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REGIONAL VARIATION IN HOME-RANGE-SCALE HABITAT MODELS FOR FISHER (*MARTES PENNANTI*) IN CALIFORNIA

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Abstract. We analyzed recent survey data and mapped environmental variables integrated over a home range scale of 10 km^2 to model the distribution of fisher (*Martes pennanti*) habitat in California, USA. Our goal was to identify habitat factors associated with the current distribution of fishers in California, and to test whether those factors differ for widely disjunct northern and southern populations. Our analyses were designed to probe whether poor habitat quality can explain the current absence of fishers in the historically occupied central and northern Sierra Nevada region that separates these two populations. Fishers were detected at 64/433 (14.8%) sample units, including 35/111 (32%) of sample units in the Klamath/Shasta region and 28/88 (32%) of sample units in the southern Sierra Nevada. Generalized additive models (GAM) that included mean annual precipitation, topographic relief, forest structure, and a spatial autocovariate term best predicted fisher detections over the species' recent historical range in California. Models derived using forest structure data from ground plots were comparable to models derived from Landsat Thematic Mapper imagery. Models for the disjunct Klamath/Cascades and southern Sierra Nevada populations selected different environmental factors and showed low agreement in the spatial pattern of model predictions. Including a spatial autocovariate term significantly improved model fits for all models except the southern Sierra Nevada. We cannot rule out dispersal or habitat in explaining the absence of fishers in the northern and central Sierra Nevada, but mapped habitat quality is low over much of the region. Landscapes with good fisher habitat may exist in rugged forested canyons of the currently unoccupied northern Sierra Nevada, but these areas are fragmented and at least 60 km from the nearest recent fisher detections.

Key words: California, USA; fisher; forest carnivore; generalized additive model (GAM); GIS; habitat model; Martes pennanti; *Receiver Operating Characteristic, ROC.*

Introduction

Predictive mapping of species distributions is used widely in conservation planning to protect and recover rare and endangered species (Guisan and Zimmermann 2000, Margules et al. 2002, Poirazidis et al. 2004). Spatially explicit statistical models of species–environment association can help to identify critical habitat areas for species protection or reintroduction and to project distribution shifts under climate change (Araujo et al. 2005, Guisan and Thuiller 2005). Such habitat modeling (Kearney 2006) assumes that the observed distribution of a species represents its true habitat needs and preferences. This assumption may be untenable for rare and endangered species whose distributions have been reduced by overharvest or historical habitat degradation. If those species have not reoccupied now-suitable habitat because of social, demographic, or dispersal factors, it will be difficult (if not impossible) to distinguish unsuitable from unoccupied habitat. Ultimately, understanding species' environmental niche relations and limits to distribution requires experimental research and long-term demographic studies (Austin 1985), which present special challenges for endangered species. In the interim, statistical models that consider spatial autocorrelation as well as multiple scales of environmental controls can strengthen inference about species' environmental niche relations and potential distributions to inform near-term conservation and management decisions (Guisan et al. 2006, Latimer et al. 2006).

Here we report research to model the distribution of fishers (*Martes pennanti*) in relation to mapped habitat variables in California, both to better understand what controls the current distribution of the species and to evaluate habitat extent and quality in the northern Sierra Nevada, where reintroduction of the species is being considered. In the western United States, the fisher

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occurred historically throughout the northern Rocky Mountains, Cascade Mountains, Coastal Ranges, and Sierra Nevada (Gibilisco 1994). The range and abundance of this forest-dwelling carnivore have decreased dramatically since Columbian times due to commercial trapping, changes in forest structure associated with logging and altered fire regimes, increased human access, and habitat loss to urban and recreational development (Powell and Zielinski 1994, Buskirk et al. 2002).

Although trapping was prohibited in California in 1946, the other threats continue. The fisher occupies less than half of its recent historical range in the state, and remnant populations in the southern Sierra Nevada are separated by more than 400 km from the nearest populations in the southern Cascades and Coast Ranges of northern California and southern Oregon (Zielinski et al. 1995, Carroll et al. 1999). Zielinski et al. (2005) hypothesized that the modern absence of fishers from the northern and central Sierra Nevada was due to timber harvest and forest management practices that reduced late-seral montane forest area from 50% of the region in 1945 to less than 5% in 1996. Fisher population decline and fragmentation have reduced genetic diversity (Drew et al. 2003), and listing of a distinct population segment of the fisher (including portions of California, Oregon, and Washington) under the U.S. Endangered Species Act is deemed "warranted" by the U.S. Fish and Wildlife Service (U.S. Federal Register, 8 April 2004). Critical habitat has not been delineated, but predictive mapping of habitat quality could support such an effort and could also aid in planning for habitat restoration and reintroduction of the species to unoccupied areas.

Spatial distribution modeling must account for characteristic scales of habitat factors associated with different levels of organization of the species: individuals, populations, species in toto (Wiens 1989, Mackey and Lindenmayer 2001, Latimer et al. 2006). At the regional scale (1000–10 000 km^2), western fisher populations generally occur in mountainous areas with extensive forest cover and low-to-moderate snowfall (Buskirk and Powell 1994, Powell and Zielinski 1994, Krohn et al. 1995). In California, Powell and Zielinski (1994) estimated the minimum area needed to support a viable fisher population to be at least 600 km^2. At the home range scale (which for fishers encompasses landscape heterogeneity over 1–10 km^2), individuals are found in areas with low levels of human activity, ready access to water, and extensive late-seral forest cover (Carroll et al. 1999). At the topo–climatic scale (1–10 ha), fishers are associated with north-facing slopes that support late-seral forest and trees of the largest size classes (Zielinski et al. 2004*a*). At the microscale (0.1–1 ha), fishers tend to rest and den in large conifers, conifer snags, and oaks (especially *Quercus kelloggii*) on steep slopes under a closed canopy of large trees (Zielinski et al. 2004*b*, 2006*b*).

These habitat associations could express both direct environmental controls on fisher distributions and indirect controls such as habitat requirements of the fisher's prey species. Fishers in California appear to prey on a greater variety of species than elsewhere in their range (Zielinski et al. 1999, Golightly et al. 2006) and preferentially select larger trees in closed forests for resting and denning (Zielinski et al. 2004*b*); thus, available evidence suggests at least some direct environmental control on fisher distribution at the scale of individual home ranges.

Modeling fisher distribution at the home range scale is particularly useful to managers evaluating the effects of vegetation management regimes on fisher habitat quality (Zielinski et al. 2004*a*). In the western United States, fisher home range size averages ~1500 ha among females and 4000 ha among males (Zielinski et al. 2004*a*). Mazzoni (2002) estimated mean home ranges for female and male animals in the southern Sierra Nevada to be 1192 ha and 2194 ha, respectively. Zielinski et al. (2004*a*) documented substantially smaller mean female home range sizes (527 ha), but similar mean male home ranges (2998 ha) in the southern Sierra. A coastal population in northwestern California, however, had larger mean home ranges (1498 and 5806 ha for females and males, respectively) than reported in the Sierra Nevada.

Fishers in the southern Sierra Nevada differ in population genetics, home range size, diet, and resting habitats from fishers in the wetter, denser forests of northwestern California (Zielinski et al. 2004*a*, *b*). Given these differences, we considered the possibility that separate distribution models might be needed for northern vs. southern populations. Region-specific habitat associations have been documented for numerous other species, but are usually not considered in building or testing distribution models (Fielding and Haworth 1995, Whittingham et al. 2003).

In addition to multi-scale habitat associations, we expected dispersal and social behavior to affect patterns of fisher occurrence. Fishers are polygnous and exhibit intrasexual territoriality; male territories usually overlap the territories of more than one female (Powell 1979, 1994). Fishers also tend to disperse relatively short distances (mean ~10 km; Arthur et al. 1993). Thus we expect fishers to be overdispersed at and below the scale of individual territories, but to be clustered at larger scales encompassing multiple territories.

To summarize, our research objective was to model the relationship between fisher distribution and mapped environmental factors and to use this relationship to map the distribution of fisher habitat within the species' historical range in California. We hypothesized that fisher occurrence in California is associated with climatic, topographic, and vegetation habitat factors measured at regional and home range scales. We further hypothesized that habitat associations at the home range scale would vary between disjunct northern and southern populations and that regional models would perform better than a statewide model for the species in

California. Lastly, we hypothesized that occurrence patterns would be spatially autocorrelated as a result of the territorial social system and local dispersal. To test these hypotheses, we fit generalized additive models (GAM) to fisher detection data based on environmental variables measured at the home range scale of 10 km^2, with and without a spatial autoregressive term. We compared habitat associations and predicted distributions of fishers in the Klamath-Cascades and southern Sierra Nevada regions of California and tested the skill of models developed in one region in predicting fisher detections in a different region. We extrapolated statewide and regional models to map fisher habitat quality in the currently unoccupied forests of the northern Sierra Nevada in order to inform ongoing planning for fisher habitat management and possible reintroduction of the species into this area.

Methods

Fisher survey data

Fisher surveys were conducted between 1996 and 2002 in California and southern Oregon, USA (Zielinski et al. 2005). We analyzed the 445 survey points that occurred in California, ranging from the Siskiyou Mountains of northwest California (42°0′ N, 124°0′ W) to the Piute Mountains of the southern Sierra Nevada (35°30′ N, 119°30′ W) (Fig. 1). We restricted the analysis to California because digital environmental data used in the analysis were not consistent between California and Oregon.

Field survey points were arrayed in a systematic-cluster design aligned with the grid established by the U.S. Forest Service Forest Inventory and Analysis (FIA) program (Bechtold and Patterson 2005). The FIA grid consists of a systematic hexagonal array of points separated by 5.47 km that are distributed across both public and private forest lands and are monitored on a 10-year interval for forest structure, composition, and condition (FIA grid *available online*).[6] Fisher survey crews surveyed alternate FIA lattice points separated by ~10 km (Zielinski et al. 2005). The sample spacing was chosen on the basis of fisher home range sizes in California to minimize the possibility that the same fisher would be detected at more than one sample unit.

