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Resting structures and resting habitat of fishers in the southern Sierra Nevada, California

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ABSTRACT

The fisher (*Martes pennanti*) is a forest mustelid endemic to North America that has experienced range reductions in Pacific states that have led to their listing under the Endangered Species Act as warranted but precluded by higher priorities. The viability of the southern Sierra Nevada fisher population is of particular concern due to its reduced historical range, isolated nature, and low genetic variability. We located resting structures of radio-collared fishers in the southern Sierra Nevada and compared resting and available habitat to examine selection for specific features of resting sites. Resting structures provide protection from predators and unfavorable weather and are believed to be the most limiting habitat element across fisher home ranges. Resting structures were found primarily in live trees (76%) and snags (15%). Trees used by fishers for resting were among the largest available and frequently had mistletoe infestations. Ponderosa pines (*Pinus ponderosa*) were used more often than expected and incense cedars (*Calocedrus decurrens*) less than expected. Snags were also large and in fairly advanced stages of decay. Habitat at fisher resting sites had higher canopy cover, greater basal area of snags and hardwoods, and smaller and more variable tree sizes compared to random sites. Resting sites were also found on steeper slopes and closer to streams. Canopy cover was consistently the most important variable distinguishing rest and random sites. In western North America, fishers are generally associated with late-successional forests, but changes in these forests due to logging and fire suppression have resulted in a transition to forest stands characterized by fewer large trees and more small stems. These conditions are consistent with our finding that the large rest structures were surrounded by smaller than average trees. Management practices that support the growth and retention of greater numbers of large trees and snags, while maintaining a minimum of 61% (based on moosehorn) or 56% (generated via Forest Vegetation Simulator) canopy cover and a complex horizontal and vertical forest structure, can improve and provide for future fisher habitat.

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1. Introduction

The fisher (*Martes pennanti*) is a forest mustelid endemic to North America that historically occupied conifer-dominated and mixed deciduous forests of Canada and the northern United States, with its distribution extending southward along peninsular mountain ranges. During the early part of the 20th century, fishers experienced significant reductions throughout their range, which

have been primarily attributed to overtrapping and habitat loss (Powell and Zielinski, 1994). Although many populations in central and eastern portions of the historic range have recovered due to trapping restrictions, reintroductions, and abandonment of farm-lands and ensuing reforestation, western populations have not (Gibilisco, 1994). Western populations were historically distributed throughout coniferous forests from British Columbia south to the Sierra Nevada of California but fishers have been extirpated from extensive portions of their historical range. West Coast fisher populations have been petitioned for listing under the federal Endangered Species Act on three occasions. The first two petitions were denied based on lack of empirical information but the most recent led to a finding of warranted but precluded by higher priorities (Federal Register, 2004).

Grinnell et al. (1937) described the distribution of fishers in California in the early twentieth century as a continuous arc from the Coast Range eastward to the southern Cascades, then south

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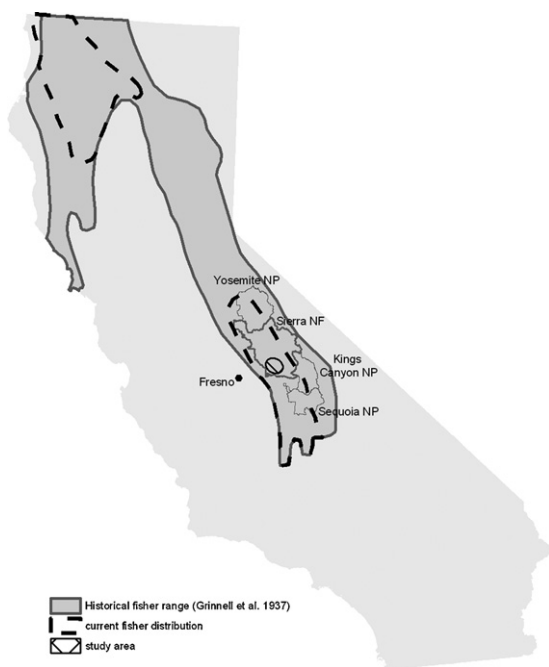


Fig. 1. Historical and current distribution of fishers (*Martes pennanti*) in California and location of study area in the southern Sierra Nevada, California, USA, where fishers were studied from 1999 through 2001.

throughout the Sierra Nevada. Fishers in California currently occupy less than half of their historic range and are absent from the northern and central Sierra Nevada (Fig. 1; Zielinski et al., 1995, 2005). The conservation of the southern Sierra Nevada population is of particular interest because it is isolated from the nearest population to the north by approximately 430 km (Zielinski et al., 2005) and has low levels of genetic diversity (Drew et al., 2003; Wisely et al., 2004), reducing the effective population size. This population represents the southernmost extension of their North American range and occupies a unique environment for fishers due to the hot, dry climate. Due to its isolation, small population size, and low genetic variability, the southern Sierra Nevada fisher population is considered vulnerable to extinction.

Fishers show greater selectivity for resting habitat than for foraging or traveling habitat, and resting and denning structures are likely the most limiting habitat elements in fisher home ranges (Zielinski et al., 2004). Resting locations are hypothesized to provide protection from predators and weather, aid in thermal regulation (respite from heat in summer and from cold and moisture in winter), and provide a place to consume prey (Kilpatrick and Rego, 1994; Aubry and Raley, 2006). Resting structures typically have low reuse rates and may be located near their last successful foraging location, suggesting that fishers require multiple resting structures distributed throughout their home ranges (Zielinski et al., 2004). We define resting location as the cavity, platform, etc. used for resting, resting structure as the habitat element (e.g., tree, snag) that contains the resting location, resting site as the habitat in the vicinity of the resting structure, and resting stand as the forest type in which the resting structure is located, following Slauson and Zielinski (2009). Taken together, resting sites and resting stands comprise resting habitat.

Suitable resting structures and habitat are essential for survival and maintaining viable fisher populations, yet are not well understood for fishers in the West, and particularly those in the Sierra Nevada. Fisher resting locations in western populations have been predominantly found in large trees, snags, and logs, although rock piles, root burrows, and cull piles have also been used (Seglund, 1995; Weir and Harestad, 2003; Zielinski et al., 2004;

Yaeger, 2005; Aubry and Raley, 2006). Research suggests that late-successional forest stands and their structural features are preferred habitat for fishers in western North America (Powell and Zielinski, 1994). These features include high canopy cover, large trees and snags, and structural complexity (Seglund, 1995; Zielinski et al., 2004, 2006; Yaeger, 2005). Zielinski et al. (2004) found that fishers in the Sierra Nevada selected resting sites with dense canopy cover and large trees in areas where structural features (except canopy cover) were most variable. Structural complexity near the forest floor has also been found to be important, with coarse woody debris an important indicator of fisher habitat use (Seglund, 1995; Weir and Harestad, 2003). In addition, the presence of trees that are alive but declining is a habitat feature typically associated with late successional forests and with fisher resting habitat. Cavities caused by heartwood decay (Zielinski et al., 2004) and platforms resulting from diseases such as mistletoe and rust brooms (Powell, 1993; Weir and Harestad, 2003; Aubry and Raley, 2006) have been used as resting locations.

Abiotic features such as distance to water, slope position, and steepness have also been shown to influence resting structure use. Proximity to water has been found important in some areas (Seglund, 1995; Yaeger, 2005), particularly in the southern Sierra Nevada (Zielinski et al., 2004). Fisher resting sites have been found more often on steep slopes (Zielinski et al., 2004, 2006) and in drainage bottoms compared to random sites (Yaeger, 2005).

