RESEARCH ARTICLE

MODELING THE EFFECTS OF FIRE SEVERITY AND SPATIAL COMPLEXITY ON SMALL MAMMALS IN YOSEMITE NATIONAL PARK, CALIFORNIA

Susan L. Roberts^{1,3,*}, Jan W. van Wagtendonk¹, A. Keith Miles², Douglas A. Kelt³, and James A. Lutz⁴

¹US Geological Survey, Western Ecological Research Center, Yosemite Field Station, El Portal, California 95318, USA

²US Geological Survey, Western Ecological Research Center, Davis Field Station, University of California, One Shields Avenue, Davis, California 95616, USA

³Wildlife, Fish, and Conservation Biology, University of California, One Shields Avenue, Davis, California 95616, USA

⁴College of Forest Resources, Box 352100, University of Washington, Seattle, Washington 98195, USA

*Corresponding author: Tel.: 001-209-735-9557; e-mail: susan_roberts@usgs.gov

ABSTRACT

We evaluated the impact of fire severity and related spatial and vegetative parameters on small mammal populations in 2 yr- to 15 yr-old burns in Yosemite National Park, California, USA. We also developed habitat models that would predict small mammal responses to fires of differing severity. We hypothesized that fire severity would influence the abundances of small mammals through changes in vegetation composition, structure, and spatial habitat complexity. Deer mouse (*Peromyscus maniculatus*) abundance responded negatively to fire severity, and brush mouse (*P. boylii*) abundance increased with increasing oak tree (*Quercus* spp.) cover. Chipmunk (*Neotamias* spp.) abundance was best predicted through a combination of a negative response to oak tree cover and a positive response to spatial habitat complexity. California ground squirrel (*Spermophilus beecheyi*) abundance increased with increasing spatial habitat complexity. Our results suggest that fire severity, with subsequent changes in vegetation structure and habitat spatial complexity, can influence small mammal abundance patterns.

Keywords: abundance, brush mice, California ground squirrel, chipmunks, deer mice, habitat complexity

Citation: Roberts, S.L., J.W. van Wagtendonk, A.K. Miles, D.A. Kelt, and J.A. Lutz. 2008. Modeling the effects of fire severity and spatial complexity on small mammals in Yosemite National Park, California. Fire Ecology 4(2): 83-104. doi: 10.4996/fireecology.0402083

INTRODUCTION

Fire is an integral process in the structure and maintenance of a variety of ecosystems throughout the world (Wright and Bailey 1982, Minnich et al. 2000). Fire regimes are so highly correlated to the habitats they shape that it is difficult to ascertain whether fire regimes drive vegetation patterns or if the vegetation drives fire regime patterns (van Wagtendonk and Fites-Kaufman 2006). Attempts to exclude fire from these systems through a century of suppression have been partly unsuccessful. The inevitable lightning strike or careless camper can lead to catastrophic wildfire when the fire occurs in areas of excessively accumulated, spatially continuous fuels. Further, long fire-free periods may be detrimental to the flora and fauna historically resident in these fire driven forests.

Fire severity refers to the magnitude of the effect that a fire has on the environment, and is commonly applied to a number of ecosystem components (van Wagtendonk 2006). Fire, both wild and prescribed, burn heterogeneously across landscapes, leaving behind a matrix of areas burned at various levels of severity, interspersed with unburned patches of various sizes and shapes. Fire suppression efforts began in earnest in the Sierra Nevada, California, in the early 1900s, greatly reducing the spatial extent of fire and, therefore, reducing its effects on the landscape. The continued. widespread efforts suppression ultimately changed the fire regime in the area such that, a century later, fires burn more intensely and create larger patches of high fire severity (Chang 1996, Sugihara and Barbour 2006).

Fire is part of a complex and dynamic feedback loop that influences the structure and composition of vegetation, which in turn shape faunal composition. The local fauna, in turn, influences habitat structure and composition; small mammals, for example, consume and

disperse seeds (Vander Wall 1993, Vander Wall et al. 2001) and hypogeous fungi (Maser and Maser 1988, Pyare and Longland 2001). Small mammals also serve an important ecological function as prey for avian, reptilian, and mammalian predators (Zielinski et al. 1983, Forsman et al. 1984, Stebbins 2003). Burned forests have complex habitat heterogeneity because fires seldom burn uniformly over the landscape (van Wagtendonk and Fites-Kaufman 2006). Fire removes the thick litter layer and exposes previously buried seeds and sprouting vegetation, thereby creating patches with increased food availability (Shaffer and Laudenslayer 2006). These burned patches are intermixed with unburned patches with an intact shrub understory that provide cover from predators (Agee 1993). A matrix of downed coarse woody debris (CWD) is also important to small mammals serving as refugia and travel corridors (Carey and Johnson 1995, Manning and Edge 2004). Ecological processes, such as fire, are interrelated with all ecosystem inhabitants; a change in one of the processes affects all of the inhabitants.