Each of the sample units consisted of six enclosed track-plate stations and 1–2 remotely triggered 35-mm cameras (Zielinski et al. 2005). A track-plate station located at the FIA point was surrounded by five additional track-plate stations equally spaced around the circumference of a 3.14-km (500 m radius) circle centered on the point. The track plate consisted of a carbon-blackened aluminum plate (20 × 76.2 × 0.1 cm) partially covered with white contact paper and enclosed in either a plywood box or a plastic canopy with a metal base (Zielinski et al. 1995, 2005). The plate was baited with raw chicken and a scent lure. Camera(s) were randomly paired with one (or occasionally two) of the track-plate stations. All stations were checked and re-baited with chicken every other day for eight visits over a 16-day survey. Scent lures were only used toward the end of a survey period if no fishers had been detected up to that time. For the rest of the paper, we will refer to individual track-plate stations as "stations" and the cluster of stations as a "sample unit."

We dropped 12 of the original 445 California sample units from the analysis, including 11 units in Yosemite National Park and one unit from Sequoia-King's Canyon National Park, because of inconsistencies in the vegetation GIS data, leaving a statewide sample of

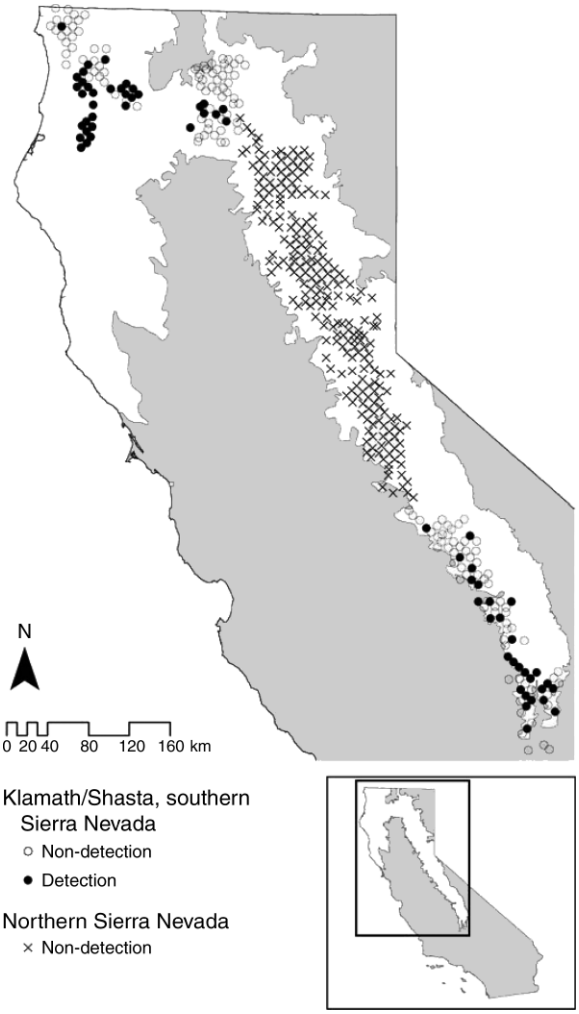

FIG. 1. Location of 433 fisher sampling units in California, USA, excluding national parks. Fisher detections (solid circles) vs. non-detections (open circles) are shown in the northern (Klamath/Shasta) and southern (southern Sierra Nevada) subregions. Locations of non-detections (crosses) in the unoccupied central and northern Sierra Nevada (northern Sierra Nevada) are also mapped. The white area is the recent historical range of the species in California, as depicted in Zeiner et al. (1990).

[6] ⟨http://fia.fs.fed.us/⟩

TABLE 1. Variables tested for association with the detection of fishers (*Martes pennanti*) in California, USA.

Variable	Variable description
Topography	
adj.elevation	Latitude-adjusted elevation.
relief	Topographic relief (standard deviation of elevation in a local 5 × 5 moving window).
Climate	
ann.ppt	Mean annual rainfall for 1960–1991 (source grid has 1-km^2 resolution).
Field vegetation	
field.CWHR	Mean fisher habitat rating (0–100) of 6–7 track plate stations at a fisher sampling unit based on the California Wildlife Habitat Relationship System (CWHR).
field.CWHR2	Mean forest habitat rating (0–100) of track plate stations at a fisher sampling unit based on a refined version of CWHR.
field.hardwood	Maximum CWHR montane hardwood or montane hardwood conifer habitat rating (0–100) of tracking plate stations at sampling unit.
field.structure	Product of a CWHR2 habitat indicator variable (1, fisher forest habitat type; 0, otherwise), forest canopy closure (centroid of class interval), and tree size (centroid of class interval), averaged over 6–7 track plate stations.
Vegetation habitat scores from remote-sensed imagery	
GIS.CWHR	Average CWHR fisher habitat rating (0–100).
GIS.CWHR2	Average refined CWHR fisher habitat rating (0–100).
GIS.structure	Product of a CWHR2 habitat indicator variable (1, fisher forest habitat type; 0, otherwise), forest canopy closure (centroid of class interval), and tree size (centroid of class interval).
GIS.dense.forest	Proportion of 1-ha cells in a 10-km^2 area classified as CWHR2 fisher forest habitat types and with 60–100% tree canopy closure.
GIS.dense.hardwood	Proportion of the 10-km^2 sample area classified as CWHR montane hardwood or montane hardwood–conifer type and with 60–100% tree canopy closure.
Road influence	
paved.roads	Mean inverse square root of distance to nearest paved road, including primary highways, secondary highways, and improved, light-duty paved roads.
improved.roads	Mean inverse square root of distance from a 1-ha cell to nearest improved road, including primary highways, secondary highways, improved, light-duty paved roads, improved light-duty gravel roads, and improved light-duty dirt roads.
Spatial autocorrelation (SA)	Spatial autocovariate term tested in the "spatial" models. Each sample unit observation (0, 1) within 20 km of the reference sample unit was weighted by its inverse squared distance to the sample unit, normalized by the sum of weights for all sample units in the 20-km region.

Notes: GIS variables are derived from source data with 1-ha spatial resolution and are the mean value of cells in a 10-km^2 circular window unless otherwise indicated. See Appendix A for a more complete explanation of variables and their derivation.

433 units (Fig. 1). We refer to this as the "statewide" data set.

To test for regional differences in habitat associations, we divided the 433 sample units into three sets (Fig. 1): (1) a "Klamath/Shasta" (KS) data set comprised of 111 sample units from the Six Rivers, Klamath, and Shasta/Trinity National Forests, which contain fisher populations; (2) 234 samples from the unoccupied northern and central Sierra Nevada region (NS) between the Pit River to the north and the Merced River to the south, located mainly in the Modoc, Lassen, Plumas, Tahoe, Eldorado, and Stanislaus National Forests, and Sequoia-Kings Canyon National Park; and (3) 88 sample units encompassing fisher populations in the southern Sierra Nevada (SS) and located in the Sierra or Sequoia National Forests.

The absence of fishers in the central and northern Sierra Nevada could reflect a lack of suitable habitat or the failure of fishers to recolonize suitable habitat in the region. If the latter were true, then including the 234 samples from the NS region in a statewide analysis should weaken the relationship between fisher detections and habitat factors. To test this idea, we excluded the NS samples and fitted habitat models to the 198 samples from the Klamath/Shasta and southern Sierra Nevada regions. We refer to this as the Klamath/Shasta + southern Sierra (KS + SS) data set.

Habitat variables

We considered five categories of landscape-scale habitat variables: topography; precipitation; field observations of forest structure and composition; vegetation structure and composition derived from Landsat Thematic Mapper imagery and digital elevation data; and road influence (Table 1; see Appendix A). Topographic variables derived from USGS 1-ha digital elevation grids included mean latitude-adjusted elevation and mean relief (the standard deviation of elevation within 500 × 500 m moving windows) in a 10-km^2 area encompassing all stations at a sample unit (Fig. 2a). To adjust for increasing latitude, we added 0.625 m of elevation per kilometer north (Schoenherr 1992). The adjustment is an admittedly crude proxy for the complex interaction of

