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USING FOREST INVENTORY DATA TO ASSESS FISHER RESTING HABITAT SUITABILITY IN CALIFORNIA

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Abstract. The fisher (*Martes pennanti*) is a forest-dwelling carnivore whose current distribution and association with late-seral forest conditions make it vulnerable to stand-altering human activities or natural disturbances. Fishers select a variety of structures for daily resting bouts. These habitat elements, together with foraging and reproductive (denning) habitat, constitute the habitat requirements of fishers. We develop a model capable of predicting the suitability of fisher resting habitat using standard forest vegetation inventory data. The inventory data were derived from Forest Inventory and Analysis (FIA), a nationwide probability-based sample used to estimate forest characteristics. We developed the model by comparing vegetation and topographic data at 75 randomly selected fisher resting structures in the southern Sierra Nevada with 232 forest inventory plots. We collected vegetation data at fisher resting locations using the FIA vegetation sampling protocol and centering the 1-ha FIA plot on the resting structure. To distinguish used and available inventory plots, we used nonparametric logistic regression to evaluate a set of a priori biological models. The top model represented a dominant portion of the Akaike weights (0.87), explained 31.5% of the deviance, and included the following variables: average canopy closure, basal area of trees <51 cm diameter breast height (dbh), average hardwood dbh, maximum tree dbh, percentage slope, and the dbh of the largest conifer snag. Our use of routinely collected forest inventory data allows the assessment and monitoring of change in fisher resting habitat suitability over large regions with no additional sampling effort. Although models were constrained to include only variables available from the list of those measured using the FIA protocol, we did not find this to be a shortcoming. The model makes it possible to compare average resting habitat suitability values before and after forest management treatments, among administrative units, across regions and over time. Considering hundreds of plot estimates as a sample of habitat conditions over large spatial scales can bring a broad perspective, at high resolution, and efficiency to the assessment and monitoring of wildlife habitat.

Key words: California; FIA; fisher; forest inventory; habitat suitability; Martes pennanti; *modeling; monitoring.*

INTRODUCTION

The goal of ecosystem management requires biological information at large spatial scales, including data to monitor populations and habitats of wildlife species of interest. At geographic scales that make experimentation difficult, habitat models provide one way to develop hypotheses about features that affect distribution (Gaston and Blackburn 1999, Manel et al. 2000). The challenge of developing habitat models at large scales, and using them to monitor habitat suitability, has been undertaken using various approaches. One involves regional landscape suitability models that characterize habitat value on the basis of aggregate features of forest type and structure that are assessed by photograph or satellite imagery. These are based on either expert opinion about the value of type and structural class polygons to a particular species, so-called knowledge-based models (e.g., California Wildlife Habitat Relations [CWHR; Mayer and Laudenslayer 1988]; Habitat Evaluation Procedures [HEP; USDI Fish and Wildlife Service 1980]; Habitat Suitability Indices [HSI; Schamberger et al. 1982, Houston et al. 1986, Johnson and O'Neil 2001]), or on empirical statistical models that generate predicted habitat values (e.g., Mladenoff et al. 1995, Carroll et al. 1999, Manel et al. 2001, Manly et al. 2002). The knowledge-based systems are often overly simplistic, make imprecise predictions, or overestimate the quantity of suitable habitat or the prediction of species occurrence (Laymon and Barrett 1986, Edwards et al. 1996, Garshelis 2000, Van Horne 2002). However, they can be useful for conservation planning at large spatial scales when their success is based on whether or not a species occurs in a region (Edwards et al. 1996).

Empirical landscape suitability models, developed by associating animal locations with a set of environmental covariates that adequately predict them, are often more

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PLATE 1. Male fisher (*Martes pennanti*) at a rest site in the Six Rivers National Forest in northwestern California, USA. Photo credit: Gregory A. Schmidt.

accurate descriptions of occupied habitat but they require new field data, are expensive to develop and apply, and often require inputs unavailable to managers (Stauffer 2002). Both approaches share the important disadvantage of excluding habitat elements (e.g., snags, logs, sources of water) from consideration that can only be detected and measured on the ground. The cost of measuring such habitat elements over a region (i.e., multiple administrative units such as a number of contiguous national forests) is usually prohibitive.

The expense of developing and applying empirical models over a region is diminished when models can be developed using pre-existing measurements of vegetation sample plots that are routinely updated. The Forest Inventory and Analysis (FIA) program provides such a system. The Forest and Rangeland Renewable Resources Research Act of 1978 authorized and promoted a nationwide survey and analysis of all renewable natural resources (Frayer and Furnival 1999); one result was the establishment of the FIA program. The design consists of sample points located in a systematic hexagonal grid (centers of each hexagon spaced 5.47 km apart) across all ownerships in the United States, with environmental variables (e.g., live and dead vegetation, topography, exposed rock) described at each point once every 10 years (Roesch and Reams 1999). FIA data are gathered and used to assist in forest management planning and monitoring of forest structure and plant communities over regions.

FIA data are useful for habitat modeling because they are a temporally and spatially reliable source of wildlife habitat data across large areas and have long-term institutional support. Previous studies have demonstrated the value of collocating animal sampling with FIA sample plots when building wildlife habitat selection models (e.g., USDA Forest Service 2000, Dunk et al. 2004; Welsh et al., *in press*). Linking models to vegetation data that are regularly resampled makes it possible to monitor the suitability of habitat over time. This approach contrasts strongly with the inferences that can be drawn using habitat suitability models developed using vegetation data collected from unique sampling protocols and whose relationship to data collected at plots used for regional inventory of forest attributes is unknown. These models would be difficult to integrate with institutional inventory programs, like FIA, and could not be easily updated with new inventory data.

Fishers (*Martes pennanti*; see Plate 1) occur in mature, structurally complex, conifer and mixed conifer–hardwood forests and have been described as one of the most habitat-specialized mammals in North America (Harris et al. 1982, Buskirk and Powell 1994). They occupy home ranges that can exceed 6000 ha (Powell and Zielinski 1994, Zielinski et al. 2004*a*). The fisher has been the subject of relatively little ecological research in western North America, yet it has been extirpated from extensive regions of its historical range in the Pacific States (Gibilisco 1994, Powell and Zielinski 1994, Zielinski et al. 1995, Aubry and Lewis 2003). In California, the fisher appears to occupy less than half of the range it did in the early 1900s and the two remnant populations are separated by a distance of

