of the status of fisher populations at the regional scale, however, is made difficult by the scarcity of geographically extensive data sets, especially in the western United States. To extract the most information from the limited amount of pre-existing survey data, we incorporated this "retrospective" data into a regional-scale habitat model. By applying the model to unsurveyed areas, we were able to delineate critical habitat areas that have priority for future survey effort. We also generated hypotheses about habitat requirements at multiple scales that could be used to direct future research. Our methodology could be applied to many species worldwide that face similar threats but for which detailed demographic data are difficult to acquire.

Methods

Study Area

The 67,000-km^2 area we analyzed includes the Klamath region of northwestern California and Southwestern Oregon and adjacent portions of the northern California coast (Fig. 1). The Klamath region lies at the juncture of several biogeographic provinces and is noted for its high biological diversity (Whittaker 1960). Elevation ranges from sea level to 2700 m. Orographic effects on precipitation are strong due to the dissected topography. Heaviest rainfall occurs in the winter months. Average annual precipitation ranges from 3000 mm a year in the northwest of the region to 500 mm in the southeast (Whittaker 1960).

Douglas-fir *(Pseudotsuga menziesii)*/mixed evergreen-hardwood is the most extensive forest type in the Klamath region. White fir *(Abies concolor)* and red fir *(Abies magnifica)* forests are found at higher elevations (Sawyer & Thornburgh 1977). To the east, more xeric forest types are dominated by pine *(Pious ponderosa* and *P. sabiniana) and* deciduous oaks *(Quercus garryana* and *Q. kelloggii*). To the west, redwood *(Sequoia sempervirens)*/western hemlock (*Tsuga beteropbylla*) forests form a landscape mosaic with patches of oak woodlands (Zinke 1977). Bordering the region to the north are the western hemlock/Sitka spruce *(Picea sitcbensis*) forests of the Oregon Coast Ranges (Franklin & Dyrness 1973). To the south, the mixed evergreen-hardwood forest has low conifer abundance (Sawyer et al. 1977). Forest types on ultrabasic parent material are common and generally show low tree cover and a well-developed shrub layer.

Approximately 43% of the analysis area is composed of public forest lands divided into three main management categories: wilderness and other protected areas (9.7%); late-successional reserves designated to protect habitat for the Northern Spotted Owl *(Strix occidentalis caurina),* where some timber harvest is permitted (11.0%); and general forest or matrix, where timber harvest is the primary management emphasis (22.2%) (U.S. Forest Service & U.S. Bureau of Land Management 1994). The coastal portion of the study area is primarily in private ownership, but it also contains the redwood parks (1.1%).

Model Development

RETROSPECTIVE SURVEY DATA

Data used to develop the habitat model came primarily from surveys conducted between 1991 and 1995 by land management agency or tribal personnel to determine the presence of fishers at sites where management activities (e.g., timber harvest, recreational development)

were planned. We refer to these as the retrospective data to distinguish them from the systematic sampling we conducted for model validation. Detection methods were of three types: 35mm camera, 110 camera, and sooted trackplate stations (Zielinski and Kucera 1995). The 35mm cameras were checked and rebaited every week, and 110 cameras and trackplate stations were checked and rebaited every 2 days. The identity of tracks and photographs was verified by W.J.Z.

The sampling design for the surveys varied from stations dispersed on roadside transects to stations dispersed throughout a 10-km^2 survey unit (Zielinski 1991; Zielinski & Kucera 1995). Average total survey duration, including multiple surveys at a single location, was 26.2 days. Because previous analyses indicated that increasing survey duration beyond 12 days had little additional effect on detections (Zielinski et al. 1997), 84 surveys of < 12 days were removed from our analysis. The 682 locations used occur over an area of approximately 15,000 km^2, or 22.4% of the total region, but the distribution of survey locations was highly uneven (Fig. 1). No standardized vegetation sampling was conducted at survey locations in the retrospective data set. Although patch-level vegetation attributes can be extracted from the GIS vegetation layer, we were not sufficiently confident of the accuracy of survey locations recorded on paper, 7.5-minute quadrangle maps to evaluate the significance of plot-level vegetation attributes derived in this manner.

Although pre-existing survey information often may be the only data available for regional-scale analyses, variations in protocols and sampling strategies are problematic. If the study organism selects for rare habitat types or resources, presence sites may be compared with random points in a case-control retrospective design, but this assumes that random points are probably unoccupied (Ramsey et al. 1994). Comparing sites with detections to sites without detections avoids this assumption,, but at the cost of reducing the generality of the observed habitat associations. The latter approach seems preferable when the surveys have the potential to detect animals over most of their home range (e.g., during foraging), as is the case with trackplate bait stations.

GIS DATA

GIS data available for analysis included information on roads, hydrology, elevation, and land-management category (U.S. Forest Service, unpublished data), as well as vegetation (California Timberland Task Force [TTF] 1993; W. Cohen, unpublished data) and precipitation (Daly et al. 1994). The TTF vegetation layer, which encompasses most of the study area, is based on a combination of unsupervised and supervised classification of Landsat Thematic Mapper (TM) imagery. The classification includes both continuous and categorical vegetation attributes, with classification accuracy for each categori-
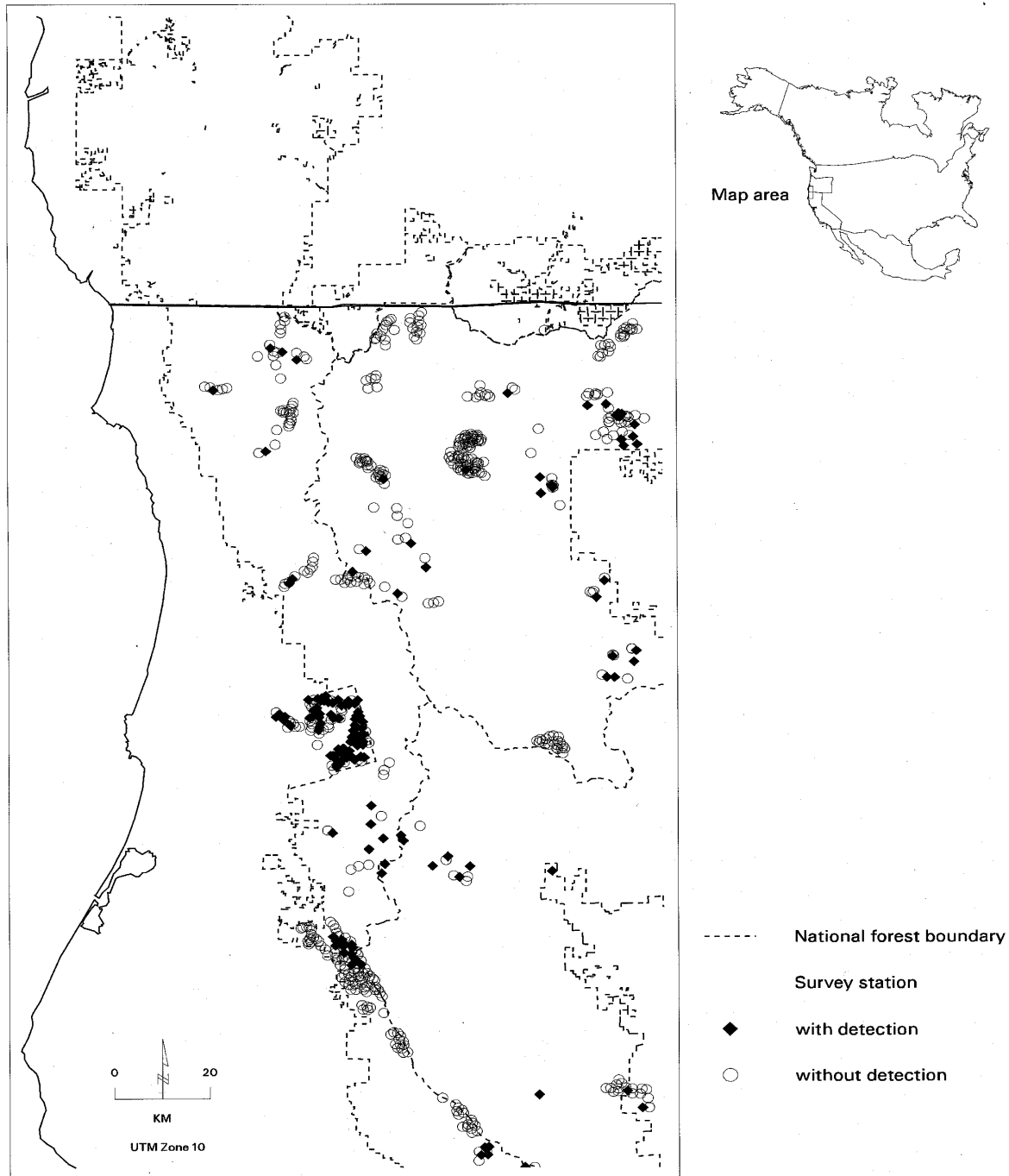
Figure 1. Map of study area with locations of survey stations used in the retrospective analysis.