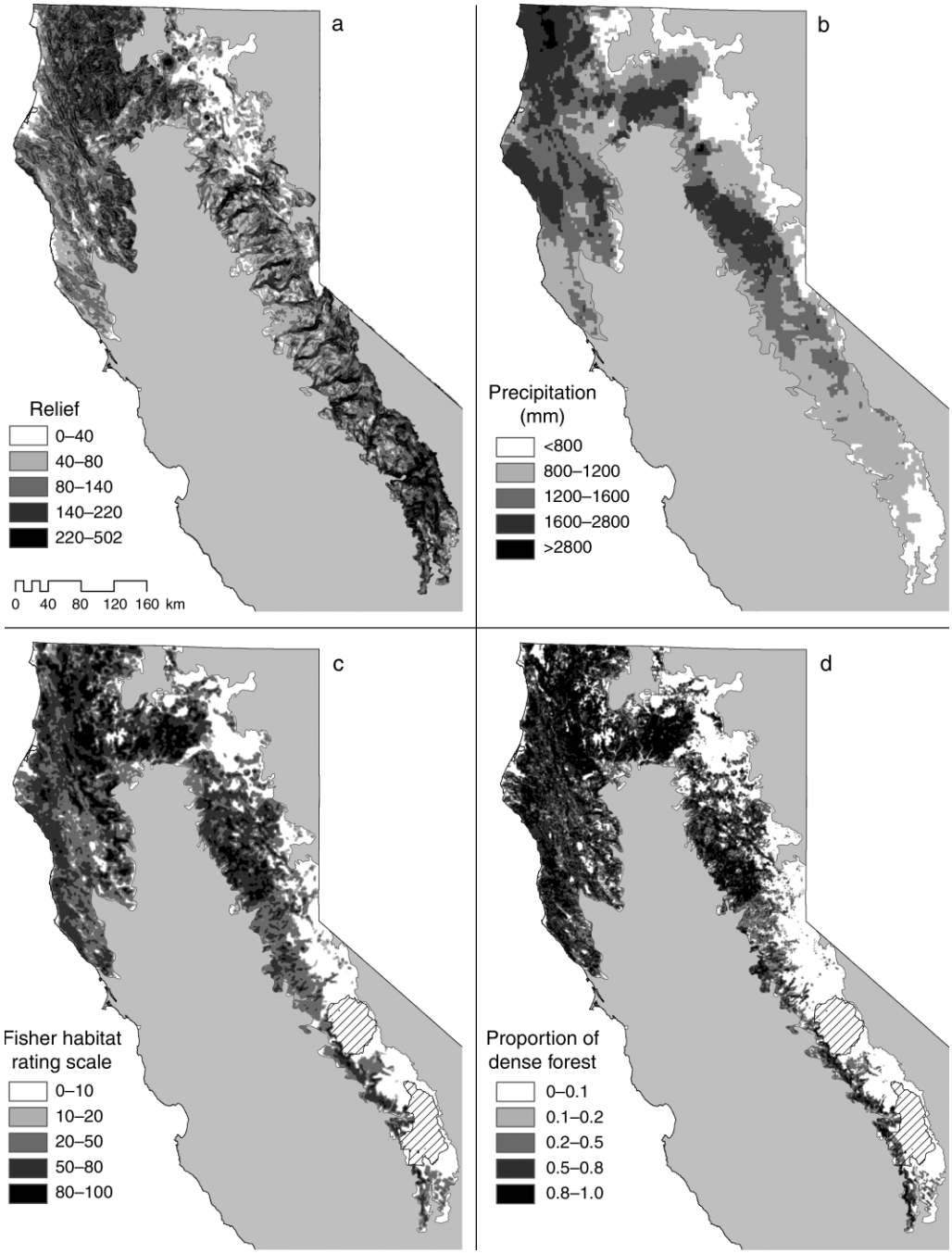

FIG. 2. Maps of selected GIS variables used to model and map the probability of detecting fishers in California, including (a) relief (calculated as the standard deviation of elevation in a local 5×5 moving window), (b) ann.ppt (annual precipitation, mm), (c) GIS.CWHR2 (average refined fisher habitat rating, 0–100, based on the California Wildlife Habitat Relationship System), and (d) GIS.dense.forest (proportion of 1-ha cells in a 10-km^2 area classified as CWHR2 fisher forest habitat types with 60–100% tree canopy closure). Vegetation variables were not mapped over most of Yosemite and Sequoia-Kings Canyon National Parks (hatched areas in panels c and d). See Table 1 and Appendix A for a description and explanation of the variables. Areas outside the fisher's recent historical range are masked.

elevation and latitude. We used latitude-adjusted elevation instead of interpolated temperature data because, although the two were significantly correlated, the former was strongly associated with fisher detections whereas the latter was not related to detections (for January minimum temperature, Wilcoxon $Z = -0.753$, $P = 0.45$), perhaps due to the coarse scale or interpolation errors in the temperature grids.

TABLE 2. Habitat rating of forest structure classes (fisher forest habitat types only) used to create landscape-scale California Wildlife Habitat Relationship (CWHR) scores.

Tree dbh size class (cm)	Canopy closure class (%)	CWHR score
<2.5	all	0
2.5–15	all	0
15–28	10–24	0
	25–39	0.07
	40–59	0.10
	60–100	0.19
28–61	10–24	0.07
	25–39	0.34
	40–59	0.69
	60–100	0.89
>61	10–24	0.21
	25–39	0.38
	40–59	0.80
	60–100	1
Multistory, trees >61 cm above trees >28 cm	>60	1

Notes: For CWHR scores, the following forest CWHR habitat types were considered fisher habitat: aspen, Douglas-fir, eastside pine, Jeffrey pine, Klamath mixed conifer, lodgepole pine, montane hardwood–conifer, montane riparian, ponderosa pine, redwood, red fir, Sierran mixed conifer, subalpine mixed conifer, and white fir. For CWHR2 ratings, aspen, eastside pine, lodgepole pine, montane riparian, red fir, and subalpine conifer were dropped from the original CWHR list.

Based on previous research (Krohn et al. 1995, 1997), we hypothesized that snowpack depth was an important climatic factor. However, given the sparse snowpack measurement network, we instead analyzed PRISM maps of mean annual precipitation for the period 1960–1991. These maps are derived by interpolating weather station data over terrain facets derived from digital elevation data (Daly et al. 1994); see Fig. 2b.

Field vegetation data were collected at every fisher survey station by trained observers, based on visual assessments. The observers classified the vegetation in the immediate vicinity of the station into general wildlife habitat type, canopy closure class, and tree size class based on version 8.0 of the California Wildlife Habitat Relationships (CWHR) system (California Department of Fish and Game 1992). We converted these data into an overall fisher habitat suitability based on the CWHR habitat rating system (Table 2). This system rates the suitability of each combination of habitat type, canopy closure class, and tree size class as high (1), medium (0.66), low (0.33), or unsuitable (0), and calculates an overall habitat suitability rating based on the arithmetic mean or geometric mean of the separate scores for reproduction, cover, and feeding. In the fisher habitat models, the structural ratings are nearly identical across suitable forest habitat types. The arithmetic mean was slightly better than the geometric mean in predicting fisher detections, based on Wilcoxon rank sum tests, so we only include arithmetic mean scores here. We scored each station for arithmetic means and then used the average score across the 6–7 stations to rate the habitat of the sampling unit (field.CWHR).

The CWHR system is based on expert judgment and continues to be evaluated and revised. Based on extensive field observations of fishers in California (W. Zielinski, *personal observation*), we believed that the current CWHR system was in error in assigning high suitability scores to upper montane, subalpine, and montane riparian forest types. To test our judgment, we modified the CWHR ratings by setting suitability scores for lodgepole pine, red fir, subalpine conifer, and montane riparian forest habitat types to 0; we retained arithmetic mean CWHR ratings for the remaining types. We refer to scores based on the revised system as CWHR2 scores; for example, field.CWHR2 is the average CWHR2 score of the stations at a sampling unit based on field vegetation surveys (Table 2).

We also created and tested new indices of forest composition and structure based on recent studies of fisher distribution in California (Table 1). We multiplied a habitat indicator variable (1, fisher forest habitat type according to CWHR2; 0, otherwise), canopy closure (centroid of class interval), and tree size (centroid of class interval) to produce a forest structure index (field.structure). Given the importance of large hardwoods, particularly black oak (*Quercus kelloggii*), in supplying resting cavities (Seglund 1995, Mazzoni 2002, Zielinski et al. 2004*b*), we calculated the maximum arithmetic mean WHR rating for montane hardwood and montane hardwood–conifer habitat types among the stations (field.hardwood) and used this to indicate high-quality montane hardwood habitat within the sampling unit.

We also modeled and mapped fisher habitat based on statewide digital vegetation data derived from satellite remote sensing. A digital vegetation database at 1-ha resolution was produced for national forest lands by applying classification models to 30-m Thematic Mapper satellite imagery and digital elevation data (Franklin et al. 2000), which are *available online*.[7] This database (see Table 1) includes CWHR habitat type, density class, and size class for each 1-ha cell, so we were able to derive the same variables from field and GIS data, including GIS.CWHR, and GIS.CWHR2 scores for 10-km^2 circular areas centered on and encompassing each sampling unit. We chose the 10-km^2 scale of analysis based on the documented home range size of fishers in California. Also, a previous landscape–fisher habitat model evaluated alternative spatial scales of analysis and concluded that model fit with observation data peaked around a 10-km^2 scale (Carroll et al. 1999). We calculated the mean of cell scores over the 10-km^2 areas centered on the sample unit for a landscape-scale measure of CWHR and CWHR2 habitat suitability (Table 1). We also calculated a forest structure index as

[7] ⟨http://frap.cdf.ca.gov/data/frapgisdata//select.asp⟩

the product of forest canopy cover and tree size for CWHR2 forest habitats (Fig. 2c).

We expected the data from remote sensing to be more accurate for canopy closure than for modeled tree size (Franklin et al. 2001); accordingly, we classified each pixel as either dense canopy (60–100% tree cover) of suitable CWHR2 forest types, or not, to derive the proportion of the 10-km^2 sampling unit area in closed-canopy forest habitat (GIS.dense.forest) (Fig. 2d). Lastly, we derived a measure of late-seral hardwood forest in the landscape as the proportion of cells in the 10-km^2 area that were classified as montane hardwood or montane hardwood–conifer forest with 60–100% tree canopy cover (GIS.dense.hardwood).

To measure road influence over the sample units, we calculated the mean square root of the distance from each cell in the 10-km^2 unit to the nearest paved road (paved.road) and improved road (improved.road).

Spatial autocorrelation

As noted previously, intrasexual territoriality (Powell 1994) and limited dispersal (Arthur et al. 1993) should result in negative autocorrelation of fisher detections at distances shorter than the typical home range radius and positive spatial autocorrelation at distances encompassing multiple home ranges. Because sampling units were deliberately spaced to avoid multiple samples per home range, we were mainly interested in the latter. To measure the degree of clustering, we created a spatial autocovariate based on the detection or non-detection of fishers at neighboring survey stations (Beard et al. 1999, Segurado and Araujo 2004, Luoto et al. 2005). Residuals from habitat models that did not include an autocovariate term generally displayed significant positive autocorrelation out to 10–20 km (see *Results*). Given this result and our expectation that fisher interactions would be localized, a spatial autocovariate (SA) was calculated by weighting the data from sampling units within 20 km of a survey point by the inverse of squared distance to the reference sampling unit, normalized by the sum of weights for all units in the 20-km region (Appendix A). Distance-weighted observations (non-detections = 0, detections = 1) were summed across all sampling units in the neighborhood. The 20 km radius (1256 km^2) is roughly twice the average distance between sampling units, encompassing 7–8 sample units and representing an area that might encompass the home ranges of 10–20 individuals (Zielinski et al. 2004*a*).

