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ABSTRACT

The fisher (Pekania pennanti; formerly known as Martes pennanti) is a North American endemic mustelid with a geographic distribution that spans much of the boreal forests of North America. In the Northern Rocky Mountain (NRM) fishers have been the focus of Endangered Species Act (ESA) listing decisions. Habitat studies of West Coast fishers in California have consistently identified late-successional forests as important, providing direct implications for forest management and fisher conservation. In the NRM range very little is known about the habitat selection patterns of fishers relative to forest age and species composition, yet ESA petitioners have repeatedly listed habitat loss and destruction as the primary threat to fisher persistence. Between 2002 and 2006 we studied NRM fishers in the Clearwater sub-basin and eastern slope of the Bitterroot-Selway Ecosystem in Idaho and Montana. We used radio-telemetry locations from collared fishers to document fisher habitat use. We developed candidate models describing tree size, species composition, canopy closure, structural diversity, and topography to assess patterns of habitat selection relative to topographic and vegetative predictor variables measured at both stand and landscape scales. Support for these models was evaluated using Akaike Information Criteria. Fishers disproportionately used both stand sites and regional landscapes characterized by large diameter trees and avoided areas with ponderosa (a shade-intolerant species characteristic of xeric sites in the NRM) and lodgepole pine according to our best supported model. These results are consistent with other studies in the western US and Canada where large trees were deemed important, although we show that this selection in the Rocky Mountains occurs at multiple scales. These results highlight the importance of late-successional forests, consistent with a recent conservation strategy for fishers, and the importance of both stand- and landscape-level factors when directing forest management of fisher habitat in the US Rocky Mountains.

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1. Introduction

In the last part of the 19th century and the early part of the 20th century trapping and habitat alteration caused the extirpation of fisher (Pekania pennanti; formerly known as Martes penannti) populations throughout the United States (Zielinski et al., 1995; Lewis and Stinson, 1998). Foresters and wildlife biologists reintroduced fishers in Washington, Oregon, Montana, Idaho, Wisconsin, West Virginia, Massachusetts, Vermont, New York and Connecticut, while augmenting populations in other regions (Powell, 1993; Powell et al., 2012). Some of these reintroductions have produced populations large enough to sustain harvests, especially in the east and mid-west of the United States and Canada (Lewis and Stinson, 1998). However, other fisher populations persist at low numbers, and remain at potentially high risk for extirpation. Limiting factors for fisher recovery include direct mortality from trapping, urban and recreational development, disease, anticoagulant rodenticide poisoning, habitat alterations (e.g., timber management and large wildfires) leading to increased fragmentation and changed forest structure, and direct and indirect impacts from road corridors (Weckwerth and Wright, 1968; Lewis and Zielinski, 1996; Weir and Corbould, 2008; Zielinski et al., 2005; Purcell et al., 2009; Gabriel et al., 2012).

Due to low abundance and documented threats, fishers have been petitioned for listing under the US Endangered Species Act in both the West Coast of the United States (California, Washington, and Oregon) and the US Rocky Mountains (Carlton, 1994;

Greenwald et al., 2000). The listing of the West Coast Distinct Population Segment of fishers was considered "warranted but precluded by higher priority actions" and this population was placed on a "candidate list" (USFWS, 2004). The United States Fish and Wildlife Service (USFWS) is currently reviewing candidate species and an updated decision is imminent. Petitioners for the Northern Rocky Mountain (NRM) population of fishers specifically argued that disease and habitat loss from logging and fire have threatened preferred habitat of fishers. Specifically, petitioners were concerned that silvicultural treatments may alter structural diversity and reduce critical cover for fishers. While the USFWS ruled that the NRM Distinct Population Segment was a "listable entity", they decided that potential factors that may affect habitat and range of fishers were not significant in magnitude to warrant listing (USFWS, 2011).

Several studies have investigated fisher habitat relationships in the West Coast population mostly with respect to fishers' use of resting structures. Resting structures are thought to be important as they provide protection from predators and moderate thermal conditions in both summer and winter (Kilpatrick and Rego, 1994; Purcell et al., 2009). Zielinski et al. (2004) studied fisher resting locations within home ranges (3rd order selection sensu Johnson (1980)) in the Coastal Mountains and Sierra Nevada of California. They found that standing California black oak (*Quercus kelloggii*) and Douglas-fir (*Pseudotsuga menziesii*) of the largest diameter available were used in each study area, respectively, and recommended forest management practices aimed at retention and recruitment of large trees, dense canopies, and structural diversity. Purcell et al. (2009) used similar methods in the southern Sierra Nevada and found fishers selected resting sites according to canopy cover, large trees and snags, and on steep slopes close to streams. They also found fishers selected for resting sites in snags with advanced stages of decay and trees with large diameter at breast height (DBH, diameter measured at 1.4 m) at sites with a high variability of tree sizes. Purcell et al. (2009) echoed the management recommendations of Zielinski et al. (2004), highlighting the importance of large trees (e.g., mean maximum DBH in stands with fisher resting sites was 141.9 cm) and snags in stands

with a minimum of 61% canopy cover and complex forest structure.

In British Columbia, Weir and Harestad (2003) found fishers selected habitat at multiple scales (i.e., from elements to stands) depending on denning, foraging, or resting behavioral states. Their results generally paralleled those of other studies, showing selection for forest overstory, coarse woody debris, and high structural diversity at the patch and stand scales. Weir and Harestad (2003) suggested that fishers can occupy heterogeneous, or patchy, landscapes that contain critical structural elements for foraging, hunting, denning and resting; thus managers can lessen negative effects of habitat alterations at large spatial scales by keeping critical elements at smaller scales. Aubry et al. (2013) conducted a meta-analysis of fisher habitat selection surrounding resting sites in 8 study areas from north-central British Columbia to the southern Sierra Nevada in California. They found that fishers selected for rest site areas that were on steeper slopes, in cooler microclimates, had dense overhead cover, in stands with greater volume of logs, and had a greater number of large trees and snags (Aubry et al., 2013).