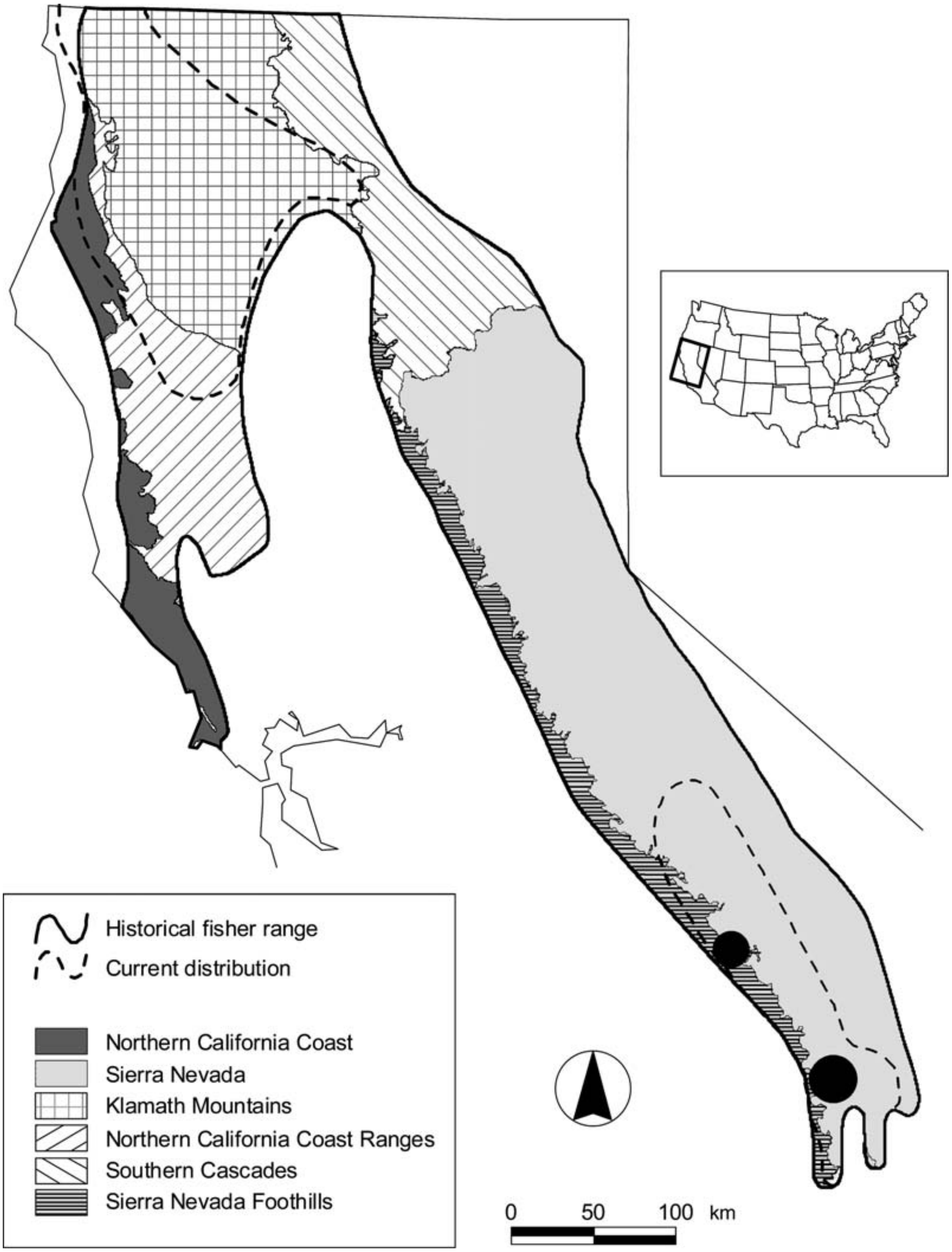

FIG. 1. Sierra National Forest (Mazzoni 2002; small circle) and Sequoia National Forest (Zielinski et al. 2004*a*, *b*; larger circle) fisher study areas relative to the approximate boundaries of existing fisher populations and Ecological Sections (Bailey 1994) within the historical range of the fisher in California (Grinnell et al. 1937).

approximately 400 km (Fig. 1; Zielinski et al. 1995). Fisher populations in the Pacific states have been petitioned for listing under the Endangered Species Act on three occasions; the most recent resulted in a finding that the fisher was warranted for listing as endangered, but that such an action was precluded by higher priorities (USDI Fish and Wildlife Service 2004).

The conservation of fisher populations in the Pacific states requires an understanding of their habitat ecology and the development of population and habitat monitoring programs. A program to monitor populations, based on detecting fishers at baited track-plate stations (Zielinski et al. 1995), has been developed and implemented in the Sierra Nevada (Zielinski and Stauffer

1996, Zielinski and Mori 2001). Although there is considerable interest in managing Sierra Nevada forests to improve habitat conditions for fishers (Center for Biodiversity et al. 2000, USDA Forest Service 2001), no program is in place to monitor changes in fisher habitat.

Fisher habitat has been described for various spatial scales and by describing their foraging, resting and denning locations (Powell et al. 2003). However, much of our view of habitats used by fishers comes from characterizing their daily resting locations. Resting locations protect forest mustelids from unfavorable weather and predators (Buskirk et al. 1989, Kilpatrick and Rego 1994, Zalewski 1997, Wilbert et al. 2000, Zielinski et al. 2004*b*), thus choosing them is probably one of the most important decisions fishers make outside of the breeding season, and is why the model we present here is based on predicting the value of resting habitat. We acknowledge, however, that foraging and denning habitats are also important, and that our description of habitat is restricted to resting habitat features. Too few natal dens have been discovered in California (fewer than 10; W. Zielinski, *unpublished data*) to model their characteristics. Although foraging sites are much more difficult to identify than resting sites, the diet of fishers in California is very diverse (Zielinski et al. 1999) such that foraging needs may be fulfilled in a diversity of environments.

Most resting structures are used by individual fishers for relatively short bouts (i.e., hours) each day and, excluding the breeding season, individual structures are infrequently reused (e.g., Jones 1991, Kilpatrick and Rego 1994, Seglund 1995, Zielinski et al. 2004*b*). Wood structures (live and dead standing trees and logs) comprise most of the resting structures used by fishers in California (Zielinski et al. 2004*b*), but fishers also rest in brush piles, rockpiles, and holes in the ground (Grinnell et al. 1937, Coulter 1966, Powell 1977, 1993, Arthur et al. 1989, Kilpatrick and Rego 1994, Zielinski et al. 2004*b*). In California, approximately 75% of resting structures were large standing trees and snags (average diameter at breast height $>$100 cm; Zielinski et al. 2004*b*), that were significantly larger, on average, than the trees that were available within their home ranges.

Previous work suggests that fishers, and the closely related American marten (*M. americana*), exhibit the greatest selection for natal dens and resting sites, and the least for foraging locations (Kelly 1977, Burnett 1981, Arthur et al. 1989, Jones and Garton 1994, Powell 1994) indicating that resting and denning structures may be their most important habitat components. Although the resting structure itself is the feature of most importance to fishers when they rest, previous work has demonstrated that environmental features in the immediate vicinity of the resting structure (the resting site) also are important predictors of resting location (Zielinski et al. 2004*b*). In the southern Sierra Nevada, in particular, resting structures were often large-diameter black oaks (*Quercus kelloggii*) and the resting site was distinguished by the presence of large diameter trees, variation in tree diameters, and steep slopes near water (Zielinski et al. 2004*b*). By centering a 1-ha FIA plot on the resting structure we chose to build a predictive resting habitat model that included the resting structure as well as the vegetation and topographic characteristics in the immediate vicinity (the resting site).

The previous use of FIA vegetation data for developing habitat models has involved taxa for which individuals, if they are present, can be expected to be discovered by searching the FIA plot (i.e., mollusks [Dunk et al. 2004]; salamanders [Welsh et al., *in press*]). Conversely, the 1-ha plot is often only a small portion of the home range of individual mammals and birds. Many of the species that use larger areas, however, often find exceptional habitat value at a limited number of point locations. Because fishers are selective about their use of resting structures and the vegetation in their immediate vicinity (Zielinski et al. 2004*b*), if we can use the vegetation and topographic data from FIA plots to develop a model that can predict the suitability of resting habitat at each plot, then we can apply this model to each of the hundreds of FIA plots in a region comprised of a number of contiguous national forests. The mean, variance and spatial attributes of the predicted suitability values in the region contain information about the general condition of resting habitat in the region each time the FIA plots are resampled and the model reapplied. This approach resembles the method used to estimate the extent of the habitat for the California Spotted Owl (*Strix occidentalis occidentalis*) using FIA plot data (USDA Forest Service 2000).

The goal of this paper is to develop and apply a model of resting habitat suitability that can be used to monitor the suitability of fisher resting habitat at FIA points distributed across the species' range in the Sierra Nevada. As such, our work shares the objective described by McDonald and McDonald (2002) of using a habitat selection model to quantify changes in the distribution or abundance of habitat.