This study was initiated to describe resting structures and resting habitat used by fishers in the southern Sierra Nevada. Previous work has described resting structures and habitat of fishers in the southern Sierra Nevada (Zielinski et al., 2004, 2006). This study replicates and builds on that work. We were especially interested in the relative importance of canopy cover, the size and density of trees and snags, and attributes of late-successional forests such as multi-layered structure and decadence, as fisher habitat suitability is expected to be negatively affected by forest management activities that affect these features (Spencer et al., 2008). To achieve this goal we compared resting structures with available trees and snags and examined selection for specific features of resting sites through the development of a logistic regression model for estimating the probability that a site will be used as a resting site. We used the model to provide quantitative recommendations for fisher resting habitat characteristics and to explore possible thresholds. Because high overhead cover has been found to be a key habitat element of fisher habitat, we explored issues related to canopy cover and closure in more depth. Our goal was to improve our knowledge of the factors that affect fisher populations and their distribution and aid in the development of practical management strategies.

2. Methods

2.1. Study area

This study was conducted from 1999 through 2001 in the Kings River Project area, High Sierra Ranger District, Sierra National Forest in Fresno County, California. Field work was carried out between 1000 and 2400 m in elevation, corresponding to fisher occurrence in the region, and the study area included a mix of public and private land. The study area was bordered by Shaver Lake to the north, state highway 168 to the west, the Kings River to the south, and the north fork of the Kings River to the east (Fig. 1). The climate is Mediterranean, with warm dry summers and cool wet winters. Precipitation falls in the form of rain and snow, mainly between November and April.

The predominant forest cover types in the area are Sierran mixed conifer, ponderosa pine (*Pinus ponderosa*), and montane

hardwood-conifer (Mayer and Laudenslayer, 1988). Logging and fire suppression have influenced stand structure. Most harvesting was selective and targeted larger stems and pines (McKelvey and Johnston, 1992). Fires in the region have been regularly suppressed since the mid-1900s. Historically, fires are thought to have been surface fires of mostly low severity with fire return intervals of 6–12 years (Phillips, 2002), or fires of varying intensity with average return intervals of large fires every 50 years (Minnich et al., 2000). Lightning was the common source of ignitions. Logging and fire suppression have led to changes from forests dominated by large, old, widely spaced trees to forests characterized by dense, fairly even-aged stands dominated by younger age classes (McKelvey and Johnston, 1992).

2.2. Trapping and handling

Live-trapping of fishers was performed during three different periods: August 1999 through October 1999, July 2000 through August 2000, and December 2000. Live traps (model 207, Tomahawk Live Trap Company, Tomahawk, WI, USA) were modified to include a plywood cubby box to provide shelter (Wilbert, 1992; Seglund, 1995). Traps were typically placed next to downed logs within 10 m of a stream. We baited traps with a piece of raw chicken securely tied to the inside of the trap and a commercial lure (Gusto, Minnesota Trapline Products, Penneck, MN, USA). Traps were checked daily and re-baited or re-scented at least every fourth day.

Captured animals were coaxed into a metal handling cone and sedated with a Ketamine hydrochloride and Diazepam mixture (1 mg Diazepam/200 mg Ketamine) injected intramuscularly. Dosage was based on estimated body weight and averaged 0.21 ml/kg (range 0.13–0.28). Each adult animal was fitted with a radiocollar (Telonics Inc., Mesa, AZ, USA) with a 16-h on- and 8-h off-duty cycling option to extend battery life and a mortality sensor. We recorded the animal's sex, age class, and weight, and a standard set of measurements were taken. Each fisher received a subcutaneous PIT tag (passive integrated transponder; 125 kHz, TX 1405L; Biomark, Boise, ID) for permanent and unique identification, and color-coded ear tags and reflective tape (Colored Rototag; Dalton Group Limited, Dalton House, Nettlebed, Oxfordshire, England). Capture and handling methods were approved under permit from CA Department of Fish and Game.

2.3. Resting structure selection

We located radio-collared fishers periodically from October 1999 through May 2000 and from October 2000 through April 2001. We used handheld receivers and antennas and standard triangulation telemetry techniques to determine approximate locations of animals. When the radio signal indicated the animal was not moving (consistent directionality and signal strength), we attempted to locate the animal on foot. A walk-in location was successful when the animal either remained at the site while the observer determined the correct location, or there was visual confirmation of the animal using the resting structure.

During the first field season, we concentrated walk-in efforts on potentially denning females, although no dens were confirmed. During the second season we attempted to locate each animal every two days by walk-in method. This increased effort resulted in a higher number of resting structure locations for all animals in the second season.

For each resting structure in a tree or snag, we recorded diameter at breast height (dbh), substrate height, tree species (for trees), and decay class of snags (Cline et al., 1980). Occurrence of dwarf mistletoe brooms was recorded for most rest structures after we noticed that many were infected. We classified decay classes of

logs according to Franklin et al. (1981). The location of the resting structure was recorded using a Global Positioning System (GPS) and entered into a Geographic Information System (GIS).

2.4. Habitat sampling

Habitat was sampled at resting sites and at random sites in the same manner. A total of 260 random sites were sampled, using a modified stratified random sampling scheme where the number of plots placed within each forest cover type were proportional to their actual distribution within the Sierra National Forest (Hyde et al., 2005). Data collected at random sites were designed to calibrate metrics derived from lidar data; random sites were centered on laser footprints and not centered on a structure. We classified habitat at resting and random sites using the California Wildlife Habitat Relations system (CWHR; Mayer and Laudenslayer, 1988). CWHR classes include habitat type, tree size class, and canopy cover class, and were assigned based on Sierra National Forest GIS vegetation layers derived from landsat imagery and air photo interpretation. From the 260 random sites sampled, we selected 160 sites located in stands with CWHR habitat types used by fishers as resting sites and in roughly equal proportions to those used by fishers in our data set. Six of these sites were dropped from analysis because they overlapped spatially with plots centered on resting structures (<112 m between plot centers; see below). CWHR habitat type of resting stands and random sites did not differ ($\chi^2_4 = 3.36, P = 0.499$).

We established concentric circular plots centered on resting structures and random sites with an inner plot of 0.07 ha (15-m radius) and an outer plot of 1 ha (56.4-m radius) (Fig. 2). We extended fiberglass tapes to create transects in four directions at right angles from each other, two parallel to the slope and two across slope from the plot center. Within the 0.07-ha circle we recorded species and diameter at breast height (dbh) for all live stems and dbh and decay class for all dead stems >10 cm dbh and

