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Estimating habitat value using forest inventory data: The fisher (*Martes pennanti*) in northwestern California

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ABSTRACT

Managing forests for multiple objectives requires balancing timber and vegetation management objectives with needs of sensitive species. Especially challenging is how to retain the habitat elements for species that are typically associated with late-seral forests. We develop a regionally specific, multivariate model describing habitat selection that can be used – when linked to an institutional forest inventory program – to assess, monitor and forecast habitat conditions for a key wildlife species. We use the fisher (*Martes pennanti*) in northwestern California as our example and develop a predictive model for resting habitat that is created using data from the specific region where it will be used. We explore how this resting habitat model differs from a similar model developed for the Sierra Nevada and consider the implications for forest management. We developed the model using MaxEnt by comparing vegetation data at 99 randomly selected fisher resting structures on public and tribal lands in northwestern California with 883 Forest Inventory and Analysis (FIA) plots within the same ecoregion. A total of 58 alternative vegetation models were specified and the top 10 were nearly identical in their performance (Gain > 1.08; Area Under the Curve [AUC] > 0.89). We chose a five-variable model (canopy closure, tree age, total basal area, volume of "large" wood and basal area of hardwoods) because it included the fewest variables and included only those that could be affected by management. This model was similar to the Sierra Nevada model, but did not include topographic features (e.g., slope) nor did it include a variable representing the density of small trees. The absence of variables related to topography may make it easier for managers to affect positive change in resting habitat suitability since all variables can be influenced by management actions. Moreover, the model indicates that small trees appear to be less important (compared to southern Sierra Nevada) and therefore the probability of producing high-value resting habitat without higher fire risk is greater. We also created a spreadsheet that simplifies the process of generating habitat predictions from new data. Since metrics of stand structure and wildlife habitat are sensitive to sample design, collecting new data with FIA protocols will provide the most accurate estimates of predicted habitat with this model. Together, the Sierra Nevada and northwest California models provide managers in California a quantitative means to assess and monitor resting habitat suitability using current and future data that are part of an institutionally supported program to inventory forest vegetation.

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1. Introduction

Providing habitat for sensitive species of wildlife is often a challenge as it must be accomplished on lands that are managed for multiple benefits. Public land management agencies can improve their decisions by using quantitative tools that allow them to understand the effects of management activities on habitat for key wildlife species. In forests, these activities are usually related to either timber production or thinning of trees to achieve fuel reduction, both of which can affect the habitat structures important to forest-dwelling wildlife species. Wildlife habitat selection occurs at multiple spatial scales, and one important scale is often referred to as microhabitat, which characterizes the specific habitat structures used for refuge, foraging, or reproduction. Determining the abundance and distribution of these small-scale features (e.g., dead trees, logs, large trees) is very difficult given that they must often be assessed using plot-based methods that are time-consuming and expensive, rather than remotely-sensed metrics that are easier to estimate over large areas. Microhabitat selection is particularly challenging to study for wide-ranging species because of the large areas that must be evaluated. For these reasons we have previously recommended the use of standardized, institutionally supported forest inventory plots to quantify habitat for various species(e.g., Dunk et al., 2004; Welsh et al., 2006; Zielinski

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et al., 2006, 2010), in particular the Forest Inventory and Analysis (FIA) program. The FIA program was mandated by the Forest and Rangeland Renewable Resources Research Act of 1978 to promote a nationwide survey and analysis of renewable natural resources, including forests (Frayer and Furnival, 1999). The current design consists of sample points randomly selected within each 2430 ha hexagon on a grid across all ownerships in the United States, with vegetation and environmental variables (e.g., live and dead vegetation, topography, exposed rock) measured at each forested plot once every 10 years in the western United States (Bechtold and Patterson, 2005). The program uses these data for the primary purpose of monitoring forest resources (e.g., Christensen et al., 2008), but the data have also been used for a myriad of other purposes (e.g., Ohmann and Spies, 1998; Iverson and Prassad, 1998; Gray, 2005).

Some of our previous work has focused on modeling habitat for the fisher (*Martes pennanti*) (Zielinski et al., 2006, 2010), a mustelid carnivore associated with late-successional mixed conifer/hardwood forests in western North America (Buskirk and Powell, 1994; Lofroth et al., 2010). Fishers choose places to rest for temporary refuge, frequently cavities in standing live and dead trees and logs (Zielinski et al., 2004a; Lofroth et al., 2010). In addition to the rest structure itself, the resting site includes nearby forest structural features described by variables such as canopy closure, tree densities and basal areas, tree size distributions, shrub density, downed logs, and other vegetation features (Zielinski et al., 2004a; Purcell et al., 2009). The fisher has been deemed "warranted but precluded" for listing under the federal Endangered Species Act (USFWS, 2004) and occurs in two disjunct populations in California (Zielinski et al., 1995). Thus, there is a need to develop methods to assess and monitor their resting habitat characteristics in each of these populations, which are separated by about 500 km (Zielinski et al., 1995).

