

## Fisher use of postfire landscapes: implications for habitat connectivity and restoration

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**ABSTRACT.**—The relationship between fishers (*Pekania pennanti*), fire, and fuel management in the Sierra Nevada region is complex and highly controversial, and the recent listing of southern Sierra Nevada fishers as endangered has brought this issue to the forefront for many land managers. While wildfire is a natural component of the historic disturbance regime in the dry, mixed conifer forests of California, it also has the capacity to destroy large swaths of suitable habitat and to fragment tenuous populations, particularly given recent shifts in wildfire scope and severity. Therefore, balancing fuel reduction with habitat conservation requires careful consideration of spatial and temporal context, cumulative effects, and management prescriptions. There are several unresolved questions pertaining to fishers, including how and when fishers begin to reuse postfire landscapes and whether this information can be applied to postfire efforts to restore habitat connectivity and limit negative impacts of population fragmentation. To better understand fisher response to postfire landscapes, and to provide land managers with guidance regarding habitat restoration efforts, we investigated fisher recolonization behavior in and around 2 recent Sierra Nevada wildfires. We hypothesized that fisher use of postfire landscapes would be driven by at least 1 of 4 primary variables: prefire habitat quality, fire severity, topography, and time since fire. We developed 5 hypotheses regarding how fishers would begin to explore postfire landscapes and tested them using a combination of fine- and coarse-scale analyses based on data collected using scat detection dogs. At fine scales, the strongest relationship we observed was the combination of fire severity and landscape curvature on fisher scat location. At coarser scales, fisher colonization rates reflected avoidance of areas dominated by higher-severity fire, and fishers had a higher probability of being found in areas with larger and more contiguous patches of low-severity fire. Our results suggest that fisher use of postfire landscapes may center on low-severity or unburned islands (i.e., fire refugia/fire skips) and on fine-scale topographic features associated with landscape concavity, such as ravines or topographic depressions. Efforts to promote a sustainable low- to mixed-severity fire regime that creates habitat heterogeneity and forest resiliency can support fisher conservation in this region, and restoration efforts that capitalize on connecting fire refugia using microtopography as a foundation may facilitate habitat connectivity for fishers more rapidly than traditional methods.

**RESUMEN.**—La relación entre las martas pescadoras (*Pekania pennanti*), el fuego y la administración del combustible en la región de Sierra Nevada es compleja y muy controvertida. Con la reciente inclusión de las martas pescadoras del sur de Sierra Nevada en peligro de extinción ha puesto este problema en primer plano para muchos administradores de tierras. Si bien los incendios forestales son un componente natural del régimen histórico de perturbaciones en los bosques secos y mixtos de coníferas de California, también tienen la capacidad de destruir grandes franjas de hábitat y fragmentar poblaciones débiles, particularmente con los cambios recientes en el alcance y la gravedad de los incendios forestales. Por lo tanto, equilibrar la reducción de combustible con la conservación del hábitat requiere una consideración cuidadosa del contexto espacial y temporal, los efectos acumulativos y las prescripciones de gestión. Una pregunta sin resolver es cómo y cuándo las martas pescadoras comienzan a reutilizar los jardines después de un incendio, y si esta información se puede aplicar a los esfuerzos de restauración para reestablecer la conectividad del hábitat y limitar los impactos negativos de la fragmentación de la población. Para comprender mejor la respuesta de las martas pescadoras en relación con los mejoramientos posteriores a los incendios y para brindar orientación a los administradores de tierras con respecto a los esfuerzos de restauración del hábitat, investigamos el comportamiento de recolonización de las martas pescadoras alrededor de 2 incendios forestales recientes en Sierra Nevada. Planteamos la hipótesis de que el uso por parte de las martas pescadoras en el mejoramiento posteriores al incendio estaría impulsado por 1 de 4 variables primarias: la calidad del hábitat antes del incendio, la gravedad del incendio, la topografía y/o el tiempo transcurrido desde el incendio. Desarrollamos 5 hipótesis sobre cómo las martas pescadoras comenzarían a explorar los lugares posteriores al incendio, y las probamos utilizando una combinación de análisis de escala fina y gruesa basados en datos recopilados con perros detectores de excrementos. A escalas finas, la relación más fuerte que observamos incluyó la combinación de la gravedad del fuego y la

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curvatura del paisaje en la ubicación de las heces de las martas pescadoras. A escalas más gruesas, las tasas de colonización de mantras reflejaron la evitación de áreas dominadas por incendios de mayor severidad, y ellas tenían una mayor probabilidad de ser encontradas en áreas con parches más grandes y cerca de incendios de baja severidad. Nuestros resultados sugieren que el uso de mejoramiento del paisaje post-incendios por parte de las martas pescadoras se centra en islas de baja severidad o no quemadas (es decir, refugios de incendios/tolvas de incendios) y en características topográficas de escala fina asociadas con la concavidad del paisaje, como barrancos o depresiones topográficas. Los esfuerzos para promover un régimen sostenible de incendios de gravedad baja a mixta que cree heterogeneidad del hábitat y resiliencia del bosque pueden apoyar la conservación de las martas pescadoras en esta región, y los esfuerzos de restauración que aprovechan la conexión de refugios contra incendios utilizando la microtopografía como base pueden facilitar la conectividad del hábitat para las martas pescadoras más rápidamente que con los métodos tradicionales.

The behavior of animals in the face of novel landscapes has recently been recognized as a critical data gap with regard to modeling habitat connectivity and predicting species movement under shifting climate and disturbance regimes. While modeling structural connectivity based on landscape composition and configuration is an integral part of habitat analyses, this method falls short when trying to understand behaviors such as dispersal or exploratory movement patterns (Vanbianchi et al. 2018). Functional connectivity modeling, which is based on integrating structural variables with behavioral response data, is emerging as a more effective way to predict and model these movements. However, this modeling method has one significant drawback: it requires data on a species' movement and selection in suboptimal habitat (Carvalho et al. 2016, Abrahms et al. 2017). While GPS collars can now provide a wealth of such data, few studies intentionally target suboptimal habitat for data collection.

In the western United States, conservation of fisher habitat poses a significant challenge for land managers for a variety of reasons. The relationship between fishers (*Pekania pennanti*), fire, and fuel management in the Sierra Nevada region is complex and can be highly controversial (Collins et al. 2010, Truex and Zielinski 2013, Spencer et al. 2015). Recently listed as endangered under the Endangered Species Act (USFWS 2020), fishers in the southern Sierra Nevada are generally associated with forested areas dominated by high overhead canopy cover, complex structure, and coarse woody debris (Purcell et al. 2009, Aubry et al. 2013, Spencer et al. 2015). These conditions are typically associated with high fire risk (Spencer et al. 2016). Fire is a natural process that, in this ecoregion, maintains habitat heterogeneity and long-term resiliency, creating critical fine-scale habitat elements such as snags and coarse woody debris (Logan et al. 2016). In recent years, however, fires

burning at the upper end or outside of the natural range of variability have removed large swaths of suitable fisher habitat and have consumed more fine-scale habitat elements than they create. For example, the 2013 Rim Fire in Yosemite National Park and the Stanislaus National Forest burned over 107,000 acres of potential fisher habitat. And in 2015, the Rough Fire burned large areas of occupied habitat in the Sierra National Forest and adjacent Giant Sequoia National Monument. Examples such as these illustrate why, in 2012, the U.S. Fish and Wildlife Service ranked uncharacteristically severe wildfire as one of the highest and most consistent threats to fisher persistence in the western United States (Naney et al. 2012). At the same time, fire suppression has been linked to increased population instability due to increasing fuel loads and increased severity of those fires that do escape initial containment (Scheller et al. 2011).