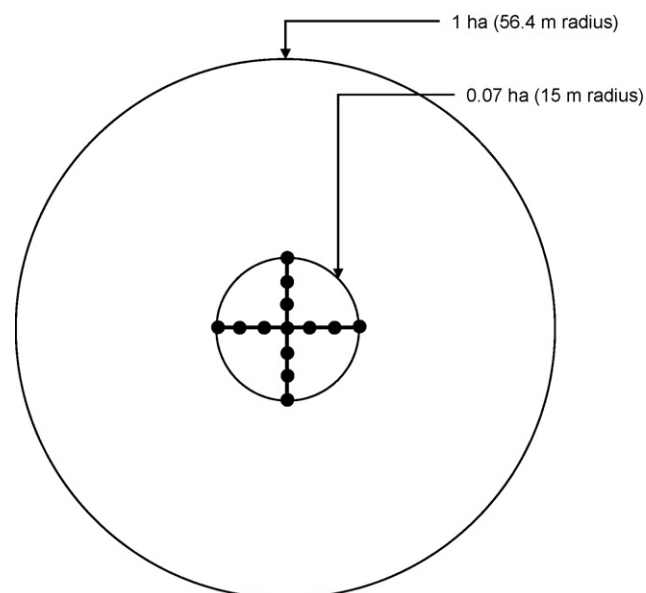


Fig. 2. Vegetation sampling design for fisher resting sites and random sites in the Sierra National Forest, 1999–2001. In the inner 0.07-ha circle, we recorded species, dbh, height, full and partial crown heights, crown wedge angle, crown slope, and crown radius for trees >10 cm dbh and dbh, height, and decay class for snags >10 cm dbh and >2 m tall. In the outer 1-ha circle, we recorded species, dbh and height for trees >76 cm dbh, and dbh, height, and decay class for snags >50 cm dbh and >3 m tall. Ground and log cover were recorded on the 4 15-m transects in the 0.07-ha circle. Canopy cover was measured using a moosehorn at the center and at 5, 10, and 15 m along each transect.

>2 m in height. These measurements were used to calculate basal area variables.

We recorded log and shrub cover to the nearest decimeter along each of the 4 transects within the 15-m circle. Logs were defined as >10 cm dbh and 2 m long with at least one-third of the log above ground. Shrub cover was recorded for shrubs <1 m and >1 m in height and measurements included only structures <10 cm dbh. We took canopy cover measurements at the center, and at 5, 10, and 15 m along each transect using a moosehorn (Moosehorn Coverscopes, Medford, Oregon). The 13 readings were averaged.

The large 1-ha plot was used to sample large trees and snags. Within the 1-ha plot, we measured tree height and dbh for trees >76 cm dbh, and height, dbh, and decay class for snags ≥ 50 cm dbh and ≥ 3 m tall. We recorded the species of each tree >76 cm dbh within all 1-ha vegetation plots for use as an index of available large trees within areas of known fisher use.

We obtained slope and aspect for rest and random sites from Sierra National Forest digital elevation model GIS layers and distances from streams and roads from stream and road coverages. Roads were not classified into types (highway, paved, gated, unimproved, etc.) due to inconsistencies between the GIS road categories and actual road conditions. Therefore roads were viewed as a gap in habitat rather than a perceived barrier due to human use.

Sample sizes vary because habitat measurements were not completed at all resting sites and log and shrub cover were not measured at two resting sites due to snow cover.

2.5. Statistical analysis

We tested for differences in resting structures and resting sites used by females and males using *t*-tests (PROC TTEST; SAS version 9.1.3, SAS Institute Inc., 2003), although sample sizes were limited for males. We tested for differences in aspect for rest and random sites using a *q*-sample Uniform Scores test (Mardia and Jupp, 2000).

We compared resting sites to available sites to develop a habitat model for estimating the probability that a site is a resting site. Because we did not know what site characteristics would best predict fisher resting sites, we created a list of variables potentially important to selection of resting sites based on results from previous work, biological relevance, relevance to land managers, and lack of multicollinearity. As a measure of canopy layering, an element associated with structural complexity associated with late-successional forests, we calculated the standard deviation of dbh of trees. We compared habitat at resting and random sites using *t*-tests to help guide variable selection.

Spline smoothing techniques were used to better understand the functional form of the selected candidate variables. We used logistic Generalized Additive Models (GAM MGCV routine, R version 6.2; R Development Core Team, 2004.) to obtain a logit response regressed on a linear combination of smoothing functions of the explanatory variables and graphs of their partial residuals to explore their significance and functional form (linear, polynomial, logarithmic, etc.) (Venables and Ripley, 1997).

To reduce the number of possible models from the set of variables and identify the final set of candidate models, we applied best subsets regression (PROC LOGISTIC; SAS version 9.1.3, SAS Institute Inc., 2003). We considered models with a maximum of 6 variables to avoid overfitting (Peduzzi et al., 1996). We selected the top 3 models with 4–6 variables, along with a null (intercept only) and a full model. We also evaluated two models from Zielinski et al. (2004): their overall model based on data from southern Sierra Nevada and coastal California populations and their model based on data from the southern Sierra Nevada only. The latter model was derived by model averaging of the two most-supported models. This resulted in a total of 13 candidate models.

We used logistic regression for fitting the probability a site is a resting site and to determine the best fitting and most parsimonious model, however our response variable is not exactly a binomial response. Our random sites represented available habitat rather than strictly unused habitat. In habitat use and availability studies such as this, random sites cannot be confirmed as unused and thus it is possible that some randomly sampled sites actually included resting sites, sometimes referred to as ‘contaminated controls.’ To remedy this potential problem, we restricted the selected random samples to those that did not spatially overlap with plots measured at resting sites and treated the data as a case–control design. We then followed procedures used by Preisler et al. (2004) as described below. A logit model was fitted using maximum likelihood estimation based on the following identity for conditional probability (Rao, 1973; Preisler et al., 2004).

$$\text{Prob}(R_i|S_i) = \frac{\text{Prob}(S_i|R_i)\text{Prob}(R_i)}{\text{Prob}(S_i)}, \quad (1)$$

where R_i = rest plot i , S_i = sampled plot i , and $\text{Prob}(R_i|S_i)$ = probability of observing a fisher resting on plot i given that this plot is in the sample, $\text{Prob}(R_i)$ = probability that plot i is a resting site, and $\text{Prob}(S_i)$ = probability that plot i is sampled. Let $\text{Prob}(R_i) = p_i$ and pr = the proportion of random sites that were not fisher resting sites. Therefore, the identity (1) becomes:

$$\text{Prob}(R_i|S_i) = \gamma_i = \frac{p_i}{p_i + (1 - p_i)pr} \quad (2)$$

Applying the logit transformation to (2), we get the following relationship:

$$\text{logit}(\gamma_i) = \text{logit}(p_i) - \log(pr) \quad (3)$$

The $\text{logit}(\gamma_i)$ differs from $\text{logit}(p_i)$ by the unknown constant pr , and since we are interested only in the relationship between the response and the explanatory variables, we modeled $\text{logit}(\gamma_i)$ as a linear regression model treating the intercept as a nuisance parameter (for more details see Manly et al., 1993; Keating and Cherry, 2004). The used logit model is as follows:

$$\text{logit}(\gamma_i) = a + g(X_i, Y_i) + \sum_j f(x_{ij}), \quad (4)$$

where a = intercept, $g(X_i, Y_i)$ = a two-dimensional smoothing function of the UTM northing and easting coordinates of plot i , and f represents parametric functional forms (polynomial) for the explanatory variables x_{ij} in plot i , where j = the number of explanatory variables. The spatial function g accounts for spatial autocorrelation, which can result from non-independence of multiple observations of the same individual, the fact that resting sites were not selected at random, or other causes. The functional form of f was determined after visually observing the partial residual graphs of the spline-smoothed form resulting from the application of GAM.