Cal attribute estimated at 60-80% (California Timberland Task Force 1993). The minimum mapping unit (MMU) for categorical attributes such as vegetation type was 4 ha. Continuous variables estimating tree canopy closure and percent conifer were derived at the original pixel resolution of 0.09 ha. All data were resampled to 1-ha resolution for our analysis.

The TTF attributes used to estimate vegetation at survey sites include tree canopy closure, tree size class, percent conifer, quadratic mean diameter at breast height (QMDBH) of hardwoods, CWHR type, and CWHR canopy closure class (Table 1). The CWHR, or California Wildlife Habitat Relationships system, is commonly used by agency and private wildlife biologists to evaluate habitat suitability for fishers and other species (Mayer & Laudenslayer 1988). It classifies vegetation into four closure classes, six tree-size classes, and a variety of forest and nonforest floristic types. A second vegetation layer was used to extrapolate predicted habitat suitability to Oregon (W. Cohen, unpublished data). These data were classified at the original pixel resolution of 0.09 ha but were resampled to 1 ha resolution for our analysis. The categorical classification used in the Oregon data (Co

hen et al. 1995) was transformed to be comparable with the continuous attributes used in the TTF data.

MULTIPLE LOGISTIC REGRESSION AND SPATIAL ANALYSIS

Multiple logistic regression was chosen as the appropriate method for the statistical analysis because of the binary nature of the response variable (presence-absence). The potential predictor variables derived from the GIS analysis were first assessed for significance in a univariate analysis using Spearman rank correlations (Table 2). Generalized additive modeling (GAM) was then used to assess curvature (Hastie 1993). Stepwise model fitting with both backward and forward selection was used to help construct a model with good fit to the data. Output from the stepwise procedure was assessed as to generality and interpretability, and alternate models were compared according to the Bayesian or Schwarz information criterion (BIC), a diagnostic statistic that penalizes for overfitting (Schwarz 1978).

The spatial correlation structure of the data was modeled as a combination of coarse-scale trend and fine-scale variation, referred to as first- and second-order ef-

Table 1. Definitions of habitat variables and terminology in development of spatial habitat models.

Term	Definition	Abbreviation
Basal area	derived from the prism tree count of a variable radius plot defined by a 20-factor prism	
Bear damage	proportion of station visits for which the station was rendered inoperable by black bear (*Ursus americanus*)	
Bayesian information criterion	penalized model-fitting statistic	BIC
Cliford-Richardson-Hemon test	test of significance of associations between spatially autocorrelated variables	CRH
California Wildlife Habitat Relationships system	system of wildlife habitat models	CWHR
Log count	log tally by size class measured along two perpendicular 25-m transects placed at an arbitrary azimuth and centered on the trackplate station	
Moving average	composite measurements derived by means of a moving-average spatial model implemented in GIS by the moving-window method	MA
Percent conifer	percentage of the total tree canopy closure attributed to conifer species	
Predicted probability	probability of fisher detection at a survey station under the multiple logistic regression model	
Quadratic mean diameter at breast height	measurement of tree diameter in centimeters that emphasizes the larger diameters	QMDBH
Road density	length per unit area of roads of all types, expressed in kilometers per square kilometer	
Transformed micro- and macroaspect	microaspect of the survey station location or macroaspect of the landform where it is located, transformed to range from zero on most-exposed southwest aspects to 2.0 on least-exposed northeast aspects	
Tree canopy closure	percentage of area covered by trees; at the plot level, a measure of the canopy closure of conifer and hardwood trees > 1 m in height by means of a hand-held densiometer; at the landscape level, derived by classification of remotely sensed imagery using plot-level data	TREE CC
Tree canopy closure and tree size variance	standard deviation of attribute values for the cells within a moving window in a geographic information system	
Tree size class	quadratic mean diameter of trees > 1 m in height as assigned to five size classes with lower thresholds of 0, 14, 25, 60, and 90 cm	
UTM	Universal Transverse Mercator map projection, zone 10	

fects (Bailey & Gatrell 1995). We modeled first-order effects through the use of linear and higher-order polynomial functions of the spatial coordinates, a technique known as trend surface analysis (Raining 1990). We modeled environmental covariates as spatially autocorrelated mesoscale or second-order variation using a moving-average (MA) function that assigns to each cell the mean value of the vegetation attributes within a circular moving window (Raining 1990; Environmental Systems Research Institute 1996). A series of multivariate models was created containing vegetation variables averaged over varying scales (1, 10, 20, 30, 50, and 100 km^2), as well as one containing the unaveraged patch-level vegetation attributes. Models with and without the trend surface component were fitted for all environmental models. The FOCALSTD function, which computes the standard deviation within the moving window, was used as an estimate of landscape diversity (Environmental Systems Research Institute 1996).

Because our retrospective data set consisted of irregularly spaced sample sites, we reduced the effect of uneven sampling effort by differentially weighting points in the model-fitting algorithm based on the area of their Thiessen polygon-a space-filling polygon surrounding the point (Bailey & Gatrell 1995). An upper limit of 60 km^2 was placed on polygon area. Cook's distance was used to assess the robustness of the model to outliers (Cook & Weisberg 1982).

Spatially autocorrelated data may pose problems for traditional significance tests due to violations of the assumption of independence (Legendre 1993; Bailey & Gatrell 1995). The Cliford-Richardson-Hemon (CRH) method adjusts the effective sample size used in significance tests based on a measure of the spatial covariance of the variables (Cliford et al. 1989; Thomson et al. 1996). The effective sample sizes given by the CRH test were used to generate corrected significance values for univariate comparisons. We chose an alpha level of 0.10 due to the exploratory nature of the analysis and the conservative effect of the CRH correction.

Model

The sampling design used in the validation surveys was a systematic-cluster design based on the National Forest Inventory (NFI) grid, a hexagonal cell-based sampling design (Stevens 1994). We surveyed alternate grid points, which are separated by approximately 10 km, to minimize the possibility that the same fisher would be detected at more than one sample unit. Each of the validation sample units consisted of five enclosed trackplate stations, equally spaced along the perimeter of a circle with a 500-m radius, and a sixth trackplate station placed at the NFI point that formed the center of the circle. A total of 468 stations grouped into 78 sample units were surveyed during 1996-1997. A systematic-cluster

design was chosen because of the coarse-scale spatial dynamics of fisher populations and the lack of a priori knowledge of habitat associations. This design also allows landscape and plot-level habitat selection to be compared (Fortin et al. 1989).

The station enclosure was constructed of either flexible plastic with a metal base or plywood (Zielinski & Kucera 1995). Stations were checked and rebaited with chicken every other day for eight visits, for a nominal survey duration of 16 days. A commercial trapping lure (M & M Fur Co., Bridgewater, South Dakota) was applied on the fourth visit to sample units that had not received a fisher detection at any of the six stations.