In contrast to the well-studied West Coast populations, very little is known about fisher habitat preferences in the Rocky Mountains of the United States. Jones and Garton (1994) showed that in central Idaho subalpine fir (*Abies lasiocarpa*) and grand fir (*Abies grandis*) old-growth forests were extensively used in the summer, while both young and old-growth forest were selected during winter. They also showed that fishers selected forest riparian habitat for resting, hunting, and travel. Jones and Garton (1994) further demonstrated that fishers did not use non-forested habitats, although the authors noted that some of their prey choices (based on a diet study) would only be found in sparsely forested habitats, suggesting forays into more open stands.

We initiated this study to examine the environmental features selected by NRM fishers at both the stand and landscape scales in the Clearwater River basin and the adjacent eastern slope of the Bitterroot-Selway Ecosystem, within the Rocky Mountains of Idaho and Montana (Fig. 1). This study area is one of few areas containing fishers with a native genetic lineage within the NRM (Vinkey et al., 2006; Schwartz, 2007; Schwartz et al., 2012). Other than
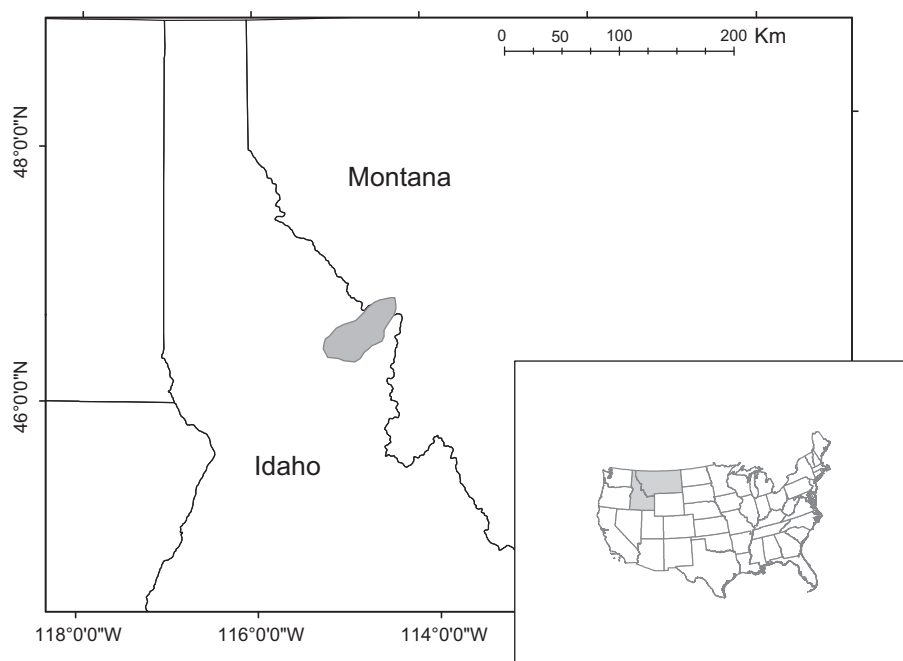

Fig. 1. Map of the study area (gray) in the Rocky Mountains of Montana and Idaho, where fishers were studies from 2002 to 2006.

the study of Jones and Garton (1994) little scientific information is available regarding fishers' use of forests in this area, likely due in part to the difficulties in accessing the greater Selway-Bitterroot Ecosystem, which contains one of the largest designated Wilderness areas in the contiguous United States. This lack of information has hindered forest management as questions concerning fisher habitat requirements have been used to legally challenge forest management activities (e.g., Idaho Sporting Congress, Inc. v. Rittenhouse, 2002; Lands Council v. McNair, 2008).

2. Methods

2.1. Study area

We studied Northern Rocky Mountain fishers in portions of north-east Idaho and west-central Montana straddled by the Bitterroot Mountain divide near Lolo Pass (Fig. 1). Our study area included approximately 100 miles of the Highway 12 corridor, which paralleled the Lochsa and Clearwater Rivers in Idaho and Lolo Creek in Montana. In the winter, the warm, moist maritime air from the Pacific penetrates into this sub-basin, resulting in a mean annual precipitation of approximately 200 cm per year (measured at Lolo Pass) and occasional years exceeding 250 cm. The abnormally high moisture (considering distance from a substantial body of water) leads to a refugia ecosystem characterized by grand fir, western red cedar (*Thuja plicata*), and hemlock (*Tsuga* spp.) stands at high and middle elevation. Intermixed with these typically coastal stands are xeric and mesic stands consisting of Douglas fir, subalpine fir, lodgepole (*Pinus contorta*) and ponderosa pine (*Pinus ponderosa*) – a more typical ecotype of the intermountain west. The area has been considered an important Pleistocene refugium based on geology, phytogeography, and phylogenetics of several key species (Daubenmire, 1975; Carstens et al., 2005; Mullen et al., 2010). The wet climate, mesic vegetation, large amounts of structure, and the presence of late successional forest stands allows the Clearwater River sub-basin to support a resident population of fishers.

2.2. Trapping, handling and telemetry monitoring

Between January 2002 and March 2006 we studied fishers by deploying conventional VHF radio-telemetry collars (150–154 MHz, Holohil MI-2 collar, Carp, Ontario; collar weight ~45 g) on a subset of 34 fishers captured within the study area (Appendix A). We captured animals using both log-cabin traps (Copeland et al., 2007) hand constructed from natural materials in the study area, and single-door box traps (1.0 × 0.3 × 0.3 m; Tomahawk Trap Co., Tomahawk, Wisconsin). Trap doors were fit with a trap-transmitter (Telonics TBT-600HC, Telonics Inc., Mesa, AZ) used to signal when the door is shut allowing remote monitoring on a daily basis.