We used an information theoretic approach to determine the most supported model for estimating the probability that a site is a resting site regressed on selected habitat variables (Burnham and Anderson, 2002). We evaluated candidate models using Akaike’s Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson, 2002). The spatial effect was forced in all the candidate models. When no single top model was identified, we applied model averaging over the entire set of models to avoid making inferences based only on the top model (the one with smallest Akaike weight) and made inferences. We also evaluated the importance of individual variables using the summed Akaike weights over all models in which that variable appeared (Burnham and Anderson, 2002).

3. Results

3.1. Resting structure selection

We obtained locations on 9 fishers (6 males and 3 females) from October 1999 through May 2000, and 7 fishers (2 males and 5 females) from October 2000 through April 2001. Because one male and one female were tracked in both years, a total of 14 individual fishers were tracked. Over two field seasons, we located 78 unique resting structures used by 11 animals (6 females and 5 males) (no resting structures were found for two males and one female). Fifty-seven were used by females and 21 by males. The number of resting structures located for individual fishers ranged from 1 to 26, with a mean of 7.1 per animal. Reuse of resting structures by the same individual was observed 4 times, and included both male and female animals. All reused sites were in live trees and included a potential, unconfirmed den site that was likely a failed attempt (Mazzoni, 2002). Resting structures located more than once were included only once in analyses.

Most (59, 76%) of the resting structures were in live trees, 12 (15%) were in snags, 3 were in logs, and 2 each were found in stumps and rock crevices. Rest trees and snags were tall, large-diameter structures (>36 m tall and >95 cm dbh, on average; Table 1). Within the 0.07 ha surrounding the rest structure, all trees and snags were ranked by size according to dbh. For 58 resting structures where the rest structure was either a live tree or snag, 55% were the largest structure in the 0.07-ha plot and 71% were the largest or second largest. Logs, stumps, and rock piles were used only rarely as resting structures. All animals in structures close to the ground were found during periods of active precipitation or immediately after snow accumulation.

Resting trees were predominantly ponderosa pine and white fir (*Abies concolor*). Of live trees used by fishers, 37% were ponderosa pine, 32% white fir, 14% California black oak (*Quercus kelloggii*), 12% sugar pine (*Pinus lambertiana*), and 5% incense cedar (*Calocedrus decurrens*) (Table 2).

We compared resting tree species with available large trees in the 1-ha plot surrounding them to examine selection in the immediate vicinity of the rest tree rather than across the landscape. The proportions of rest tree species used differed from available large trees ($\chi^2_4 = 16.73$, $n = 933$, $P = 0.002$). Chi-square values for individual tree species suggest that incense cedar was used less than expected and ponderosa pine was used more than expected (Table 2). In addition, there was some evidence that California black oaks were also selected for (14% of rest trees vs. 9% of available trees).

Most snags used for resting were in fairly advanced stages of decay. Of the 12 snags used for resting, half were classified as decay

Table 1
Mean diameter at breast height (dbh) and height of fisher rest trees and snags in the Sierra National Forest, CA, 1999–2001.

	Dbh (cm)			Ht (m)		
	n	Mean	SD	n	Mean	SD
All live	57	95.32	29.09	49	36.67	12.01
F	47	97.89	30.16	39	37.24	11.99
M	10	83.20	20.40	10	34.45	12.45
Conifers only	49	94.45	30.96	342	39.76	9.94
F	40	97.40	32.30	33	40.84	9.10
M	9	81.33	20.71	9	35.82	12.38
Snags	12	116.75	47.23	11	16.94	14.43
F	6	98.83	31.91	6	14.97	12.11
M	6	134.67	55.86	5	19.31	18.01

Data for resting structures in live conifers excluded black oaks (*Quercus kelloggii*), which were shorter and had larger diameters.

Table 2

Tree species used by fishers as resting structures and the number of available large trees (>76 cm dbh) within 52 1-ha plots centered on resting structures in live trees in the Sierra National Forest, CA, 1999–2001.

Species	All	Females	Males	Available	χ^2 value ^a
Incense cedar	4	3	1	222	9.16
White fir	20	19	1	236	0.46
Sugar pine	8	7	1	144	0.61
Ponderosa pine	23	17	6	193	4.85
California black oak	9	8	1	78	1.65

The overall χ^2 test was significant ($\chi^2 = 16.73$, $df = 4$, $P = 0.002$). The χ^2 contribution for each tree species to the overall test is provided for comparison.

^a χ^2 contribution by tree species for analysis comparing all resting structures with available.

class 5 (the most advanced stages of decay), and none were in classes 1 or 2. Of 45 rest trees (oaks and cedars excluded) for which mistletoe occurrence was recorded, 38 (84%) had obvious mistletoe infestations.

3.2. Resting habitat selection

Based on CWHR classification of the stands within which fisher resting structures were found, fisher resting sites occurred most often in Sierran mixed conifer and ponderosa pine forest types, but some were classified as montane hardwood-conifer, montane hardwood, and montane chaparral (Fig. 3). Average tree sizes in the stands were small, with 55% of the stands with trees in the 28–61 cm dbh size class (11–24 in.), but with high canopy cover (70% had >60% canopy cover).

Although sample sizes for male resting sites were small, we found no differences between sexes for any variables except distance to ephemeral stream (females: $\bar{x} = 46.3$ m, $n = 57$, males: $\bar{x} = 28.9$ m, $n = 21$, $t_1 = 2.55$, $P = 0.013$), suggesting that males select resting structures closer to streams than females. Resting and random sites did not differ in mean aspect (rest: $\bar{x} = 191.6^\circ$, random: $\bar{x} = 186.3^\circ$, $w_2 = 0.188$, $P = 0.910$).

We identified 12 candidate variables for inclusion in habitat selection models: percent canopy cover, average dbh of trees, standard deviation of the dbh of live trees, basal area of conifers, hardwoods, and snags, percent cover of logs, number of large trees per ha, number of large snags per ha, maximum dbh of trees in 1 ha plot, percent slope, and distance to stream (Table 3). GAM analyses suggested that all variables responded in a linear fashion except for percent canopy cover, which was best explained by a concave quadratic function, and seemed to indicate that the probability a site is a resting site is maximized at some canopy cover value (Fig. 4).

Of the 13 models tested, the most-supported model, with an Akaike weight of 0.39, included linear and quadratic effects of canopy cover and linear effects of basal area of snags, average dbh of trees, the standard deviation of dbh, slope, and hardwood basal area (Table 4). The second-most supported model had ΔAIC_c of 0.69, an Akaike weight of 0.28, and differed in only one variable: distance to stream replaced hardwood basal area. No other models had ΔAIC_c values <3. The spatial effect for the top model was significant ($P \approx 0.003$), and increased the explained deviance from 33.5 to 48.8%.

Because no one model accounted for a majority of the Akaike weight, we used model averaging to reduce model selection bias. Regression estimates for the two top models were similar to the model-averaged estimates and were well within the 95% confidence intervals for the estimates. Regression coefficients indicated that resting sites had higher canopy cover, higher basal area of snags and hardwoods, more variable tree diameters, were surrounded by smaller diameter trees, and were found on steeper slopes and closer to streams, compared to random sites (Table 5).