This conflict presents a significant challenge to forest land managers in the western United States, who, with limited resources, are mandated to reduce wildfire behavior while conserving high-quality habitat as well as to restore postfire landscapes to a forested condition. The challenge is enhanced by the fact that fisher habitat in the Sierra Nevada is found primarily in a narrow north–south band along the range's western slope, bounded by elevation and periodically constrained by the bottlenecks created by large, steep, east-to-west-oriented river canyons. Described as “habitat linkage areas” (Spencer et al. 2015), these bottlenecks restrict movement and genetic flow between larger areas of suitable habitat. Fires that occur in these canyons have the potential to fragment the population, resulting in population-level effects far greater than the direct result of habitat loss (Scheller et al. 2011, Tucker et al. 2014, Spencer et al. 2015).

Managing fisher habitat in the Sierra and Cascade regions is now deeply intertwined

with fire and fuel management, and understanding the potential for fishers to use and/or traverse burned landscapes is therefore a priority. Predicting and promoting movement, particularly across potentially inhospitable matrix habitat such as a postfire landscape, requires an understanding of how fishers may respond to new environments. While resource selection data gleaned from the species' movements within suitable habitat may reflect its preferences, such data are limited in their ability to inform dispersal or exploratory movements. Understanding an animal's functional response to a novel landscape instead requires data on the species' movement and behavior in sub-optimal or infrequently used habitat. While this type of data is often scarce, there is a growing understanding of its importance in corridor or fragmentation analyses (Carvalho et al. 2016, Abrahms et al. 2017, Vanbianchi et al. 2018).

Fuel reduction efforts can reduce wildfire intensity, limit extent, and protect critical structures used by fishers for resting and reproduction; however, at the same time, these activities come with short-term reductions in habitat quality (Scheller et al. 2011, Truex and Zielinski 2013, Hanson 2013, Sweitzer et al. 2016). Balancing fuel reduction with habitat conservation requires careful consideration of spatiotemporal context, cumulative effects, and management prescriptions (Lindenmayer et al. 2006), and recent work suggests that the 2 objectives are not necessarily mutually exclusive (Zielinski et al. 2013, Truex and Zielinski 2013, Sweitzer et al. 2016, Thompson and Purcell 2016). Other authors have suggested that fishers are not negatively impacted by large high-severity wildland fires (Hanson 2013, DellaSala et al. 2017) and that greater harm is posed by mechanical thinning (Odion et al. 2014, Hanson 2015). There are several unresolved questions about fishers, including how and when they begin to reuse postfire landscapes, and whether this information can be applied to postfire restoration efforts in order to restore habitat connectivity and limit the negative impacts of population fragmentation.

To better understand fisher response to postfire landscapes, and to provide land managers with guidance regarding habitat restoration efforts, we investigated fisher behavior in and around 2 adjacent wildfire footprints in the Sierra National Forest—the French Fire

(2014) and the Aspen Fire (2013)—for between 1 and 3 years following fire. We used a noninvasive survey technique, scat detection dogs, to document fisher use of postfire landscapes (Thompson et al. 2012, Hanson 2013). We hypothesized that fisher use of postfire landscapes could be driven by any of 4 primary variables: prefire habitat quality, fire severity, topography, and/or time since fire. We developed a suite of hypotheses regarding how fishers would begin to explore postfire landscapes, and we tested our hypotheses using a combination of fine- and coarse-scale analyses based on scat locations in and around the fire footprints.

Our hypotheses were as follows:

*Hypothesis 1.* Fisher exploration and use of postfire landscapes would be unrelated to fire intensity or topographic variables. Under this scenario, we predicted that fisher use would begin near the fire perimeter and gradually work inward over time. Fishers would not show a preference for patches of different fire severity.

*Hypothesis 2.* Fisher use could be preferentially related to prefire conditions, either through spatial memory or a relationship between prefire conditions and postfire remnant structure (e.g., snags, coarse woody debris, etc.). Fishers might be motivated by a memory of prefire habitat conditions and would seek to preferentially use and recolonize areas of high prefire habitat suitability (Spencer 2012, Merkle et al. 2014). A relationship between scat location and prefire habitat quality would indicate support for this hypothesis.

*Hypothesis 3.* In the absence of suitable vegetative habitat (e.g., complex forest structure, overhead cover), fishers would rely on topographic variation to provide security while exploring and recolonizing postfire landscapes. Under this scenario, fisher use would be associated with fine-scale topographic features such as ravines or drainages. Use and occupancy would be unaffected by fire severity.

*Hypothesis 4.* Fishers would rely on unburned and lightly burned portions of the postfire landscape (fire refugia) to provide security while recolonizing burned areas. In this scenario, use and recolonization would focus on areas of lower burn severity (Volkman et al. 2020).

*Hypothesis 5.* Fisher behavior would exhibit some combination of hypotheses 2, 3 and 4, where fisher use of a postfire landscape is guided by multiple factors.

We assumed that any resident fisher would have either perished or fled during the fire and that the landscape was unoccupied immediately postfire. We therefore focused our analyses on attempting to determine what landscape factors may have guided fishers from surrounding areas as they reentered the area postfire. While the term *colonization* is often associated with population-level changes, we use it here in reference to metrics commonly associated with occupancy analyses, namely, the probability of an unoccupied area becoming occupied in a subsequent survey. Information on when, where, and how fishers recolonize postfire landscapes will help guide managers not only in restoration efforts, but also in minimizing the impacts of fuel reduction activities on fisher habitat connectivity.

#### Study Area

In the Southern Sierra Nevada Fisher Conservation Strategy (Spencer et al. 2016), the section of the San Joaquin River drainage directly below Mammoth Pool Dam is identified as Linkage Area D, a bottleneck of fisher habitat between 2 larger areas of suitable habitat (Fig. 1). In this area, the mixed conifer forest consists primarily of ponderosa pine (*Pinus ponderosa*), incense cedar (*Calocedrus decurrens*), and white fir (*Abies concolor*), interspersed with California black oak (*Quercus kelloggii*) and manzanita (*Arctostaphylos* spp.). The western side of the drainage is relatively steep and rocky, with forested areas patchily distributed among a shrub-dominated landscape. Beyond the river canyon, the forest becomes denser and includes additional species such as sugar pine (*Pinus lambertiana*) and mountain dogwood (*Cornus nuttallii*). The eastern side of the drainage has a more moderate slope, and the forest cover is more contiguous, though it is relatively open in structure and has a prominent hardwood component.