Understanding how the attributes of a fire regime (e.g., season, spatial complexity, and severity) influence the flora and fauna is important for predicting the effects of regime changes and for planning management actions (Shaffer and Laudenslayer 2006). Monroe and Converse (2006) found little temporal effect resulting from the season of prescribed fire on deer mice (*Peromyscus maniculatus*) and chipmunks (*Neotamias* spp.) in the southern Sierra Nevada, but little information exists on how spatial aspects of fire (e.g., fire severity) affect wildlife.

As part of a study to assess the influence of fire on California spotted owls (*Strix occidentalis occidentalis*) at a landscape scale, we sampled their mammalian prey at a series of burned sites with known fire histories in Yosemite National Park, California. Our goal in this paper is to identify the impact that fire

severity and related spatial and vegetative parameters have on small mammal populations and to develop habitat models to evaluate the effect of fire severity on small mammals. We hypothesized that fire severity would influence the abundances of small mammals via changes in vegetation composition, structure, and spatial complexity. We pursued our analyses on the four most commonly captured small mammals in our study area: deer mice, chipmunks, brush mice (*Peromyscus boylii*), and California ground squirrels (*Spermophilus beecheyi*).

METHODS

Study Area

Yosemite National Park encompasses over 302688 ha in the central Sierra Nevada, approximately 224 700 ha of which comprises contiguous lower and upper montane mixedconifer forests. These forests occur between 1000 m and 3450 m elevation on the western slope of the range and support a diverse faunal community (Graber 1996). White fir (Abies concolor), ponderosa pine (Pinus ponderosa), black oak (Quercus kelloggii), incense-cedar (Calocedrus decurrens), and sugar pine (P. lambertiana) dominate the lower montane The upper montane forests are forests. dominated by red fir (A. magnifica), white fir, sugar pine, and Jeffrey pine (*P. jeffreyi*). Forest stands in our study area were dominated by either P. jeffreyi (for higher elevation sites) or P. ponderosa, with a mix of white fir in the overstory and understory.

Prior to European settlement, these forests experienced low- to medium-severity fires every 2 yr to 20 yr (Skinner and Chang 1996). In 1970, the park developed a prescribed burning program to reduce fuels and lower the risk of stand-replacing fires while conserving the selection pressures that fire historically imposed on these ecosystems (van Wagtendonk

et al. 2002). All fires that have occurred in the park since 1930 have been dated, mapped, and digitized for use with geographic information system (GIS) software. Thode (2005) created a digital map depicting fire severity for fires >40 ha that burned since 1974.

Plot Selection

We restricted our efforts to areas that burned between 1989 and 2004, because this 15-year interval falls within the range of the historic fire return interval (2 yr to 20 yr) for these forest types (Skinner and Chang 1996). We limited our trapping effort to sites <6 km from a road or trailhead because of the logistical difficulties in carrying traps and other equipment long distances over rugged terrain. Because the objective was to obtain reliable indices of population sizes between burned areas, we emphasized increased spatial coverage at the expense of re-sampling.

We used the ArcMap 9.1 GIS to delineate all fires that burned in the mixed-conifer zone of Yosemite since 1989. We then generated 100 random points across that burned landscape and stratified the points according to logistical constraints of accessibility and crew safety. We selected the first 10 random points that occurred at sites with >40% overstory canopy cover based on the lower limit of spotted owl habitat requirements (Figure 1). Each of these points served as the origin of a spotted owl sampling area, within which we established trap lines to quantify small mammal assemblage structure and composition.