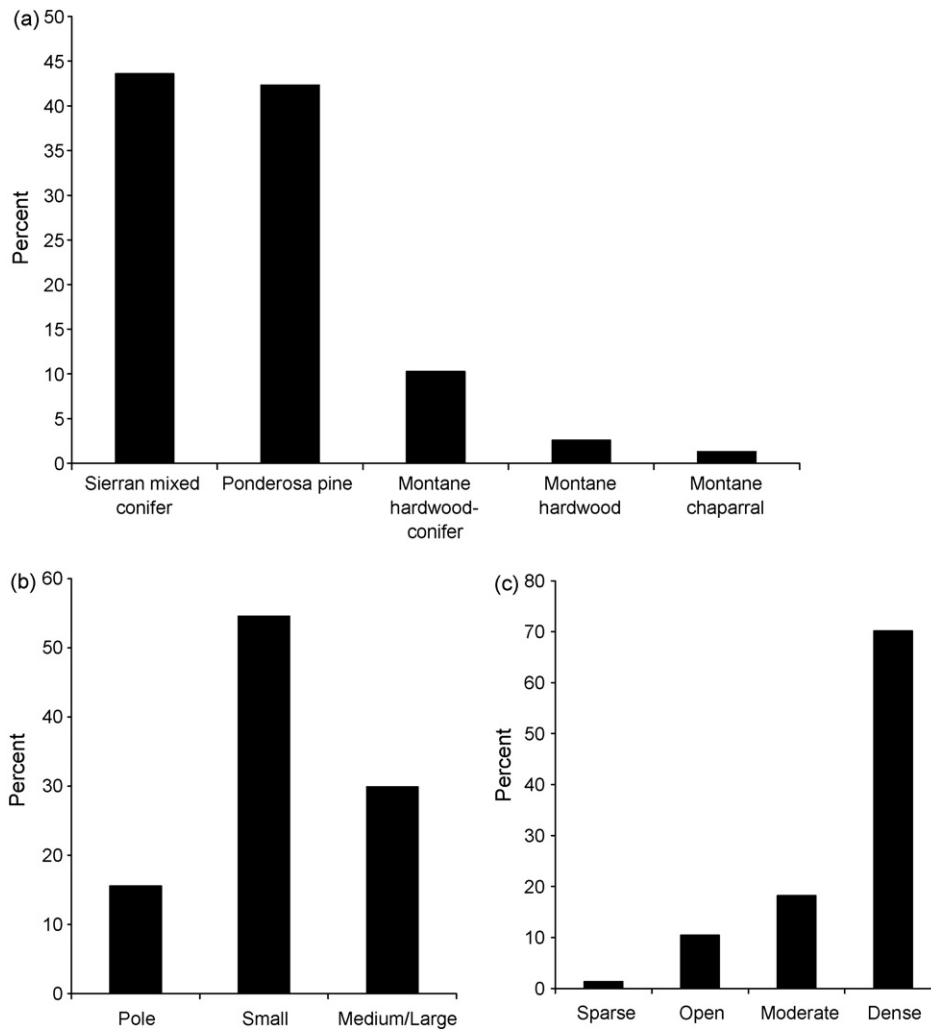


Fig. 3. California Wildlife Habitat Relationships (CWHR) classification of resting habitat in the Sierra National Forest from 1999 through 2001 for (a) forests type, (b) tree size class, and (c) cover class, based on Sierra National Forest GIS vegetation layers. Tree size classes include pole (15–28 cm dbh; 6–11 in.), small (28–61 cm dbh; 11–24 in.), and medium/large (> 61 cm dbh; >24 in.). Cover classes are sparse (10–24% cover), open (25–39%), moderate (40–59%) and dense (> 60%).

Table 3
Means (SD) for habitat variables measured at fisher resting sites and random sites in the Sierra National Forest, CA, 1999–2001.

Variable	Resting sites		Random sites	
	Mean (SD)	n	Mean (SD)	n
Canopy cover (%)	73.7 (12.5)	61	55.3 (22.3)	154
No. trees (>10 cm dbh)	40.9 (17.7)	61	28.5 (16.8)	154
Average dbh of trees (>10 cm)	29.7 (7.1)	61	33.2 (11.6)	154
No. snags (>10 cm dbh, >2 m tall)	5.9 (6.0)	61	3.8 (5.2)	154
Standard deviation dbh live trees	22.2 (6.4)	61	20.3 (92.0)	154
Crown layering	2.36 (0.49)	61	2.22 (0.55)	154
Basal area live conifer trees (>10 cm dbh)	3.7 (1.6)	61	2.9 (1.7)	154
Basal area hardwoods (>10 cm dbh)	0.4 (0.6)	61	0.2 (0.4)	154
Basal area snags (≥26 cm dbh)	0.5 (0.7)	61	0.2 (0.4)	154
Shrub cover <1 m (%)	24.9 (22.6)	59 ^a	27.4 (24.8)	154
Shrub cover >1 m (%)	14.5 (13.6)	59 ^a	11.9 (13.9)	154
Log cover (>10 cm dia, >2 m long; %)	3.8 (3.1)	59 ^a	2.7 (3.6)	154
No. large trees in 1 ha plot (>76 cm dbh)	18.8 (11.6)	61	14.0 (12.8)	154
No. large snags in 1 ha plot (>50 cm dbh)	5.7 (3.6)	61	4.0 (4.2)	154
Max. dbh trees in 1 ha plot (cm)	141.9 (30.2)	61	125.7 (36.2)	154
Slope (%)	37.3 (19.1)	78	27.8 (14.6)	154
Distance to stream (m)	41.6 (29.4)	78	56.6 (51.9)	154
Distance to road (m)	150 (101)	78	180 (133)	154

Variables selected for inclusion in final models are shown in bold.
^a Shrub and log cover were not measured at two sites due to snow cover.

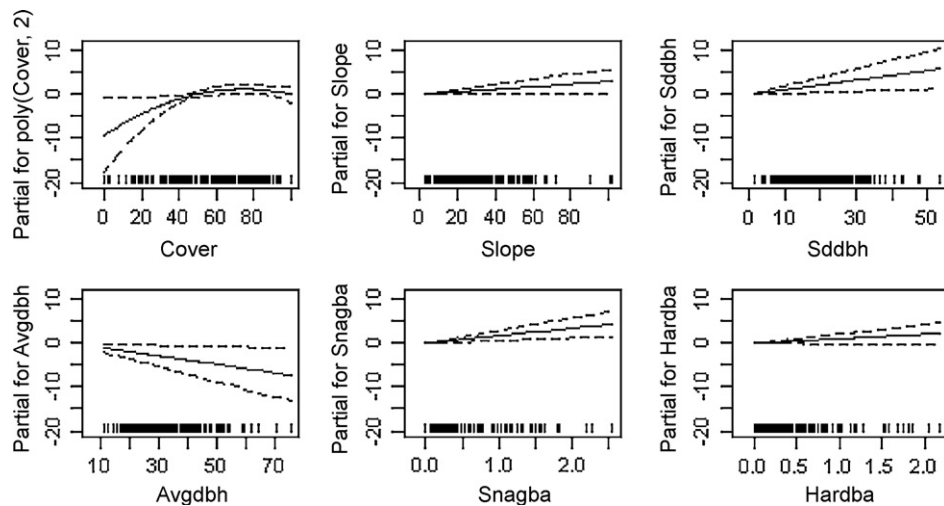


Fig. 4. Plots of partial residuals for variables included in the most-supported habitat model for estimating the probability that a site is a resting site in the Sierra National Forest, CA, 1999–2001. The model included a spatial effect variable, which is not shown here. Tick marks along the x-axis represent the data points.

Table 4

Model selection results for models distinguishing fisher resting sites from random sites in the Sierra National Forest, CA, 1999–2001.