METHODS

Study area

The data used to develop the habitat model were collected in conjunction with two different studies on the resting habitat ecology of fishers in the Sierra Nevada. Both studies were conducted within the Sierra Nevada Mountain and Sierra Nevada Foothill ecosections (Bailey 1994). The first was conducted from April 1994 to October 1996 on 300 km^2 in the Sequoia National Forest in Tulare County (Zielinski et al. 2004*b*; Fig. 1), and the second was conducted from October 1999 to May 2000 on 260 km^2 of the Sierra National Forest in Fresno County (Mazzoni 2002; Fig. 1). Elevations ranged from approximately 800 m to 2500 m. The primary vegetation types (Mayer and Laudenslayer

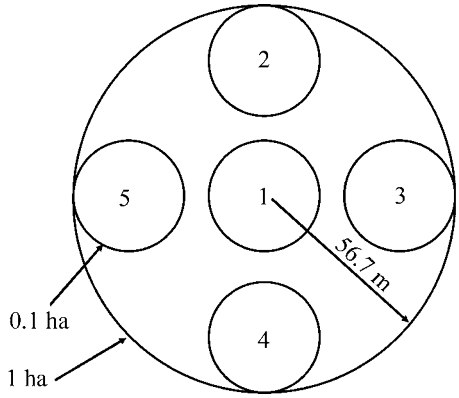

FIG. 2. Schematic drawing of the Forest Inventory and Analysis (FIA) sampling plot.

1988) were Sierran mixed conifer, ponderosa pine (*Pinus ponderosa*), red fir (*Abies magnifica*), montane hardwood, and various chaparral types. Lodgepole pine (*Pinus contorta murrayana*), Jeffrey pine (*Pinus jeffreyi*), and grassland/meadow types comprised less than 10% of the area. Individual-tree-selection harvest has been the dominant silvicultural technique within the study areas (McKelvey and Johnson 1992), but there has been little timber harvest activity since the mid-1990s.

Fisher resting sites and FIA vegetation data

The fisher field studies used similar methods to identify the resting locations of radio-collared fishers. Every few days an observer tracked each study animal on foot to a resting structure (Mazzoni 2002, Zielinski et al. 2004*b*) resulting in a total of 78 and 397 resting occasions from 11 (four males and seven females) and 12 individuals (four males and eight females) on the Sierra and the Sequoia study areas, respectively. Most (86%) were standing live or dead trees and logs. Seventy-five resting locations (35 from the Sierra and 40 from the Sequoia National Forest study areas) were randomly selected for vegetation sampling using the USDA Forest Service Region 5 FIA protocol (USDA Forest Service 1999); a few resting locations had to be reselected due to difficulties relocating them. In the Sequoia study area only, the number of resting locations selected was proportional to the numbers used by each sex.

The FIA protocol involves the collection of vegetation data at five 0.1-ha subplots enclosed in a 1.0-ha circle (Fig. 2). Within each subplot, individual trees and shrubs are identified to species, and a comprehensive list of vegetation structure and composition variables are either measured or estimated (e.g., percentage of canopy cover, diameter at breast height, age). In addition, the quantity of downed wood (measured in various size classes), rock, and other physical features are estimated (see USDA Forest Service 1999 for details on FIA sampling protocols and data availability). For plots sampled at fisher resting sites, the resting structure served as plot center and was included in measurements taken at the plot.

Analyses

We built fisher resting habitat suitability models by comparing the vegetation characteristics at sites used by fishers for resting with those in FIA plots located in comparable environmental conditions (Fig. 3). Thus, our habitat model was developed by comparing data collected at plots that were used by fishers with a set of plots that were available to them (Boyce et al. 2002). Our model assumes that we are distinguishing used from random locations (e.g., Henner et al. 2004), not from non-used locations. As is typical for this form of analysis, we assumed that the available sites were a random selection of locations where the probability of use was low; an assumption that justified the use of the logistic regression model. Low use of these sites was expected due primarily to the fisher's naturally low density and large individual home ranges (Zielinski et al. 2004*a*).

We limited the available data set to include only those 232 FIA plots within the approximately 2230 km^2 area between suitable elevations (1100 and 2300 m; Zielinski et al. 1997) that also were within either the Sierra Nevada (code M261E) or the Sierra Nevada Foothills ecosection (code M261F) of the Ecological Unit of California system (Bailey 1994; Fig. 3). The area includes primarily federal lands and overlaps much of the Mariposa and Minarets Ranger Districts, and the west side of the Pineridge and Kings River Ranger Districts of the Sierra National Forest. On the Sequoia National Forest the area includes the Hume Lake, Tule River, Hot Springs Ranger Districts and west side of the Greenhorn Ranger District. This region included each of the fisher study areas and overlapped significantly with the currently occupied portion of the historical range of the fisher on the western slope of the southern Sierra Nevada (Grinnell et al. 1937, Zielinski et al. 2005). We collected the FIA-protocol vegetation data at fisher resting sites in 1999 and 2000. The FIA data we used to assess available habitat was collected in 1997 and 1998 by contractors hired by the USDA Forest Service.

We used nonparametric logistic regression models, specifically generalized additive regression models (GAMs; Hastie and Tibshirani 1990), to develop a resting habitat suitability model for distinguishing FIA inventory plots from those centered on fisher resting structures. We used this model to predict the suitability of inventory plots as resting habitat. GAMs are an excellent tool for data exploration (Yee and Mitchell 1991) as well as prediction (Pearce and Ferrier 2000). They relax distributional assumptions about the dependent variable and they do not assume any specific relationship with the predictor variables. Instead, the data define the form of the relationship between response and predictor(s), which is estimated simultaneously using a loess smoothing function (Cleveland and Devlin 1988). Our approach defines a relative measure of resting habitat suitability as the predicted probability of having been drawn from the