We immobilized captured fishers with a ketamine/xylazine mixture (22 mg ml^{-1} ketamine/kg and 10 mg ml^{-1} xylazine per animal) administered with a jab stick. Once anesthetized, ophthalmic ointment was placed onto the fisher's eyes for protection, and a small hood was fit over its face. While under the dissociative anesthetic fishers were instrumented with the radiocollar, weighed, physically examined, and tagged at the base of the anterior edge of the ear using Dalton Rototags (Dalton Supplies Ltd., Nettlebed, England). A small tissue punch and hair sample (~50 hairs) was collected for DNA analysis (Vinkey et al., 2006; Knaus et al., 2011). We conducted all trapping and handling procedures under Institutional Animal Care and Use Committee oversight and under scientific collecting permits (#011211 from Idaho Fish and Game and #1520 from Montana Fish Wildlife and Parks).

During the winters of 2002 and 2003, all captured fishers (11 males, 6 females) were instrumented with radio-telemetry collars. Due to limited monitoring resources and the difficulty associated with locating male fishers, collaring from 2004 onward was limited to females, and collars were removed from re-captured males. Incentive for focusing data collection on adult female fishers included the importance of adult female survival in driving fisher population dynamics (sensitivity = 0.71; M. Schwartz unpublished data). In total, 23 males and 11 females were captured during the study, and data from nine females were used for this habitat analysis (two juvenile females were never relocated).

Radio-tagged fishers were located by one of three techniques. The primary method (64% of locations) involved using ground telemetry to detect an individual fisher at distance and subsequently walking into the stand where the fisher was present. If the fisher was resting the technician circled the stand and noted the group of trees where the fisher was located, therefore eliminating telemetry error. We rarely visually observed the fisher using this method. Secondary methods included aerial telemetry (27%) and ground triangulation (9%; White and Garrott, 1990), where locations could be attributed to specific structural elements in a stand. Locations where we could not localize a structure in a stand, or where researchers could not be at 90 degree angles from one another at distances less than 100 m, were discarded.

2.3. Vegetation and physical sampling

We sampled used and available habitat associated with telemetry locations and randomly selected locations within 10 km of Highway 12, which bisected the study area along the major drainage basin (Fig. 1). To minimize the degree of contamination of our available sample with habitats actually used by fishers (Johnson et al., 2006), we deployed non-invasive genetic sampling devices at each random location (see Zielinski et al., 2007; Kendall and McKelvey, 2008; Wasserman et al., 2010 for details on this device). Non-invasive snares were set for 2 periods of 14 days. Upon return, when hair was present, the sample was removed and placed in a 50 mm plastic centrifuge vial filled with 6–16 mesh silica desiccant (Fisher Scientific, Pittsburg PA, USA), and Standard species identification approaches were subsequently followed in a genetics laboratory (Schwartz and Monfort, 2008). During the summer of 2004 we deployed 74 devices at randomly selected sites within 10 km of Highway 12 to characterize habitat availability regardless of landscape designation (e.g., Wilderness, roadless, or managed) or access issues. We used those stations that did not detect a fisher (*n* = 67) as a sample of available habitat points, although admit that fisher may have been present, but not detected.

At each used and available location we recorded habitat characteristics at multiple, nested scales. Broadly we characterized the heterogeneity in habitat characteristics at used and available locations at two scales: a stand scale describing features in the immediate vicinity of the location and a landscape scale describing features within a 1 km surrounding radius. For stand-level measurements, vegetation sampling plots of several sizes were centered around locations and additional topographic variables (slope, aspect, elevation, distance to edge of patch, type of edge, distance to water, and snow depth) were recorded to characterize the stand and available elements (Table 1). At the largest plot size (36 m radius), we estimated tree density and basal area. We also recorded the tree species present, DBH, and whether cavities or snags were present. Within a mid-sized plot (18 m radius) we established line intercept transects from plot center in each cardinal direction and measured DBH of trees greater than 1 m, species, length, and log decay (Sollins index of log decay; Sollins, 1982) of downed trees, stumps, snags, and ground cover. Logs were defined as horizontal trees >8 cm DBH and >2 m long. For all snags we

Table 1
A list of habitat variables measured at sites of fisher use and at random sties in the Rocky Mountains of Montana and Idaho, 2002–2006. Vegetation was measured at a plot level and a landscape level (1 km buffer), structural elements were noted at a plot level, and physical variables were estimated at both scales. DBH is diameter of a tree measured at 1.4 m. TPI is an index of landscape convexity.

Categories	Specific variables	Subcategories
Vegetation (Plot level)	DBH	Max, Mean, Standard Deviation
	Tree count	Total, Grand fir (*Abies grandis*), Subalpine fir (*Abies lasiocarpa*), Larch (*Larix occidentalis*), Lodgepole pine (*Pinus contorta*), Ponderosa pine (*Pinus ponderosa*), Engelmann spruce (*Picea engelmannii*), Douglas fir (*Pseudotsuga menziesii*), Western red cedar (*Thuja plicata*), Mountain hemlock (*Tsuga mertensiana*)
	Shrub	Count
Vegetation (Landscape level – 1 km buffer GIS)	Tree size	Sapling, small, medium, large
	Grass	Proportion of buffer
Structural	Cavity	Presence, Count
	Logs	Mean DBH, count, volume
	Canopy	Density (field measured), Buffered 1 k (low, mid, high)
	Snags	Max DBH, Count
	Stumps	Presence
Physical	Point	Elevation, Slope, Aspect
	I km Buffer	TPI, Slope, Roughness

noted if cavities were present. At this mid-scale we also calculated mean canopy cover (hereafter canopy cover) by measuring canopy cover at the center and at each end of the transects using a spherical convex canopy densitometer (Forest Densiometers, Oklahoma, USA). Lastly, we established a 9-m radius plot and measured shrub and understory variables. We recorded the shrub species between 0.5 m and 2 m in height and the approximate ground cover at the plot center and in each of the cardinal directions 9 m from plot center using a gridded meter square box. Within the 1 m² box we estimated cover of nonvascular plants, graminoids, forbs, and shrubs.