Model	K	AIC _c	ΔAIC _c	w _i	Deviance explained (%)
Cover ² + snagba + avgdbh + sddbh + slope + hardba	23	173.7318	0.00	0.39	48.8
Cover ² + snagba + avgdbh + sddbh + slope + streamdist	23	174.4263	0.6946	0.28	48.4
Cover ² + snagba + avgdbh + sddbh + slope + log	23	177.1826	3.4508	0.07	44.1
Cover ² + snagba + slope + sddbh + avgdbhtree	22	177.5097	3.7779	0.06	43.4
Cover ² + snagba + avgdbh + sddbh + hardba	22	177.6050	3.8732	0.06	46.7
Full	29	177.6631	3.9313	0.06	52.4
Cover ² + snagba + avgdbh + slope + maxdbh	22	178.9364	5.2046	0.03	42.9
Cover ² + snagba + avgdbh + slope + hardba	21	179.2888	5.5570	0.02	45.4
Cover ² + snagba + avgdbh + sddbh	21	180.2620	6.5302	0.02	42.0
Cover ² + snagba + avgdbh + slope	21	181.2349	7.5031	0.01	44.5
Cover ² + slope + maxdbh ^a	20	187.5384	13.8066	0.00	37.7
Sddbh + maxdbh + slope + streamdist ^b	20	190.2938	16.5620	0.00	39.6
Intercept	16	207.1401	33.4083	0.00	29.7

Thirteen models were considered, including a full model, a null model, and two models based on Zielinski et al. (2004). Variables included linear and quadratic effects of canopy cover (Cover²) and linear effects of basal area of snags (snagba), basal area of hardwoods (hardba), average dbh of trees (avgdbh), maximum dbh (maxdbh), standard deviation dbh of live trees (sddbh), percent slope (slope), percent cover of logs (log), distance to stream (streamdist), percent cover of logs (log), maximum dbh of trees (maxdbh), conifer basal area, and the number of large (>50 cm dbh) snags and trees per ha. In addition, all models included a spatial effect (that included 15 parameters) to control for spatial autocorrelation. Sample sizes were 61 for resting sites and 154 for random sites.

^a Overall model from Zielinski et al. (2004) based on data from southern Sierra Nevada and coastal California populations.

^b Sierra model from Zielinski et al. (2004) based on data from the southern Sierra Nevada population only.

Table 5

Estimated regression coefficients and *P*-values for most-supported model, model-averaged regression coefficients, and summed Akaike weights over all models in which that variable appears for fisher resting sites and random sites in the Sierra National Forest, CA, 1999–2001.

Parameter	Estimated regression coeff. in logit scale for top model	<i>P</i> -value for top model	Model-averaged regression coeff. in logit scale	Frequency	Sum of the Akaike weights
Intercept	-6.147	<0.001	-5.335	13	1.00
Cover	26.060	0.004	25.048	11	1.00
Cover ²	-15.418	0.021	-13.360	11	1.00
Snagba	1.768	<0.001	1.559	10	1.00
Avgdbh	-0.095	0.004	-0.094	9	0.97
Sddbh	0.111	0.002	0.109	8	0.94
Slope	0.030	0.005	0.030	10	0.93
Hardba	1.039	0.019	1.050	4	0.53
Streamdist			-0.010	3	0.34
Log			8.306	2	0.13
Maxdbh			0.013	4	0.09
Coniferba			0.392	1	0.06
Lgsnag			0.007	1	0.06
Lgtree			-0.039	1	0.06
Spatial effect		≈0.003		13	1.000

Variables included linear (Cover) and quadratic (Cover²) effects of canopy cover and linear effects of basal area of snags (Snagba), standard deviation dbh of live trees (Sddbh), average dbh of trees (Avgdbh), slope (Slope), basal area of hardwoods (Hardba), distance to stream (Streamdist), percent cover of logs (Log), maximum dbh of trees (Maxdbh), basal area of conifers (Coniferba), and number of large snags and trees (>50 cm dbh) per ha (Lgsnag, Lgtree), and a spatial effect to account for spatial autocorrelation resulting from autocorrelation of multiple resting sites of the same individual. The overall spatial effect is shown but not the 15 coefficients because they are considered nuisance parameters. Frequency is the number of models in which each variable appeared.

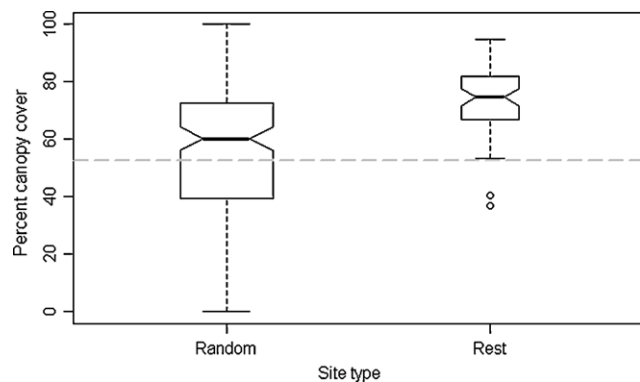


Fig. 5. Notched box plots of percent canopy cover for random sites and resting sites used by fishers in the Sierra National Forest from 1999 through 2001. The dark horizontal line in the notched portion of the box marks the median, the notch width represents the 95% confidence interval, and the upper and lower edges forming the box represent the first and third quartiles (or the 25th and 75th percentiles). The upper and lower whiskers represent the smallest non-outlier values (not more than 1.5 times the interquartile range). The lowest non-outlier value for resting sites (53%) is noted by a dotted line. The circles below 53% represent outliers.

The sum of the Akaike weights over all models in which that variable appeared suggested that the variables most important for resting site selection are canopy cover and basal area of snags, followed by average dbh of trees, standard deviation of dbh of trees, percent slope, hardwood basal area, and distance to stream (Table 5).

The partial residuals for canopy cover showed that the probability a site was a resting site increased to an apparent threshold at roughly 50–55% canopy cover, after which increases in canopy cover did not appear to substantially increase the probability that a site was a resting site (Fig. 4). Below this threshold sites are unlikely to be used for resting, which is confirmed by the fact that 97% of resting sites had >53% canopy cover, with only two observations with lower cover (Fig. 5). To further investigate canopy cover conditions at resting sites, applying partial derivatives and using the estimated cover coefficients, we calculated the value of the canopy cover (and the 95% confidence interval) that maximized the probability that a site is a resting site. The probability that a site was a fisher resting site was maximized at 72% canopy cover (95% confidence interval: 61–82%). Because the confidence interval did not include values in the apparent threshold range (50–55%) we conducted a sensitivity analysis to investigate the effect of reducing canopy cover below

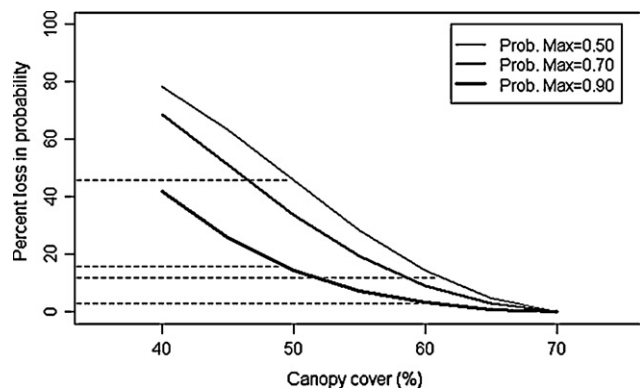


Fig. 6. Sensitivity analysis of the effect of reducing canopy cover levels on the maximum probability a site is used as a fisher resting site. Horizontal lines show the relative change in the probability a site is a resting site when canopy cover is decreased from 72% (where the probability is maximized) to 50% (threshold value) and 61% (lower confidence interval) canopy cover according to the logistic regression model for maximum probabilities ranging from 0.50 to 0.90.

the optimal value (72%) for different values of the maximum probability that a site is a resting site. Results showed that the probability the site is a resting site decreases with decreasing canopy cover, and the decrease is more pronounced for a lower quality site compared to a higher quality site that has other key features of resting sites (Fig. 6). The sensitivity analysis suggested that the loss in probability when canopy cover decreases from 72 to 50% ranges from 16 to 46% for maximum probabilities ranging from 0.90 to 0.50 (Fig. 6). The loss when canopy cover is decreased from 72 to 61% (the lower confidence interval) cover is substantially lower, ranging from 3 to 12% for maximum probabilities ranging from 0.90 to 0.50.