Plot Vegetation Data at Validation Survey

A potential weakness of the use of the retrospective data is the inability to analyze the importance of microhabitat associations. To remedy this, vegetation data were collected on the ground at each trackplate station in the validation surveys.

Canopy closure and log tally by size class were measured along two perpendicular 25-m transects placed at an arbitrary azimuth and centered on the trackplate station. Diameter at breast height (DBH) and condition of all snags and trees by species, as well as basal area, were measured for a variable radius plot defined by a 20-factor prism (Wenger 1984). Visual estimates of tree and shrub cover by species; CWHR type; size and closure class; approximate distances to water, logged areas, and roads; and aspect and slope were also recorded. A cosine transformation was used to convert aspect to a variable that ranged from zero on the most-exposed (southwest) aspects to 2.0 on the least-exposed (northeast) aspects (Beers et al. 1966).

Results

Univariate

Although correlations between fisher detections in the retrospective data and several habitat variables were significant at the level of $p < 0.10$ with the conventional sample size ($n = 682$), only tree canopy closure, hardwood diameter, and conifer variance remained significant when the effective sample size was corrected for spatial autocorrelation (Table 2). The reduction in effective sample size was greatest in the moving-average variables due to the effects of the spatial averaging process, and it increased with the size of the moving window.

Moving-average indices for landscapes of different sizes were highly correlated ($r_s > 0.8$) and the QMDBH of conifers was highly correlated with overall QMDBH ($r_s = 0.96$). All other correlations between variables were <0.72.

Table 2. Station attributes of sites with and without detections of fishes in retrospective data set, with rank correlation between habitat variables and fisher detection*.

| | Detection | | | | | |
| | no (n = 508) | yes (n = 174) | Rank | p | p | Effective |
Variable	mean (SD)	mean (SD)	correlation	(conventional)	(CRH corrected)	sample size
Tree canopy closure	58.2 (25.5)	65.6 (27.7)	0.156	<0.001	0.097	114
Tree canopy closure MA (km^2)						
1	60.7 (13.3)	67.3 (12.9)	0.230	<0.001	0.128	45
5	60.5 (11.8)	66.9 (11.9)	0.264	<0.001	0.113	37
10	60.5 (11.2)	66.7 (11.5)	0.267	<0.001	0.125	34
20	60.5 (10.6)	66.5 (11.2)	0.275	<0.001	0.133	31
30	60.5 (10.2)	66.3 (11.0)	0.278	<0.001	0.142	29
50	60.3 (10.0)	66.0 (11.1)	0.280	<0.001	0.155	27
100	60.1 (9.7)	65.6 (11.3)	0.267	<0.001	0.192	25
Percent conifer	69.0 (26.0)	63.9 (24.9)	-0.102	0.008	0.125	227
Percent conifer MA (10 km^2)	67.4 (9.6)	65.7 (9.6)	-0.099	0.010	0.440	62
Tree size class	2.30 (1.09)	2.32 (1.13)	0.018	0.636	0.805	186
Tree size class MA (10 km^2)	2.28 (0.36)	2.29 (0.34)	-0.026	0.494	0.840	60
Conifer QMDBH	21.4 (7.5)	22.1 (8.3)	0.042	0.269	0.604	151
Hardwood QMDBH	10.6 (3.4)	11.5 (3.5)	0.146	<0.001	0.080	146
Hardwood QMDBH MA (10 km^2)	6.18 (2.14)	7.04 (2.22)	0.212	<0.001	0.107	59
CWHR fisher habitat index	2.55 (0.90)	2.71 (0.70)	0.076	0.049	0.190	301
CWHR index MA (10 km^2)	2.51 (0.34)	2.61 (0.25)	0.117	0.002	0.236	104
Tree canopy closure variance MA (10 km^2)	2.26 (3.11)	2.19 (3.06)	-0.091	0.017	0.273	145
Tree size variance MA (10 km^2)	1.01 (0.11)	0.98 (0.10)	-0.118	0.002	0.356	62
Conifer variance MA (10 km^2)	2.42 (3.11)	2.27 (2.63)	-0.238	<0.001	0.007	128
Road density (km/km^2)	1.54 (0.86)	1.63 (0.85)	0.047	0.222	0.632	106
UTM easting (10^5 m)	4.68 (0.25)	4.66 (0.27)	-0.080	0.037	0.689	26
UTM northing (10^6 m)	4.57 (0.06)	4.55 (0.05)	-0.168	<0.001	0.217	55
Annual precipitation (10^3 mm)	1.55 (0.52)	1.44 (0.42)	-0.109	0.004	0.518	36
Elevation (10^2 m)	11.24 (3.75)	9.98 (4.09)	-0.136	<0.001	0.337	51
Total survey duration (days)	26.8 (13.0)	24.4 (8.3)	-0.106	0.006	0.377	70

Refer to Table 1 for explanation of terms and abbreviations.

Model Fitting

The moving-average variables selected in the final model were functions of tree canopy closure, tree size class, and percent conifer. Among the series of models representing different scales, the combined models at scales of between 10 and 50 km^2 achieved the best BIC (Fig. 2). Although the 10-km^2 model showed a marginally poorer BIC than the 20-km^2 model (-3918 versus -3922), it was selected as the final model to limit the effect of the increase in spatial autocorrelation with larger moving-window sizes that was revealed by the CRH analysis (Table 2).

The tree canopy closure MA was consistently significant in the multivariate models. After the addition of this variable, the QMDBH hardwood MA and elevation variables became nonsignificant (p = 0.59 and 0.48, respectively). Seasonal effect as measured by the survey starting date was nonsignificant in the multivariate model (p = 0.42). Residuals from the final model and the validation data also showed no seasonal pattern.

The GAM assessment suggested that regional variation should be modeled with a linear term for precipitation and a quadratic function for UTM northing. Although the BIC of the model incorporating precipitation was

poorer (-3918) than an alternative incorporating UTM easting (-3951), we chose to retain the more process-oriented variable, precipitation, to increase model generality (Austin & Meyers 1996). Two interaction terms were significant and were included in the model: tree canopy closure MA by percent conifer MA and tree size class MA by precipitation. The equation for the final model was

$$\text{logit}(p) = -2401 + 0.6023\text{TREECCMA} - 12.07\text{SIZMA} + 0.4911\,\text{CONMA} - 0.01307\text{PRECIPANN} + 0.001059\text{UTMN} - 1.176 \times 10^{-10}\text{UTMN}^2 - 0.006251\text{TREECCMA} \times \text{CONMA} + 0.005004\text{SIZMA} \times \text{PRECIPANN},$$

where p is the probability of fisher detection, TREECCMA is tree canopy closure moving average, SIZEMA is tree size class moving average, CONMA is percent conifer moving average, and PRECIPANN is annual precipitation. The detection probability values were calculated from the logit value by the equation $p = 1/(1 + e^{-\text{logit}(p)})$. Model coefficients, standard errors, and significance values are reported in Table 3.