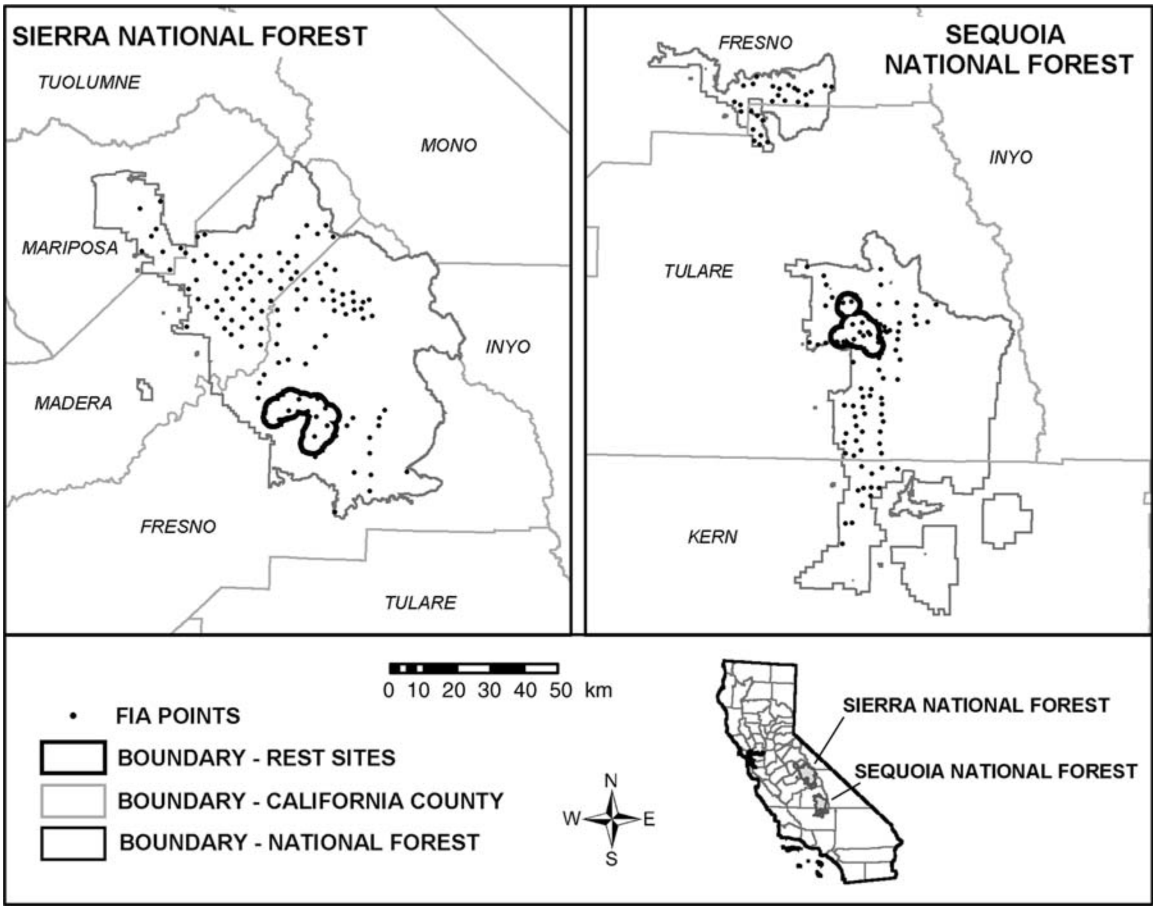

FIG. 3. Spatial distribution of locations of fisher resting structures included in the sample of used locations (polygons) and the FIA vegetation plots (black dots) that constituted the set of available plots. FIA plots were included if they fell between 1100 and 2300 m elevation and were also within either the Sierra Nevada (code M261E) or the Sierra Nevada Foothills section (code M261F) of the Ecological Unit of California system (Bailey 1994). The area includes primarily federal lands and overlaps much of the Mariposa and Minarets Ranger Districts, and the west side of the Pineridge and Kings River Ranger Districts of the Sierra National Forest. On the Sequoia National Forest, the area includes the Hume Lake, Tule River, and Hot Springs Ranger Districts, and the west side of the Greenhorn Ranger District.

set of fisher resting plots; this value is calculated for each inventory and resting plot using the model.

Model development

We applied an information-theoretic approach (Burnham and Anderson 2002) to model development and selection, seeking the maximum predictive power with the fewest variables. We compared models using Akaike's Information Criteria ($\mathrm{AIC_c}$; Akaike 1973) and we calculated the weights of $\mathrm{AIC_c}$ values (Burnham and Anderson 2002) and the relative likelihood of the best model compared to all others ([$\mathrm{AIC_c}$ weight of the highest ranking model]/[$\mathrm{AIC_c}$ weight of model *i*]). We evaluated each model's deviance reduction relative to the deviance of the null model using D^2 values (Guisan and Zimmerman 2000), which index the percentage of the deviance explained (analogous to R^2 in linear regression [Yee and Mitchell 1991]). We were less interested in classifying individual FIA plots as either "suitable" or "unsuitable" (i.e., discriminatory ability [Vaughan and Ormerod 2005]) than in deriving a quantitative measure of the probability of resting habitat suitability value, from 0 to 1, at each plot. Because discriminatory ability is a commonly reported classification diagnostic, we evaluated it using Cohen's Kappa (Cohen 1960, Manel et al. 2001), assuming a probability threshold of 0.5.

We restricted the large number of potential FIA variables to those, or their surrogates, that were used or selected by fishers in previous studies (i.e., Buck et al. 1994, Seglund 1995, Mazzoni 2002, Zielinski et al. 2004*b*). Most of the variables included were related to vegetation (tree and shrub) density, seral stage, conifer and hardwood tree size, standing and downed wood, conifer/hardwood ratio, and local topography (Table 1). To assist interpretation, we conducted univariate comparisons (resting site plots vs. inventory plots) for

TABLE 1. Abbreviations and descriptions of variables used in candidate a priori fisher resting-habitat suitability models.

Abbreviation	Description
CC	canopy cover: sum of percent cover of dominant and codominant trees, including overlaps
CC_STD	standard deviation of canopy cover
HC	hardwood cover (%)
SC	shrub cover (%)
BA	total basal area (m^2/ha)
BA_S	basal area of small ($5 < x < 51$ cm dbh) trees (m^2/ha)
BA_QUKE	basal area of *Quercus kelloggii* (m^2/ha)
CBA	conifer basal area (m^2/ha)
HBA	hardwood basal area (m^2/ha)
DBH	mean diameter at breast height
DBH_HWD	mean dbh of hardwoods
DBH_MAX	diameter of largest tree
LOWSHRUB	cover (%) of 16 species of shrubs not expected to provide cover above the head of a fisher, in the genera *Arctostaphylos, Mahonia, Ceanothus, Chamaebatia, Symphoricarpos, Vaccinium*
HIGHSHRUB	cover (%) of all shrubs expected to provide some overhead cover to fishers, including all species classified as shrubs that are not also low shrubs (see previous cell)
AGE	mean age, determined by coring, of up to 10 dominant conifer trees (>2/subplot)
CONSNAG	diameter of largest conifer snag
LRG_SNAG	number of snags $\geq$ 38.1 cm dbh
LRG_WD	volume of large downed wood (>25.4 cm diameter at largest end)
SLOPE	slope (%)
CROWN VOLUME	volume of tree canopy (crown ratio × tree height × crown width)

many of the variables that were included in the candidate models.

We grouped variables into 188 single or multivariate a priori models (Burnham and Anderson 2002). Some models were based on the collection of variables that had been demonstrated to have explanatory power (i.e., Buck et al. 1994, Mazzoni 2002, Zielinski et al. 2004*b*), but most were based on our knowledge about the combination of forest characteristics that may interact to influence habitat use by fishers. Our previous work led us to hypothesize that selection of resting habitat was based on the combination of features related to forest density (e.g., canopy closure, basal area, tree size and density, shrub density) and important woody habitat elements (e.g., large snags and logs, large live and dead oaks [*Quercus* sp.], maximum conifer size); thus candidate models reflected differing contribution of variables from each of these two primary categories.

Parameter estimation

Nonparametric logistic regression is useful for evaluating the relative importance of predictor variables and for describing the shape of response curves. However, simpler parametric models make understanding the contribution of individual variables more straightforward (e.g., Knapp and Preisler 1999). Parametric models result in an algebraic expression of predicted habitat suitability, which can more easily be applied by practitioners, whereas calculating suitability using the nonparametric terms requires the application of statistical software with loess smoothing. Thus, we also produced a parametric version of the best non-parametric model by evaluating the shapes of the response curves of each of the variables and substituting an approximate parametric form (e.g., linear, polynomial, logarithmic). Slopes and intercepts for the parametric functions were estimated using general linear models.

Model evaluation

We evaluated the stability of the selected model by conducting a 10-fold cross-validation procedure. We randomly divided the original data into 10 equal-sized segments, estimated the model with nine segments (training data) and classified the remaining (10%) segment (test data; see Fielding 2002). This procedure was repeated 10 times. To evaluate the stability of the model's predictions, we inspected the distribution of predicted probabilities for the test data and correct classification rates. Because GAMs have the best inference when the test data fall within the range of the original covariate values, the total sample of classified observations was less for the cross-validation evaluation than for the entire data set.