4. Discussion

4.1. Resting structures

Large trees, snags, and logs were used as resting structures and resting trees or snags were generally the largest or second largest structure in the vicinity of the resting structure. Live trees were the most frequently used resting structure. If sufficient quantities of large trees are present over the landscape, requirements for large snags will likely also be met. It should be noted, however, that fishers used trees as small as 43 cm dbh and snags as small as 34 cm dbh, suggesting that large size is not absolutely essential if certain structural conditions are met (as discussed below).

Ponderosa pines and white firs were the most commonly used tree species. Compared to trees available in the immediate vicinity, ponderosa pines were used more often than expected, incense cedars were used less than expected, and white firs were used in proportion to their availability. We found some evidence of selection for California black oaks and Zielinski et al. (2004) found that black oaks comprised 38% of resting structures in the southern Sierra Nevada. It is important to note that only living oaks, not snags, were used as resting structures in this study and in Zielinski et al. (2004).

Shade tolerant species such as white fir and incense cedar have increased in abundance in these fire-suppressed forests while shade intolerant species such as pines and oaks are less abundant compared to historical numbers (McDonald, 1990; Minnich et al., 1995; Roy and Vankat, 1999). We suspect that white firs may have been used less and ponderosa pines and black oaks used more in the past. Species preferences are likely based on factors such as the tendency to form cavities and the presence of platforms or witches brooms suitable for resting.

Resting locations used by fishers included cavities, old squirrel nests or platforms, witches brooms, and large branches. Although no data were collected on the proportion of trees infested with mistletoe over the study area, a significant number of resting structures exhibited some degree of infestation. Selection for ponderosa pine and white fir was likely related to the occurrence of mistletoe brooms in these species (Hawksworth and Wiens, 1972). Aubry and Raley (2006) found that fishers used mistletoe brooms more than any other microsite.

Mistletoe does not contribute to the formation of brooms in either incense cedars or black oaks (Hawksworth and Wiens, 1972). Animals resting in incense cedars were usually found in a cavity or on a large branch and the lack of cavities and platforms in incense cedars may explain the low use of this species for resting. California black oaks have a propensity to form cavities as they mature and all resting locations found in black oaks were in cavities. Cavities suitable for resting are also found in snags.

Reuse rates of resting structures from previous studies in western populations have ranged from 3 to 27% (Seglund, 1995; Zielinski et al., 2004; Yaeger, 2005; Aubry and Raley, 2006), which includes both reuse by the same individual or a different

individual. Similar to previous work, we found infrequent reuse of resting structures (5%), which suggests a need for numerous quality resting structures throughout the home range of an individual fisher. The assumption that re-use is rare is based on a small subset of the structures actually used because animals are not located daily and all resting structures are not identified.

4.2. Resting habitat selection

Our findings suggest that structurally complex forests with dense canopies, large trees, and snags and hardwoods are key features of resting habitat for fishers. Our model results predicted increasing fisher resting habitat suitability as canopy cover, basal area of snags and hardwoods, tree size variability, and slope steepness increase, and average tree size and distance to streams decreases. Models that did not include both canopy cover and basal area of snags received virtually no support. These two variables were clearly important predictors of resting site use in our study. While the Zielinski et al. (2004) models we tested did not predict fisher resting sites in our study area, our ability to test these models was perhaps limited by differences in how variables were measured. For example, we measured distance to streams from GIS layers, but did not determine whether water was present at the time the fisher was using the site. Zielinski et al. (2004) recorded presence of water within 100 m of the rest site as a categorical variable. Random sites in Zielinski et al. (2004) were also structure-centered, which would make differences in tree size and canopy cover harder to detect. Nevertheless, all of the variables included in their models were important in ours, with the exception of the dbh of the largest tree in the vicinity of the resting structure.

Throughout their range, fishers have consistently been shown to prefer habitat with high overhead tree cover (Powell, 1993; Powell and Zielinski, 1994). In our study, canopy cover was clearly the most important variable distinguishing resting sites from available sites. Canopy cover was the first variable selected in all of the best subsets logistic regression models, was included in all the top logit models, and had the maximum summed Akaike weight over all models in which it appeared. The importance of canopy cover is likely related to the preference of fishers for mesic environments, protection from predators due to their agility in trees, and prey availability (Powell, 1993).

Caution is required in interpreting canopy cover estimates. Results based on different techniques are not equivalent and there is confusion over what is actually being measured. Canopy cover is the area of the ground covered by a vertical projection of tree canopies, while canopy closure is the proportion of the sky hemisphere obscured by vegetation when viewed from a single point (Nuttall, 1997; Jennings et al., 1999). We measured canopy cover using moosehorns, which employ a fairly small field of view of approximately 10°. Most previous fisher research in California and southern Oregon has used concave spherical densiometers, which provide a measure of canopy closure based on a fairly wide angle of view of (approximately 30°; Cook et al., 1995). We used data from a study assessing several methods of estimating canopy cover done in the Sierra National Forest (M. Landram, U.S. Forest Service, Pacific Southwest Region, unpublished report) to create regression equations to allow comparison across studies using different methods. In addition to spherical densiometer and moosehorn, we included cover estimates generated by Forest Vegetation Simulator (FVS) growth models, a method typically used by the USDA Forest Service to plan and evaluate management treatments. While linear relationships are probably not appropriate for extrapolation to cover levels below 50% (Fiala et al., 2006), they are appropriate for the range of values used here and the fit of the regression lines was good (R^2 values from 0.84 to 0.91). Average canopy closure estimates from studies of fisher

Table 6

Canopy cover and closure measurements (%) from fisher resting site studies in California and southern Oregon and from this study, calibrated across measurement methods.

Study	Spherical densiometer	Moosehorn	FVS ^a
Seglund (1995)	85.4	68.4	61.4
Zielinski et al. (2004)			
Northwest coastal California	95.0	79.5	69.0
Southern Sierra Nevada	92.1	76.2	67.0
Yaeger (2005) ^b	50.0	27.4	32.2
	75.0	56.4	52.8
Aubry and Raley (2006)			
Females	84.0	66.8	60.3
Males	82.0	64.5	58.6
This study	85.6	73.7	64.0

Calibration equations are based on data from Landram (U.S. Forest Service, Pacific Southwest Region, unpublished report). Field measurements were collected using concave spherical densiometers in all studies except the current study, where moosehorns were used. See literature cited for references.