In July 2013, the Aspen Fire was ignited by lightning and burned 22,800 acres on the eastern side of the San Joaquin River drainage. In July 2014, an untended campfire started the French Fire, which eventually burned 13,837 acres on the western side of the drainage, directly opposite the Aspen Fire (Fig. 1). The Aspen Fire was generally considered a mixed-severity fire, with approximately 18%, 54% and 28% of the burned area burning at low, moderate, and high severity, respectively. In

contrast, nearly 55% of the French Fire burned at high severity and only 9% qualified as low severity according to Monitoring Trends in Burn Severity (MTBS) data (<http://www.mtbs.gov>). Taken together, the 2 fires effectively consumed 1 of the 6 important habitat linkage zones identified in a recent conservation strategy (Spencer et al. 2016).

## METHODS

### Scat Detection Dog Surveys

We conducted 3 scat detector dog surveys of the French and Aspen Fire landscape in October 2015, May 2016, and November 2016. To distribute the survey effort consistently across the landscape, we identified twelve 10-km<sup>2</sup> hexagonal sampling units, approximately the size of a female fisher home range (Spencer et al. 2016). Hexagonal units included a range of burn severities, including unburned areas outside but adjacent to the fire perimeter. For each survey, we minimized the effect of environmental and behavioral variability by (1) sampling each unit twice, with approximately 1 week between sampling efforts and (2) assigning different dog/handler teams for each unit during the second sampling period. Scat detection dog teams were provided by the University of Washington, Center for Conservation Biology's (UWCBC) Conservation Canines program.

Dog/handler teams were assigned a different sampling unit each day, and each team surveyed all units at least one time. Surveys began at an arbitrary location along a road within the target unit. From that point, dogs were allowed to search off-leash; however, their overall search pattern was dictated by the handler, who ensured that the dog investigated all desired habitat patches and elements, that the use of air currents was maximized, and that the survey remained within the target unit (Wasser et al. 2011). Each dog carried a miniature GPS receiver that logged the survey team's location every 60 s. While exhaustively searching each cell was not possible, teams surveyed large swaths of each unit, focusing on habitat and structures that would likely be used by a fisher, and the GPS track-log provided a detailed depiction of survey effort. Successful use of detector dogs depends on experience and a strong relationship between the dog and handler; we used teams trained

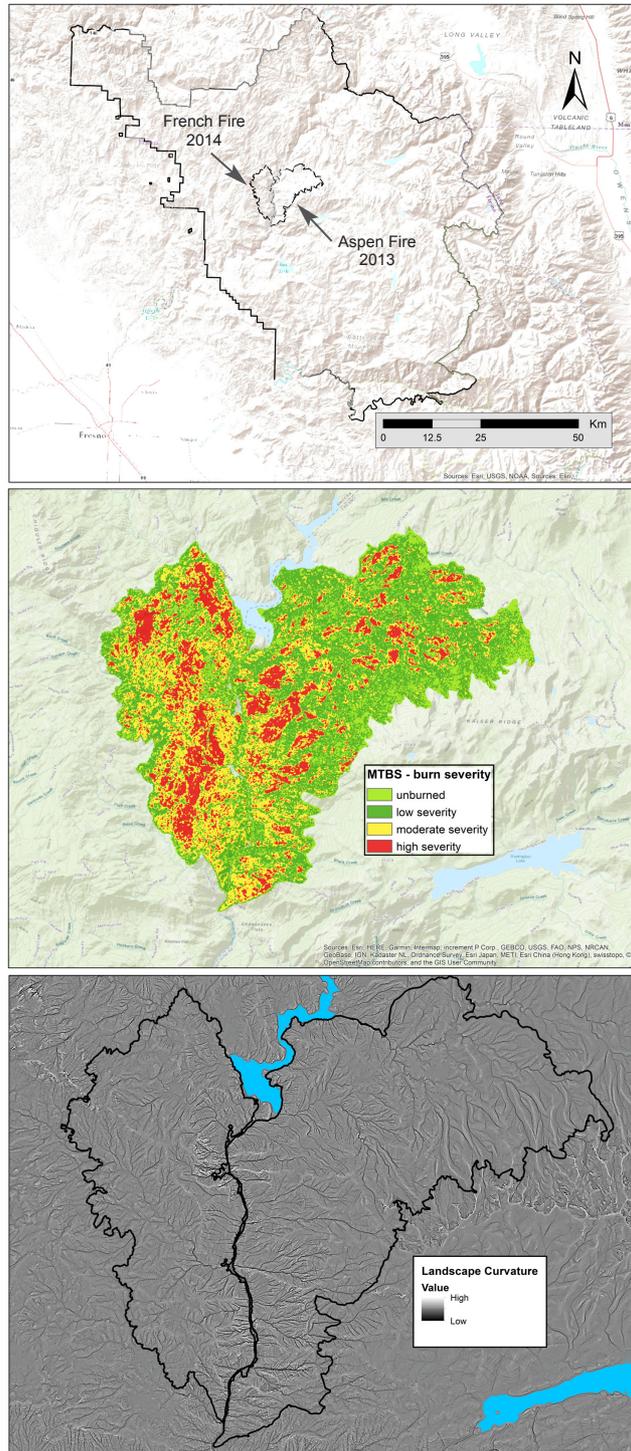


Fig. 1. *Top panel*, Location of the French and Aspen Fires on opposite sides of the San Joaquin River in the Sierra National Forest, California. The Aspen Fire occurred on the eastern side of the San Joaquin River drainage in 2013, and the French Fire occurred on the western side in 2014. *Middle panel*, Burn severity based on Monitoring Trends in Burn Severity (MTBS) data for the French and Aspen Fires. *Bottom panel*, Landscape curvature for the French/Aspen Fire landscape.

on the nearby Kings River Fisher Project, a long-running U.S. Forest Service fisher research project that used detector dogs to conduct semiannual occupancy surveys between 2007 and 2018.

Due to the large number of mesocarnivores with overlapping diets in the region, and due to the risk of field misidentification, all potential scats (i.e., not cougar or deer) located by the dogs were collected regardless of the handler's opinion. This resulted in numerous false-positive detections, but due to the nature of the project (i.e., surveying for a low-density population in atypical habitat), this was expected. We approached the surveys in this way to minimize the risk of missing a valid detection. Detection dogs are able to pick up on a wealth of different odors in each individual sample, so if a fisher was eating manzanita berries, for example, and the dog was rewarded for a scat with manzanita in its contents, then it follows that the dog has been reinforced to detect scats with manzanita, which many species consume seasonally in this region. All scats collected were dried and sent to the UWCBC genetics lab for species identification (Wasser et al. 2004, Vynne et al. 2011).