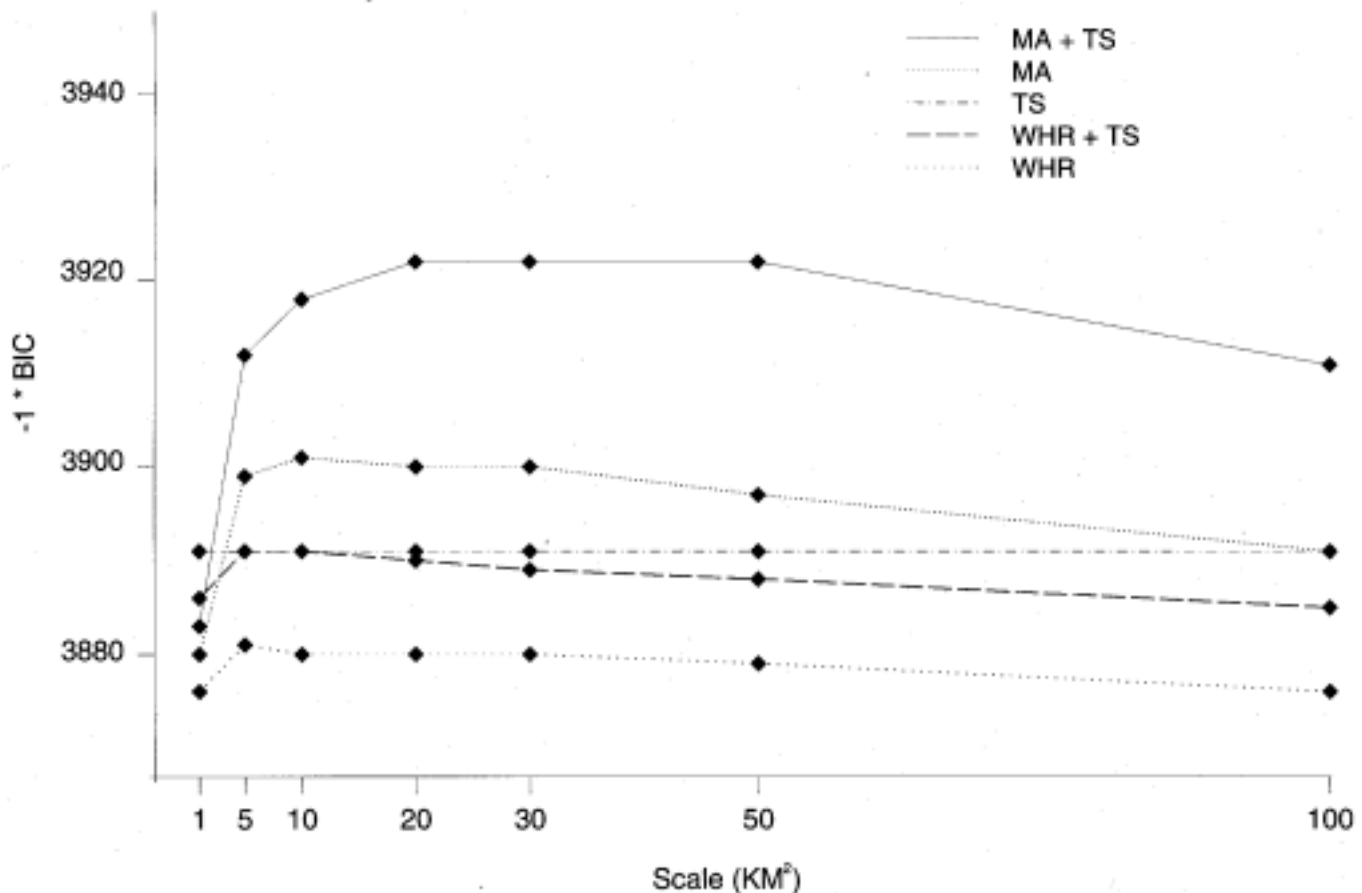Even after penalties for the inclusion of additional vari-

Figure 2. Plot of spatial scale of analysis versus predictive power of multivariate habitat models predicting the probability of fisher detection (MA, moving average; TS, trend surface; WHR, California Wildlife Habitat Relationships model).

ables, the model containing both moving-average and trend-surface variables fit the data better than models containing either group of variables alone. The BIC of the combined model was -3918, compared with the moving-average model at -3901 and the trend-surface model at -3891 (null model = -3738). Models derived from the CWHR values for fishers performed poorly at all scales when compared to the vegetation moving-average models, with a difference in BIC of between 18 and 37. Although among the standard deviation (FOCALSTD) attributes the percent conifer variance retained the highest CRH-corrected significance in univariate analysis ($p < 0.01$), only the variance in tree size class remained significant in the multivariate models (BIC reduced from -3918 to -3920).

Fifteen sites, located on the eastern and northwestern edges of the data set, were identified as outliers by means of Cook's distance. Models with these outliers removed or with data not weighted by Thiessen polygon area gave results similar to those of the final model. We chose to retain the outliers because their removal may magnify errors in extrapolating to boundary areas of the data set, where nonlinearities in spatial trends become most noticeable.

At an optimal cutpoint of 0.24, the final model showed a correct classification rate of 80.4% (Table 4). An optimal cutpoint here is a value that minimizes the total errors of commission and omission. This cutpoint value is close to the proportion of stations receiving detections (0.255), as expected in well-calibrated models. The calibration plot (Fig. 3), however, shows some underestimation of actual detection probabilities in the lower range of predicted probability values.

Comparison of mean predicted probabilities of fisher detection between land-management categories reveals that among U.S. Forest Service lands, late-successional reserves had a higher predicted probability (0.128) than wilderness (0.103) or matrix lands (0.087). The redwood parks had high probability (0.347), and nonpublic lands as a whole ranked relatively low (0.062) with important exceptions, such as the Hoopa Indian Reservation in the lower Trinity River area (0.440).

Model Validation

In the validation surveys, fishers were detected at 17.9% of the stations and at one or more station of 37.2% of the

Table 3. Variables in multiple logistic regression model showing coefficients, standard errors, and significance values derived from the chi-square test (df = 1)*.

Variable	Coefficient	Standard error	p
Intercept	-2400.547	1490.377	
TREECCMA	0.6023069	0.1294571	<0:0001
SIZMA	-12.07156	3.047576	0.0015
CONMA	0.4910782	0.1131558	0.0559
PRECIPANN	-0.01307159	0.00435792	<0.0001
UTMN	0.001059108	0.000656653	0.0108
$UTMN^2$	$-1.176063 \times 10^{-10}$	7.217931×10^{-11}	0.0093
TREECCMA:CONMA	-0.006251404	0.001685051	0.0002
SIZMA:PRECIPANN	0.005003867	0.001810565	0.0006

78 six-station sample units. Average latency to first detection at the sample units or stations that received detections was 7.4 days and 9.3 days, respectively. The correct classification rate for the validation data at the sample unit level was 71.8% (Table 4). The cutpoint used here (0.171) was derived from the probability of receiving no detections at six randomly selected sites in the retrospective data set: $(1 - 0.255)^6$.

The original goal had been to predict presence or absence at the spatial scale of an entire sample unit, because we thought that the number of stations within each unit that received a detection would be independent of predicted habitat suitability. Contrary to expectations, the validation data showed a significant positive correlation between predicted probability and number of stations in a sample unit with detections (Fig. 4), both over all 78 sample units ($r = 0.59$, $p < 10^{-7}$, df.= 76) and over the 29 sample units that received at least one detection ($r = 0.51$, $p < 0.01$, df = 27). The binary classification accuracy of the model at the station level (78.6%) using the same cutpoint as in the retrospective analysis

(0.24) was similar to that in the retrospective data set (Table 4). Model calibration appears better for the validation data than for the retrospective data (Fig. 3).

Plot Vegetation Data at Validation Sample Sites

When plot-level attributes from the validation survey stations were compared, hardwood QMDBH, conifer and total basal area, and transformed micro- and macroaspect remained significantly higher ($p < 0.10$) at fisher detection sites after spatial autocorrelation was accounted for (Table 5).

Addition of plot-level variables to the landscape-level model, however, did not significantly improve model performance. An appropriate comparison, given that the plot-level model was elaborated after the validation surveys, was between a plot-level model and a new model containing landscape variables alone. The BIC was -2470 for the plot-level model, -2600 for the landscape model, and -2601 for a combined model (null model = -2431). Hardwood diameter was highly significant ($p < 0.01$) in both the plot-level and combined models.

Discussion

In our construction of a model of fisher distribution, the best predictors proved to be landscape- and regional-scale variables, rather than the fine-scale variables often used in wildlife-habitat models. If, as our study suggests, habitat selection by fishers is dominated by factors operating at the home-range scale and above, regional-scale conservation planning for the fisher may be possible without fine-scale data on vegetation or prey abundance. Fishers appear strongly associated with forest cover, and this attribute is relatively easy to measure with satellite imagery. Although this approach is also valuable for other mesocamivores that are less strongly associated with forest cover, prediction accuracy may be lower (Carroll et al. 1999).