We have previously developed a habitat model, using FIA-generated variables, to predict the relative suitability of a site as resting habitat for the fisher population in the southern Sierra Nevada (Zielinski et al., 2006). Our purpose here is to develop a region-specific model for the other fisher population, in northwestern California. This is a different ecoregion than the southern Sierra, with different climatic and topographic influences. Fisher habitat, diet and genetics differ substantially between the two populations (Zielinski et al., 1999; Wisely et al., 2004; Zielinski et al., 2004a,b; Golightly et al., 2006; Davis et al., 2007). Because habitat features important to fishers differ between the regions, methods to evaluate and monitor resting habitat will likely differ between the regions as well. Here we develop a regionally specific resting habitat model for fishers in northwestern California and contrast it with the southern Sierra model, and evaluate what implications this may have for forest management. We continue our practice of constructing the model using predictors from the FIA program to reap the myriad benefits that occur when a wildlife habitat model is explicitly linked to a regularly sampled system of forest inventory plots.

2. Materials and methods

2.1. Study area

The study area was an approximately 27,344 km^2 region defined by the Eastern and Central Franciscan subsections (codes M261Ba and M261Bb) of the Northern California Coast Ranges ecosection and the western portion (west of −122.75 latitude) of the Klamath Mountains ecosection (code M261A) in northwestern California (Bailey, 1994) (Fig. 1). This largely forested area was selected because the fisher resting data used to construct the model (see below) was collected during two different research studies located within these specific physiographic regions and, therefore, we anticipated that the model we developed could be justifiably applied to FIA plot locations within these larger ecoregions (the "modeled region"). Only the western portion of the Klamath Mountains section was included because the eastern portion includes high-elevation areas with vegetation types that are not represented elsewhere in the modeled region or within the fisher research areas where the resting habitat data were derived. The modeled region includes portions of Humboldt, Del Norte, Siskiyou, Trinity, Shasta, Tehama, Glenn and Mendocino counties in northwestern California (Fig. 1) and is represented by 63.9% public and 36.1% private land (including tribal) with elevations ranging from 20 to 2,697 m. This region overlaps considerably with the currently occupied portion of the historical range of the fisher in northwestern California (Zielinski et al., 1995). The primary vegetation types (Mayer and Laudenslayer, 1988) were Douglas fir, Montane Hardwood, Klamath Mixed Conifer, Mixed Hardwood Conifer, and Montane Chapparal. Regeneration harvest, via clearcutting, has been the dominant silvicultural technique in the modeled region but most of the harvest activity since the mid-1990s has been on private lands.

Developing the predictive model required sampling vegetation at known fisher resting sites. We selected these at random from those sites that had been discovered during two different studies that used radio-marked fishers to study the resting habitat ecology of fishers in northern California. The first was conducted from 1993 to 1997 on 400 km^2 of the Six Rivers and Shasta-Trinity national forests in Humboldt and Trinity counties (Zielinski et al., 2004a,b). This study had 2 subareas: the northern Pilot Creek and the southern Cedar Gap (Fig. 1). The second study was conducted from 1996 to the present on the 362 km^2 Hoopa Valley Indian Reservation (Higley and Mathews, 2009) (Fig. 1). Elevations within the fisher study areas varied from 600 to 1800 m. A notable difference between the 2 research study areas was that tan oak (*Lithocarpus densiflora*) was a much more dominant tree species in the Hoopa area than on the national forest research area.

2.2. Fisher resting sites and FIA vegetation data

The development of the predictive resting habitat model required sampling vegetation characteristics in the immediate vicinity of resting structures (Zielinski et al., 2006). We located resting sites by homing on telemetry signals from radio-collared individuals. Many more resting sites were identified during the original studies than we were able to revisit for this study. Thus, we randomly selected 74 resting sites from the national forest study area and 25 resting sites from the Hoopa study area, for a total of 99 resting sites. These sites were used by a total of 34 individual fishers (8M:26F).