Habitat Variables

We used satellite imagery compiled by Thode (2005) and Miller and Thode (2007) to determine the effects of fire severity and spatial complexity on small mammal capture rates. These authors used Landsat Thematic Mapper

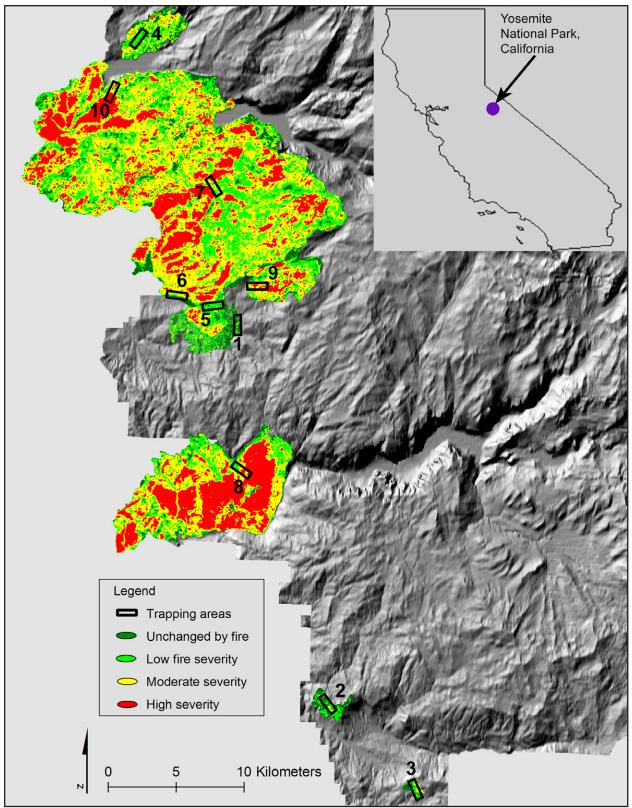


Figure 1. Locations of 10 burned small mammal live-trapping areas (2004-2005) in Yosemite National Park, California. Burned areas experienced either wildfire or prescribed fire between 1989 and 2004. Site numbers adjacent to each trapping area correspond to the site numbers in Figure 3 and Table 1.

(Landsat TM) imagery to map fires from 1984 through 2005 using the Normalized Burn Ratio (NBR). The NBR uses Landsat TM bands seven (mid-infrared) and four (near infrared), making it particularly sensitive to changes in the amount of live green vegetation, moisture content, and certain soil conditions that may occur after fire (Key 2006, Miller and Thode 2007). We used the Relative differenced NBR (RdNBR) to account for heterogeneity of prefire vegetation among fires mapped with TM imagery (Thode 2005, Miller and Thode 2007). RdNBR is a unitless index that is a derivative of NBR that corrects for the pre-fire vegetation and is relative to the vegetation for our particular study area (Miller and Thode 2007).

Thode (2005) determined numerical thresholds to distinguish between portions of a fire that burned at low, moderate, and high severities, as well as areas that were unchanged between pre-fire and post-fire satellite images. Unchanged areas usually reflected low intensity surface fires that burned beneath the overstory canopy and that did not burn or scorch the overstory canopy. She classified areas within the digitized fire history perimeters as unchanged if the severity was so low that she could not detect a change in the images that were one year post-fire, and she extended the perimeters to include areas that showed a change due to fire but were outside of the recorded perimeters. The RdNBR thresholds were: unchanged – less than 42; low – greater than or equal to 42 and less than 220; moderate - greater than or equal to 220 and less than 566; and high – greater than or equal to 566. The RdNBR value is influenced by the substrate, ash cover, and soil moisture at a site, which causes the value to vary after total canopy mortality in the high severity polygons (Kokaly et al. 2007). Therefore, there is no upper limit to the high severity category in our Thode (2005) used these threshold study. values to create each fire severity patch and assigned the levels with integers: 1, 2, 3, and 4, respectively.

We calculated a total fire severity index (FSI) for each trapping area by multiplying the integer RdNBR levels by the proportion of the area they encompassed and summing the products. Total fire severity index therefore was a continuous variable that ranged from 0, a completely unburned area, to 4, an area completely burned at high severity.

Spatial heterogeneity in the habitat is a consequence of fires as they burn across landscapes, resulting in patches of varied fire We examined several spatial severity. variables: patch squareness, total patch perimeter, and distance to fire edge. From the center point of each trapping area, we used GIS to determine the distance to the nearest To investigate how fire unburned edge. severity patch size diversity influences small mammal captures, we calculated total patch perimeter and patch squareness for each small mammal trapping area using FRAGSTATS (McGarigal et al. 2002) and GIS. Total patch perimeter is a measure of patch heterogeneity calculated by summing the perimeter of each fire severity patch contained within the boundaries of the trapping area. Because all of the small mammal trapping sites were equal in size, the site with the highest total patch perimeter indicates a site with more patches of differing fire severities, and therefore a site with higher burn heterogeneity. Patch squareness describes patch shape complexity and is an index that ranges from 0 (square, less edge, minimum complexity) to 1 (least squarelike, more edge, high complexity) (Frohn 1998). Unlike contagion and fractal dimension, total patch perimeter and patch squareness are optimized for use with data arranged in rasters, as with Landsat data (Frohn 1998).