Statistical analysis

We measured pairwise association between environmental factors and fisher detections using Wilcoxon rank sum tests. Multivariate habitat models were produced using stepwise generalized additive modeling, GAM (Hastie and Tibshirani 1987, Yee and Mitchell 1991, Guisan et al. 2002). We chose GAM because it consistently outperformed General Linear Modeling (GLM) and Classification and Regression Trees (CART), and GAM models were easier to interpret than neural network models (which had slightly higher skill in fitting the data).

GAM analyses were conducted using S-PLUS version 6.0 (Insightful Corporation 2001) with GRASP 3.0 (General Regression Analysis and Spatial Prediction; Lehmann et al. 2002, 2004). Alternative multivariate models were generated by stepwise GAM modeling and a best model was selected using the Akaike Information Criterion, AIC (Hastie 1992, Manel et al. 2001, Burnham and Anderson 2002, Thuiller 2003). We integrated the Area under the Receiver Operating Characteristic (ROC) curve (AUC) to evaluate the classification skill of the models (Altman and Bland 1994, Fielding and Bell 1997). A model with no classification skill produces an AUC of 0.5, whereas a perfect model corresponds to an AUC of 1.0.

Model robustness was tested using fivefold cross-validation of the fitted models. Both presence and absence data were divided into five equal partitions, one partition was withheld for testing, and the model was fitted using the remaining data. The process was repeated five times and the mean performance of the five trials was calculated. We report both the model AUC and cross-validated AUC. When the model is sensitive to moderate changes in the input data set, the cross-validated AUC will be substantially lower than the AUC from the full data set.

GAM models can be unstable and goodness-of-fit statistics can be biased downward when there is concurvity (the nonparametric analogue to multicollinearity in generalized linear models) (Ramsay et al. 2003). Latitude-adjusted elevation, relief, precipitation, and road indices were not highly correlated, and of these variables, only elevation was moderately, negatively correlated with vegetation habitat indices (Appendix B). The vegetation habitat indices, on the other hand, were highly correlated (r values > 0.5). To reduce the potential impact of concurvity in the GAM models, we limited the number of candidate vegetation variables for stepwise selection. Rather than entering all vegetation variables into the stepwise GAM models, we first fitted and compared a large set of full models that included precipitation, elevation, relief, one forest structure variable (e.g., field.CWHR2), and one measure of hardwood fraction (e.g., field.hardwood), separately testing all possible vegetation variables. For stepwise modeling, we included only the forest structure variable and hardwood variable that produced the best fit among the set of models. Also, we did not include field and GIS variables in the same model.

We analyzed spatial autocorrelation in GAM model residuals using spatial correlograms (Moran's I) (Legendre and Fortin 1989, Lichstein et al. 2002). Significance of the autocorrelation term as a function of distance was determined using a two-tailed global Bonferroni test.

We fitted "spatial GAM models" by including the environmental variables selected in stepwise GAM

TABLE 3. Univariate tests of association between fisher detections and environmental factors based on the Wilcoxon *U* test.

Variable	Statewide (n = 433)		KS + SS (n = 199)		Klamath/Shasta (n = 111)		Southern Sierra (n = 88)	
	Wilcoxon	*P*	Wilcoxon	*P*	Wilcoxon	*P*	Wilcoxon	*P*
adj.elevation	**3.400**	**0.001**	1.456	0.146	1.860	0.063	0.184	0.854
relief	**−6.630**	**<0.001**	**−4.167**	**<0.001**	**−4.135**	**<0.001**	−1.429	0.153
ann.ppt	0.824	0.410	0.126	0.900	1.860	0.063	1.778	0.075
paved.roads	**−3.089**	**0.002**	**−3.087**	**0.002**	**−2.821**	**0.005**	−1.653	0.098
improved.roads	−1.275	0.202	−0.308	0.758	−1.038	0.299	0.506	0.613
field.CWHR	**−2.219**	**0.027**	**−2.898**	**0.004**	**−3.805**	**0.000**	0.063	0.950
field.CWHR2	**−3.473**	**0.001**	**−3.616**	**0.000**	**−4.276**	**<0.001**	−0.799	0.425
field.hardwood	**−6.455**	**<0.001**	**−3.456**	**0.001**	**−4.072**	**<0.001**	−0.598	0.550
field.structure	**−3.693**	**0.000**	**−3.847**	**0.000**	**−4.681**	**<0.001**	−0.843	0.399
GIS.CWHR	**−2.979**	**0.003**	**−3.318**	**0.001**	**−3.337**	**0.001**	−0.999	0.318
GIS.CWHR2	**−4.483**	**<0.001**	**−3.464**	**0.001**	**−3.706**	**0.000**	−1.330	0.183
GIS.structure	**−3.529**	**0.000**	**−3.259**	**0.001**	**−3.538**	**0.000**	−1.035	0.301
GIS.dense.hardwood	**−5.629**	**<0.001**	**−2.602**	**0.009**	**−2.670**	**0.008**	−0.481	0.631
GIS.dense.forest	**−5.773**	**<0.001**	**−3.489**	**0.001**	**−2.659**	**0.008**	**−2.280**	**0.023**

Notes: Separate tests were performed for the indicated subregions; KS + SS is Klamath/Shasta and southern Sierra. Cell entries are two-tailed *P* values and have not been adjusted to account for spatial autocorrelation. See Table 1 for an explanation of the variables. Sample size (n) is the number of sample units (each with six track-plate stations and 1–2 remotely triggered cameras). Values are negative when the variable has higher values at sites with fisher detections than those with non-detections. Values in bold indicate P values < 0.05.

modeling plus the spatial autocovariate. When included as a variable in stepwise GAM modeling, the spatial autocovariate term was usually selected first and its strong effect tended to mask the role of other environmental factors (see Miller and Franklin [2002] for a discussion of this issue in spatial autoregressive models). Constraining the SA term to enter after the best environmental variables had been identified allowed us to better model the combined effect of environmental habitat factors and autocorrelation on patterns of fisher detections. We also fitted models based solely on the spatial autocovariation. Comparing the three classes of models (environmental, environmental plus spatial autocovariation, spatial autocovariation) helped us to tease apart environmental vs. spatial associations in the fisher distribution data.

Based on AUC statistics, we measured the classification skill of a model developed for one region in predicting fisher detections in other regions. For example, we compared the performance of statewide vs. KS + SS models in predicting patterns of fisher detections in the KS + SS area.

Habitat envelope modeling

To further probe whether the lack of fishers in the northern and central Sierra is better explained by habitat limitations or dispersal, we created a more liberal habitat envelope model based on statewide presence-

TABLE 4. Summary of generalized additive models to predict fisher detections derived using field-based and GIS-derived vegetation data.

Model and vegetation data	*N* (prevalence)	Nonspatial GAM model			
		Variables	AUC	CV AUC	AIC
Statewide	433 (0.15)				
Field		ann.ppt, relief, field.hardwood	0.84	0.79	303.0
GIS		ann.ppt, GIS.dense.forest, relief	0.85	0.81	290.4
KS + SS	199 (0.32)				
Field		relief, ann.ppt, field.CWHR2	0.77	0.7	228.9
GIS		ann.ppt, GIS.CWHR2, relief	0.80	0.72	220.3
Klamath/Shasta	111 (0.32)				
Field		ann.ppt, field.CWHR2, relief	0.90	0.82	103.7
GIS		relief, GIS.structure, ann.ppt	0.89	0.84	99.7
Southern Sierra	88 (0.32)				
Field		ann.ppt	0.70	0.58	110.51
GIS		ann.ppt, GIS.dense.forest, adj.elevation	0.83	0.73	104.10

Notes: Variables are listed in their order of contribution to the final models, by subregion; KS + SS is Klamath/Shasta and southern Sierra. For fisher prevalence, the first number is sample size (number of sample units); the number in parentheses is the proportion of sample units with fisher detections. Model AUC (area under the curve), and fivefold cross-validated AUC (CV AUC) values are also tabulated. See Table 1 and Appendix A for an explanation of the variables and their abbreviations. Blank cells indicate that no data are possible.

only data and GIS-based habitat data using maximum entropy (MAXENT) modeling (Phillips et al. 2006). Absence data were generated by statewide random sampling. The MAXENT approach performs better with presence-only data than other methods such as bioclimatic envelope modeling or genetic algorithms (Elith et al. 2006). In comparing GAM and MAXENT outputs, we reasoned that the habitat-based explanation would be reinforced if both GAM and maximum entropy models produced low habitat suitability scores for the unoccupied region, whereas the dispersal explanation would be strengthened if the GAM models produced low scores and the MAXENT model produced high habitat scores over much of the region.

Results

Fishers were detected at 14.8% (64/433) of sample units including 32% (35/111) of sample units in the Klamath/Shasta region and 32% (28/88) of sample units in the southern Sierra Nevada (Fig. 1). One fisher was detected at the extreme southern end of the 234 sample units in the central and northern Sierra Nevada.

Based on AUC and AIC values, GAM models derived using the vegetation GIS data performed as well as or better than the models using field vegetation data (see Table 4). Given our focus on predictive mapping, we concentrate on the GAM models derived using GIS vegetation variables. We report summary statistics for both classes of model and consider the implications of the better performance of the GIS-based models in the *Discussion*.

Statewide model

Fisher detections were significantly associated (Wilcoxon Z, $P < 0.05$) with latitude-adjusted elevation (–), relief (+), and paved roads (+), as well as all of the field-based and GIS-based measures of vegetation structure (Table 3). Detections were most associated with the landscape fraction of late-seral forest (GIS.dense.forest) and late-seral hardwood forest (field.hardwood, GIS.dense.hardwood), and were more likely in forested areas with high tree cover and larger tree sizes (positive associations with field.CWHR, GIS.CWHR, field.structure, and GIS.structure). Detections were more strongly associated with high field- or GIS-based CWHR2 ratings than with the original CWHR ratings, supporting our expectation that fishers are less likely to use upper montane and subalpine forests than lower-to-mid elevation conifer and mixed conifer–hardwood forest types.