Vegetation attributes at fisher resting sites were measured using the FIA vegetation sampling protocol (USDAFS, 2007; Christensen et al., 2008). Technicians that were specially trained by the FIA program collected the data after centering the plot on the resting structure, which was usually a live or standing dead tree. The FIA protocol involves the collection of detailed vegetation data at four subplots within a 1.0 ha circular area. Within each subplot, a nationally standardized set of attributes are measured or estimated, including live and dead trees, topography, stand structure, and disturbance history. In addition, regionally important measurements are collected, including understory composition, the quantity of downed wood and litter, ground cover, and other physical features (see http://fia.fs.fed.us and http://www.fs.fed.us/pnw/fia/publications/fieldmanuals.shtml for details on national and regional FIA sampling protocols and data availability).

2.3. Analyses and model development

We developed a predictive resting habitat model by comparing characteristics at the 99 fisher resting sites with the characteristics

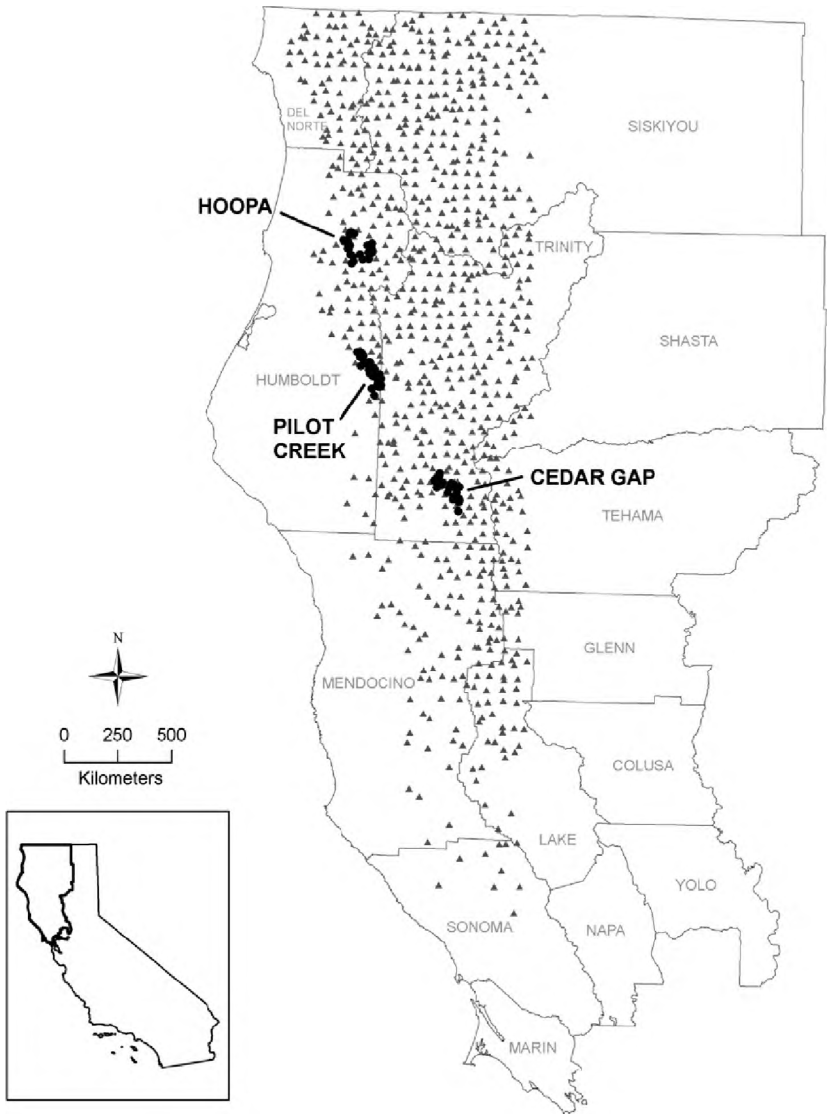

Fig. 1. The modeled region, in northwestern California, including the 883 Forest Inventory and Analysis (FIA) points (gray triangles) that fall within the Eastern and Central Franciscan subsections (codes M261Ba and M261Bb) of the Northern California Coast Ranges ecosection and the western portion (west of -122.75 latitude) of the Klamath Mountains ecosection (code M261A) in northwestern California (Bailey, 1994). The 3 clusters of black circles represent the 99 fisher rest site locations that we used to create the model representing sites on the Hoopa Indian Reservation study area ($n = 25$ rest sites), the Pilot Creek subarea ($n = 49$ rest sites) and the Cedar Gap subarea of the Six Rivers National Forest study area ($n = 25$ rest sites).

at the 883 regularly sampled FIA plots within the study area. We settled on the latter number after determining – via simulation using only those 378 FIA points that were within a 40-km buffer around the fisher research study areas – that there was no sample selection bias (Phillips et al., 2009). Sample selection bias can occur when the two sets of data, the animal occurrence plot data and the available plot data, are drawn from significantly different geographic areas. To be assured that differences between the two sets of data were unrelated to this bias we compared the predicted values from a set of candidate models that were evaluated using the smaller set of FIA plots close to the fisher plots ($n = 378$) and then using the larger set of FIA plot data ($n = 883$). The predictions from the two data sets were highly correlated, so we used the larger set of FIA plots for this analysis.