^a Forest Vegetation Simulator (FVS) estimates of canopy cover generated from species-specific relationships between tree size and canopy cover, corrected for crown overlap.

^b Actual canopy closure measurements were not reported but 87% and 98% of resting sites had >50% canopy closure and 60% and 88% had >75% canopy closure at Hoopa Indian Reservation and Shasta-National Forest, respectively.

resting sites in the Pacific states based on spherical densiometer readings ranged from 82 to 95%, which translate into moosehorn estimates from 65 to 80% and FVS estimates from 59 to 69%—substantial differences (Table 6).

Our results suggest that fisher resting habitat suitability improves with increasing canopy cover up to approximately 50–55%, below which resting sites were rarely found (Figs. 5 and 6). Zielinski et al. (2006; Fig. 4a) also found a non-linear relationship with canopy cover at resting sites, with a similar threshold. Thresholds can be misused as targets for management and must be carefully applied. Our sensitivity analysis suggested that lowering canopy cover to these levels could substantially reduce the probability a site is used.

High basal area of snags, an important predictor of resting sites, can be a result of size class distributions that include many small snags, a few large snags, or a range of size classes. A closer look at our data suggests that the high basal area of snags at resting sites was primarily due to the presence of large snags (i.e., higher average dbh of snags and number of large snags/ha; Table 3). Because only 15% of resting structures were snags, the value of large snags to fishers may be related to other factors such as foraging habitat and the availability of prey. Snags with cavities and loose bark provide nesting and roosting sites and refugia for small mammals, bats, and birds (Mannan et al., 1980; Raphael and White, 1984; Carey, 1995; Loeb, 1996, 1999).

Resting habitat was characterized by trees with variable sizes, a result consistent with Zielinski et al. (2004). We calculated the standard deviation of dbh of trees as a proxy for canopy layering, a habitat element associated with structural complexity associated with late-successional forests. Variability in tree size underscores the importance of complex vertical structure.

Fishers in the Pacific states are widely regarded as old-growth associates. One finding unique to our study was that, although resting structures were large, the trees surrounding them were small compared to those at random sites. Previous work has found larger trees with higher mean dbh at resting sites rather than fewer (Seglund, 1995; Zielinski et al., 2004, 2006). In our study, these smaller trees appeared to provide the requisite canopy cover and adequate resting habitat, provided a suitable resting structure was available. Late seral habitat has been altered by changes stemming from logging and fire suppression. These forests have undergone a

transition from forests dominated by large trees and snags to dense stands with size class distributions that include more small stems and fewer large stems (Vankat and Major, 1978; Minnich et al., 1995; Goforth and Minnich, 2008). In stands previously logged using large tree selection, we would expect to find a few large trees surrounded by smaller, suppressed trees. In other stands, the age classes would be more evenly distributed with a larger average tree size.

Similar to Zielinski et al. (2004), we found that slope and presence of water were both important predictors of resting sites in the Sierra Nevada. Seglund (1995) and Yaeger (2005) found that fishers rested most often in drainage bottoms but concluded that it was difficult to ascertain whether close proximity to water or some other factor such as riparian habitat was attracting fishers to these locations. Proximity to water, steepness, aspect, slope position, dense riparian habitat (potentially providing high prey densities and protection from predators), past management history of riparian corridors, and the role of these factors in tempering direct solar radiation are all intricately interrelated. Research is needed to clarify the relative importance of these factors and determine the causal factors. It seems likely that the ultimate reason for selection is related to preferred microclimates and meeting the physiological needs of fishers in the hot, dry climate of a species normally found at higher latitudes. If thermal regulation is an important factor in fisher resting site selection, larger bodied males may be more selective than females in terms of distance to streams, as our data suggest. A study of California spotted owls (*Strix occidentalis occidentalis*) found that they were relatively intolerant to heat compared to other species and suggested that the owls preferred late seral stage forests because they provided favorable microclimates (Weathers et al., 2001). Understanding more about the thermal ecology and ecological energetics of fishers in the southernmost extent of their range where climate conditions are hot and dry is needed, particularly in light of uncertainty associated with climate change.

Field-based research is needed on the direct effects of forest management activities on fisher population ecology. Changes in the quality, quantity, and distribution of available habitat can affect occupancy. Our study does not provide answers regarding optimal arrangements of patches of resting habitat that will best retain habitat value for fishers. Research on the trade-offs of direct and indirect effects of fuel reduction treatments on fisher habitat will lead to more informed management decisions and increased ability to provide for viable, well-distributed fisher populations.

5. Management implications

Management strategies for public lands in the southern Sierra Nevada are being developed with a focus on the protection of this fisher population. The results of this study provide insights into the habitat requirements of this species, however caution is advised in inferring optimum, preferred, or suitable fisher habitat based on our results. Although we have identified certain habitat characteristics associated with use, we cannot say which habitat characteristics fishers would select if they were available or what habitats are most productive.

Our results suggest that large trees and snags are probably limiting to fishers. Large trees, especially pines and oaks, are less abundant than they were historically, and large trees and snags are beneficial to a wide variety of wildlife species (e.g., Verner et al., 1992; Noss et al., 2006; Purcell, 2007; Bagne et al., 2008). We encourage management practices that retain large trees, snags, and logs and support the growth of greater numbers of large trees while maintaining dense cover and a complex vertical and horizontal forest structure. Trees with decadence or poor growth form are sometimes removed if deemed to pose a hazard risk. Trees

with defects such as multiple tops, rot, and cavities often result from injury and there is no genetic reason for removal (North et al., 2009). Disease incidence may not indicate genetic susceptibility. Rather, disease may be related to spatial proximity to other diseased trees or stochastic events related to dispersal (North et al., 2009). Retaining trees with defects and decadence should be considered in thinning and fuels reduction activities. If large-diameter trees or snags must be removed for safety considerations, leaving them on the ground may provide some mitigation. Protection of large snags may be warranted during prescribed burning applications (Bagne et al., 2008).

Hardwoods, particularly California black oaks, are an important source of cavities and mast but have declined in many areas. Black oaks require disturbance for regeneration and, without disturbance, they are shaded out by faster growing conifers and crowded out of the most productive sites (McDonald, 1990). We recommend retaining large, decadent oaks and thinning around the most productive acorn producers to create openings favorable for oak regeneration (Purcell and Drynan, 2008; North et al., 2009).

Canopy cover requirements of fishers are one of the most problematic issues facing land managers in western forests where fishers occur. Ongoing and proposed management activities aimed at reducing the wildfire risk and restoring forests to historical conditions through uneven-aged management typically involve thinning trees, consequently reducing canopy cover. Clearly, reducing the risk of wildfire through fuels treatments and restoring forests to historical conditions is a desirable goal as long as we can concurrently maintain healthy fisher populations. A recent effort that modeled the effects of wildfires and fuels management on fisher population sizes found that, while fuel treatments had direct, negative effects on habitat suitability, those effects were overshadowed by benefits related to limiting fire risk on the landscape (Spencer et al., 2008). Because canopy cover generally recovers quickly compared to the time required to replace large trees and snags, some reduction in canopy cover is probably acceptable as long as other fundamental habitat elements are retained. Our results suggest that, to retain suitable fisher resting habitat, a minimum target for canopy cover should be no less than 61% (Moosehorn; 56% FVS equivalent), based on the lower 95% confidence interval for maximum probability a site is a resting site.

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