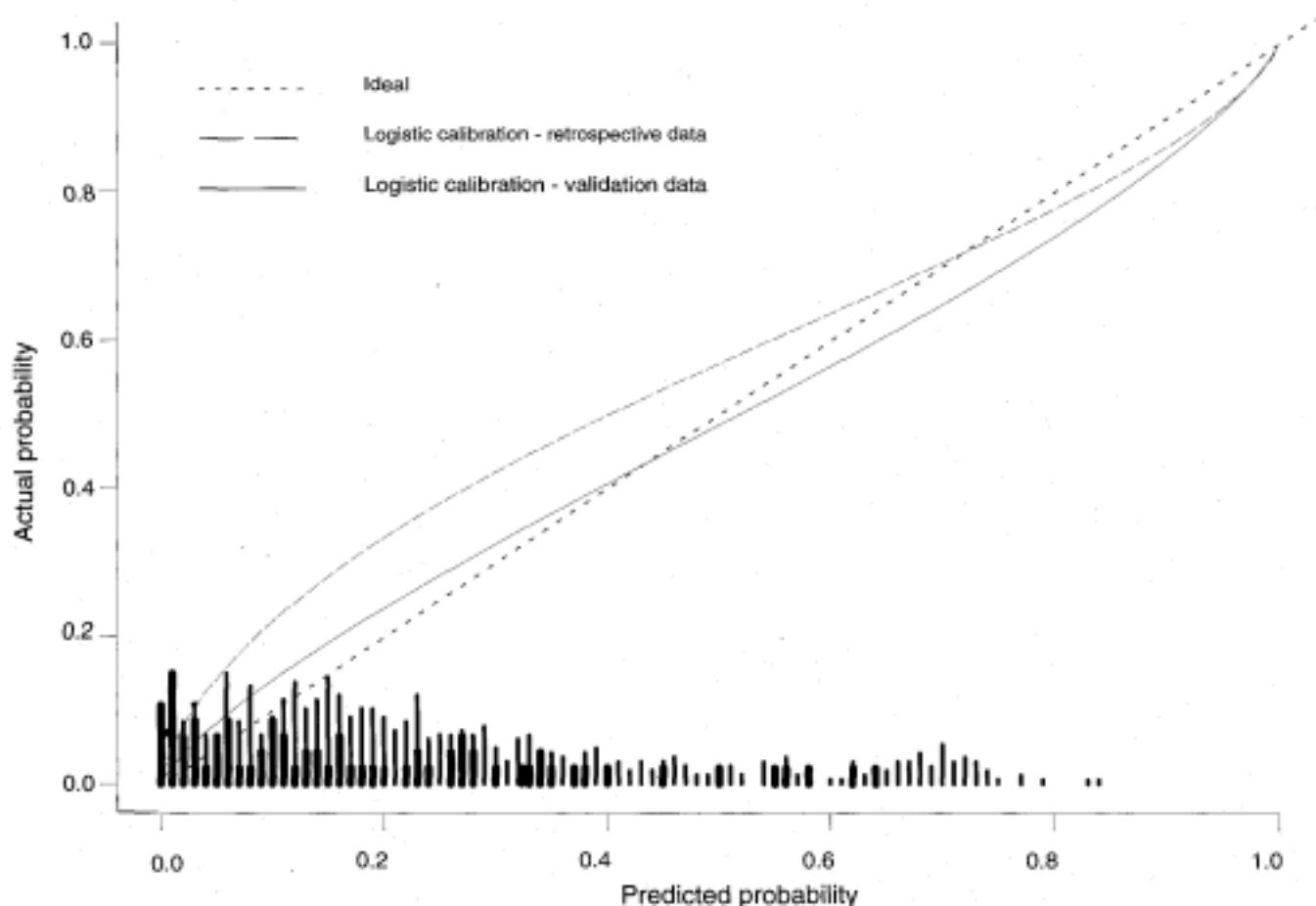Although plot-level variables in general show low sig-

Table 4. Classification table showing performance of logistic regression model with retrospective data and validation data on fisher distribution.

Data*	Classified present	Classified absent	Total
Retrospective			
(0.240; 0.804)			
Presence	98	76	174
Absence	58	450	508
Total	156	526	682
Validation by station			
(0.240; 0.786)			
Presence	55	29	84
Absence	71	313	384
Total	120	348	468
Validation by sample unit			
(0.171; 0.718)			
Presence	17	12	29
Absence	10	39	49
Total	27	51	78

*cutpoint = 0.240, correct classification rate = 0.804.

*Figure 3. Calibration plot of predicted versus observed fisher detection probabilities for retrospective and valida
tion data sets. Bars along x-axis indicate distribution of data in retrospective (thin bars) and validation (thick
bars) data sets.*

nificance in our analysis, hardwood diameter is highly
significant in all comparisons. Two factors may explain
the importance of large hardwoods for fishers. Cavities
in large hardwoods are frequently used as resting and
denning sites (W. Zielinski, unpublished data), and
these trees produce mast, which may stimulate higher
prey densities (Powell & Zielinski 1994). Information on
the distribution of these resources may be important in
the management of habitat quality and connectivity
at the within-home-range scale to complement land-
scape-level planning.

Methods such as the CRH test appear useful in analysis
of data sets such as this one that show a strong spatial
structure that is either intrinsic or produced through the
GIS moving-window process (Thomson et al. 1996). In-
creased correlation at coarser scales may be due to in-
creased biological significance of landscape-level effects
or to high apparent predictability (sensu Wiens 1989*b*).
In the validation-plot data, the CRH test is capable of dis-
tinguishing between shrub cover, a variable whose un-
corrected significance is due to data from only one por-

tion of the study area, and hardwood diameter, whose
correlation with fisher detection is more widely charac-
teristic of the region.

Among the vegetation variables, the tree canopy closure
MA has the highest significance and the clearest biological
interpretation. Landscapes with higher levels of overhead
cover may provide increased protection from predation,
lower the energy costs of traveling between foraging sites,
and provide more favorable microclimate and increased
abundance or vulnerability of preferred prey species
(Buskirk & Powell 1994; Powell & Zielinski 1994).

The percent conifer MA is only marginally significant
in its main effect but retains significance through its in-
teraction term. The negative interaction between the
percent-conifer MA and the tree canopy closure MA sug-
gests that increasing tree canopy closure has a more pos-
itive effect in mixed conifer/evergreen-hardwood land-
scapes than in purely conifer landscapes.