We used maximum entropy models (MaxEnt ver. 3.3.3e, Phillips et al., 2006) to conduct the modeling because it is specifically designed to use "presence only" data, similar to our fisher resting site data, when creating a predictive model. In our case, MaxEnt compared alternative models that were generated by contrasting features at resting sites with those generally available in the region at large, represented by the grid of FIA plots in the study area. Because we were unaware of the use by fishers of the FIA inventory plots (i.e., some may have been used, at some point in time, as a resting site by a fisher) the FIA plots could not be considered, in this habitat selection analysis, as sites where fishers were absent. Instead, we considered them as "availability" sites, representing the range of environmental conditions in the modeled region. These availability data, which we use to represent the range of environmental conditions that are available to fishers in the modeled region, are often referred to as "background" or "pseudo-absence" data when conducting habitat selection modeling (Phillips et al., 2009). The outcome of our analysis, comparing used data from the fisher rest sites, and available data from the background FIA plots, resulted in estimates of Relative Resting Habitat Suitability (RRHS). The FIA vegetation data were collected at the selected fisher resting sites from 2005 to 2007 whereas the FIA data used to assess availability were collected from 2001 to 2006. We used the Species with Data (SWD) format in MaxEnt and restricted the functional relationships between variables and the response (called "features" in MaxEnt) to either linear, threshold or quadratic forms; otherwise we used the default features in MaxEnt.

We restricted the large number of potential FIA variables to those, or their surrogates, that were used or selected by fishers in previous studies (Buck et al., 1994; Zielinski et al., 2004a; Purcell et al., 2009) (Table 1). Most of the variables included were related to vegetation (tree and shrub) density, conifer and hardwood tree size, standing and downed wood, conifer/hardwood ratio, and local topography. We grouped variables into 58 single or multivariate *a priori* candidate models (Burnham and Anderson, 2002). The models were largely a subset drawn from biologically based models that were specified in a previous, companion, project to create a resting habitat model for fishers in the southern Sierra Nevada (Zielinski et al., 2006). We reviewed this larger set of models for relevance to characteristics of forests in northwest California. This previous work led us to hypothesize that selection of resting habitat was based on the combination of features related to forest density and important dead wood habitat elements; thus most candidate models reflected contributions of variables from each of these two categories (Appendix A).

We compared models using two measures of model fit to the data: the gain (Phillips et al., 2006) and the Area under the Receiver Operating Characteristic (ROC) curve (AUC) (Altman and Bland, 1994; Fielding and Bell, 1997). The gain is closely related to deviance, a measure of goodness of fit used in generalized additive and generalized linear models. It starts at 0 and increases towards an asymptote and is defined as the average log probability of the presence samples, minus a constant that makes the uniform distribution have zero gain (www.cs.princeton.edu/~schapire/maxent/tutorial/tutorial.doc). Gain (actually calculated as exp(gain)) represents the average difference in RRHS between used and available plots. A model with an AUC value of 0.5 has the classification skill that would be expected by chance, whereas a model with perfect classification skill corresponds to an AUC of 1.0. Model robustness and stability were tested using cross validation of the fitted models. We randomly removed 10% of the fisher locations 15 times, each time with replacement, and evaluated whether the RRHS scores were similar to that obtained when all the fisher location data were used. Similarity of scores would indicate that the model is robust to modest changes in the source data used to create it.

We also used the predicted RRHS value at each location to estimate the distribution and abundance of categories of varying predicted value (Boyce et al., 2002; Hirzel et al., 2006). We generated the "predicted to expected ratio", P/E (Hirzel et al., 2006), as a measure of strength of habitat selection. This was calculated by dividing the proportion of fisher resting sites that occurred in a RRHS window that was 0.1 wide (i.e., RRHS values could range from 0 to 1, starting at a value of 0.05, then moving up to 0.75 in 0.01 increments)by the proportion of the FIA sites in the modeled region in the same window. The strength of selection index is <1 when a RRHS category is selected against and >1.0 when it is selected for; we calibrated the values so that they could vary from negative to positive infinity. A good model should show a monotonically increasing P/E curve.