The positive association of fisher detections with proximity to paved roads runs counter to our expectation that fishers would avoid areas of high human activity. The correlation could be spurious, given the tendency for roads to have been located along waterways and near high-value timber stands at mid-to-low elevations (Riitters and Wickham 2003). These relationships are evident in the moderate ($0.3 < r < 0.5$) correlations between the index for improved roads and topographic and vegetation factors (Appendix B). Correlations between the paved road index and topographic or vegetation variables, however, are relatively low ($r < 0.2$; Appendix B). The index is positively correlated with average distance in the 10-km^2 sample unit area to major streams and rivers depicted in 1:100 000 scale topographic maps ($r = 0.27$), but fisher detections are not directly associated with this hydrologic variable (Wilcoxon $Z = 0.05$, $P = 0.96$). Because we have no ecological interpretation for the positive association with paved roads, and because including the paved road index did not improve the fit of the GAM models based on AIC values or the classification skill based on AUC values, we opted to exclude road variables from further analyses.

The best nonspatial GAM model using statewide GIS vegetation data includes ann.ppt, relief, and GIS.dense.forest (Table 4, Fig. 3). Model residuals (observed – predicted) are significantly positively autocorrelated up to 20 km (Fig. 4a), mainly because the model underpredicts fisher detections in the Klamath/Shasta and southern Sierra regions, producing large regions of positive residuals, and overpredicts fisher detections in the unoccupied northern Sierra Nevada, producing a cluster of negative residuals (Fig. 5a). Adding the spatial autocovariate improves model classification skill, indicated by an increase in cross-validated AUC from 0.81 to 0.90, and model residuals are spatially uncorrelated (Table 4). The model based solely on spatial autocovariation has comparable skill to that combining environmental variables and the spatial autocovariate term (cross-validated AUC = 0.89), and slightly lower goodness of fit (AIC = 232 vs. 226).

Table 4. Extended.

Spatial GAM models			
Variables	AUC	CV AUC	AIC
SA	0.90	0.89	232.2
ann.ppt, relief, field.hardwood, SA	0.93	0.90	232.1
ann.ppt, GIS.dense.forest, relief, SA	0.93	0.90	226.6
SA	0.76	0.75	206.8
relief, ann.ppt, field.CWHR2, SA	0.85	0.78	203.3
ann.ppt, GIS.CWHR2, relief, SA	0.86	0.76	202.4
SA	0.89	0.88	89.9
ann.ppt, field.CWHR2, relief, SA	0.96	0.86	84.3
GIS.structure, relief, SA	0.95	0.89	82.0
SA	0.60	0.45	114.4
ann.ppt, SA	0.72	0.53	114.9
ann.ppt, GIS.dense.forest, adj.elevation, SA	0.84	0.61	112.5

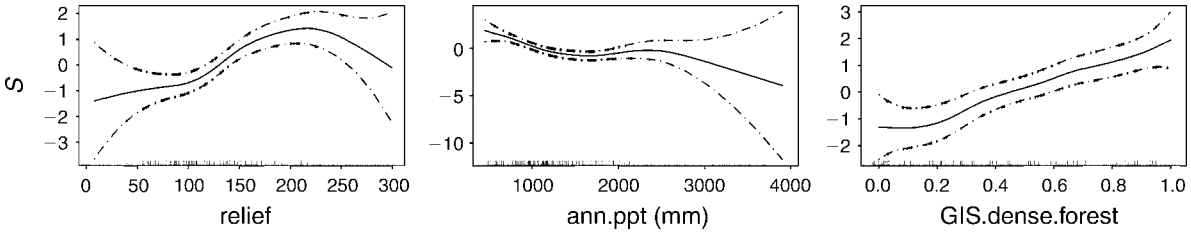

FIG. 3. Partial response curves for the statewide GAM (generalized additive model) based on topographic relief (relief, calculated as the standard deviation of elevation in a local 5 × 5 moving window), annual precipitation (ann.ppt), and forest structure (GIS.dense.forest, calculated as the proportion of 1-ha cells in a 10-km^2 area classified as CWHR2 fisher forest habitat types with 60–100% tree canopy closure). The *x*-axis is the value of the model independent variable, and the *y*-axis (*S*) is the additive contribution of the variable to the nonparametric GAM smoothing function. Dashed curves are two standard errors about the estimated function.

When evaluated against the regional subsets of the data, the nonspatial and spatial statewide models perform best at predicting the lack of fisher detections in the northern Sierra and worst at predicting fisher detections and non-detections in the southern Sierra Nevada (Table 5). The models perform nearly as well in the Klamath/Shasta region (spatial model AUC = 0.93) as for the statewide data set (spatial model AUC = 0.95), again indicating that the statewide GAM models are particularly poorly specified for the southern Sierra Nevada.

Klamath/Shasta + southern Sierra (KS + SS) model

When samples from the unoccupied northern Sierra Nevada region are excluded, fisher detections in the KS + SS regions are significantly associated with relief, paved.roads, and every vegetation variable (Table 3). The main difference in pairwise associations between KS + SS vs. statewide data sets is the lack of association of fisher detections with latitude-adjusted elevation in the KS + SS data. Fisher detections are positively associated with late-seral stages of mid-montane forest types, late-

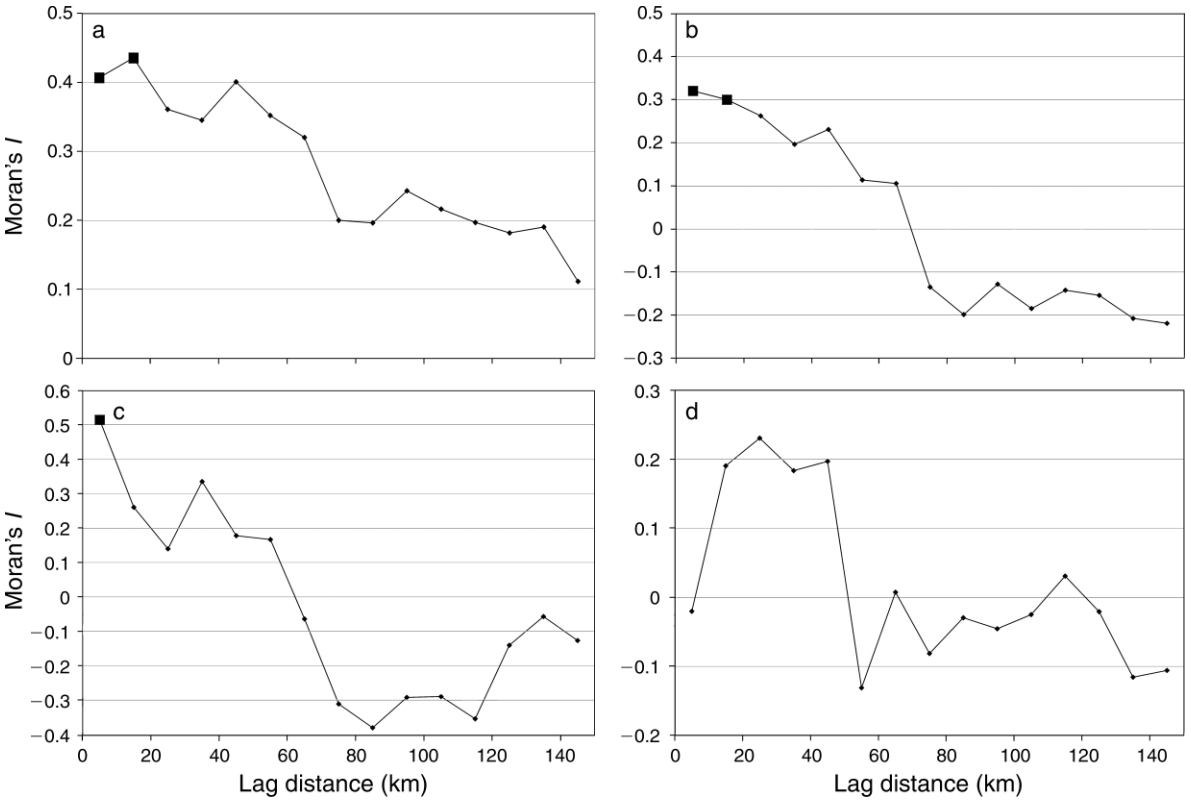

FIG. 4. Moran's *I* spatial correlograms of GAM model residuals from the nonspatial models based on GIS vegetation data. The *x*-axis shows the distance between site pairs. Models include (a) statewide, (b) Klamath/Shasta + southern Sierra (KS + SS), (c) Klamath/Shasta (KS), and (d) southern Sierra (SS). Significant ($P < 0.05$) values of Moran's *I* are indicated with solid squares.