The tree size MA has low univariate significance, and
its effect in the multivariate model is generally negative.
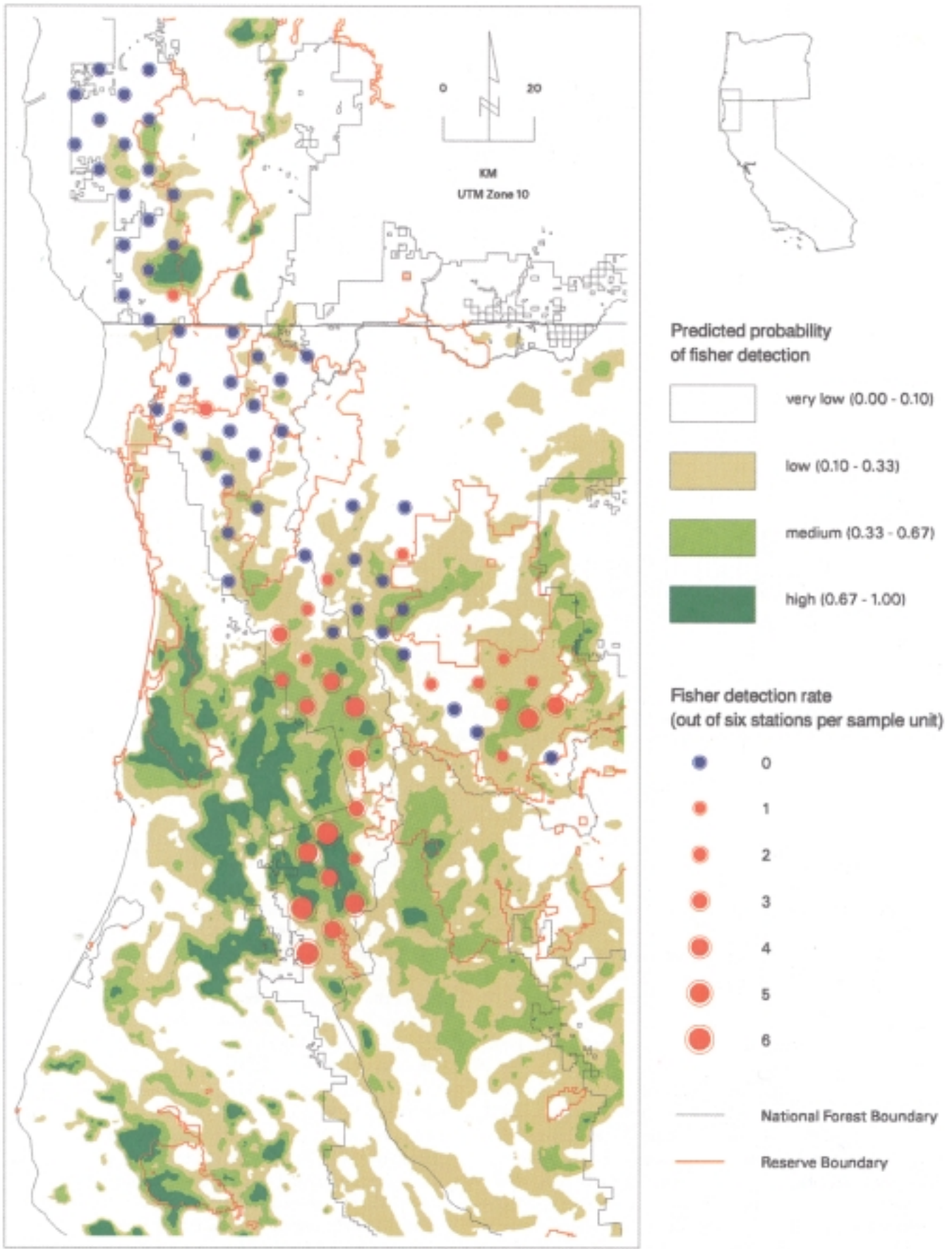This contradicts results from fine-scale studies of fishers

Figure 4. Results of validation surveys superimposed on fisher detection probability as predicted by the model based on the retrospective data set. Each symbol represents a sample unit of six survey stations.

Table 5. Station attributes of sites with and without detections of fishers in validation surveys, with rank correlation between habitat variables and fisher detection*.

Station attributes	Detection no (n = 384) mean (SD)	yes (n = 84) mean (SD)	Rank correlation	p (conventional)	p (CRH corrected)	Effective sample size
GIS attributes						
Tree canopy closure MA (10 km^2)	68.5 (10.9)	71.3 (8.5)	0.091	0.050	0.506	55
Percent conifer MA (10 km^2)	69.9 (11.2)	63.5 (10.8)	-0.219	<0.001	0.379	17
Tree size class MA (10 km^2)	2.55 (0.58)	2.45 (0.29)	-0.071	0.123	0.759	19
Annual precipitation (10^3 mm)	2.06 (0.70)	1.44 (0.40)	-0.292	<0.001	0.422	8
UTM easting (10^5 m)	4.37 (0.28)	4.56 (0.19)	0.285	<0.001	0.471	8
UTM northing (10^6 m)	4.62 (0.47)	4.55 (0.29)	-0.535	<0.001	0.176	7
Predicted probability	0.12 (0.14)	0.33 (0.23)	0.393	<0.001	0.087	20
Field measurements						
Elevation (m)	769 (357)	852 (406)	0.064	0.164	0.684	41
Slope	42.8 (20.7)	44.0 (18.3)	0.023	0.614	0.755	179
Transformed macroaspect	0.986 (0.696)	1.218 (0.762)	0.132	0.004	0.028	278
Transformed microaspect	0.958 (0.702)	1.168 (0.763)	0.108	0.020	0.028	415
Total basal area (m^2/ha)	37.4 (20.2)	47:3 (20.0)	0.187	<0.001	0.058	104
Conifer basal area	21.1 (17.8)	26.5 (15.9)	0.151	0.001	0.039	188
Hardwood basal area	12.2 (15.6)	16.1 (15.8)	0.111	0.017	0.128	189
Snag basal area	4.1 (6.4)	4.7 (7.1)	0.015	0.749	0.792	318
Mean QMDBH (cm)	53.7 (31.6)	61.8 (28.4)	0.114	0.014	0.228	114
Conifer QMDBH	59.6 (42.4)	64.9 (38.3)	0.058	0.211	0.476	153
Hardwood QMDBH	16.6 (19.7)	27.4 (26.2)	0.164	<0.001	0.046	150
Snag QMBDH	25.9 (39.0)	35.4 (47.5)	0.043	0.356	0.294	605
Canopy closure (%)	78.1 (27.1)	87.1 (13.6)	0.046	0.317	0.485	229
Log count (15-30 cm class)	2.03 (2.93)	1.94 (2.54)	0.018	0.697	0.898	52
Log count (30-60 cm class)	0.96 (1.59)	0.96 (1.48)	0.006	0.891	0.956	76
Log count (60-90 cm class)	0.42 (0.86)	0.44 (0.78)	0.028	0.539	0.731	147
Log count (>90 cm class)	0.28 (0.64)	0.27 (0.81)	-0.026	0.572	0.776	119
Bear damage (% of visits)	17.2 (22.3)	14.5 (20.4)	-0.044	0.344	0.685	87
Ocular estimates						
Overstory canopy closure	42 (24)	43 (22)	0.028	0.550	0.585	392
Understory canopy closure	34 (24)	41 (24)	0.115	0.013	0.129	174
Overstory + understory canopy closure	76 (24)	85 (15)	0.127	<0.001	0.102	166
Shrub canopy closure	55 (29)	38 (25)	-0.215	<0.001	0.312	23
Percent conifer	64 (30)	64 (26)	-0.014	0.761	0.827	243

*Refer to Table 1 for explanation of terms and abbreviations.

in this region that show an association of fisher rest sites with large trees (W. Zielinski, unpublished data). The contrast between the landscape-level and patch-level associations may be due to characteristics of the mesic mixed evergreen-hardwood forests of the region that allow younger stands to exhibit relatively high canopy closure and structural complexity. Examination of alternate models reveals, however, that the coefficient of the tree size-class term is most strongly affected by multicolinearity between the three vegetation attributes. This limits the interpretability of this model component. In addition, the different effects of hardwood and conifer diameter in the patch-level data, as well as the significance of the variance (FOCALSTD) function of tree size, suggest that tree size has the most complex effect of the three vegetation attributes.

Elevation was not significant in the multivariate model, perhaps because of its correlation with percent conifer ($r_p = 0.70$). This suggests that correlations of fisher distribution with elevation may alternately be attributed to

the effects of vegetation, either directly or as a mediator of snow condition (Krohn et al. 1997). Road density at the landscape level was not significant in either univariate or multivariate analyses. Roads may show negative correlations with fisher distribution either by providing access for trappers or by their association with habitat alteration. Trapping intensity is low in the Klamath region. Public lands in the Klamath have historically experienced lower levels of habitat alteration in the form of logging than have other parts of the Pacific Northwest (Noon & McKelvey 1996), a factor that may help explain the persistence of fishers in our study region. Regional gradients in forest structure and productivity may still be as significant as anthropogenic impacts in determining habitat quality.