To characterize landscape-scale heterogeneity, we quantified a suite of GIS-based metrics describing features within a 1 km radius of locations. We generally followed Squires et al. (2008) and characterized a set of topographic and vegetative variables using point estimates at each location as well as mean estimates within 1000-m radius buffer surrounding each location. We used a 30 m digital elevation model (US Geological Survey, 2000) to characterize elevation, slope, aspect, topographic position, and roughness. Slope and aspect were derived using the Spatial Analyst extension for ArcGIS Desktop 9.2 (ESRI, Redlands, CA, USA), and we transformed aspect into an index of the SSW-NNE axis using the cosine of the angle minus 35° (Cushman and Wallin, 2002). We calculated a continuous topographic position index (TPI) that indexed landscape convexity (positive values indicative of ridges) versus concavity (negative values suggesting drainages). We used the TPI extension (v. 1.3a; Jenness, 2006) for ArcView 3.2a to estimate TPI at a 1 km neighborhood scale surrounding each location. We estimated roughness as the ratio of 3-dimensional surface area to 2-dimensional surface area (Jenness, 2004) using the Surface Areas and Ratios feature of the Elevation Grid v 1.2 extension for ArcView 3.2.

We used the US Forest Service's Northern Region Vegetation Mapping Project layers (VMAP v. 6; Brewer et al., 2004) to characterize land cover type, canopy closure, and tree size according to the proportionate area of each of several categories per variable within 1000-m circular landscapes surrounding point locations. We simplified the VMAP species composition layer into four cover type categories to parsimoniously characterize study area vegetation as grass, shrubs, shade-intolerant forest (included single-species and mixed stands of ponderosa pine, Douglas fir, western larch (*Larix occidentalis*), and lodgepole pine) and shade-tolerant forest (included single-species and mixed stands of grand fir, subalpine fir, Englemann spruce, western red cedar, and mountain hemlock). We characterized canopy closure and tree size layers in forested habitats using canopy closure categories of low (10–24.9%), medium (25–59.9%), and high (>60%) canopy closure and tree size categories of saplings (0–13 cm DBH), small (13–25 cm), medium (25–38 cm), and large (>38 cm; Brewer et al., 2004).

2.4. Data analyses and model selection

We evaluated fisher habitat preferences by comparing the suite of vegetative and physical resources at used fisher telemetry locations to those at randomly available sites. All statistical analyses were conducted in Stata 10 (StataCorp, 2007). We began analyses with an information-theoretic model selection approach (Burnham and Anderson, 2002) to assess the relative evidence for five basic habitat factors shown to drive fisher habitat selection in a recent meta-analysis (Aubry et al., 2013). We selected this approach as a first step to avoid over-fitting our modest data set with the full suite of possible models available, and instead explore the relative support among few biologically meaningful hypotheses (Burnham and Anderson, 2002). For each of the five habitat factors, we developed sets of 5–15 *a priori* candidate models containing combinations of predictor variables that best characterized the resources of hypothesized importance (Table 2).

First, we developed candidate models describing tree size at both stand and landscape-scales as a means of assessing the support for large trees as key components of fisher resting and denning habitat (Aubry et al., 2013; Zielinski et al., 2004, 2006; Purcell et al., 2009; Table 2). Second, we used species composition models differentiating tree species indicative of both mesic and xeric microclimates (Zielinski et al., 2004; Purcell et al., 2009; Aubry et al., 2013). Third, we evaluated models characterizing canopy closure at multiple scales (Weir and Harestad, 2003; Zielinski et al., 2004; Raley et al., 2012), and fourth, we separately tested models parameterizing structural diversity as predictive of fisher habitat selection, including quantification of snags and tree cavities to assess the evidence for thermal and other cover as provided by these structural components (Buskirk and Powell, 1994; Raley et al., 2012; Table 2). Lastly, we compared topographic models that explained fisher resting and denning habitat in previous studies, including variables regarding slope, aspect, and topographic position (Table 2). We used Akaike Information Criteria (AIC) to assess the relative support for each of these hypothesized drivers of fisher habitat selection, as quantified by both ΔAIC differences between each model and the lowest model score, as well as AIC model weights (*w*; Burnham and Anderson, 2002). We used the variables from the most supported models in each of the 5 analysis per habitat factor to build and evaluate 30 composite models that

Table 2
Five sets of *a priori* candidate models containing combinations of predictor variables that best characterized the resources of hypothesized importance of fishers in the Rocky Mountains of Montana and Idaho, 2002–2006. Variables in bold were most supported. Landscape variables were evaluated at the 1 km scale.