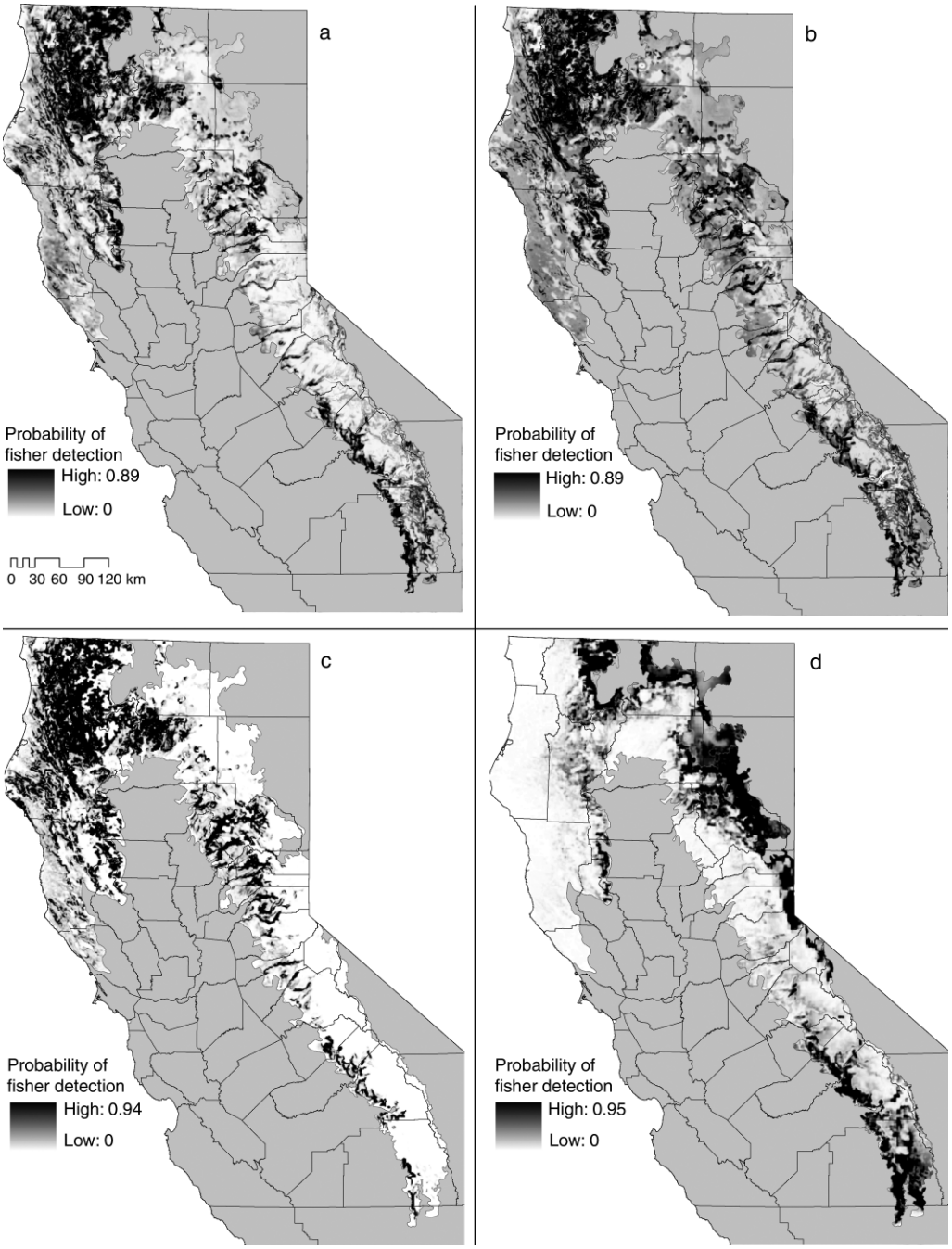

FIG. 5. Mapped probability of fisher detection within the historic range of fishers in California based on (a) statewide, (b) Klamath/Shasta + southern Sierra (KS + SS), (c) Klamath/Shasta (KS), and (d) southern Sierra (SS) GAM models and GIS data. Darker areas have higher calculated probabilities.

seral hardwood forest, and the fraction of the landscape occupied by dense mid-montane forest.

The nonspatial GAM model includes ann.ppt, GIS.CWHR2, and relief (Table 4, Fig. 6). Model residuals are significantly spatially clustered to a lag distance of 20 km, due to underprediction of fishers in the occupied subregions and overprediction of detections in the unoccupied northern and central Sierra Nevada region (Fig. 4b).

The KS + SS models have a lower classification skill than the statewide models, with cross-validated AUC values of 0.7–0.75. The nonspatial KS + SS models have AUC values equivalent to the statewide model when applied to the statewide data set (Table 5), although the patterns of predicted detections are somewhat different,

TABLE 5. AUC (area under the curve) measures of model performance for GAM models in the calibration region (rows) and test region (columns).

Model	AUC				
	Statewide	KS + SS	Klamath/Shasta	Southern Sierra	Northern Sierra
Statewide					
Nonspatial	0.85	0.76	0.81	0.70	0.89
Spatial	0.93	0.84	0.92	0.70	0.98
KS + SS					
Nonspatial	0.84	0.80	0.87	0.71	0.88
Spatial	0.93	0.86	0.93	0.73	0.96
Klamath/Shasta					
Nonspatial	0.74	0.73	0.89	0.61	0.91
Spatial	0.80	0.77	0.95	0.61	0.97
Southern Sierra	0.69	0.68	0.52	0.73	0.70

Notes: Spatial models include a spatial autocovariate term. Results are for the GAM models based on GIS-derived measures of vegetation structure and composition. The spatial autocovariate term was not significant in the southern Sierra, so only the nonspatial models are shown. KS + SS is Klamath/Shasta and southern Sierra.

partly due to the higher model prevalence. The nonspatial KS + SS model yields a high probability of fisher detections in east–west running river canyons of the northern Sierra Nevada (Fig. 5b).

Inclusion of a spatial autocovariate term improves the skill of models using either field or GIS vegetation data, although the models are weaker than their statewide counterparts (Table 4). Model residuals are not significantly autocorrelated at any lag distance. Including environmental variables offers only a slight improvement in model fit over the model based simply on spatial autocovariation (AIC of 202.4 vs. 206.8; Table 4).

The KS + SS models are equivalent to, or better than, the statewide models at predicting survey results statewide, in the Klamath Shasta region, and in the southern Sierra Nevada (Table 5). Excluding the 233 non-detections from the unoccupied region in the statewide model does not improve model fit to statewide patterns in fisher detections.

Klamath/Shasta model

Despite the smaller sample size, fisher detections in northern California are strongly associated with all predictor variables except proximity to improved roads (Table 3). Relief, field.structure, field.CWHR2, and field.hardwood exhibit the strongest association with the pattern of fisher detections, although the associations with field vegetation data are only slightly stronger than with GIS vegetation data (Table 3).

GAM models based on relief, ann.ppt, and GIS.CWHR2 have good classification skill for the survey data from northwestern California, with cross-validated AUC values of 0.84 (Table 4, Fig. 7). Higher misclassification rates occur in the northwest corner of the region, where the model overpredicts fisher detections. Model residuals are significantly positively autocorrelated to a lag distance of 10 or 20 km (Fig. 4c). The addition of the SA term increases the cross-validated AUC from 0.84 to 0.89 for the GIS-based model (Table 4), and the model produced by fitting environmental factors and then SA is superior to the model based solely on SA (AIC values of 82.0 vs. 89.9; Table 4).

The Klamath/Shasta models perform relatively well in the Klamath/Shasta and northern Sierra Nevada test regions, but poorly in the southern Sierra Nevada (Fig. 5c, Table 5). In the southern Sierra, the few survey units where the model correctly predicts fisher detections tend to be western units at the lower elevations in areas of lower precipitation.

Southern Sierra model

Physical and vegetation factors at the 10-km^2 scale are weakly associated with fisher detections in the southern Sierra, and only GIS.dense.forest is significant at $P <$

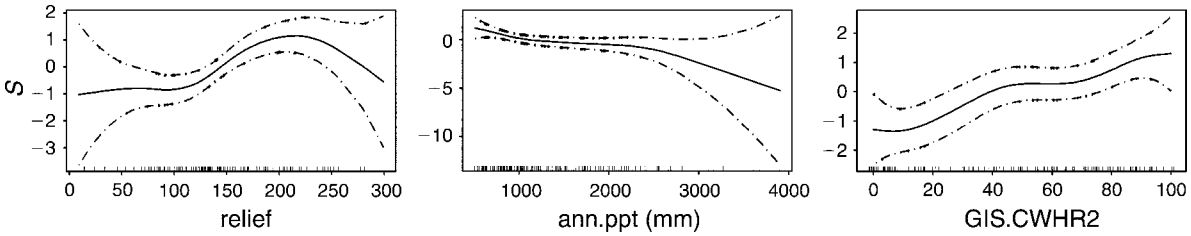

FIG. 6. Partial response curves for the Klamath/Shasta + southern Sierra GAM model based on topographic relief (relief), annual precipitation (ann.ppt), and forest structure (GIS.CWHR2). See Fig. 3 for an explanation of the response curves.

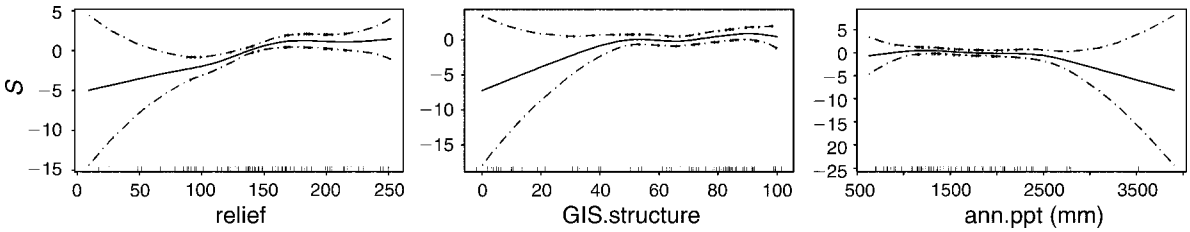

FIG. 7. Partial response curves for the Klamath/Shasta GAM model based on topographic relief (relief), forest structure (GIS.structure), and annual precipitation (ann.ppt). See Fig. 3 for an explanation of the response curves.

0.05 (Table 3). Although the sample size is small ($n = 88$ sample units, each with six track-plate stations and 1–2 remotely triggered cameras), the result is puzzling, given the strong association of fisher detections with relief and other vegetation variables in the statewide and northern data sets.

GAM models based on GIS vegetation data have higher skill than those based on field vegetation data (Table 4), but none of the nonspatial or spatial models provides a good fit to the survey data (Table 4). We hypothesized that this might be due to the greater heterogeneity and finer grain of vegetation mosaics in the southern Sierra compared to northwestern California, in which case, fisher survey data should be more strongly associated with vegetation variables integrated over smaller areas. In the southern Sierra, fisher detections are slightly more strongly associated with vegetation variables assessed at 3 km^2 than at 10 km^2, whereas in the Klamath/Shasta region, stronger association can be at 3-km^2 or 10-km^2 scale, depending on the variable (Table 6). The differences in association are small and dependence on spatial scale does not seem to explain the systematically lower association of fishers with GIS and field vegetation variables in the region.