Our selected model was intended primarily to help managers predict, and then to monitor, RRHS over the modeled region. However, we realize that it would be useful to provide information about the values for many of the key variables that were associated with various categories of RRHS. Thus, we divided RRHS into 4 bins – from low to high – and calculated the mean and 95% confidence interval for each variable considered (for an example, see Dunk and Hawley, 2009). Thus, our overall analysis provides (1) a quantitative prediction of the RRHS for any location where values for the variables in the final model can be collected and (2) a summary of the environmental conditions in areas of low, intermediate, and high predicted RRHS.

Finally, it may be difficult for those unfamiliar with MaxEnt to generate predictions of RRHS for lands that they are responsible for within our study area. Thus, to assist in the practical use of our model, we developed an Excel spreadsheet that automatically calculates RRHS when the user enters the values for the variables in our final model.

3. Results

The top 10 models all had similar performance measures, with gain values ranging from 1.080 to 1.118 and AUC values ranging from 0.890 to 0.899 (Table 2). Four of the same variables occurred in all 10 models (canopy closure, mean age, total basal area, and volume of large-sized downed wood) and a fifth variable occurred in the majority of the models (basal area of hardwoods). We chose model 14 for further evaluation for two reasons: (1) parsimony; it

Table 1
Abbreviations and descriptions of variables used in candidate *a priori* fisher resting site habitat suitability models for northwestern California.

Abbreviation	Description
CC	Canopy cover (%), calculated from crown width equations (Warbington and Levitan, 1992) for dominant and co-dominant trees and summing area without overlap
CC_STD	Standard deviation of canopy cover among subplots (%)
HC	Percent hardwood cover (all tree sizes)
SC	Percent shrub cover
BA	Total basal area of live trees ($m^2 ha^{-1}$)
BA_S	Basal area of small (12.5 < x < 51 cm dbh) trees (m^2 ha^{-1})
BA_QUKE	Basal area of *Quercus kelloggii* (m^2 ha^{-1})
CBA	Conifer basal area (m^2 ha^{-1})
HBA	Hardwood basal area (m^2 ha^{-1})
DBH	Mean diameter at breast height (cm)
DBH_HWD	Mean dbh of hardwoods (cm)
DBH_MAX	Diameter of largest live tree (cm)
HIGHSHRUB	Percent cover of shrub species expected to provide overhead cover to fishers.
AGE	Mean age of dominant conifer trees (determined by coring a subsample of trees).
CONSNAG	Diameter of largest conifer snag (cm)
LRG_SNAG	Density of snags >38.1 cm dbh (N ha^{-1})
LRG_WD	Volume of large downed wood (>25.4 cm diameter at largest end) (m^3 ha^{-1})
SLOPE	Percent slope
CROWN VOLUME	Volume of tree canopy (crown ratio * tree height * crown width) (m^3 ha^{-1})

Table 2
List of variables included in the top 10 best-fitting candidate fisher resting habitat models in northwestern California, and their gain and area under the curve (AUC) values.

Model	Variables								Gain	AUC
31	CC	AGE	BA	LRG_WD	HBA	SLOPE	HIGHSHRUB	CONSNAG	1.118	0.899
20	CC	AGE	BA	LRG_WD	HBA	SLOPE	CONSNAG		1.106	0.897
43	CC	AGE	BA	LRG_WD	HBA	SLOPE	HIGHSHRUB	LRG_SNAG	1.098	0.896
36	CC	AGE	BA	LRG_WD	HBA	SLOPE	LRG_SNAG		1.089	0.894
26	CC	AGE	BA	LRG_WD	HBA	SLOPE	HIGHSHRUB		1.089	0.893
37	CC	AGE	BA	LRG_WD	HBA	LRG_SNAG			1.088	0.893
27	CC	AGE	BA	LRG_WD	HBA	HIGHSHRUB			1.089	0.892
46	CC	AGE	BA	LRG_WD	CONSNAG	BA_QUKE			1.083	0.892
13	CC	AGE	BA	LRG_WD	HBA	SLOPE			1.083	0.892
14	CC	AGE	BA	LRG_WD	HBA				1.080	0.890

had the fewest variables, and (2) practicality; it did not include a topographic variable (e.g., slope) which our interviews with managers suggested would be preferable because topography is not amenable to manipulation by managers.