We also examined model performance by investigating the pattern of predicted values for partitioned test data against categories (bins) of predicted values (Boyce et al. 2002). A Spearman-rank correlation between area-adjusted frequency of cross-validation points within bins (a bin equals a range of predicted values, e.g., 0–0.075, 0.076–0.149, and so on) and the bin rank (lowest category of predicted value = 1, highest = 10) was calculated for each cross-validated observation. Area-

TABLE 2. Univariate comparisons of vegetation and topographic variables (means, with SE in parentheses) measured at fisher resting sites ($n = 75$) and Forest Inventory and Analysis (FIA) plots ($n = 232$) on the Sierra and Sequoia National Forests, California, USA.

Parameter	Resting plots	FIA plots
Elevation (m)	1621.9 (22.7)	1767.0 (20.2)
Vegetation cover (%)		
Hardwood	14.1 (1.9)	17.6 (1.8)
Shrub	13.3 (1.4)	24.8 (1.6)
Low shrub	11.6 (1.7)	7.8 (0.8)
Basal area (m^2/ha)		
Total	58.7 (2.5)	40.1 (1.6)
Small tree (<51 cm dbh)	25.0 (1.4)	15.5 (0.7)
Large tree (>52 cm dbh)	11.6 (1.8)	7.0 (0.7)
Quercus kelloggii	5.6 (0.7)	3.1 (0.4)
Conifer	51.6 (2.6)	35.2 (1.7)
Hardwood	7.1 (0.8)	4.9 (0.5)
No. conifer stems	1120.6 (90.9)	531.4 (33.8)
Tree dbh (cm)		
Mean tree	19.4 (0.9)	23.7 (0.9)
Mean hardwood	20.3 (2.1)	14.2 (1.1)
Maximum tree	145.6 (7.3)	111.3 (3.2)
Tree age (yr)		
Mean	118.4 (3.9)	113.9 (4.1)
Minimum	38.3 (1.9)	42.2 (2.3)
Maximum	317.4 (23.1)	230.8 (10.5)
Largest conifer snag (cm dbh)	110.6 (5.5)	79.8 (3.1)
Number of large snags (>38.1 cm dbh)	15.4 (1.1)	10.7 (0.8)
Volume of logs (m^3/ha)	169.4 (33.4)	118.0 (9.7)
Number of downed logs/ha	64.6 (4.1)	48.4 (2.5)

adjusted frequencies were the frequency of cross-validated resting structure plots within a bin, divided by the number of FIA plots that had predicted values within the range of values in the bin. Adjusted frequencies should be highly correlated with the predicted values if the model performs well. This particular application of k-fold cross validation is especially useful for evaluating designs like ours that are based on comparing use with availability (Boyce et al. 2002). All regression-related calculations were done using the S-Plus statistical package (MathSoft, Seattle, Washington, USA).

RESULTS

Univariate results

The mean values of most variables were dissimilar when fisher resting sites ($n = 75$) were compared to the FIA inventory plots ($n = 232$; Table 2). Particularly disparate were values for total basal area, conifer basal area, small (<51 cm dbh) tree basal area, large tree (>52 cm dbh) basal area, black oak basal area, number of conifers, number of large (>38 cm dbh) snags, number of downed logs, maximum diameter at breast height (dbh), percentage of high shrub, and maximum tree age; all had substantially larger values at fisher resting sites than at the available FIA inventory plots (Table 2). In contrast, fisher resting sites and FIA plots were similar in respect to percent hardwood, percent low shrub, mean age, and volume of downed logs.

Non-parametric habitat models

The top-ranked (selected) model represented a dominant portion of the AIC_c weights (0.87 of 1.0); the next best model had a weight of only 0.02 (Table 3). Because a single model accounted for the majority of the AIC_c weight, we did not consider additional models. The selected model explained 31.5% of the deviance, and included the following variables: average canopy cover, basal area of small trees (<51 cm dbh), hardwood dbh, maximum tree dbh, percentage of slope, and dbh of the largest conifer snag. Response curves for individual variables indicated that most responses were non-linear (Fig. 4A–F). The variables that were most responsible for the decrease in deviance, in decreasing order of importance, were maximum tree dbh, basal area of small trees (<51 cm dbh), slope, canopy cover, maximum conifer snag dbh, and hardwood dbh (Table 4). The distribution of habitat suitability values predicted by the best model indicated that few of the FIA inventory plots had suitability values that exceeded 0.30, but the resting plots had suitability values that were distributed across all probability categories (Fig. 5A). The lowest predicted suitability values (<0.09) were overwhelmingly represented by the inventory plots and the highest values (>0.60) were represented by the fisher resting plots. Using a cut-point of 0.50, 81.8% of the records were correctly classified (kappa = 0.45). Most of this success was attributed to correct classification of FIA inventory plots, only 7% of which were misclassified as fisher resting plots. Conversely, only 48% of the fisher resting plots were classified as such. Thus the model more easily distinguished FIA plots from resting structure plots than visa versa.

Cross-validation revealed that the best model had slightly lower correct classification rates for the sets of 10% of the data that were excluded (79.3% correct classification; Cohen's kappa = 0.34; Fig. 5B). The Spearman rank correlation of bin rank (prediction) and area adjusted frequency of cross-validation was 0.903 ($P = 0.001$) suggesting strong agreement between predicted

TABLE 3. Akaike's information criterion (AIC_c), ΔAIC_c, and Akaike weights (AIC_c wt) for the top five fisher resting-site habitat models developed from data collected in 2000 and 2001 on the Sequoia and Sierra National Forests.

Model†	AIC_c	ΔAIC_c	AIC_c wt
CC, BA_S, DBH_HWD, DBH_MAX, SLOPE, CONSNAG	272.4	0.00	0.879
CC, BA, HBA, SLOPE, LRG_WD	279.9	7.52	0.020
CC, BA, HBA, SLOPE	280.0	7.56	0.020
CC, DBH_MAX, SLOPE, CONSNAG	280.5	8.13	0.015
CC, BA, HBA, SLOPE, HIGHSHRUB	281.2	8.76	0.011

† Variables are defined in Table 1.