Residuals from the GAM model based on adj.elevation, ann.ppt, and GIS.dense.forest exhibit no spatial autocorrelation in the southern region (Moran's $I = -0.01$, $P > 0.10$) (Table 4, Figs. 4d and 8). In other regions, the southern Sierra model produces strikingly different patterns of fisher habitat than those observed or predicted by the other models (Fig. 5d). Low predicted probabilities of occurrence prevail over most survey points in the northern Sierra Nevada and Klamath/Shasta regions, and high detection probabilities are mapped at high elevations in drier regions to the east of actual fisher detections. Fisher surveys occurred at systematically higher adjusted elevations in the southern Sierra (2808 ± 482 m, mean ± SD) than in the Klamath/Shasta (2358 ± 476 m) region, and also systematically drier locations. The association of fishers with precipitation is also different: in the southern Sierra, fisher detections are more likely at lower and drier sites, whereas in the Klamath/Shasta, fishers are only lacking at the very wettest sites. These differences in environmental associations are indicated by the poor fit of the southern Sierra model to the other regional and subregional data sets, in particular to the Klamath/Shasta data set, where an AUC value of 0.52 is hardly better than a random association between predicted and observed values (Table 5).

Statewide habitat envelope model

The MAXENT model based on fisher detections and pseudo-absences drawn from statewide environmental data selected ann.ppt, GIS.dense.forest, and relief and produces a probability map similar to the statewide GAM model (Fig. 9). The correlation between GAM and MAXENT scores at sampling unit locations is 0.83. As expected, the MAXENT model identifies more area with high probability of predicted occurrence, especially in the Klamath/Shasta region and at middle elevations of the southern Sierra Nevada. Like the GAM models, MAXENT models predict low probabilities of occurrence over much of the northern and central Sierra Nevada.

DISCUSSION

We first discuss our findings in the light of current understanding of fisher habitat associations before turning to the role of spatial autocorrelation. We then

TABLE 6. Univariate tests of association between fisher detections and selected vegetation factors in the Klamath/Shasta and southern Sierra region at two different spatial scales based on the Wilcoxon U test.

		Scale 3 km^2		Scale 10 km^2	
Region	Variable	Wilcoxon Z	P	Wilcoxon Z	P
Klamath/Shasta	GIS.dense.forest	−3.253	0.001	−2.659	0.008
	GIS.CWHR2	−3.694	<0.001	−3.706	<0.001
Southern Sierra	GIS.dense.forest	−2.576	0.015	−2.280	0.023
	GIS.CWHR2	−1.649	0.099	−1.330	0.183

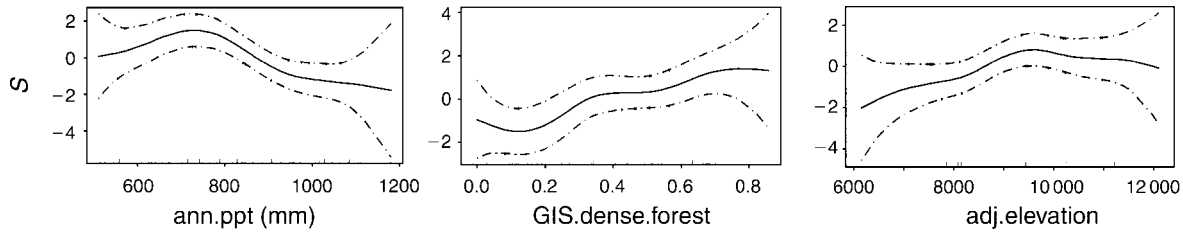

FIG. 8. Partial response curves for the southern Sierra GAM model based on annual precipitation (ann.ppt), forest structure (GIS.dense.forest), and latitude-adjusted elevation (adj.elevation). See Fig. 3 for an explanation of the response curves.

consider possible explanations for the absence of fishers in the northern and central Sierra Nevada and conclude with a brief discussion of the management implications of our findings.

Fisher habitat relations

Habitat associations of fisher detections in the statewide survey reinforce current scientific understanding of the species as inhabiting rugged terrain with extensive closed-canopy, mid-to-late seral mixed conifer or mixed hardwood–conifer forest. We have shown that fishers are less likely to occur in subalpine forest types such as red fir (*Abies magnifica*) or lodgepole pine (*Pinus contorta*) forests, and we recommend revising the California Wildlife Habitat Relationship System model for fishers to reflect the low association of fishers with these habitat types.

Fishers are associated with dense forest cover in both the Klamath/Shasta region and the southern Sierra Nevada, but these populations differ in the details of their habitat associations. Fisher detections in the Klamath/Shasta region were clustered at mid-elevations in rugged mountainous areas and were negatively associated with highest levels of precipitation. Like Carroll et al. (1999), we found that fisher detections in northwestern California were positively associated with the proportion of the landscape in mature montane forest and montane hardwood forest, and with increasing average tree size and canopy closure. These relationships hold for both field-based and satellite-derived estimates of forest extent, composition, and structure. As noted by Carroll et al. (1999), fishers may associate with landscapes with a high fraction of mature forest because those areas pose a lower risk of predation by raptors and other mammalian carnivores (Powell et al. 2003) and offer higher levels of forest-associated prey.

In contrast, fisher detections in the southern Sierra region were associated with satellite-derived estimates of dense cover, but were not strongly associated with topography, forest composition, or structure. This pattern may partly reflect undersampling of lower elevations in the southern Sierra region. The survey grid may not have spanned a sufficient range of climatic, topographic, and vegetation conditions to allow fisher habitat preferences to be discriminated. Campbell (2004) using a similar set of data, also described fisher occurrence on the basis of a simple model that included only slope as a predictor (although this was correlated with other vegetation features).

Another circumstance that may be responsible for the unique set of predictors associated with fisher occurrence in the southern Sierra is the fisher's diverse diet in this region. Zielinski et al. (1999) found that the diet of fishers in the southern Sierra Nevada includes prey items from both forest and non-forest habitats. Porcupines and snowshoe hares, which are staples of fisher diets elsewhere, do not occur in the southern Sierra Nevada, where fishers eat lizards, birds, and insects in addition to mammal prey (Zielinski et al. 1999). This suggests that

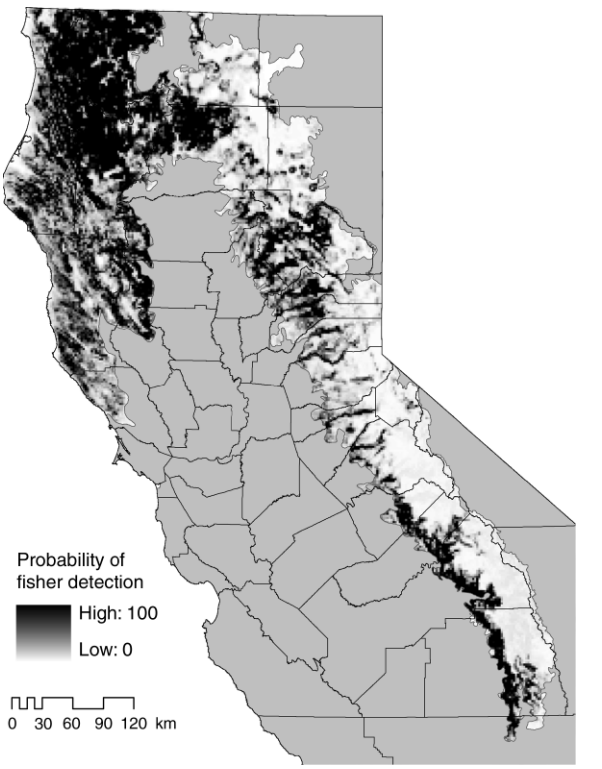

FIG. 9. Mapped probabilities of fisher detection within the species' historic range in California based on the MAXENT model and statewide survey data. Darker areas have higher calculated probabilities.

fishers may be foraging across a wide range of montane habitats in the southern Sierra.

Spatial autocorrelation in fisher detections

The fisher survey data reveal two dominant scales of distribution pattern: regional and local. Statewide, three regions emerge, including the occupied Klamath/Shasta and southern Sierra Nevada regions, where fishers were detected at roughly one-third of the sampling units, and the central and northern Sierra Nevada, an unoccupied area representing more than half of the species' historical range in the state. None of the spatial or nonspatial models fits this biogeographic pattern closely, in part because of the different habitat associations of northern vs. southern populations and in part because the statewide average frequency of detections (model prevalence) yields models that underpredict fisher detections in the occupied regions and overpredict detections in the unoccupied region. The spatial autocorrelation structure of model residuals for the nonspatial GAM models reflects these large-scale effects, showing significant positive autocorrelation up to 20 km and decreasing autocorrelation with increasing distance for 50–100 km.

Fisher detections in the Klamath/Shasta are locally clustered and the pattern suggests the effect of territorial and dispersal behavior on current fisher distributions in the region. GAM models based solely on environmental factors produce autocorrelated model residuals at the 10-km scale and are weaker than a simple spatial autoregressive model or the model combining both environmental factors and the spatial autoregressive term (Table 4). We can say little about the relative roles of environment vs. movement behavior in the distribution of fishers in the southern Sierra Nevada. Of the environmental factors, detections are associated only with dense forest and are not spatially autocorrelated at a scale of 10–20 km. Monitoring of the survey localities over a longer term and expansion of the survey to lower elevations are necessary to better understand the environmental, behavioral, and demographic controls on the species' distribution in this region.

The absence of fishers in the northern and central Sierra Nevada

Habitat quality, dispersal limitation, and demography may all be contributing to the current absence of fishers in the northern and central Sierra. Several lines of evidence indicate limited high-quality habitat in the unoccupied region. All of the models estimate low detection probabilities over much of the area (Fig. 5). The nonspatial statewide GAM model is more skillful than the model excluding data from the unoccupied region (KS + SS). Both the GAM models based on detection vs. non-detection and the more liberal MAXENT model (based on detections only) indicate extensive areas of unsuitable habitat, especially in the far northern Sierra. Forests of the northern Sierra Nevada have been more extensively impacted by historical logging than those farther south, where Yosemite and Sequoia-King's Canyon National Parks still harbor extensive late-seral forests (Franklin and Fites-Kaufmann 1996, Zielinski et al. 2005). Late-seral forests now occupy <10% of the northern region compared to >40% in the mid-20th century (Franklin and Fites-Kaufmann 1996, Zielinski et al. 2005). The highest habitat scores in the northern Sierra Nevada occur in steep, east–west running canyons such as the canyon of the north fork of the American River in Nevada County and the Middle Fork of the Feather River in Plumas County. These areas were identified by Franklin and Fites-Kaufmann (1996) as supporting much of the remaining late-seral old-growth forest on public lands in the northern and central Sierra Nevada.