To verify species ID, all scat samples were extracted in duplicate using a modified version of Qiagen's DNeasy tissue extraction kit and then amplified in duplicate with Qiagen's Multiplex PCR kit using a restriction fragment length polymorphism marker. Both positive and negative controls were used in amplification for quality control. All PCR products were run on an ABI 3730 Genetic Analyzer (Applied Biosystems, <https://www.thermofisher.com/appliedbiosystems>) and then analyzed using GeneMarker software (SoftGenetics, State College, PA). The DNA extracts for confirmed fisher scats were further concentrated twofold using a Savant SpeedVac DNA Concentrator (Thermo Scientific™). Duplicate extracts were then PCR amplified 4 times using 2 previously developed and validated sex ID DNA markers targeting the ZFX/ZFY locus on the X and Y chromosomes (Statham et al. 2007) and the DBY locus on the Y chromosome (Tucker et al. 2017). Both markers were amplified together in a 17- $\mu$ L multiplex reaction using Qiagen's Multiplex PCR kit. Fragments were separated by size using capillary electrophoresis on an ABI 3730 Genetic Analyzer and were then visualized and scored

using GeneMarker software. Negative controls were used throughout each step of the process, and positive controls of known fisher DNA were amplified along with field samples.

#### Landscape Data Acquisition

Data on fire severity were obtained from the MTBS program (<https://www.mtbs.gov/>). MTBS provides burn severity data in raster format at a 30-m resolution, categorized into 4 severity classes defined by differences in the normalized burn ratio (dNBR): unburned to low, low, moderate, and high. While there are a number of different approaches to assessing fire severity, MTBS focuses on the impacts of fire on vegetation, particularly overstory (Eidenshink et al. 2007), which is highly relevant to species such as fishers that rely on overhead cover and complex forest structure for resting and denning sites, security, and access to prey (Zielinski et al. 2004, Purcell et al. 2009). The spatial configuration of fire severity classes was analyzed using FRAGSTATS (version 4.1; McGarigal and Marks 1995). Spatial metrics calculated included cohesion and Shannon's diversity index at the landscape scale, as well as percent of landscape and largest patch index for the 4 severity classes (Table 1).

Topographic variables were constructed using a 30-m digital elevation model (DEM) and the DEM Surface Tools package for ArcGIS (Jenness Enterprises 2013) and were included in order to investigate the potential use of terrain features as surrogates for vegetative cover by fishers. Variables calculated included surface area and general landscape curvature. Surface area, calculated from the estimated distance between the center of the target cell and the center of each of the 8 surrounding cells, is an indicator of topographic ruggedness and is limited to the estimated surface area of the target cell. Landscape curvature is based on an analysis of the relative position of 9 raster pixels: a target pixel and the 8 surrounding pixels. Negative values indicate a relatively concave arrangement such as a ravine, while positive values indicate a convex arrangement such as a ridge (Jenness Enterprises 2013).

Animals may recall certain habitat conditions or associations in a postdisturbance landscape (Gautestad 2011, Spencer 2012, Gautestad et al. 2013) and therefore may exhibit behavior in response to structures that are no

TABLE 1. Landscape variables used in resource selection (fine-scale) and occupancy (mid-scale) analyses of postfire fisher scat locations in the Sierra National Forest, California.

Landscape variable description	Fine-scale analysis	Mid-scale analysis	Variable name
Burn severity (unburned [c1], low [c2], moderate [c3], and high severity [c4])	X		MTBS
Spatial metrics of burn severity patches			
Shannon's diversity index		X	SHDI
Largest patch index (4 classes)		X	LPI-c1, c2, c3, c4
Cohesion (5 classes)		X	Cohesion L, c1, c2, c3, c4
Percent landscape (4 classes)		X	%land c1, c2, c3, c4
Surface area	X		surface area
Landscape curvature	X		curvature
Prefire habitat quality	X	X	Land08
Slope	X		slope
Distance to fire perimeter (m)	X	X	Dist to fireline
Distance to low-severity or unburned patch (m)	X		Dist to unburned patch
Time since fire (months)		X	tsf

longer present on the landscape. Therefore, we included an assessment of prefire habitat quality using a landscape-scale fisher habitat model developed by the Conservation Biology Institute (Spencer et al. 2011). The model is based on a combination of latitude-adjusted elevation, annual precipitation, and above-ground biomass of trees, and it accounted for 53% of the variation in fisher occupancy in a region-wide forest carnivore monitoring program (Spencer et al. 2011).

We calculated additional spatial variables, such as slope, distance to fire perimeter, and distance to closest low-severity patch, using standard tools in ArcGIS v10.3 (ESRI, Redlands, CA). Distance to fire perimeter was calculated based on how far within the overall fire footprint a scat was located, measured in meters to the nearest edge. Scats outside the fire perimeter received a distance score of 0. Low-severity patches were defined as areas comprising >0.5 ha of contiguous unburned or low-severity land (MTBS code 1 & 2) within the fire perimeter. While subjective, this threshold allowed us to exclude small slivers and individual raster cells that were unlikely to influence fisher behavior. We examined correlations between variables, and when the correlation between 2 variables exceeded 0.6, one of the variables was excluded (Appendix 1). Time since fire was calculated according to the number of months between the fire and the survey. This number varied between the 2 fires, since the Aspen Fire burned in 2013 and the French Fire burned in 2014.

#### Fine-scale Analysis

To characterize fisher use of postfire landscapes at a fine spatial scale, we constructed a suite of resource selection functions using the GLM package in R (R Core Development Team 2013). The locations of genetically verified fisher scats defined our set of used locations. Available locations, 25 per used location, were randomly placed within a 100-m buffer along the detector dog survey routes in order to constrain the available set to areas actually surveyed. Distance-based metrics were square root transformed to minimize the effect of skewness. Initially, we created 7 univariate random-effect models and ranked them using Bayesian information criterion (BIC) values, with fire (French or Aspen) as a random effect. We examined potential interactions between the top-ranked variable and all 6 remaining variables. We then constructed bivariate models using the top-ranked variable and all 6 remaining variables and again ranked the models according to BIC scores. This process was repeated a third time, resulting in a suite of trivariate models (Table 2).

#### Mid-scale Analysis

Detector dog surveys are most effective when the dogs are allowed to follow air currents and associated scents, but consequently this does not provide a precise characterization of space such as is provided by a fixed array of cameras or defined survey transects. We created this characterization by overlaying

TABLE 2. Univariate, bivariate, and trivariate resource selection models indicating the fine-scale relationship between fisher locations and landscape metrics on the French and Aspen Fire landscapes in the Sierra National Forest, California.  $\Delta$ BIC values are calculated in relation to the best-performing model overall.