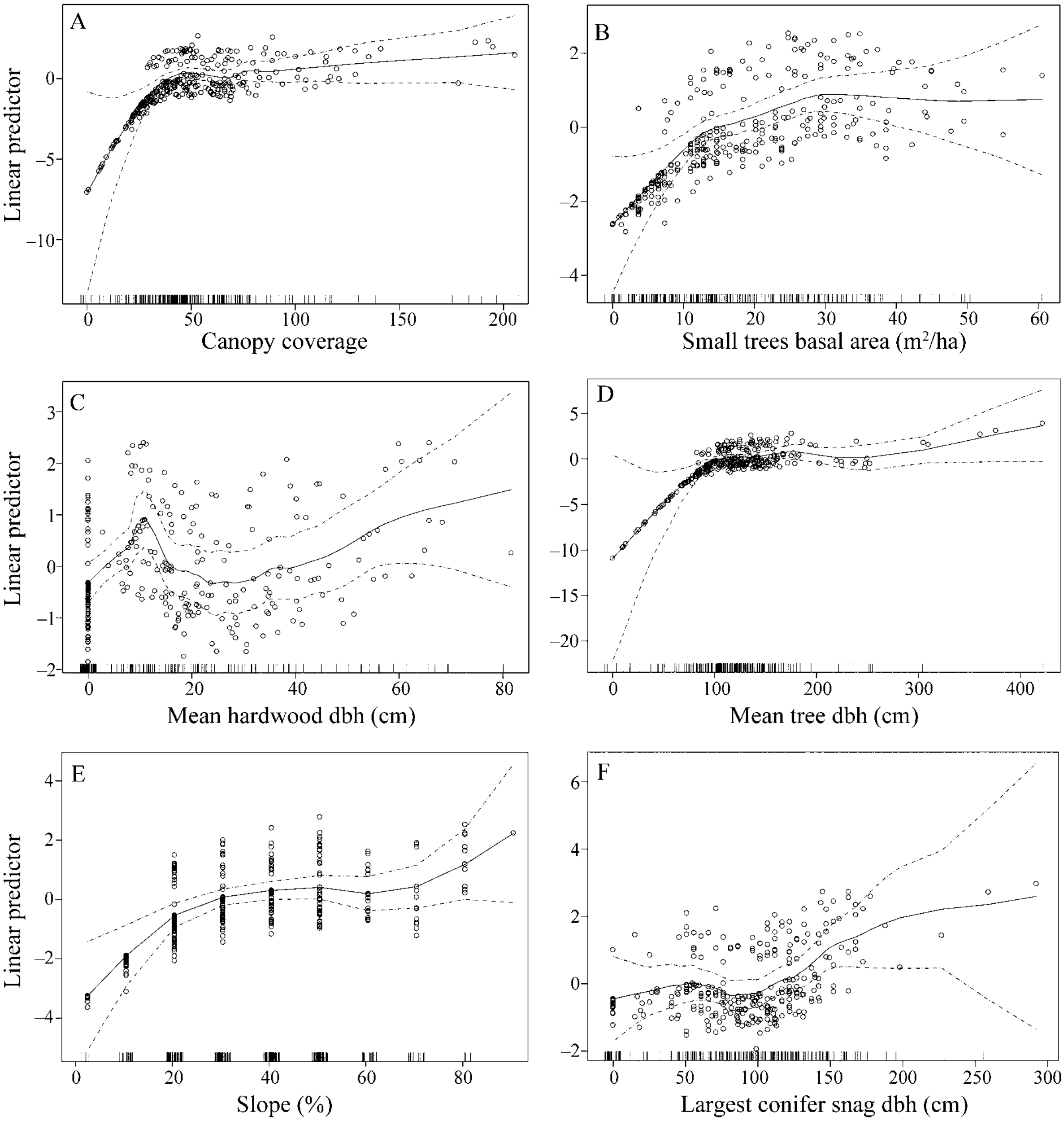

FIG. 4. The relationship of each independent variable in the best model (including 95% CI, dot-dashed lines) on the probability of resting site habitat suitability (span [a smoothing parameter] = 0.5). Variables are (A) canopy closure, (B) basal area of trees <51 cm diameter at breast height (dbh), (C) average hardwood dbh, (D) maximum tree dbh, (E) slope, and (F) maximum conifer snag dbh. These functional forms represent the effect of each independent variable on the probability of resting habitat suitability, given the presence all other variables in the model. Hatch marks above the x-axes indicate the observed values for each independent variable.

fisher suitability value and proportion of fisher plots that occurred within an ordered range of area-adjusted predicted values (Fig. 6).

Parametric fit to best model

The response surfaces for five of the six variables in the best model (canopy closure, basal area of trees <51 cm dbh, hardwood dbh, maximum tree dbh, and slope) could be approximated with a logarithmic function; number of large conifer snags was approximated using a linear function. Specifying these forms of the parameters allowed us to estimate coefficients and standard errors for each variable (Table 5).

DISCUSSION

Wildlife-habitat relationship models are usually developed to understand mechanisms of habitat selection; less commonly are models proposed as a means for

TABLE 4. Residual deviance and its change when individual variables are removed from the top fisher resting site habitat model.

Variable removed	Residual deviance	Change in residual deviance
Largest tree dbh	238.22	22.682
Basal area of small trees	232.02	16.483
Slope	231.69	16.149
Canopy cover (density)	230.74	15.199
Largest conifer snag dbh	225.97	10.425
Hardwoods dbh	224.87	9.332
None (full model)	215.54	0

assessing, and then monitoring over time, the status of habitat suitability. This is probably because most models are generated using independent variables that are measured and selected by the investigator and which, therefore, cannot easily be collected in other areas or repeatedly over time. Our alternative approach is driven by the need to generate a habitat suitability model that selects from only the variables that are routinely collected at plots that are part of the national Forest Inventory and Analysis program. Although the universe of potential variables to draw from is predetermined, the model has the advantage of being applicable to all appropriate sample points in the population, every time each point is resampled. This approach may be less desirable if the goal is to build a model that seeks to understand the mechanisms by which fishers select habitat, but it is an extremely efficient tool for assessing and monitoring relative habitat suitability.

Although we were constrained to use only the variables available from the FIA sampling protocol, we were able to generate models that shared variables (or their surrogates) with those that have previously been demonstrated to predict habitat use by fishers. In particular, the model we selected here shared two variables with the top resting habitat selection function that Zielinski et al. (2004*b*) developed for the southern Sierra Nevada, from a different data set. The fourth-ranked model in the current analysis also was adopted from this previous work, suggesting that we have identified a robust set of variables that collectively represent features that are important predictors of resting site choice.

The considerable amount of unexplained deviance, however, suggests that the model excludes other important factors that influence the choice of resting structures and the features in their immediate vicinity, or reflects a random element to the choice of a resting site by fishers. In addition, the set of sites used by fishers was compared to a set of FIA inventory plots that were a random selection of available sites. This form of habitat selection analysis makes it more difficult to discriminate and identify the features that drive habitat selection (Johnson 1980, Boyce et al. 2002, Manly et al. 2002). It is important to note also that the inclusion of a variable in the best model is not proof of that variable's importance to fishers, nor is the absence of a variable from the best model proof of its lack of importance.

An important advantage of our approach is that it was based on an empirical model that was developed using local information collected on the ground. This is not, however, a general criticism of knowledge-based habitat relationship systems (e.g., Mayer and Laudenslayer 1988) which are often constrained by their need to be applied consistently to all species of vertebrates over all land ownerships. We also believe that the approach promoted here, of applying a standard vegetation monitoring protocol at a plot centered on an important habitat feature, is better than trying to use FIA variables as surrogates for informative variables that were identified during independent wildlife research projects, but were measured differently (e.g., FIA-based model for the California Spotted Owl [USDA Forest Service 2000]). Even if both protocols measure the same variable, the sampling designs usually vary (e.g., 0.1-ha vs. 1.0-ha plots) and additional field data or analyses are necessary to be confident that the vegetation measures collected at FIA plots have the same statistical properties as the surrogates that were collected by wildlife biologists during independent studies of habitat selection.

Using a cutpoint of 0.5, the model was better at distinguishing FIA inventory plots from fisher resting structure plots than it was at distinguishing resting structure plots from FIA inventory plots. This meant that suitability values at resting plots were more evenly distributed between 0 and 1 than were suitability values at FIA plots, of which >50% had resting habitat probability values <0.1. The relatively low Kappa value (kappa = 0.34) that resulted was not particularly discouraging, however, given that the intended use of the model is to evaluate status and relative change in resting habitat suitability over time. Moreover, relatively low Kappa values are not uncommon. Manel et al. (2001) developed models for 34 taxa of aquatic invertebrates and, using the categories of Landis and Koch (1977), the models were viewed as excellent (kappa > 0.8) in only 3% of the cases, good (kappa = 0.4–0.8) in 21%, and poor (kappa = 0–0.4) in 76% of the cases. Developing empirical habitat suitability models based on presence/absence data is challenging, even when potential predictor variables are abundant and, as in the case of aquatic invertebrates, are strongly linked to the viability of the species. More relevant to our situation than classifying the probability of use on the basis of a 0.5 cutpoint, is the strong relationship between the ranks of bins of predicted values and the area-adjusted frequency of cross-validation points within bins shown in Fig. 6. The fact that more of the fisher resting plots (area-adjusted) continually fall within higher predicted value bins is a good indication of predictive success (Boyce et al. 2002). This result acknowledges the strength of models that produce quantitative predic-