Performance measures of model 14 were quite acceptable, even though it had marginally lower AUC and gain values compared to the other models in the set. For example, an AUC value of 0.89 means that if we were to randomly select a fisher rest site location and a FIA plot location from the pool of samples, 89% of the time the fisher rest-site location would have a higher RRHS value than the FIA plot location. Similarly, a gain of 1.080 means that the mean RRHS score for fisher rest-sites is 2.945 times larger (calculated as exp[*gain*]) than the values at FIA plot locations. The variables most responsible for the increase in gain, in decreasing order of importance, were total basal area (72.4%), abundance of large-sized downed wood (11.4%), basal area of hardwood (8.8%), canopy cover (3.9%) and mean tree age (3.5%). Response curves suggested that the two basal area variables had a threshold relationship with RRHS and the remaining 3 variables had a quadratic relationship.

Cross validation resulted in nearly identical distributions of proportions of fisher resting sites in the RRHS categories (Fig. 2). Moreover, the cross validated data revealed a mean (CI) AUC among the 15 replicates of 0.896 (0.875–0.917), compared with 0.890 for the full model. These results suggest that model 14 is robust to changes in the data set used to develop it. Strength of selection analysis illustrates that below a RRHS value of 0.15, selection is quite strongly negative (selection values ranging from −2.9 to −30) and that selection is neutral when RRHS ranges from 0.15 to 0.35 (Fig. 3). Above 0.35 the selection values steadily increase

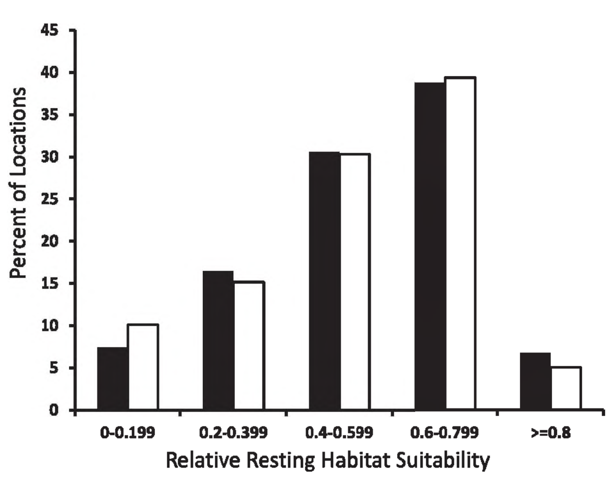

Fig. 2. Predicted fisher resting site classification in northwestern California, by RRHS bins, for model 14 using all data (open bars) and the classification of the cross-validated data (black bars).

until they reach their maxima of ~120 around 0.70–0.75 (0.75 being the highest predicted value among the FIA points). Thus, there is a conspicuous pattern of stronger selection for high RRHS values (up to 120 times greater than expected) compared with the selection against low RRHS values (up to 30 times less than expected).

We also examined the variables as a function of how they changed with increasing RRHS value. Using 4 categories of RRHS values, <0.15, 0.15–0.329, 0.33–0.61, >0.61 (which were informed by the strength of selection analysis described above), we found the expected relationships (i.e., quadratic, threshold) for the 5 variables included in model 14. For example, mean age of trees on the plot was 98.1 years for FIA points with RRHS values <0.15, 144.1 years for values between 0.15 and 0.3299, 152.6 years for values between 0.33–0.61 and 144.5 years for FIA points with values >0.61. There were few additional variables, however, that demonstrated functional relationships with RRHS, exceptions being diameter at breast height (DBH) of the largest tree on the plot and DBH of largest conifer snag (Table 3).

4. Discussion

This model, like its predecessor (Zielinski et al., 2006, 2010), was developed for a unique purpose: to assess and potentially monitor relative resting habitat suitability across a particular region. The primary goal is not to understand mechanisms of habitat selection, but instead to find the most efficient and effective system for collecting, interpreting, and applying information that is relevant to fisher habitat management at the microhabitat scale. This is the reason that we built the model from predictors available in an institutionalized forest inventory system, the FIA program, instead of based on a set of unique predictors measured using a non-standard protocol (e.g., Zielinski et al., 2004a).Building our model to link to a standard forest inventory system allows managers to update the predicted RRHS values at the 883 FIA points every time they are resampled, which occurs about every 10 years. This is accomplished by simply downloading the inventory data for the 5 predictor variables at each of the FIA points in the area of inference each time the plots are resampled, thus no new or additional field work is required to monitor RRHS. This link to the FIA program also permits the model to be used to forecast change in future resting habitat value when the model is integrated with a forest vegetation simulator (e.g., Zielinski et al., 2010). Thus, the model we developed here is built with implementation in mind, fully integrated with other inventory systems to perform a number of important forest planning and monitoring functions. And, to assist managers in using this new model we developed a spreadsheet to simplify the process of generating predictions from new plot data (see Appendix A, Supplementary data).