Climatic gradients in precipitation and temperature associated with a coastal-interior transect are, along with elevation, influential abiotic factors controlling the distribution of the region's diverse flora. These floristic changes may alter the relationship of forest structure to

fisher distribution through effects on prey species composition. The interaction term of precipitation by size class MA suggests a regional gradient in the association between tree size and fisher presence. This parallels the findings of habitat studies of the Northern Spotted Owl, which reveal stronger selection for large-diameter stands in more coastal areas (Noon & McKelvey 1996).

The quadratic function of UTM northing shows fisher detection probability decreasing north and south of a region centered on the lower Trinity River (Humboldt Co., California; Fig. 4). The significance of trend surface variables 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 the effects of local habitat selection (Pulliam 1988). Strong regional-scale trends have been evident in previous studies of the fisher (Klug 1996) and the American marten (*Martes americana*; Chapin et al. 1998). Dispersal rates may dominate the demographics of some fisher populations, suggesting the existence of innate dispersal tendencies even when density and fecundity are low (York 1996). This tendency may lower population viability in fragmented habitat (Doak 1995). Testing of the source-sink hypothesis against alternate explanations, such as climatic or floristic gradients, is difficult because of the nonreplicable nature of regional-scale biogeographic processes. The most persuasive evidence would come from intensive studies of dispersal, survivorship, and reproduction. Repeated surveys of the same locations may also help identify sink populations by high temporal variability in detections (Howe et al. 1991).

Role of Modeling in Conservation Planning

Recent developments in dynamic modeling have popularized the use of spatially explicit population models that combine demographic data with GIS maps of landscape composition and pattern. Sensitivity to error-propagation from poorly known parameters, however, may limit the use of dynamic models even with well-studied species (Karieva et al. 1996). This problem has led to the search for modeling techniques that can use coarser-resolution data such as presence-absence records (Hanski 1996). We found static spatial habitat modeling an attractive alternative for species such as the fisher for which demographic data are extremely difficult to collect. Results from static models can be incorporated into population viability analyses through the use of resource selection functions and other techniques (Boyce & McDonald 1999).

A comparison of model diagnostics across a range of scales (Coulson et al. 1997) may aid in the selection of indicator species based on the scale at which they most strongly respond to landscape attributes. Species may

group into a limited number of locations along the continuum of possible scales because of interactions between morphological constraints and the spatial structure of the environment (Honing 1992). Monitoring of habitat change at multiple scales is facilitated by selecting representative species from among these spatial "guilds." Nonvolant habitat specialists, such as the fisher and marten, whose distribution is controlled by regional-scale processes are good candidates for such focal species (Buskirk 1992). An interpenetrating grid design such as that used here facilitates the incorporation of several such guilds into a single sampling program (Stevens 1994). Analysis of the spatial correlation structure of pilot survey data may also provide direction as to the optimal distance between sampling sites and may identify environmental gradients over which to establish sampling transects (Haining 1990; Austin and Heyligers 1991), information that can be used to refine sampling programs in an "adaptive monitoring" strategy (Legendre et al. 1989).

One of the weaknesses of the moving-average model we used is that correlation quickly decays to zero with distance (Haining 1990). This forces the use of trend surface variables and limits model generality (Bailey & Gatrell 1995). Other spatial models, such as the spatial autologistic, avoid the necessity for trend surface variables but are more computationally intensive (Wu & Huffer 1997). We are currently exploring their application to the modeling of carnivore distribution.

Approximately two-thirds of the variance in fisher distribution remains unexplained in both the retrospective and validation data sets. This is partly due to problems associated with the use of retrospective data. Nonsystematic sampling requires extrapolation of spatial trends to areas without survey effort, creating regions with large estimation error. We attribute additional error to inaccuracies in the GIS vegetation layer (California Timberland Task Force 1993). Structural attributes such as tree size class are typically more difficult to measure with TM satellite imagery than are attributes such as canopy closure. Classification to floristic type is often even lower in reliability (Cohen et al. 1995), and the lack of significance of floristic type (i.e., CWHR type) in the analysis may be influenced by this error.

Other sources of unexplained variance include factors at and below the patch level that may influence fisher occurrence. Although the plot-level vegetation variables we examined had little explanatory power, they were measured at a scale of approximately 0.05 ha and may not fully represent the characteristics of a vegetation patch. Other fine-scale attributes such as spatial and temporal variation in prey abundance may also be important. Some proportion of the variation in the distribution and abundance of a species will be determined by factors unrelated to the current habitat pattern, such as historical effects and stochastic variability in habitat occu-

pancy. The relationships between fisher detections and fisher population density and between density and individual survival and reproduction are also untested here (Van Home 1983).

The persistence of fishers in the Klamath region focuses attention on regional-scale floristic and land-use patterns that distinguish this region from other parts of the western United States from which fishers have been extirpated. The Klamath region represents a continental-scale ecotone between Madrean evergreen hardwood forests to the south and the northern coniferous forests (Whittaker 1960; Sawyer et al. 1977). The Douglas-fir/mixed evergreen-hardwood forests of the region may produce an optimal combination of habitat resources for fishers: high levels of canopy closure, large wood provided by conifers, and mast and refuges provided by hardwoods. The sprouting ability of both evergreen hardwoods and redwoods allows these forest types to recover canopy closure more rapidly, making their habitat resources more resilient to disturbance. In contrast, forest types in other parts of the western United States require longer periods after disturbance to recover important structural habitat attributes such as canopy closure. Comparisons between regions of the degree of sensitivity of American marten to landscape disturbance show similar gradients (Bissonette et al. 1997).

Our study further documents the discontinuous distribution of fishers in the Pacific coastal states. If the metapopulation concept is applicable here, as has been proposed (Heinemeyer & Jones 1994), the isolation of fisher populations in the western. United States from one another and from the more continuous populations in northern Canada and the eastern United States may be of concern. Gaps in fisher distribution also exist within the study region. This may be of particular concern in the coastal portion of our study area, which is largely in private ownership. Current land-use strategies that incorporate short timber harvest rotations may isolate remnant areas of fisher habitat. Regional or landscape-level thresholds of habitat value, area, or connectivity may exist below which population viability is compromised due to an imbalance between immigration and emigration (Lande 1987; Noon & McKelvey 1996). Maintaining viable and well-distributed fisher populations may require increased levels of canopy closure and retention of large hardwoods on managed lands, especially in areas that appear from habitat analyses to be plausible regional habitat linkages. Conservation planning for nonfederal lands-for example, through development of habitat conservation plans-should prioritize surveys to validate the .areas of potential habitat identified in regional-scale analyses.

The evaluation of the representation of fisher habitat by management category shows that late-successional reserves represent a greater proportion of fisher habitat than do strictly protected areas now in existence, with the exception of the redwood parks. The designation of late-successional reserves represents a shift in conservation priorities toward an increased focus on low-elevation, biologically productive areas. Although low-elevation forests may retain only fragmented old-growth habitat, these patches may be more valuable as nuclei for biodiversity reserves than their size or connectivity would indicate (Franklin 1993; Spies et al. 1994). Because little low-elevation forest is contained within existing protected areas, conservation of forest carnivores such as the fisher may depend on multi-ownership cooperative management at the regional scale (Mladenoff et al. 1995).

Acknowledgments

Literature Cited

Allen, T. F. H., and T. B. Starr. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago.

Aubry, K. B. 1997. Ecological characteristics of fishers in southwestern Oregon: progress report: February 1997. Pacific Northwest Research Station, U.S. Forest Service, Olympia, Washington.

Aubry, K. B., and D. B. Houston. 1992. Distribution and status of the fisher in Washington. Northwestern Naturalist 73:69-79.

Austin, M., and P. C. Heyligers. 1991. New approach to vegetation survey design: gradsect sampling. Pages 31-36 in C. R. Margules and M. P. Austin, editors. Nature conservation: cost effective biological surveys and data analysis. Commonwealth Scientific, Industrial, and Research Organization, Melbourne, Australia.