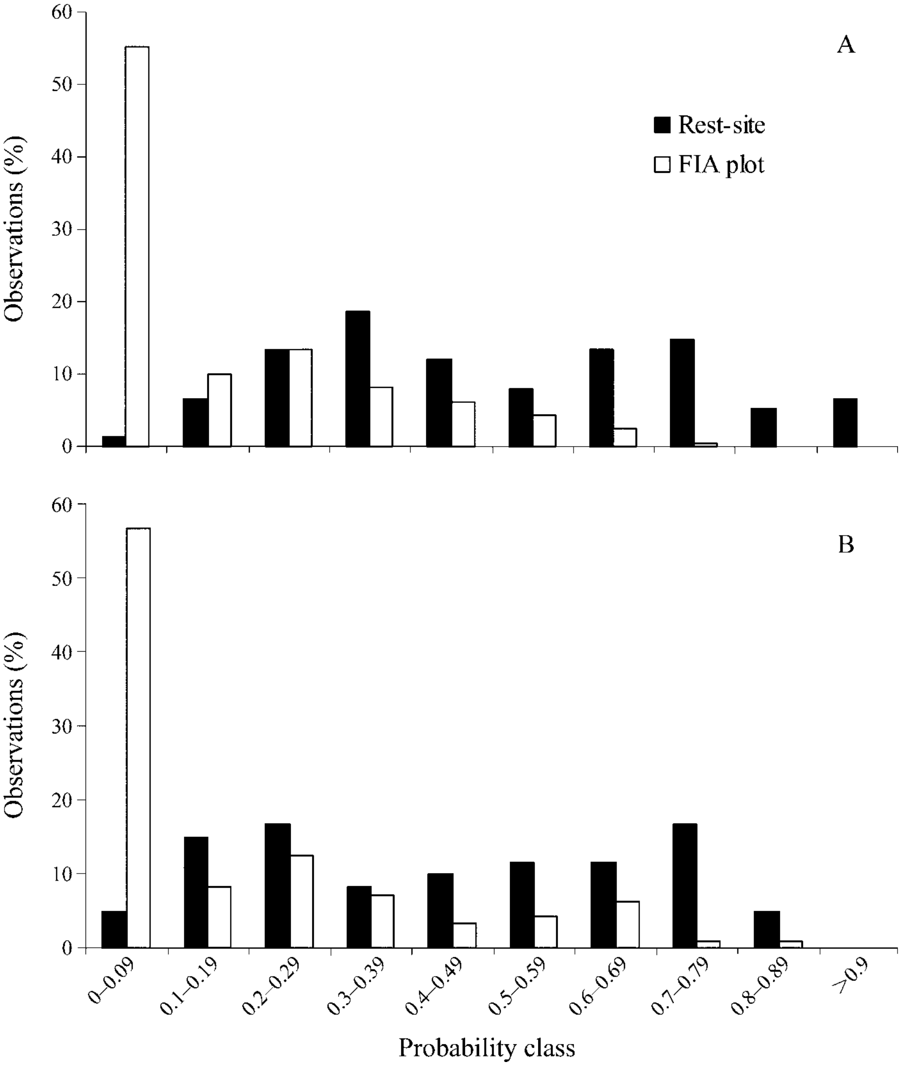

FIG. 5. Percentage of correct classification of (A) the data used to develop the best model and (B) the cross-validation data sets, as a function of the predicted probability values for fisher resting-site plots and FIA inventory plots.

tions, which provide more information of conservation value than discriminatory models that divide sites crudely into two opposing categories (Vaughan and Ormerod 2005).

One important feature distinguished the fisher resting plots and the inventory plots to which they were compared: the presence of a central large woody structure. Our inclusion of the resting structure may have contributed to the fact that these plots had greater values for a number of structural variables (Table 2), and thus may represent a bias. We believe, however, that this bias is inconsequential, given our objectives, for a variety of reasons. First, in previous work, we compared models for fisher resting habitat selection that used either tree-centered or non-tree-centered random plots, and fisher resting plots had significantly greater values for measures of tree size and volume than both types of plots (Zielinski et al. 2004*b*; W. Zielinski, *unpublished data*). Thus, even when resource availability plots were pre-selected to include a large central structure, the fisher resting sites still had significantly greater estimates of tree sizes and volumes. Second, FIA plots are significantly larger (1.0 ha) than plots used to assess availability in our previous studies (i.e., 0.1 ha) and those of many other wildlife researchers. This larger size mitigates the influence of any single feature on most measurements of vegetation structure and size. Finally, we believe the issue becomes moot when we focus on the goal of developing a method for assessing change in the relative suitability of fisher resting site habitat. Fishers select locations to rest that have larger trees and more tree volume and canopy closure than randomly located sites in the forest (Zielinski et al. 2004*b*).

Because of the history of timber harvest in the Sierra Nevada, forests currently lack many large tree and snag components that once characterized them (Franklin and

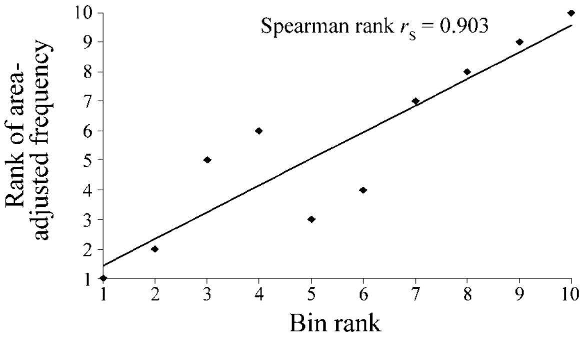

FIG. 6. The relationship between ranks of bins of predicted values (a bin equals a range of predicted values; 1, 0–0.075; 2, 0.076–0.149; 3, 0.15–0.2235; 4, 0.2236–0.298; 5, 0.299–0.3725; 6, 0.3726–0.447; 7, 0.448–0.5215; 8, 0.5216–0.596; 9, 0.597–0.6705; 10, >0.6705) and the area-adjusted frequency of cross-validation points within bins for each cross-validated model. Area-adjusted frequencies were the frequency of cross-validated use sites within a bin, divided by the number of FIA plots that had predicted values within the range of values in the bin (see Boyce et al. 2002).

Fites-Kaufman 1996, Bouldin 1999). Thus, we fully expect that most FIA plots will have lower measures of tree and snag volume than the places where fishers choose to rest. The model output can be used to track the *relative* change in habitat suitability, regardless of whether the model was developed using inventory plots that were or were not centered on large structures. One way to specifically evaluate the effect of a large central feature on predicted habitat suitability would be to develop alternative models that distinguish the vegetation information from the *central* FIA subplot (where the resting structure is located) from the surrounding subplots. This would require a new protocol for the format of the FIA vegetation reports, however, because data are routinely reported at the plot level only.

Potential applications

We view the selected model as a potentially important tool for evaluating the status and trend of fisher resting habitat suitability on the west slope of the Sierra Nevada. However, we caution that it should be applied only within the southern Sierra Nevada, within the area that included the set of inventory plots used to develop the model. We foresee managers in this region using the parametric form of the model to generate predicted resting habitat suitability values using the FIA vegetation data that are routinely provided to them. Values for the predictors in the final model (i.e., canopy closure, basal area of small trees, mean dbh of hardwoods, maximum tree dbh, slope, and dbh of largest conifer snag) would be extracted from the data for each FIA plot and each would be multiplied by their respective coefficients to yield a resting habitat suitability value ranging from 0 to 1. Here are a few examples of applications we can envision that apply to various spatial scales and administrative levels:

1. *Local spatial comparisons.*—The fisher currently appears to occupy more of its former range on the Sequoia than the Sierra National Forest. The manager on the Sierra National Forest could conclude that the difference is not a consequence of inadequate resting habitat if the mean resting suitability value from FIA plots on the Sierra National Forest is no different than on the Sequoia National Forest.