Although we did not build the model to reveal mechanisms of habitat selection, or functional relationships between variables

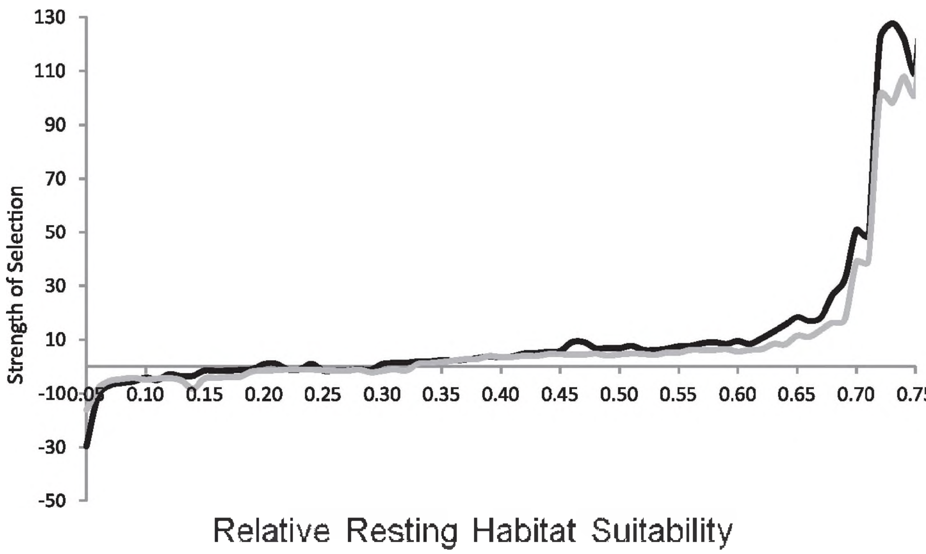

Fig. 3. Strength of selection (*sensu* Hirzel et al., 2006) calculated for the full fisher resting site data set using model 14 (black line) and the cross-validated data (gray line) represented against the midpoint of the predicted RRHS values. Positive strength values represent selection *for* the characteristics represented by the predicted values and negative value represent selection *against*.

Table 3
Mean and 95% confidence intervals of variable compared among values of four relative resting habitat suitability (RRHS) bins. Bins were determined based on their strength of selection values. The <0.15 bin represents areas strongly selected against by fishers and the >0.61 bin represents areas that were strongly selected for by fishers. The bottom rows refer to the percent of FIA and fisher resting sites within each bin.

Variable	Mean and 95% confidence interval among RHS bins			
	<0.15	0.15–0.3299	0.33–0.61	>0.61
BA ($m^2\ ha^{-1}$)	23.4 (22.2–24.7)	49.1 (47.2–51.0)	65.1 (62.7–67.6)	88.3 (80.0–96.6)
CBA ($m^2\ ha^{-1}$)	15.2 (14.0–16.4)	35.8 (33.3–38.4)	48.7 (44.8–52.6)	69.7 (59.0–80.5)
HBA ($m^2\ ha^{-1}$)	8.2 (7.4–9.0)	13.2 (11.4–15.1)	16.4 (13.7–19.1)	18.5 (14.5–22.5)
BA_QUKE ($m^2\ ha^{-1}$)	1.5 (1.2–1.8)	1.5 (1.1–2.0)	2.2 (1.4–2.9)	1.5 (0.6–2.4)
BA_S ($m^2\ ha^{-1}$)	12.2 (11.4–13.0)	21.8 (20.3–23.3)	22.8 (20.9–24.8)	23.8 (20.3–27.4)
LRG_SNAG ($N\ ha^{-1}$)	8.4 (7.0–9.7)	13.3 (10.7–15.8)	14.9 (12.2–17.6)	14.0 (10.6–17.4)
DBH_MAX (cm)	77.9 (74.6–81.1)	120.0 (114.7–125.4)	139.2 (133.4–145.1)	152.2 (140.9–163.4)
CONSNAG (cm)	42.3 (38.6–46.0)	73.8 (67.0–80.5)	90.8 (80.9–100.6)	112.5 (96.8–128.1)
SLOPE (%)	45.5 (44.1–47.1)	50.3 (47.4–53.1)	46.6 (43.9–49.3)	44.7 (40.5–48.8)
HIGHSHRUB (%)	25.3 (23.4–27.1)	15.9 (13.5–18.3)	15.6 (12.8–18.4)	14.7 (9.0–20.5)
AGE (years)	98.1 (91.2–105.0)	144.1 (131.7–156.4)	152.6 (139.5–165.7)	144.5 (126.7–162.3)
LRG_WD ($m^3\ ha^{-1}$)	31.9 (25.9–37.8)	54.6 (45.1–64.1)	89.6 (74.5–104.6)	147.6 (119.5–175.7)
CC (%)	55.3 (51.9–58.6)	67.2 (62.4–72.1)	71.4 (66.0–76.8)	71.8 (63.7–79.8)
CC_STD (%)	8.7 (7.9–9.4)	8.0 (7.2–8.7)	8.1 (7.2–8.9)	8.7 (7.4–9.9)
HC (%)	59.9 (54.0–65.9)	79.0 (67.0–91.0)	88.5 (74.7–102.3)	94.3 (72.6–116.0)
DBH (cm)	19.6 (18.3–20.8)	21.4 (19.9–23.0)	23.2 (20.1–25.8)	26.5 (22.7–30.4)
DBH_HWD (cm)	12.1 (11.1–13.1)	15.4 (13.8–17.0)	16.1 (13.2–19.0)	24.6 (18.1–31.1)
Percent of 883 FIA plots	70.3	18.3	9.7	1.6
Percent of 99 fisher rest sites	4.0	12.1	43.4	40.4