Univariate RSF models	BIC	$\Delta$ BIC	$P$ (var1)		
MTBS	381.9	11.4	<0.0001		
Dist to unburned patch	403.5	33.0	<0.001		
Curvature	415.2	44.7	<0.0001		
Dist to fireline	418.0	47.5	<0.0001		
Slope	425.8	55.3	<0.01		
Surface area	426.5	56.0	<0.01		
Land08	434.5	64.0	0.960		
Interactions	BIC	$\Delta$ BIC	$P$ (MTBS)	$P$ (var 2)	$P$ (MTBS* var2)
MTBS * curvature	377.0		<0.0001	0.007	0.428
MTBS * surface area	389.8		0.412	0.032	0.309
MTBS * slope	390.7		0.155	0.047	0.312
MTBS * Land08	393.1		0.002	0.352	0.156
MTBS * dist to fireline	390.6		0.015	0.628	0.348
MTBS * dist to unburned patch	395.3		<0.001	0.345	0.321
Bivariate RSF models	BIC	$\Delta$ BIC	$P$ (MTBS)	$P$ (var 2)	
MTBS + curvature	370.5	0.00	<0.0001	<0.0001	
MTBS + surface area	383.9	13.4	<0.0001	0.014	
MTBS + dist to fireline	384.4	13.9	<0.0001	0.032	
MTBS + slope	384.6	14.1	<0.0001	0.032	
MTBS + Land08	388.2	17.7	<0.0001	0.365	
MTBS + dist to unburned patch	389.0	18.5	0.0004	0.828	
Trivariate RSF models	BIC	$\Delta$ BIC	$P$ (MTBS)	$P$ (curvature)	$P$ (var 3)
MTBS + curvature + surface area	373.7	3.2	<0.0001	<0.0001	0.03
MTBS + curvature + slope	373.7	3.2	<0.0001	<0.0001	0.044
MTBS + curvature + Land08	376.4	5.9	<0.0001	<0.0001	0.274
MTBS + curvature + dist to fireline	373.5	3.0	<0.0001	<0.0001	0.045
MTBS + curvature + dist to unburned	377.6	7.1	0.001	<0.0001	0.768

a finer grid (1-km<sup>2</sup> hexagon) over the original sampling unit array and considering each 1-km<sup>2</sup> grid cell to be a distinct sampling unit (Thompson et al. 2012). Pseudoreplication is a significant concern in the analysis of scat location data, as the deposition of scat by many animals is nonrandom and can be influenced by the presence of other individuals or territory boundaries. Based on our experience working with fishers, we assumed that a 1-km<sup>2</sup> resolution was small enough to capture landscape variability yet large enough that a detection in one cell was unlikely to influence the probability of a detection in an adjacent cell (Thompson et al. 2012). The detection of a scat within a grid cell identified that cell as occupied versus

unoccupied; additional scats or the presence of a latrine within a cell did not alter this.

We conducted an occupancy analysis using program PRESENCE (Hines 2006) with the 1-km<sup>2</sup> grid cells as the sampling units and with 3 sampling seasons. Because sampling intensity varied between cells, we used the length of the georeferenced tracklog to generate an estimate of survey effort. The length of a tracklog in a particular cell varied according to terrain and forest structure, and not every grid cell was surveyed in every season depending on the route a dog chose to follow. Therefore, survey effort (i.e., length of the tracklog in a cell) was included as a covariate in the occupancy model associated with probability

TABLE 3. Univariate and bivariate occupancy models indicating the mid-scale relationship between fisher locations and landscape metrics on the French and Aspen Fire landscapes in the Sierra National Forest, California. Coefficients include occupancy (psi), colonization (gamma), extinction (eps), and detection (p). Only models within 5 AIC points of the top models, either within group or overall, are reported.

Models	AIC	Within-group ΔAIC	Overall ΔAIC
Univariate occupancy models			
psi(), gamma(%high), eps(), p(effort)	157.39	0.00	1.72
psi(), gamma(LPI_c2), eps(), p(effort)	160.26	2.87	4.59
psi(), gamma(%land_c2), eps(), p(effort)	160.45	3.06	4.78
psi(), gamma(cohesion_c2), eps(), p(effort)	160.56	3.17	4.89
psi(), gamma(), eps(), p(effort) [NULL]	162.71	5.32	7.04
Multivariate occupancy models			
psi(%land_c2), gamma(%high), eps(), p(effort)	157.20	0.00	1.53
psi(cohesion_c1), gamma(%high), eps(), p(effort)	157.42	0.22	1.75
psi(%land_c2+ cohesion_c1), gamma(%high), eps(), p(effort)	157.94	0.74	2.27
psi(tsf), gamma(%high), eps(), p(effort)	158.07	0.87	2.40
psi(%land_c2 + tsf), gamma(%high), eps(), p(effort)	158.64	1.44	2.97
psi(cohesion_c1 + tsf), gamma(%high), eps(), p(effort)	160.20	3.00	4.53
psi(%land_c2), gamma(LPI_c2), eps(), p(effort)	160.27	3.07	4.60
psi(%land_c2+ cohesion_c1), gamma(LPI_c2), eps(), p(effort)	160.49	3.29	4.82
psi(tsf), gamma(LPI_c2), eps(), p(effort)	160.96	3.76	5.29
psi(cohesion_c1 + tsf), gamma(LPI_c2), eps(), p(effort)	161.54	4.34	5.87
Variable detection probability			
psi(tsf), gamma(%high), eps(), p(effort * survey)	155.67	0.00	0.00
psi(%land_c2), gamma(%high), eps(), p(effort * survey)	155.80	0.13	0.13
psi(cohesion_c1), gamma(%high), eps(), p(effort * survey)	155.80	0.13	0.13
psi(lpi_c2), gamma(%high), eps(), p(effort * survey)	156.23	0.56	0.56
psi(tsf + %land_c2), gamma(%high), eps(), p(effort * survey)	156.81	1.14	1.14
psi(), gamma(%high), eps(), p(effort * survey)	157.08	1.41	1.41
psi(cohesion_c1), gamma(%high), eps(), p(effort * survey)	157.42	1.75	1.75
psi(cohesion_c1 + %land_c2), gamma(%high), eps(), p(effort * survey)	157.63	1.96	1.96
psi(), gamma(), eps(), p(effort * survey) [NULL]	159.83	4.16	4.16
psi(cohesion_c1 + tsf), gamma(%high), eps(), p(effort * survey)	159.98	4.31	4.31

of detection. Because we were interested in the relative contribution of landscape variables in explaining the behavior of fishers in burned landscapes, we wanted to avoid inadvertently including uninformative parameters (Arnold 2010). We therefore screened variables for potential contribution by creating a set of univariate occupancy models and ranking these models based on AIC values. We also assessed correlations among variables using Pearson’s correlation coefficient and identified pairs of variables with correlations significantly different from 0 (Appendix 1). Based on this information, we identified a subset of potentially informative variables related to our initial hypotheses and conducted a structured all-subsets analysis while avoiding correlated pairings (Conner et al. 2018). Based on univariate model rankings and variable correlations, we included 5 variables in the development of multivariate occupancy models: 3 as coefficients on the occupancy estimate (percent low-intensity burn [%land\_c2], cohesion of unburned

land [cohesion\_c1], time since fire [tsf]) and 2 as coefficients on the colonization estimate (percent high-severity burn [%high], largest patch index for low-severity fire [LPI\_c2]; Table 3). We also considered the potential for detection probability to vary by survey, resulting in 40 potential models. The probability of extinction was assumed to be constant throughout the study. To evaluate the relative importance of each variable, we again ranked all models that outperformed the null model using AIC, and for each variable we summed the weights of the models that included that variable.