We hypothesized that of the three fire severity levels (excluding the unchanged areas), the low severity patches would be the most valuable to small mammals, assuming lower fire severity in those patches would have resulted in a forest with higher structural heterogeneity and, therefore, more refugia with

adjacent clear areas for easy foraging (Shaffer and Laudenslayer 2006). Therefore, we calculated patch squareness for only the low severity patches within each of the burned trapping areas.

To match the scale of the fire severity GIS patches (30 m pixels), we measured the other habitat variables using remote sensing methods. To characterize post-fire vegetation, we estimated dominant overstory canopy cover, oak (*Quercus* spp.) tree cover, and shrub cover at the stand level for each trapping area using data classified from aerial photographs taken in 1997 and from the GIS. The majority of our small mammal trapping areas burned between 1989 and 1996, before the aerial photographs were taken for the park-wide vegetation mapping. In those few instances where the fires burned after the photographs were taken, we verified the vegetation map characteristics using USGS Digital Ortho Quarter Quadrangle (DOQQ) aerial photographs that were taken after the fire. If the characteristics varied between the digital vegetation map and the current DOQQ photographs, we reclassified the vegetation polygons within the mammal trappings using the same methods that the National Park Service (1997) used to create the digital vegetation map. The final digital vegetation map included polygons of dominant overstory and understory vegetation types, with a cover class assigned to each polygon (National Park Service 1997). We superimposed the mammal census areas onto the vegetation map and calculated the area of each vegetation type polygon contained within each trapping area. In our study area, overstory trees consist predominately of conifers, with black oak usually growing in the understory or in canopy gaps. We calculated overstory canopy cover for each mammal trapping area by multiplying the mid-point of each cover class polygon by the proportion of area defined by that polygon within the trapping area. We followed the

same procedure for calculating understory and oak tree cover; however, if a cover class was not provided by the map, we used a default cover of 7.5 %, assuming that the cover had to be \geq 5 % to 10 % for the photo interpreter to list it as part of the vegetation type for that polygon.

Small Mammal Sampling

We oriented 500 m × 1500 m small mammal trapping areas within spotted owl sampling areas (Figure 2). The total trapping area used in the spatial analyses was 64 ha, which included a 50 m buffer on all sides. In each trapping area, we censused terrestrial small mammals using four parallel trap lines established to maximize trap success (Pearson and Ruggiero 2003). We conducted censuses only once at each site and each census was five

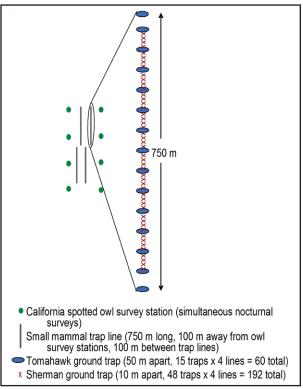


Figure 2. Small mammal trap line configurations within California spotted owl survey areas (from simultaneous study on effects of fire on spotted owls) in Yosemite National Park, California.

consecutive 24 h periods, checking traps in early morning and afternoon, from April through July in 2004 and 2005. Each trap line was 750 m long and was separated by 100 m from adjacent lines (Figure 2). Each trap line included 15 Tomahawk live traps (13 cm × 13 cm × 41 cm) at 50 m intervals, with four Sherman traps (8 cm \times 9 cm \times 23 cm) at 10 m intervals between consecutive Tomahawk traps starting with the second and ending with the fourteenth Tomahawk trap (n = 48 Sherman traps per line; Figure 2). We placed all traps on the ground, covered each with bark, and provided polyester batting for protection from inclement weather. Each trap line consisted of 63 traps, for a total of 252 traps per census area (Figure 2).

We identified all captured animals to species (chipmunks [Neotamias spp.] were identified to genus only) and marked them with uniquely numbered ear tags (National Band and Tag Co. Newport, Kentucky). We recorded gender, reproductive condition, and standard body measurements (weight, length of hind foot, ear, and tail), and released each individual at the point of capture. All procedures were approved by the University of California, Davis, Institutional Animal Care and Use Committee, and met guidelines recommended by the American Society of Mammalogists (Gannon et al. 2007).