Model	Variables	ll (model)	df	AIC	ΔAIC	wAIC
Habitat factor 1: Importance of large trees						
M1a	Maximum DBH in trees in the stand	−55.7826	2	115.5651	4.3909	0.0632
M1b	Mean DBH in trees in the stand	−65.0273	2	134.0545	22.8803	0.0000
M1c	Standard deviation in DBH in trees in the stand	−57.9918	2	119.9836	8.8094	0.0069
M1d	**Maximum DBH + Proportion of large trees (landscape)**	**−52.5871**	**3**	**111.1742**	**0**	**0.5677**
M1e	Mean DBH + Proportion of large trees in landscape	−59.5949	3	125.1899	14.0157	0.0005
M1f	Standard Deviation in DBH + Prop. of large trees (landscape)	−53.0383	3	112.0767	0.9025	0.3615
M1 g	Proportion of large trees (landscape)	−62.2423	2	128.4846	17.3104	0.0001
Habitat factor 2: Importance of species composition						
Model	Variables	ll (model)	df	AIC	ΔAIC	wAIC
M5a	Number of grand fir	−70.6549	2	145.3099	7.4264	0.0114
M5b	Number of western red cedar	−71.2118	2	146.4236	8.5401	0.0065
M5c	Number of ponderosa pine	−67.7906	2	139.5813	1.6978	0.1999
M5d	Number of Douglas fir	−72.9638	2	149.9276	12.0441	0.0011
M5e	**Number of lodgepole pine + Number of ponderosa pine**	**−65.9417**	**3**	**137.8835**	**0**	**0.4672**
M5f	**Number of ponderosa pine + Number of western red cedar**	**−66.3769**	**3**	**138.7538**	**0.8703**	**0.3023**
M5 g	Number of western red cedar + Number of grand fir	−69.6425	3	145.285	7.4015	0.0115
Habitat factor 3: Importance of canopy cover						
M2a	Canopy cover	−55.6711	2	115.3422	3.878	0.0733
M2b	Canopy cover + Canopy cover^2	−55.5635	3	117.1269	5.6627	0.0300
M2c	**Proportion of high canopy cover (landscape)**	**−53.7321**	**2**	**111.4642**	**0**	**0.5096**
M2d	Canopy cover + Proportion of high canopy cover (landscape)	−53.3215	3	112.643	1.1788	0.2827
M2e	Canopy cover + Canopy cover^2 + Prop. of high canopy cover (landscape)	−53.3179	4	114.6357	3.1715	0.1044
Habitat factor 4: Importance of structure						
M3a	Presence of snags	−72.5473	2	149.0946	5.2354	0.0299
M3b	Presence of tree cavities	−70.7687	2	145.5373	1.6781	0.1770
M3c	Total log volume	−73.2393	2	150.4786	6.6194	0.0150
M3d	**Presence of snags + Presence of tree cavities**	**−68.9296**	**3**	**143.8592**	**0**	**0.4096**
M3e	Presence of snags + Total log volume	−72.1173	3	150.2346	6.3754	0.0169
M3f	Presence of tree cavities + Total log volume	−70.3796	3	146.7592	2.9	0.0961
M3 g	Presence of snags + Presence of tree cavities + Total log volume	−68.4015	4	144.803	0.9438	0.2555
Habitat factor 5: Importance of topography						
M4a	TPI	−69.7269	2	143.4537	6.7773	0.0186
M4b	Slope	−73.1455	2	150.291	13.6146	0.0006
M4c	Aspect	−73.6048	2	151.2095	14.5331	0.0004
M4d	Slope (landscape)	−70.888	2	145.776	9.0996	0.0058
M4e	TPI + Slope	−69.0009	3	144.0018	7.3254	0.0141
M4f	TPI + Aspect	−69.7166	3	145.4332	8.7568	0.0069
M4g	TPI + Slope (landscape)	−68.0464	3	142.0928	5.4164	0.0367
M4h	Slope + Aspect	−73.1387	3	152.2773	15.6009	0.0002
M4i	Slope + Slope (landscape)	−67.0479	3	140.0958	3.4194	0.0996
M4j	Aspect + Slope (landscape)	−70.8752	3	147.7504	11.074	0.0022
M4k	TPI + Slope + Aspect	−68.995	4	145.99	9.3136	0.0052
M4l	**TPI + Slope + Slope (landscape)**	**−64.3382**	**4**	**136.6764**	**0**	**0.5507**
M4m	TPI + Aspect + Slope (landscape)	−68.0461	4	144.0922	7.4158	0.0135
M4n	Aspect + Slope + Slope (landscape)	−66.9754	4	141.9508	5.2744	0.0394
M4o	TPI + Slope + Slope (landscape) + Aspect	−64.3217	5	138.6435	1.9671	0.2060

compared the relative support for combinations of each of our broad habitat factors of tree size, species composition, canopy cover, structural diversity, and topography as drivers of fisher habitat selection.

Following this information-theoretic approach to model selection, we conducted *post hoc* exploratory analyses of univariate and multivariate relationships of all measured variables as potential drivers of habitat selection. These analyses were conducted to explore all relationships in the data for this poorly studied population of fishers, and consider alternate multivariable models for explaining fisher habitat beyond those developed *a priori*. We used Wald statistics (z) to assess the univariate importance of all vegetation and physical variables measured and then conducted multivariable model selection on the subset of variables with weak univariate significance ($p < 0.25$), following Hosmer and Lemeshow (2000). We used a manual forward stepping approach to assess multivariable models according to both individual variable Wald statistics and the effects of multicollinearity among moderately ($r < 0.7$) correlated variables as evidenced by variance inflation

and changing of coefficient signs (Hosmer and Lemeshow, 2000; Copeland et al., 2007). We evaluated overall model fit using receiver operating characteristic (ROC) curves which have been shown to be a conservative indicator of RSF performance and predictive power (Cumming, 2000; Boyce et al., 2002) and the likelihood ratio chi-squared test.