Austin, M., and J. A. Meyers. 1996. Current approaches to, modeling the environmental niche of eucalypts: implication for management of forest biodiversity. Forest Ecology and Management 85:95-106.

Bailey, T. C., and A. C. Gatrell. 1995. Interactive spatial data analysis. Addison-Wesley, Reading, Massachusetts.

Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. Journal of Forestry 64:691-692.

Bissonette, J. A., D. J. Harrison, C. D. Hargis, and T. G. Chapin. 1997. Influence of spatial scale and scale-sensitive properties in habitat

selection by American marten. Pages 368-385 in J. A. Bissonette, editor. Wildlife and landscape ecology: effects of pattern and scale. Springer-Verlag, New York.

Boyce, M. S., and L. L. McDonald. 1999. Relating population to habitats using resource selection functions. Trends in Ecology and Evolution 14:268-272.

Buskirk, S.W. 1992. Conserving circumboreal forests for martens and fishers. Conservation Biology 6:318-320.

Buskirk, S. W., and R. A. Powell. 1994. Habitat ecology of fishers and American martens. Pages 283-296 in S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, editors. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, New York.

California, Timberland Task Force. 1993. Report. California Department of Forestry and Fire Protection, Sacramento.

Carroll, C., R. F. Noss, and P. C. Paquet. 1999. Carnivores as focal species for conservation planning in the Rocky Mountain region. World Wildlife Fund, Toronto, Ontario.

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.

Cliford, P., S. Richardson, and D. Hemon. 1989. Assessing the significance of the correlation between two spatial processes. Biometrics 45:123-134.

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.

Cook, R. D., and S. Weisberg. 1982. Residuals and influence in regression. Chapman and Hall, London.

Coulson, T., S. Albon, F. Guinness, J. Pemberton, and T. Clutton-Brock. 1997. Population substructure, local density, and calf winter survival in red deer (*Cervus elapbus*). Ecology 78:852-863.

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.

Environmental Systems Research Institute. 1996. Arc-Info, version 7.0. Redlands, California.

Fortin, M. J., P. Drapeau, and P. Legendre. 1989. Spatial autocorrelation and sampling design in plant ecology. Vegetatio 83:209-222.

Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? Ecological Applications 3:202-205.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. General technical report PNW-8. Pacific Northwest Research Station, U.S. Forest Service, Portland, Oregon.

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, Massachusetts.

Haining, R. 1990. Spatial data analysis in the social and environmental sciences. Cambridge University Press, Cambridge, United Kingdom.

Hanski, 1. 1996. Metapopulation ecology. Pages 13-44 in O. E. Rhodes, R. K. Chesser, and M. H. Smith, editors. Population dynamics in ecological space and time. University of Chicago Press, Chicago.

Hastie, T. J. 1993. Generalized additive models. Pages 249-308 in J. M. Chambers and T. J. Hastie, editors. Statistical models. Chapman and Hall, New York.

Heinemeyer, K. S., and J. L. Jones. 1994. Fisher biology and management in the western United States: a literature review and adaptive management strategy. U.S, Forest Service Northern Region, Missoula, Montana.

Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs 62:447-502.

Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of "sink" populations. Biological Conservation 57:239-255.

Karieva, P., D. Skelly, and M. Ruckelshaus. 1996. Reevaluating the use of models to predict the consequences of habitat loss and fragmentation. Pages 156-166 in S. T. A. Pickett, R. S. Ostfeld, M. Schachak, and G. E. Likens, editors. The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity. Chapman and Hall, New York.

Klug, R. R., Jr. 1996. Occurrence of Pacific fisher *(Martes pennanti)* in the redwood zone of northern California and the habitat attributes associated with their detections. M.S. thesis. Humboldt State University, Arcata, California.

Krohn, W. B., W. J. Zielinski, and R. B. Boone. 1997. Relations among fishers, snow, and martens in California: results from small-scale spatial comparisons. Pages 211-232 in G. Proulx, H. N. Bryant, and P. M. Woodard, editors. *Martes:* taxonomy, ecology, techniques, and management. Proceedings second international *Martes* symposium. Provincial Museum of Alberta, Edmonton.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. American Naturalist 130:624-635.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659-1673.

Legendre; P., M. Troussellier, V. Jarry, and M. J. Fortin. 1989. Design for simultaneous sampling of ecological variables: from concepts to numerical solutions. Oikos 55:30-42.

Mayer, K. E., and W. F. Laudenslayer Jr. 1988. A guide to wildlife habitats of California. California Department of Forestry and Fire Protection, Sacramento.

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.

Noon, B. R., and K. S. McKelvey. 1996. Management of the Spotted Owl: a case history in conservation biology. Annual Review of Ecology and Systematics 27:135-162.

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.

Powell, R. A. 1993. The fisher: life history, ecology, and behavior. 2nd edition. University of Minnesota Press, Minneapolis.

Powell, R. A., and W. J. Zielinski. 1994. Fisher. Pages 38-73 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, technical editors. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine. General technical report RM-254. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

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. Wiley, New York.

Sawyer, J. O., and D. A. Thornburgh. 1977. Montane and subalpine vegetation of the Klamath mountains. Pages 699-732 in M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. Special publication 9. California Native Plant Society, Davis, California.

Sawyer, J. O., D. A. Thornburgh, and J. R. Griffin. 1977. Mixed evergreen forest. Pages 359-382 in M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. Special publication 9. California Native Plant Society, Davis, California.

Schwarz, G. 1978. Estimating the dimension of a model. Annals of Statistics 6:461-464.

Spies, T. A., W. J. Ripple, and G. A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecological Applications 4:555-568.

Stevens, D. L. 1994. Implementation of a national monitoring program. Journal of Environmental Management 42:1-29.

Thomson, J. D., G. Weiblen, B. A. Thomson, S. Alfaro, and'P. Legendre. 1996. Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. Ecology 77:1698-1715.

U.S. Forest Service and U.S. Bureau of Land Management. 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. U.S. Forest Service, Portland, Oregon.

Van Home, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Wenger, K. F. 1984. Forestry handbook. 2nd edition. Wiley, New York.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:279-338.

Wiens, J. A. 1989a. The ecology of bird communities. Volume 1. Foundations and patterns. Cambridge University Press, New York.

Wiens, J. A. 1989b. Spatial scaling in ecology. Functional Ecology 3: 385-397.

Wiens, J. A., N. C. Stenseth, B. Van Home, and R.A. Ims. 1993. Ecological mechanisms and landscape ecology. Oikos 66:369-380.

Wu, H., and F. W. Huffer. 1997. Modelling the distribution of plant species using the autologistic regression model. Environmental and Ecological Statistics 4:49-64.

York, E. C. 1996. Fisher population dynamics in north-central Massachusetts. M.S. thesis. University of Massachusetts, Amherst.

Zielinski, W. J. 1991. A survey protocol to monitor forest carnivores in proposed management activity areas. Pacific Southwest Research Station, U.S. Forest Service, Arcata, California.

Zielinski, W. J., and T. E. Kucera. 1995. American marten, fisher, lynx, and wolverine: survey methods for their detection. General technical report PSW-GTR-157. Pacific Southwest Research Station, U.S. Forest Service, Albany, California.

Zielinski, W. J., T. E. Kucera, and R. H. Barrett. 1996.The current distribution of fishers (*Martes pennanti*) in California. California Fish and Game 81:104-112.

Zielinski, W. J., R. L. Truex, C. V. Ogan, and K. Busse. 1997. Detection surveys for fishers and American martens in California, 1989-1994: summary and interpretations. Pages 372-392 in G. Proulx, H. N. Bryant, and P., M. Woodard, editors. *Martes*: taxonomy, ecology, techniques, and management. Proceedings of the Second International Martes Symposium, Provincial Museum of Alberta, Edmonton.

Zinke, P. J. 1977. The redwood forest and associated north coast forests. Pages 679-698 in M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. Special publication 9. California Native Plant Society, Davis.