## RESULTS

Across all 3 surveys, detector dogs located 157 scats in and around the French and Aspen Fire landscapes (Fig. 2). Of these, 49 (31%) were genetically confirmed as fisher scats. An additional 10 scats amplified as multiple species, including fisher and other mesocarnivores such as fox or skunk. This may reflect territorial

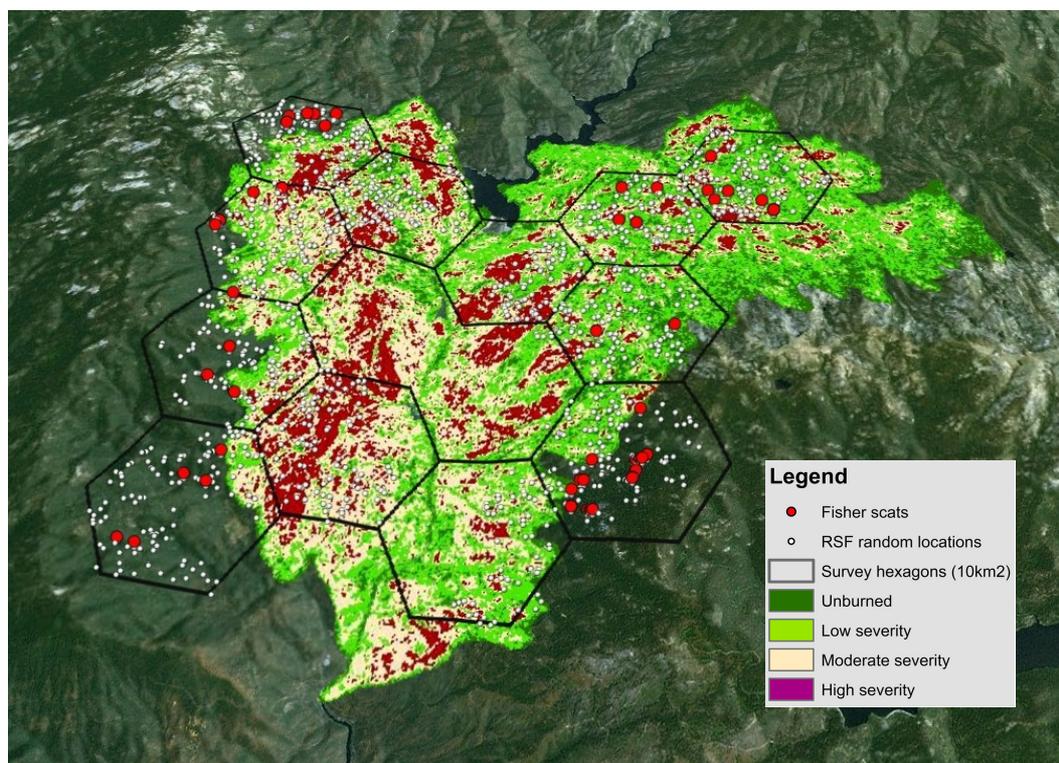


Fig. 2. Results of scat detector dog surveys for fisher presence within the French and Aspen Fire landscapes in the Sierra National Forest, California, 2015–2016. Green to red shading indicates fire severity; dark outlines indicate 10-km<sup>2</sup> survey hexagons. Red dots indicate the locations where fisher scats were collected, and white dots indicate the random locations chosen for fine-scale resource selection function (RSF) analysis.

overmarking, but these locations were excluded from analysis because we were unable to exclude the possibility of intraguild predation or scavenging. Forty-two scats failed to amplify, and the remaining scats primarily included gray fox (*Urocyon cinereoargenteus*) and ring-tail (*Bassariscus astutus*).

Survey effort varied widely between coarse-scale hexagonal survey units and the 1-km<sup>2</sup> sampling units used for RSF analysis. Hexagonal survey units were intentionally surveyed during each effort, with an average of approximately 5.5 h spent surveying each unit. Coverage of the 1-km<sup>2</sup> RSF sampling units varied; not every unit was sampled in each season, because teams were not tasked with sampling at this scale and because the 1-km<sup>2</sup> grid was overlaid on tracklogs post hoc. Of the one hundred and fifty-four 1-km<sup>2</sup> RSF sampling units in the study area, an average of 86 were sampled in each season (90 in fall 2015, 87 in spring 2016, 81 in fall 2016). When a sampling

unit was surveyed, an average of 65 min was spent surveying the unit (range 1–214 min).

Of the 49 confirmed fisher scats, 24 were confirmed to sex (14 male, 10 female). An additional 10 samples amplified according to sex (2 males, 8 females) but failed to meet the quality assurance standard for confirmation. The remaining 15 samples failed to amplify. Male scats were detected fairly evenly across all seasons (4 in fall 2015, 5 in spring 2016, 5 in fall 2016), while 80% of female fisher scats were detected in spring 2016. Of the 49 confirmed fisher scats, 16 were located within the fire perimeters (7 confirmed male, 2 confirmed female, 1 suspected female, 6 sex undetermined). These scats were located an average of 1793 m within the fire footprint (range 216–3025 m).

#### Fine-scale Habitat Selection

Univariate RSF models indicated that of the 7 landscape variables considered, fisher scat

location was most strongly associated with burn severity, indicating an avoidance of high and moderate severity classes (Table 2). No other models were competitive, including interaction terms. Bivariate models indicated that an additive model based on burn severity and landscape curvature outperformed the burn severity model by 11.4 BIC points (Table 2). No trivariate model outperformed the burn severity + landscape curvature model.

#### Mid-scale Habitat Selection

At the mid scale, the highest-performing univariate model consisted of a colonization estimate based on the percent of high-severity fire within the target cell. This model outperformed the null model by 5.32 AIC points. Adding the percentage of low-intensity fire as a covariate on the occupancy estimate improved the AIC value slightly ( $\Delta\text{AIC} = -0.19$ ) (Table 3). The only other competitive multivariate models were the percent high-severity fire as a coefficient on colonization and the cohesion of unburned pixels as a coefficient on occupancy ( $\Delta\text{AIC} = 0.22$ ).

Relaxing the assumption of a consistent probability of detection resulted in the creation of 8 additional competitive models (Table 3). In all top models, the consistent feature was a negative association between the percentage of high-severity fire within a grid cell and the probability of fisher colonization. Comparable AIC values ( $<2$  AIC points) resulted from a variety of occupancy coefficients: fisher scats were located in cells with higher percentages of low-intensity fire, higher cohesion of unburned land, and larger patches of low-intensity fire. However, the overall top model indicated that the probability of occupancy increased in relation to the time since fire; this model outperformed a null model, assuming variable detection probability, by 4.16 AIC points.

#### DISCUSSION

Little published literature exists on how mesocarnivores respond to both wildland and prescribed fire (Fisher and Wilkinson 2005, Wasserman 2015). What does exist focuses on generalist species and suggests a wide variety of responses depending on the physiology and ecological relationships of the focal species. Foxes have been observed using burned land-

scapes more often than expected (Schuette 2007, Thompson et al. 2008, Borchert 2012), though postfire declines have also been documented (Cunningham et al. 2006). Coyote use of postfire landscapes has been observed to increase (Schuette et al. 2014), decrease (Schuette 2007, Borchert 2012), and remain constant (Cunningham et al. 2006). Lindenmayer et al. (2008) observed a mixed response to wildland fire by Australian mesocarnivores; long-nosed bandicoot (*Perameles nasuta*) and common brushtail possum (*Trichosurus vulpecula*) detections increased, while detections of common ringtail possums (*Pseudocheirus peregrinus*) decreased. Extensive scavenging of fire-killed large mammals by large carnivores has been documented (Singer et al. 1989, Blanchard and Knight 1990), and it is logical to assume that mesocarnivores may exploit a similar bounty following higher-severity fires.