2. *Evaluating the effects of specific forest management activities.*—Managers often lack quantitative expressions of habitat suitability that can be used to evaluate the effects of proposed land management activities. For example, fire exclusion has led to the increased growth and survival of fire-sensitive trees species, which now occur at densities that are far higher than would normally occur in the presence of periodic natural, low-intensity fires (McKelvey and Busse 1996, Skinner and Chang 1996). We have no clear understanding of how the management activities designed to reduce fuel loads and to reintroduce fire will affect the resting habitat components important to fishers in California, but our model could be used to index changes in resting habitat suitability caused by fuels treatments. This would require that managers compare resting habitat suitability values before and after area treatments are applied, using the data from FIA plots that happen to occur in the treatment area, or that they install a separate set of FIA plots in areas scheduled for treatment. Both options would require the flexibility to sample FIA plots at times that may not always occur on the 10-yr schedule.

3. *General standards for performance.*—The manager of a national forest wishes to take actions to improve—or at least not retard the development of—fisher resting habitat. For example, the current mean predicted suitability at FIA plots could be used as a standard below which future mean values should not fall. Success at achieving the restoration of fisher resting habitat could be evaluated by verifying that mean resting habitat suitability increases with the evaluation of every new set of FIA data.

4. *Regional monitoring.*—The predicted fisher resting habitat suitability at each FIA point is a source of data for evaluating change in suitability over time. This can

TABLE 5. Coefficients for each variable in the approximated parametric version of the top nonparametric fisher resting-habitat model and the *t* statistic testing significance of departure from 0.

Variable	Coefficient (SE)	*t*	*P*
Intercept	–22.12 (3.61)	–5.99	<0.00001
log(largest tree dbh)	4.55 (1.31)	3.41	0.0007
log(small trees basal area)	2.15 (0.69)	3.09	0.002
log(slope)	2.16 (0.75)	2.85	0.005
log(canopy cover)†	2.46 (3.61)	2.84	0.005
Largest conifer snag dbh	0.008 (0.004)	1.94	0.054
log(hardwoods dbh)	0.47 (0.25)	1.81	0.072

† A measure of density.

be conducted at the level of a single administrative unit, but would achieve better statistical power if it included the FIA plots that occur over a much larger region. The trend in mean predicted suitability value over the region (stratified by administrative unit if necessary) can be evaluated over time for statistical departures from 0 slope. Significant increases can be evaluated against some historical benchmarks for habitat availability to determine when sufficient resting habitat has been achieved. This form of habitat monitoring could, for example, be an important complement to the current fisher population monitoring program in the Sierra Nevada (Zielinski and Mori 2001; R. Truex, *personal communication*). Changes in the distribution of resting habitat could be compared with changes in the distribution of fishers, to help determine if changes in the frequency of detection of fishers are linked to changes in habitat suitability. The current FIA 10-yr resample interval would appear to be a reasonable period of time to reassess the status of fisher resting habitat. However, a 5-yr sampling frequency would allow comparisons with the fisher population monitoring data which is scheduled for assessment every five years.

5. *Reintroduction*.—Fishers are currently absent from a large portion of their historical range in the central and northern Sierra Nevada, and conservation options include the possibility of reintroducing fishers from elsewhere into suitable portions of this region. We anticipate that the model developed here could be used to assist in the choice of a preferred location. However, because the model was developed using data from the southern Sierra Nevada, extrapolation should be applied with discretion until a suitable substitute model for the northern Sierra is developed.

It is important to note that resting habitat is an important component of fisher habitat, but it is not the only one. The habitat features associated with natal dens, foraging locations, and the composition of home ranges and landscapes should all be considered in a complete habitat monitoring plan. Fisher natal dens share many features with the structures that they select for daily resting bouts (Powell et al. 1997; W. Zielinski, *personal observation*), thus, the possibility that monitoring resting habitat suitability is an adequate proxy for monitoring natal denning habitat should be investigated further. It is possible that foraging habitat, like resting habitat, could be routinely assessed using vegetation data from FIA plots, by comparing the characteristics at FIA plots to those sites where active (and presumably hungry and foraging) fishers visit track plate stations provisioned with small baits (Zielinski and Stauffer 1996). Incorporation of foraging habitat into a complete assessment of fisher habitat suitability will be a challenge because the fisher diet is very diverse and because recording foraging locations is difficult. However, apparent flexibility of the fisher's dietary habits in the southern Sierra Nevada (Zielinski et al. 1999), and the possibility that fishers are less selective of foraging than resting habitat (Powell 1994), may make monitoring foraging habitat less critical than resting habitat. Until this assumption is verified in the Sierra Nevada, however, foraging habitat should be considered an important component of a complete approach to monitoring fisher habitat.

A focus on resting habitat features, as important as they appear to be, overlooks the need to understand the integration of these and other habitat elements over large spatial extents (i.e., home range and landscape). It is for this reason that we strongly endorse a companion element of a fisher habitat monitoring program that assesses landscape suitability over time, preferably one that, like the FIA program, enjoys strong institutional support and is routinely updated. Models of landscape suitability for fishers have been developed from survey data and tested in northwestern California (Carroll et al. 1999) and in the southern Sierra Nevada (R. Truex, *unpublished data*), each by relating fisher detections to a set of predictors derived, directly or indirectly, from features remotely sensed by satellite imagery.

We envision a future fisher habitat monitoring program in the Sierra Nevada that is linked to two sources of routinely updated vegetation and topographic information: (1) the FIA plot data, which can be used to index the status of predicted resting habitat (as demonstrated here) and, when developed, predicted foraging habitat and (2) some reliable form of remotely sensed data that can be used to predict landscape habitat suitability. These sources of information would provide land managers an invaluable assessment of many of the dimensions of fisher habitat condition. Moreover, when FIA and remotely sensed vegetation data are used by forest managers in models to simulate changes in forest structure and composition (e.g., Spectrum; USDA Forest Service 1995), due either to forest management or other factors (e.g., climate change), the fisher resting habitat models could be applied to the result of these simulations to predict effects on future resting habitat values.

In considering these applications, the potential for periodic changes in the FIA system protocol must be considered. For example, the FIA program has recently replaced the five-subplot design that relied on variable-radius plot methods, which was used in California (and implemented here), with a four-subplot design that used fixed plot methods (USDA Forest Service 2004). Because of the premium placed on consistency in estimating trend in forest vegetation over time, the new protocol is assumed to simply be a more efficient method for estimating the same variables. For consistency, one of the subplots will be the same when sites measured under the old protocol are remeasured under the new one. Researchers and forest managers can estimate forest vegetation variables at FIA sites with either protocol and they should produce similar results when aggregated at the site level. Analyses to confirm this assumption are being conducted by the FIA program, and the results will allow us to adapt the model for use of data derived from the four-subplot sampling method.

Systematically collected forest inventory data can have significant value in developing wildlife habitat models when combined with samples of animal occurrence. We were able to develop a credible species–habitat model using vegetation plot data that are widely available to federal land managers. We encourage researchers and managers to consider how FIA data might be used in their specific geographic regions and to engage in a dialogue with those individuals and entities responsible for the periodic gathering of FIA plot data. It is possible that for a modest increase in funding, relevant species-specific habitat data could be collected, and the FIA program could be more broadly integrated into ecological studies of species–habitat relationships as well as the application of species–habitat models to questions of interest to land managers.

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