3. Results

We first evaluated variables associated with large trees at stand and landscape scales (Fig. 2). The model with most support included both maximum DBH at the stand scale and the proportion of large trees within the landscape scale (Table 2). We subsequently evaluated tree species composition variables and found that a model showing avoidance of both ponderosa and lodgepole pine species was the most supported, suggesting avoidance of xeric stands. A univariate model including the proportion of high density canopy cover within 1-km landscapes was the most supported
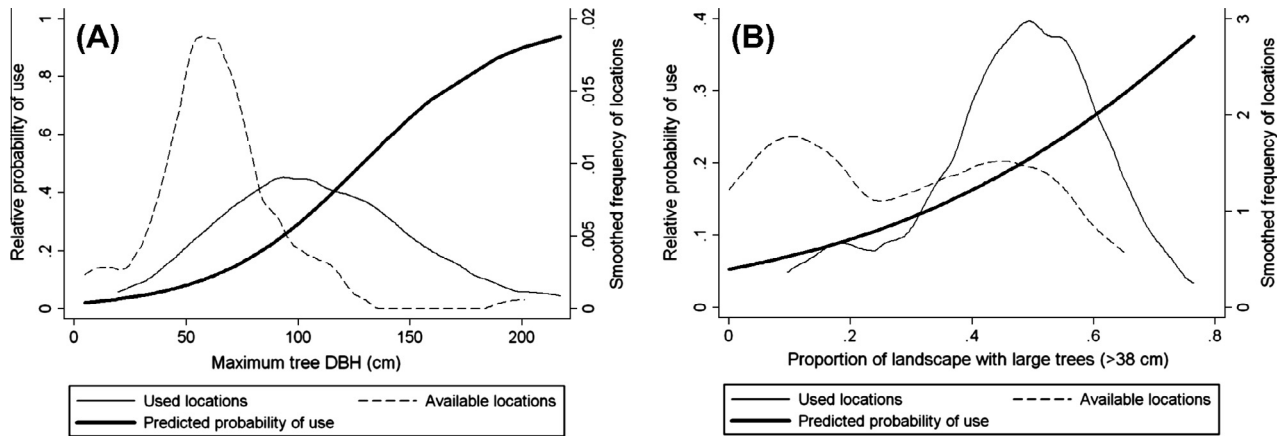
Fig. 2. Kernel smoothed densities of used and available locations according to (a) stand-scale maximum tree DBH measurements within the plots and (b) landscape-scale measurements of the proportion of large (>38 cm) within 1000 m circular radii from plot centers, as well as the respective corresponding predicted probabilities of use by fishers from the best model describing fisher habitat selection in the Rocky Mountains of Montana and Idaho, 2002–2006.

model characterizing canopy closure (Table 2). Comparing the stand structure models, the most supported model included snags and tree cavities present (Table 2). Lastly, of the 15 topographic models assessed, the most supported model included TPI, and two scales of slope measured both locally at the plot center and as an average within a 1-km radius (Table 2).

We combined the top models describing each of these five basic habitat factors to create 30 additional models representing all possible combinations of these factors. The most supported model contained two factors: tree size and species composition. Specifically, this model revealed selection for large maximum tree DBH ($\beta = 0.031$, $P < 0.001$), high proportion of large trees in a 1 km buffer ($\beta = 3.097$, $P = 0.048$), and avoidance of stands with ponderosa pine and lodgepole pine ($\beta = -0.375$, $P = 0.09$ and $\beta = -0.002$, $P = 0.97$; Tables 3 and 4).

Our *post hoc* analysis began with univariate analysis of all recorded variables and revealed several statistically significant relationships (Appendix B). As found by our model selection approach above, fishers preferred sites with trees of larger maximum DBH ($Z = 4.63$, $p < 0.001$). They preferred sites with large standard deviations in DBH ($Z = 4.63$, $p < 0.001$), though this variable was highly

correlated with DBH Max ($r = 0.91$). Among tree species, the most preferred species was grand fir ($Z = 2.23$, $p = 0.026$). Stand structure and complexity variables revealed fisher selection for sites with large logs ($Z = 2.22$, $p = 0.027$) and presence of tree cavities ($Z = 2.23$, $p = 0.026$). Consistent with the need for structure, there was also selection against grass cover across a 1 km buffer ($p = 0.031$; $Z = -2.16$). Topographic variables were also important. At the stand level fishers selected for lower elevations ($Z = -4.18$, $p < 0.001$), while at the landscape scale fishers selected steeper slopes ($Z = 2.26$, $p = 0.024$) higher surface roughness ($Z = 2.21$, $p = 0.027$), and concave, or drainage-like, topographical positions ($Z = -2.53$, $p = 0.011$).

A manual stepping multivariable model selection approach produced a nearly identical best model as reached by the information theoretic approach, differing only in its exclusion of the lodgepole pine variable (Appendix B). Generally both exercises indicated that fishers selected sites with larger diameter trees, in landscapes with large trees, while avoiding stands of primarily xeric species composition. The predictive capacity of the model was good, with a pseudo-$R^2 = 0.33$ and ROC = 0.86, and a significant likelihood ratio chi squared = 48.3 (Appendix B).

Table 3
Comparison of the most supported habitat factors (see Table 2) combined to assess the relative importance of large trees, canopy cover, structure, topography, and species composition for fishers in the Rocky Mountains of Montana and Idaho, 2002–2006. Thirty models were evaluated (all combinations of models 1–5, removing those nested models where addition of a new variable did not improve the AIC score by two points as in Arnold, 2010), but only the top 10 models (ranked by AIC) are displayed here.

Model	ll (Model)	df	AIC	BIC	Work	ΔAIC	wAIC
Large Trees + Species Composition	−49.445	5	108.890	122.392	1	0	0.234
Large Trees	−52.587	3	111.174	119.276	0.3191	2.2845	0.075
Large Trees + Canopy Cover	−51.866	4	111.733	122.535	0.241352	2.843	0.057
Large Trees + Canopy Cover + Topography	−49.169	7	112.338	131.242	0.178298	3.4486	0.042
Large Trees + Topography	−50.251	6	112.502	128.705	0.164269	3.6125	0.038
Large Trees + Structure	−52.572	4	113.144	123.946	0.119171	4.2544	0.028
Large Trees + Canopy Cover + Structure	−51.863	5	113.727	127.229	0.089046	4.8372	0.021
Large Trees + Canopy Cover + Structure + Topo	−49.164	8	114.328	135.932	0.065924	5.4385	0.015
Large Trees + Structure + Topography	−50.226	7	114.452	133.355	0.06197	5.5622	0.015

Table 4
Variables that comprise the best supported model of fishers habitat use in the Rocky Mountains of Montana and Idaho considers variables including the size of trees and tree species composition. Support for this model is seen in Table 4.