The absence of fishers from areas predicted to have high suitability in the northern Sierra Nevada could be due, at least in part, to their inaccessibility to fishers or because surplus individuals are not being produced in the occupied regions. Individuals attempting to disperse into the northern Sierra Nevada from the closest occupied sites south of Lake McCloud in the Shasta National Forest would encounter numerous barriers, including the Pit River and the Highway 299 corridor (where much of the land cover is chaparral, early-seral forest recovering from the 1992 Fountain Fire, or agriculture), only to reach fragmented forests of the Lassen National Forest (Fig. 10). The northern limit of fisher detections in the southern Sierra occurs inside Yosemite National Park just south of the Merced River and Yosemite Valley. The limit is not obviously associated with major gaps in forest habitat, although forest habitat is extensively modified in the surrounding national forest lands to the north and east, largely as a result of fires and timber harvest.

Even allowing for dispersal routes into the unoccupied northern Sierra region, if fisher populations are not increasing in their current distribution, there may not be a steady supply of emigrating individuals to reoccupy these areas. Recent reviews of the vital rates of fishers in California, and the effect of these rates on viability, do not forecast significant growth in the fisher population (Powell and Zielinski 1994; R. H. Lamberson, R. L. Truex, W. J. Zielinski, and D. MacFarlane, *unpublished manuscript*). Unfortunately, detailed demographic data are not available and we cannot parameterize a spatially explicit dynamic population model to examine this possibility (Guisan and Zimmerman 2000).

Management implications

The conservation of fishers is a major concern to conservation biologists in the western United States, as evidenced by the favorable response of the U.S. Fish and Wildlife Service to the most recent petition to list the fisher as endangered in the Pacific States (U.S. Federal Register, 8 April 2004). Ecologists increasingly use species distribution models to address conservation

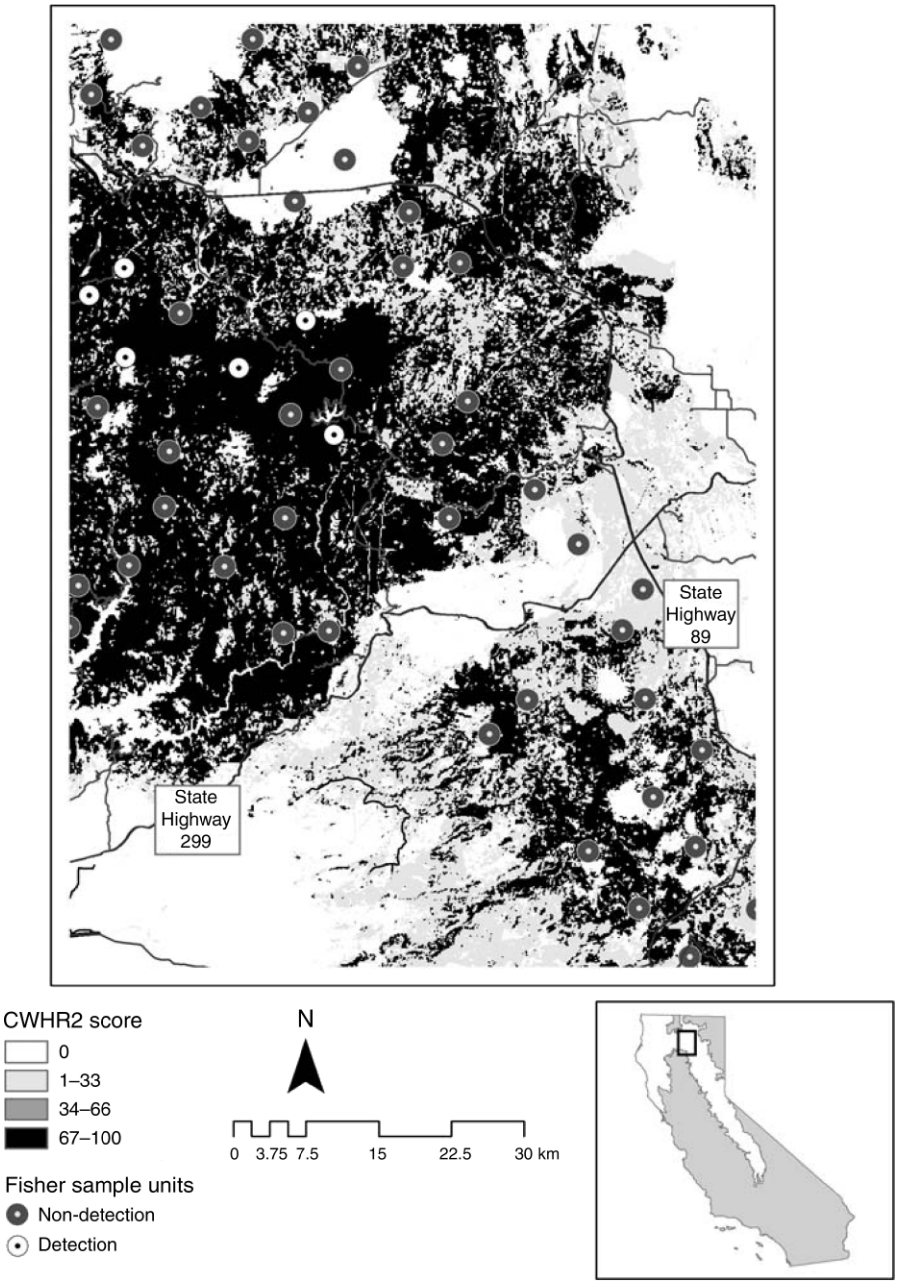

FIG. 10. Map of fisher habitat quality in the area between the Klamath/Shasta and northern Sierra Nevada subregions. Fisher sampling unit locations (fisher detections vs. non-detections) are superimposed on GIS.CWHR2 scores (see Table 1) derived from U.S. Forest Service vegetation maps. Higher scores indicate higher habitat suitability. State highways 299 and 89 are labeled.

and management issues (Scott et al. 2002, Latimer et al. 2006), and our model and its successors could be used by managers and policy makers to inventory and monitor fisher habitat extent and condition, to identify regional bottlenecks in fisher habitat connectivity, to identify areas for fisher habitat maintenance or restoration, to consider candidate areas for reintroduction, and to explore implications of regional climate change. Such applications would be strengthened by additional studies of GIS data quality and model sensitivity and uncertainty (Hines et al. 2005).

The reliability of existing digital vegetation maps has been of particular concern, given the documented affinity of fishers with late-seral montane forests in California and the known limitations of satellite-derived vegetation maps (Miller and Franklin 2002, Hines et al.

2005). The USFS databases used here have been documented as having only moderate (70–80%) site-level accuracy for vegetation type and lower accuracy for canopy cover class (50–60%) and crown size class (30–40%) (Franklin et al. 2000, Hines et al. 2005). The moderate correlation ($0.37 < r < 0.72$) between field-based and GIS-based vegetation variables was higher than we expected, as was the highly significant association between fisher detections and GIS vegetation data and the close similarity of predictive models derived from field and GIS data. The agreement between field and GIS results is presumably because the data were integrated over large assessment areas (10 km^2) rather than applied at the pixel or site scale. At this scale, the analysis appears to be relatively robust to local inaccuracies in the GIS data.

Our finding that vegetation databases derived from remotely sensed imagery perform at least as well as field vegetation data implies that fisher habitat at the home range scale can be monitored using public geospatial databases that are being maintained by state and federal agencies (Franklin et al. 2000, Rogan and Chen 2004), and that field collection of habitat data could focus on refining and validating remote-sensing models and quantifying map data quality (Zielinski et al. 2006*b*). Maintenance of a regionally consistent database across state and agency jurisdictional boundaries would enable range-wide monitoring of fisher habitat conditions and progress toward restoring habitat conditions in the central and northern Sierra.

Could fishers be successfully reestablished in unoccupied regions of the central and northern Sierra Nevada? Our data suggest that the distribution of potential habitat in this region is limited to a few areas associated with the densely forested river canyons of the northern Sierra. These potential habitat areas are smaller and less well connected than areas within the currently occupied regions of the Klamath/Shasta region or the southern Sierra. This suggests caution in implementing a reintroduction and we would recommend additional analyses to determine the likelihood that these areas could sustain a viable population. In the near term, however, the potential habitat areas that were identified in the northern Sierra Nevada would be places to focus future surveys because these are the most likely settling places for fishers that may naturally disperse south and east from the Klamath region. In this regard, our statewide model (Fig. 5a) was the best at predicting absence in the northern Sierra Nevada and should probably be used to map habitat and for other fisher conservation applications in this region.

Fishers currently occur in portions of Oregon, Idaho, Montana, British Columbia, and Alberta. Developing empirical landscape habitat-suitability models will assist conservation in these regions. Fishers have been extirpated from Washington, but plans for reintroductions have included an expert-derived habitat model that has been used to select from candidate reintroduction sites (Lewis and Hayes 2004). Future modeling efforts, however, are likely to be built using detection data that come with more information than simple occurrence. Identification of sex and individuals is possible using genetic samples derived from scat and hair (Eggert et al. 2003, Riddle et al. 2003, McKelvey et al. 2006), and methods have been developed to collect hair when fishers visit enclosed track plate stations (Zielinski et al. 2006*a*). Future models will be able to link habitat value to demographic information, which will add considerably to the utility of empirical habitat models for conservation planning.

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APPENDIX A

Descriptions of variables tested for association with the detection of fishers in California (*Ecological Archives* A017-090-A1).

APPENDIX B

Correlations among environmental variables applied to fisher habitat modeling (*Ecological Archives* A017-090-A2).