and selection, a limited amount of interpretation is possible. For example, the top model in a previous model of fisher resting habitat suitability in northwestern California (Zielinski et al., 2004a) included canopy cover, maximum tree dbh and the presence of a large (>102 cm) dbh conifer snag. All of the top models in our exercise here identified canopy closure as an important predictor and 3 of the 10 top models also included large conifer snag. Fishers are strongly associated with closed canopy forests (Buskirk and Powell, 1994; Powell and Zielinski, 1994; Purcell et al., 2009; Lofroth et al., 2010) primarily because this is where they forage and find suitable resting structures. Thus, the inclusion of dense canopy and large conifer snags as predictors in models predicting fisher resting habitat suitability are not unexpected.

The model we selected for northwestern California fisher resting habitat was, however, distinctly different than the previous model we developed using FIA data for the southern Sierra Nevada (Zielinski et al., 2006) in that it did not include any topographic features (e.g., slope) nor did it include a variable representing the density of small trees. The absence of variables related to topography may make it easier for managers to affect positive change in RRHS since all variables in the selected model can be influenced by management actions. Managers we contacted were generally more favorable toward models that included variables that can be manipulated. The lack of a predictor related to the density of small diameter trees may be because fire is a less influential disturbance in northwest California than the Sierra Nevada, and thus the effects of fire suppression may not have resulted in an abundance of small trees associated with fisher rest structures in the northwest. Moreover, the model indicates that small trees appear to be less important (compared to the southern Sierra Nevada) and therefore the probability of producing high-value resting habitat without higher fire risk is greater.

High suitability resting habitat is apparently a rare commodity, as indicated by the paucity of FIA plots with high predicted value. Of the almost 900 FIA points in the modeled region, the highest RRHS value estimated at any of these points was 0.715. However, 21 of the 99 fisher rest sites (21.2%) had RRHS values >0.715. Thus, even though the FIA plots were randomly allocated in space, and are intended to be a representative sample of conditions on the ground, they did not often represent the environmental conditions that fishers selected most strongly for rest sites. And, fisher selection for these characteristics was strong; there is a conspicuous pattern of greater selection for high RRHS values compared to selection against low RRHS values. This highlights the rarity of the special conditions on the landscape that are attractive to fishers as resting sites.

The form of the strength-of-selection relationship reveals that fisher resting habitat selection is affected by more factors than were included in the selected model. That the relationship resembles a step function, rather than the monotonically increasing linear function, indicates that other factors – not accounted for in the model – also affect resting site choice. No single model can easily predict habitat choice, particular one that focuses only on plot-level variables (Shirk et al., in press). Habitat choice is a multi-scale phenomenon, and we did not consider here, for example, the location of plots relative to landscape attributes like patch size or distance to water. Furthermore, our model does not include the influence that prey or competitor distribution may have on resting habitat choices. Nonetheless, we believe that the selected model is a credible framework for characterizing resting habitat that can be easily integrated into the forest planning process by its association with the FIA program. One important shortcoming, however, is that the model predicts resting site habitat suitability, not the availability of resting structures (i.e., the specific trees, logs and other structural elements where a fisher rests). Resting structures were the center of the plots used to characterized resting sites, so their effect on the plot characteristics were accounted for, but we do not predict with our model the probability that any particular structural element will be used by a fisher. This is a challenge for the future and one that will reveal additional dimensions of fisher resting habitat.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2012.03.008.

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