Variable	Coefficient	Standard error	Z	P > z	95% CI	
Maximum DBH (stand)	0.031	0.008	3.66	0	0.0143	0.0474
Proportion of large trees (landscape)	3.097	1.568	1.98	0.048	0.0237	6.1700
Mean Number of Lodgepole Pine (stand)	−0.002	0.060	−0.04	0.968	−0.1200	0.1152
Mean Number of Ponderosa Pine (stand)	−0.375	0.222	−1.69	0.090	−0.8097	0.0592
ConstantConstant	−3.977	0.919	−4.33	0	−5.7783	−2.1757

4. Discussion

4.1. Habitat selection

Perhaps the most compelling result from this study was the consistent selection by female fishers for large trees at both stand and landscape scales. Our best multivariable model contained both maximum DBH at the stand level and a proportion of large tress within 1 km circular landscapes. Large trees occur in many settings throughout the study area, including remnant stands surrounded by forests that are highly altered by recent and historical logging, landscapes with large trees only in riparian areas, and patches of large trees embedded in wilderness and other highly inaccessible lands. However, it appears in our study area that the most preferred stands with large DBH trees (average maximum DBH in used habitats = 107.77 cm versus 64.224 cm in unused habitats) also occur in landscapes with large trees (used landscapes were composed of 47% large tree stands versus 29% in available landscapes). Thus, we recommend that silvicultural treatments of stands consider not only the retention of large trees, but consider the larger landscape when managing for fishers.

Maximum DBH best explained the differentiation between used and available habitats, yet it was highly correlated with mean DBH and the variation (standard deviation) in DBH. While the top model characterizing tree size included DBH max and proportion of a landscape with large size trees, the next most supported model contained the standard deviation in tree size at the stand scale and the proportion of large trees at the landscape scale (Table 2). This suggests that stands most used by fishers are those mature forests with both large and smaller trees, consistent with evidence that fishers need cover for hunting efficiency or predator escape purposes. These results are similar to Jones and Garton (1994) who found fishers selecting mature and old growth forests during the summer in Idaho. Yet, during the winter, they found fishers using a wider array of habitats, although still selecting for the larger diameter trees compared to random (Jones and Garton, 1994). Zielinski et al. (2004) studied West Coast fisher habitat selection at resting locations in the Coastal Mountains and Sierra Nevada of California. They found that standing trees of California black oak and Douglas-fir of the largest diameter available were used in each area, respectively. In their Sierra study area their resource selection function showed that fishers selected sites nearby water, on steeper slopes, with larger maximum DBH trees at sites with more variable tree DBH than random. They interpreted these results to suggest that managers can maintain fisher resting habitat by retaining large trees and using forest management practices that aid in the recruitment of trees that achieve the largest sizes. They also recommend increasing structural diversity at these sites. We concur with these forest management recommendations in reference to NRM fishers as well. Similarly, Purcell et al. (2009) found fishers selected sites with larger DBH trees and higher variance in the DBH of trees. This is consistent with a recent meta-analysis of 8 studies by Aubry et al. (2013) where there were significant summary effects sizes in mean DBH of live conifers $\geqslant 10$ cm DBH, and mean DBH of live hardwoods $\geqslant 10$ cm DBH, suggesting fishers' selection for larger diameter trees.

Our modeling efforts also showed tree species selection with avoidance of ponderosa pine and lodgepole pine stands. Ponderosa pine is generally considered a semiarid or xeric species although at mid-elevations and in more northern latitudes ponderosa pine can be an early seral stage of Douglas-fir or grand fir forest (Barrett, 1988; Keeling et al., 2006). In other moist forests the species is found on drier south facing aspects (Graham and Jain, 2005). Lodgepole pine is widely distributed throughout the study area, although it is generally considered a pioneer species first colonizing after a fire and then dominating early seral stages through rapid juvenile growth (Coops and Waring, 2011). Fishers likely avoid the ponderosa pine stands as they reflect the drier environments in the study area and generally have less understory cover to offer protection (Graham and Jain, 2005; Keeling et al., 2006). Avoidance of lodgepole pine is likely related to the relatively small diameter of even the oldest trees (i.e., mature sizes of lodgepoles in the Northern US Rocky Mountains is between 18 and 33 cm DBH; Burns and Honkala, 1990). This is consistent with evidence for fisher's selection for western red cedar stands, a species with large DBH and associated with wetter, more structure filled environments. In our preliminary evaluations of species composition, models characterizing selection for western red cedar were nearly equivalent to those describing selection against ponderosa pine (delta AIC = 0.87).

Interestingly, abundance of western red cedar and grand fir may be higher now than in historical times when western white pine (*Pinus monticola*) dominated moist, mid-elevation forests. However, this major element of inland northwest forests was substantially reduced in abundance due to white pine blister rust (*Cronartium ribicola*), mountain pine beetles (*Dendroctonus ponderosae*), and fire exclusion (Loehman et al., 2011). In fact, western white pine is now at less than 5% of historical range in the inland northwest; instead of being the dominant species in many stands it is widely scattered with limited natural regeneration potential (Harvey et al., 2008). Current management objectives are to restore western white pine ecosystems, which may have significant ramifications for fishers given our findings, as young white pine stands may not have the structural diversity in the understory, and be too open at maturity. On the other hand, the cones may serve as an important food source for small mammals, a primary food resource for fishers, and burned pine snags can persist for decades potentially providing denning habitat for female fishers. Thus, we recommend initiation of extensive studies of the potential impacts of white pine restoration on this rare species.