Statistical Analyses

Because we estimated the landscape-level habitat variables at different scales, we applied non-metric multidimensional scaling (NMDS) to assess the orientation of the 10 burned sites in relation to each other in terms of the habitat variables. The NMDS uses the rank order of Sørenson distances (Sørenson 1948, Bray and Curtis 1957) to establish similarities between sites and the environmental variables measured at each site. The sites closest together in NMDS space share the most similarities in the

measured environmental variables. The axes of the NMDS ordination represent gradients that are a composite function of the variables. The dissimilarity between the distribution of data points in the original data space and the reduced ordination data space is quantified as "stress," which scales from 0 to 100; values <15 may be interpreted as "quite satisfactory" (McCune and Grace 2002). We selected the dimensionality of the NMDS ordination using scree plots, which depict how stress decreases with increasing dimensions. Pearson's coefficient of determination to quantify the proportion of variation (fit between the original data space and the distance in the ordination) represented by each To reduce skew, we composite axis. transformed the data using either arcsinesquare root (proportional data; canopy closure, oak cover, shrub cover, and patch squareness) or natural logarithm (distance variables; distance to fire edge, and total fire severity patch perimeter). We did not transform the fire severity index as it was already normally distributed. To regulate differences in scale, we adjusted all values to the standard deviation of the mean for each variable. We used PC-ORD (MiM software design, http://home. centurytel.net/~mjm/) to perform the NMDS according to guidelines outlined by McCune and Grace (2002).

Due to the infrequency of recaptures at a few of the trapping areas, we used capture rate (C) as an index for abundance. To standardize across all trapping areas, we calculated capture rates for each trapping area as the number of unique individuals per 1000 trap nights following the equation of Nelson and Clark (1973):

$$C = (I \times 1000) \div (T - S/2) \tag{1}$$

where I = number of individuals captured, T = number of traps, and S = number of traps

sprung. We chose to calculate capture rates using Nelson and Clark's (1973) formula in favor of alternative methods (e.g., CAPTURE), because this metric incorporates the number of traps sprung or rendered dysfunctional during a trapping session. An important source of capture variability in our study resulted from traps sprung from known (e.g., predators) and unknown reasons and traps that were dysfunctional for the entire trapping session due to extreme weather (e.g., trap mechanisms frozen).

To limit the number of zeros in the data matrix, we excluded rare species (i.e., <5 individuals captured or <3 sites of capture) from analyses (Legendre and Legendre 1983, Brazner and Beals 1997); this left four "common" species (deer mouse, brush mouse, chipmunks, and California ground squirrel) in our dataset. We assessed habitat associations of the four species based on comparisons among sets of linear regression models, in which we selected the regression covariates a priori (see Habitat Models, below). Because individual species are unique in their habitat requirements, we determined the best fit model for each species separately. We compared competing models using Akaike information criteria (Akaike 1973) corrected for low capture rates (AIC_c; Akaike 1973, Hurvich and Tsai 1989). The information theoretic (AIC) approach allows for quantifiable, simultaneous model comparison and provides insight into which habitat variables were important to each of the common species (Burnham and Anderson 2002).

Habitat Models

We considered only one- and two-variable regression models on abundance because of the low number of independent sites trapped for small mammals (n = 10) (Burnham and Anderson 2002). We used SAS 9.13 (SAS 2002-2003) to calculate the residual sum of

squares for each model and followed the guidelines detailed by Burnham and Anderson (2002) for AIC calculations.

We developed model sets a priori to reduce the risk of spurious model selections (Anderson et al. 2001). Because fire severity is a derivative measure of post-fire vegetation structure and composition (van Wagtendonk and Fites-Kaufman 2006), we did not include the total fire severity index with any of the vegetation variables in the same model. We used total canopy cover, shrub cover, and oak tree cover as indicators of the various food types (conifer seeds, shrub seeds and fruits, and acorns, respectively) consumed by the four encountered commonly small mammal species.