The 5 potential hypotheses we postulated each suggest a different combination of landscape variables as primary influences on fisher scat locations. The majority of the fisher scats we located were found outside the fire footprint, indicating that fishers remained in the surrounding forest and began to penetrate the burned landscape 2–4 years after the fires occurred. The fact that time since fire emerged in one of the top models suggests that fisher exploration of burned landscapes is a gradual process. Despite the fact that distance to fire perimeter was not a strong predictor of occupancy or colonization, it was correlated with time since fire (Pearson's correlation coefficient 0.625,  $R^2 = 0.39$ ,  $P = 0.0006$ ), indicating that fishers continued to venture farther into the fire interior over time. Ten of 13 scats found within the fire perimeter were detected  $\geq 36$  months postfire. In particular, a number of scats were located well within the northern portion of the Aspen Fire, an area that burned at a mixed severity.

At fine scales, the strongest relationship we observed included the combination of fire severity and landscape curvature on fisher scat location. Fisher scats were more often located in areas of lower-severity fire and in areas of concave topography, such as ravines or canyon bottoms. At coarser scales, fisher colonization rates reflected avoidance of areas dominated by higher-severity fire, and fishers had a higher probability of being found in areas with larger and more contiguous patches of low-severity

fire. Variables such as prefire habitat quality and distance to fire perimeter did not appear to influence fisher scat locations in a noticeable way. Based on the pattern of relationships we observed, fishers appeared to recolonize burned landscape in accordance with our fifth hypothesis, utilizing a combination of fine-scale topography and unburned or lightly burned patches within the fire perimeter. Similar behavior has been reported for American black bears (*Ursus americanus*; Cunningham et al. 2003) and Canada lynx (*Lynx canadensis*; Vanbianchi et al. 2017). Cunningham et al. (2003) found that bears relied on unburned islands within the perimeter of large fires for bedding and feeding sites. Similarly, Vanbianchi et al. (2017) reported that lynx in northern Washington used burned areas within 1 year of the Tripod Fire, but also that they avoided areas of high-severity fire, instead focusing their activity within the fire perimeter on unburned or lightly burned islands (fire skips) with residual trees and high canopy cover.

It is worth noting that our evaluation of fisher response to prefire habitat quality and distance to fire perimeter are both based on assumptions. We did not attempt to determine individual ID or age for detected fishers; therefore, we are assuming that the animals we detected came from the local area and were potentially familiar with the prefire landscape. If these animals were juveniles or dispersers from outside the local area, our rejection of the idea that they would respond to prefire habitat quality would be invalid. Furthermore, fire perimeters are rarely as distinct on the landscape as they are on a map. They are often better characterized as a patchwork or gradient of fire severity. However, our analysis assumed that fishers observed the fire edge as we defined it—not a likely scenario, but a necessary assumption in the absence of better data.

It is extremely difficult to acquire empirical data on the response of secretive, highly mobile forest carnivores such as fishers to unpredictable events such as wildfire. To our knowledge, only one other study has attempted this. Hanson (2013, 2015) used detector dogs to survey the McNally (2002) and Manter (2000) Fire footprints on the Sequoia National Forest for fisher scat 10–12 years postfire. The author reported fisher scats in both postfire and unburned areas, and fisher selection of closed-

canopy mature/old forest prior to the fire at the same level as similar unburned areas. Based on this evidence, the author concluded that mixed-severity and high-severity fire did not represent a loss of habitat for fishers and that fishers may select a combination of burned/unburned areas for foraging and resting, respectively.

Our results differed from Hanson (2013) and Hanson (2015) in several ways. We found no evidence of a relationship between fisher scat detection and prefire habitat quality. Fishers on the Aspen/French Fire landscapes appeared to avoid areas of high and moderate fire severity and instead used islands of unburned forest or low-intensity patches to facilitate movement within the fire perimeter. They also appeared to use fine-scale topographic features such as movement corridors, which likely provide some degree of security in an open postfire landscape and may have provided refuge for small mammals during the fire. Only one fisher scat was located in an area classified as high-intensity fire, and this scat was located in a small ravine under a spanning log. One area of agreement between the 2 studies may be the idea that fishers' willingness to use a postfire landscape increases over time. Although the majority of scats were located outside the fire perimeter in all our surveys, the detection of scats deeper within the fire perimeter increased in later surveys. This result loosely corresponds with the Hanson (2013) report of fisher scats within the McNally and Manter Fire perimeters 10+ years postfire. Similarly, Vanbianchi et al. (2017) reported that lynx activity within the Tripod Fire was primarily limited to within 1 km of the fire perimeter during the first year postfire. In the Sierra Nevada region, it is common for shrubs to respond strongly and dominate postfire landscapes that burned with moderate to high severity (Collins and Roller 2013). As shrubs develop, they provide vegetative cover and likely increase a fisher's willingness to explore the postfire landscape.

Pseudoreplication is a significant concern when using scats to indicate a species' presence or activity, as the placement of scats is autocorrelated and the associated clustering can lead to biased results (Thompson et al. 2012). This problem is particularly acute with small sample sizes and with species such as fishers that may use latrines or mark territory

boundaries with scat. Instead, when evaluating scat data without individual genetic information, it is necessary to identify some independent spatial sampling unit appropriate for the species (e.g., a transect, grid cell, etc.) and then to examine occupancy or abundance within that unit (Smith et al. 2005, Long et al. 2007, Thompson et al. 2012). To help address this issue, we analyzed our data at 2 spatial scales and compared the results of multiple analytical techniques. Hanson (2013) relied on a one-tailed chi-square analysis to assess habitat selection without accounting for autocorrelation or multiple comparisons, and in a subsequent publication Hanson stated that the absence of statistical significance supported the conclusion of no difference in selection of burned and unburned habitat (Hanson 2015), as opposed to a failure to reject a null hypothesis of differential selection (Anderson et al. 2001). Such misapplication of statistical techniques can create difficulties for land managers who are required to consider “all relevant science” when developing management actions (Safford et al. 2008, Peery et al. 2019).