Structure and cover have been considered critical elements for fisher habitat (Raley et al., 2012; Weir and Corbould, 2010; Truex and Zielinski, 2013). In our initial models to characterize structure, the most supported model was the landscape model with a high proportion of stands with high canopy cover. Weir and Corbould (2010) found that fishers selected stands with greater than 30% canopy cover; Purcell et al. (2009) found canopy cover was the most important variable at predicting fisher resting sites; and Zielinski et al. (2004) showed that higher average canopy cover was critical for predicting fisher resting habitat. Alternatively at the stand scale we did not detect an effect of canopy cover on habitat selection by female fishers. This may be an effect of our study area, a mesic environment where relatively high canopy cover is ubiquitous and stands have ample mean canopy cover (e.g., our random locations had greater than 50% canopy cover) meeting threshold requirements. A similar area with dense forests, the Hoopa Valley of California, also did not show canopy cover being a limiting factor.

With our initial forest structure models we found the most support for fishers selecting structure in the form of stands with abundant snags and cavities. This is consistent with Zielinski et al. (2004) where the presence of conifer snags was significant. We recommend retention of large decadent trees and snags in areas with large trees to provide denning habitat for female fishers. While we identified univariate patterns of selection for variables that indicate structure, we also found avoidance of variables such as landscapes with a high proportion of grass, suggesting the corollary – avoidance of open areas - is also true. This is similar to results from Weir and Corbould (2010), where fishers avoided open areas, non-forested ecosystems, and areas with recent logging.

We evaluated 15 topographic models, as topographic features have been important for predicting fisher occurrence elsewhere (Purcell et al., 2009; Zielinski et al., 2004; Aubry et al., 2013). Both Purcell et al. (2009) and Zielinski et al. (2004) showed the importance of steep slopes for predicting fisher habitat use. Our most supported initial model contained both slope and TPI suggesting fishers' selection for steeper slopes and more concave environments, although neither was retained in our final multivariable models. TPI likely is a surrogate for moisture as fishers are selecting for wetter environments where vegetation is typically denser and larger.

4.2. Limitations of study

Fishers proved to be very difficult to detect and monitor in our study area, even when fitted with radio-collars, as the study area is largely roadless and mostly designated as federal Wilderness (the Selway-Bitterroot Wilderness alone is >500,000 ha). We culled male detections from our analysis as we were concerned about the bias introduced by not detecting males for months at a time, suggesting they often had lengthy movements beyond our study area. For example, one juvenile male captured in a trap in January 2005 was incidentally detected in June 2006 in a hair-snare device 91.5 km from the original trap site, across the Selway-Bitterroot Wilderness. Newer and lighter satellite based telemetry will improve our ability to study fishers in the future in these remote landscapes (e.g., Brown et al., 2012). Although even the newest satellite-based approaches will not be a panacea for the study of fishers given the dense vegetation, use of remote habitats in the Rocky Mountains, and the species penchants for using tree cavities and rock piles, which shield satellite communication. Fortunately, instrumented females exhibited much smaller areas of movement, with an average use area of 9.1 km^2. In the future we hope to combine satellite telemetry with remote download stations to improve our study of female fisher habitat use.

Our sample size was very limited. Despite the fact that this area likely has one of the densest populations of fishers in the US Rocky Mountains, we were only able to capture 11 females over 4 years, indicative of the relatively low density typical of this species in the Rocky Mountains. We opted to maximize sample size by lumping all locations across all females. This approach prevented us from making assertions regarding individual or annual differences. We also may have missed detection of selected habitat features that were of small selection effect or proportionate availability, yet important to fisher habitat selection. While we would normally be reluctant to present data sets of this modest size, there are almost no available data on fishers in the Rocky Mountains, except Jones and Garton (1994) who radiocollared 13 fishers in Idaho between 1985 and 1988 and obtained 88 observations at resting sites, comparable to the size of our dataset.

5. Conclusions and management implications

One of the most pressing questions regarding fisher management in the Rocky Mountains is the degree to which fishers are sensitive to habitat modification at a scale larger than the stand or the specific element in the stand. In this study, we found that females are indeed selecting habitat at two scales: a stand scale as indicated by stands that have large mean and maximum DBH trees (as well as a large variation in tree size) and a landscape scale as indicated by the preference for landscapes with a high proportion of large trees. Thus, it appears that while fishers can be detected in riparian stringers that bisect open landscapes, this habitat may not be sufficient for persistence. The converse is also likely true. Landscapes that do not have variation in large trees, snags, and cavities,

and drier landscapes (i.e., landscapes with ponderosa and lodgepole pine) are probably not sufficient for fisher persistence either.

Forest activities that promote the growth of multi-stage stands with ample structure and variation in tree widths and ages will provide the best habitat for fishers. Retaining trees that have decadence, disease, or defects will help provide some of this habitat. These recommendations may be resisted as forests implement fuel treatments that often aim to limit the availability of ladder fuels. Fortunately, preferred habitat appears to be in moister topographic settings that create mesic stands, which should prove more resistant to wildfire and require less fuel treatments (Spies et al., 2006). Agee (2003) estimated fire return intervals of 75 years for mesic stands in Washington State and Camp et al. (1997) estimated that some mesic stands had a fire interval greater than 150 years. Similarly, according to Cilimburg and Short (2005), the mean fire return interval across 51 fire studies in the moist montane forests of western Montana and northern Idaho was 78 years. On balance this suggests that fire was not a large part of these wetter ecosystems except during extreme droughts. Purcell et al. (2009) and Spencer et al. (2008) noted that fuel treatments in California would have direct, negative impacts on fisher habitat suitability; however, these negative effects may be offset by the reduction in large fire risk. They suggested that the recovery of canopy cover from forestry treatments and wildfire may be relatively fast compared to the growth of large trees that would be removed should fire occur (Purcell et al., 2009).

Fishers clearly avoided openings such as clearcuts, open areas, and grassy slopes which were selected against in all of our models. They also avoided uniform early seral forests, like many of the lodgepole pine stands seen in the study area. Overall, our results suggest that the maintenance of suitable habitat for fishers will take planning at multiple scales with a focus on maintaining large trees in mesic forests.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.05.014.

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