Issues are further confounded by Hanson's (2013, 2015) choice of fire severity classes. Hanson (2013) defines low-severity fire as areas with <15% basal area mortality (<316 RdNBR), moderate-severity fire as areas with 15% to 50% basal area mortality (316–477 RdNBR), and higher-severity fire as areas with >50% basal area mortality (>477 RdNBR). Management agencies, on the other hand, generally define low-severity fire as <25% basal area mortality, moderate as 25% to 75% basal area mortality, and high as >75% mortality. Furthermore, to account for small sample sizes, the author combined the “moderate-” and “higher-” severity fire categories into a single broad category, effectively biasing subsequent interpretation toward higher-severity fire (Fulé et al. 2014). While there is no precise agreed-upon threshold of high-severity fire, Safford et al. (2008) recommended a 75% basal area mortality threshold, given that the most commonly used thresholds in the literature range from 70% to 80%. It is worth noting that careful examination of the maps provided by Hanson (2013, 2015) suggests that the surveys were conducted in areas of mixed-severity fire and not within large high-severity patches. Labeling these areas as high-severity fire, based on a threshold of 15% basal mortal-

ity (moderate + high severity), notably undervalues the importance of variability in fire severity and the potential for fire refugia to serve as key “stepping-stone” habitat. Regardless, the use of common standards and definitions across studies will facilitate comparisons and further our understanding of wildlife response to fire.

More appropriate context for our results may come from a telemetry study of marten response to postfire landscapes in the Alaskan taiga (Paragi et al. 1996). The authors reported that marten abundance and activity was highest within a recent (<10 years) burned landscape, which contained lower canopy cover but higher coarse woody debris than older burned or unburned landscapes. However, they also reported that there was high population turnover and that the vast majority of animals using the burned landscape were juveniles. They reported higher biomass and diversity of small mammals within the burned landscape and expected to find higher use of habitat near the fire perimeter, where martens could rest in unburned habitat and forage within the burned area. Instead, they reported very low use of edge habitat. The authors concluded that postfire habitat lacked the conditions necessary for marten reproduction and instead acted as a population sink. Dispersing animals from nearby mature forest were attracted to the postfire landscape due to availability of unoccupied territories and high prey density; however, these animals frequently died before reproducing. Similar dynamics, as described by Van Horne (1983), have been observed in other boreal marten populations exposed to both fire (Vernam 1987, Latour et al. 1994) and intensive logging (Chapin et al. 1998).

Martens and fishers display significant overlap in their habitat selection and behavior, so the evidence above suggests that fisher use of postfire landscapes should be interpreted carefully. Relating population density to habitat quality in the absence of survival or other corroborating demographic data risks mistaking potential population sinks as high-quality habitat (Van Horne 1983). Without demographic data, it is difficult to know whether fisher use of postfire landscapes indicates a resident or transient population or whether species like the fisher may experience higher mortality in postfire landscapes. At the same time, some authors have suggested that a

landscape mosaic created and supported by a mixed-severity fire regime could provide a diversity of habitat and prey while protecting against large habitat losses associated with large or uncharacteristically severe disturbances (Koehler and Hornocker 1977).

Predicting an animal's behavior in a novel landscape is difficult, and insights gained from research in more typical habitat may not always apply (Carvalho et al. 2016, Abrahms et al. 2017, Vanbianchi et al. 2018). Density in atypical habitat may be low, further weakening researchers' ability to discern patterns. Scat detector dogs are uniquely qualified to provide initial information in these situations; they are able to cover large areas quickly without bias, and the probability of detecting a target animal, if present, is high (Wasser et al. 2004, Long 2006). While GPS collar technology has greatly increased researchers' ability to collect large amounts of precise data on an individual animal's movement, capturing and collaring the few animals that will choose to explore a novel environment or disperse across a barrier is extremely difficult and can require an extended period of monitoring to document such relatively rare events. By providing initial information on how animals move in sub-optimal or unique environments, detector dog surveys can inform subsequent research efforts, including trapping or camera surveys. Radio or GPS telemetry and scat detection dogs are often viewed as "alternatives," but each has its own strengths and weaknesses and can answer different questions, and consequently, these methods may be best used as complementary efforts. While our sample size in this analysis was low ( $n = 49$ ), our experience of over a decade researching fisher ecology in the Sierra Nevada region (Thompson et al. 2012, Sweitzer et al. 2016, Green et al. 2018), including extensive scat detection dog surveys and telemetry work, suggests that we did identify the low level of fisher activity present on a recent postfire landscape. Subsequent research efforts should build on this foundation and apply different tools to expand our understanding of fisher behavior in novel, disturbed, or otherwise suboptimal habitats.

Our results suggest that fisher use of post-fire landscapes centers on low-severity or unburned islands (i.e., fire refugia/fire skips) and on fine-scale topographic features associated with landscape concavity, such as ravines

or topographic depressions. These results may be linked, as landscape concavity is often associated with water accumulation and therefore may represent landscape patches that are less likely to burn, are quicker to recover some form of vegetative cover, and may contain remnant prey populations. Where possible, fishers may use unburned islands to traverse burned landscapes and, in the absence of vegetative cover, may use topography as a surrogate. Fisher and Wilkinson (2005) write that "these structural features [fire skips], where examined, were revealed as important predictors of mammalian use of burned and harvested stands for all mammal species groups" and suggest that a "more explicit examination of the influence of live residual trees and their influence on recolonization and persistence of mammal species post disturbance is required."

Our results differed from the one other study that, to our knowledge, attempted to quantify fisher use of postfire landscapes in the Sierra Nevada. These differences may have stemmed from the amount of time after the fire that sampling was conducted. Hanson (2013, 2015) sampled >10 years postfire, when vegetation recovery may have provided greater cover and structure. In contrast, our sampling occurred in years 2–4 following fire, when only limited vegetation recovery had occurred. Of particular concern is Paragi et al.'s (1996) conclusion that postfire habitat may not serve as breeding habitat for martens and may instead serve as a population sink attracting dispersing juveniles into a hazardous landscape. Dispersing fishers may be similarly drawn toward landscapes with increased prey availability and reduced conflict with territorial adults. However, without key habitat elements such as resting and denning structures, postburn habitat may not support reproduction, at least in the short term, and may expose fishers to predators such as bobcats that often use post-fire shrub-dominated areas (Wengert 2013).

Given the recent USFWS decision to list the Southern Sierra Nevada fisher population as endangered (USFWS 2020), it is crucial that we clarify the species' relationship with postfire landscapes and identify potential opportunities for restoring habitat connectivity. Efforts to promote a sustainable low- to mixed-severity fire regime that creates habitat heterogeneity and forest resiliency may provide a

buffer against population decline. In addition, connecting unburned islands within the fire perimeter and using microtopography as a template may present opportunities for post-fire restoration to more rapidly promote habitat connectivity.

#### DECLARATIONS

*Ethics approval and consent to participate.* All animal capture and handling was conducted under the guidelines of the American Society of Mammalogists (Sikes et al. 2016); procedures were reviewed and approved by the California Department of Fish and Wildlife (permit #SC-2730).

*Consent for publication.* The authors consent to publication of all details and images contained herein.

*Availability of data and material.* All data sets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

*Competing interests.* The authors declare that they have no competing interests.

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*Authors' contributions.* CT coordinated the research effort, conducted analyses, and was the primary writer of the manuscript. KP acquired funding, assisted with analyses, and was a major contributor to editing the manuscript. RG oversaw the field aspects of the research effort and assisted with writing and editing the manuscript. HS managed the data collection and contributed to the methodology section of the manuscript. SW provided logistical and laboratory support.

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