Variables representing spatial complexity (FSI, fire severity patch squareness [hereafter patch squareness], and fire severity total patch perimeter [hereafter patch perimeter]) are a function of how fire burned across the landscape, and we included them in the models for all four species. The fire severity of an area influences what post-fire forage is available for consumer groups, and we included FSI in some of the models for each species. included distance to the nearest edge of the burn as a single-variable model for each species, because it is known to influence deer mouse abundance (Schwilk and Keeley 1998), and we hypothesized it would be important to the other species as well. However, we expected distance to the nearest burned edge to be least important to California ground squirrels, which are the largest of the species and, therefore, presumed to be the most mobile with the largest home range (Kelt and Van Vuren 1999). Therefore, we only included distance in one model with California ground squirrels to confirm that it had little influence. Acorns are an important food source for deer mice (Jameson 1952, Monroe and Converse 2006), brush mice (Jameson 1952), chipmunks (Travis 1952, McShea 2000), and California ground squirrels (Schitoskey and Woodmansee 1978). Therefore, we included oak tree cover in the model set for all four species. Deer mice (Jameson 1952) and chipmunks (Travis 1952) both consume conifer seeds in the spring, especially in the absence of acorns. Summers and Proctor (2005) showed that pine seed fall in a dense plantation of Scots pine (Pinus sylvestris) was greater than that in three natural woodlands with sparser tree cover. absence of a direct measure of conifer seed availability at our sites, we used canopy cover as a surrogate for this metric. Brush mice consume the fruits of various shrubs (Jameson 1952), and California ground squirrels eat many grasses and herbaceous species in the absence of shrub cover (Schitoskey and Woodmansee 1978). We represented shrub production in a trapping area using shrub cover in the model set for these two species.

established Researchers have annual variation in capture rates for many small mammal species (Wolff 1996, Converse et al. 2006, Monroe and Converse 2006). However, we hypothesized that the various habitat variables would have a more direct effect, and we included year only as a single-variable model for each species. We also minimized annual variation in capture rates by timing the trapping in the spring, before the influx of juveniles into the local populations, and by only conducting analyses on adult individuals. To account for variability due to the trapping period within a year, we included trap week (week one through week five for each year) to represent the week during which the trapping occurred at a site.

The lowest AIC_c and the largest Akaike weight (w_i) determined the best model (Burnham and Anderson 2002). The Akaike weight represents the probability that a particular model provides the best explanation of the data of the tested set of models. The difference in the AIC_c of each alternative model with the lowest AIC_c (best model) is

referred to as ΔAIC_c , and can be used to evaluate the level of support for the alternative models. Models with $\Delta AIC_c \leq 2$ have "substantial" support, whereas models with $\Delta AIC_c > 10$ have essentially no support (Burnham and Anderson 2002). The evidence ratio is calculated as $w_1 \div w_2$, where w_1 and w_2 refer to Akaike weights for two models being compared; evidence ratios allow alternative models to be ranked relative to another candidate model. There is a substantial level of support for the model being compared if the evidence ratio is ≤ 2.7 (Burnham and Anderson 2002).

We used SigmaPlot v10.0 (Systat Software, San Jose, California) to display the linear regressions in a heuristic sense and graphically show the effect of these habitat variables on the abundance of each of the commonly captured species. We graphed the predictive response of the alternative model(s) when the evidence ratio showed enough support. For multivariate models (>1 habitat variable in the best model), we graphed the regressions on each habitat variable separately to improve the interpretability of the response.

RESULTS

The NMDS ordination for the habitat variables at the 10 burn sites (Figure 3) was best represented in two dimensions (stress = 4.0); the proportion of variation represented by axes 1 and 2 was 0.78 and 0.18, respectively. The lack of apparent clumping of trapping sites along either axis indicates that they differed in most of the habitat variables recorded. These axes represent composites of the habitat variables that were influential in explaining the variability in the data, and each axis represents a gradient in these variables. Trapping sites in the bottom left corner of the ordination had higher fire severity, greater distances from unburned edge, less patch complexity (i.e., more patch squareness and

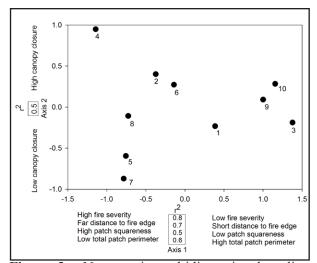


Figure 3. Non-metric multidimensional scaling ordination for the seven habitat variables that were estimated using remote sensing techniques for 10 burned small mammal trapping sites in Yosemite National Park, California. The variables with a coefficient of determination >0.5 are listed on each axis. The point labels correspond to the site numbers in Figure 1 and Table 1.

low patch perimeter), and low canopy closure (Figure 3). The FSI varied from 1.41, at a site encompassing mostly areas unchanged by fire with low severity patches scattered throughout, to 3.46, at a site that incorporated all fire severity levels and had large patches of moderate and high severity (Table 1). We used the FSI as a continuous variable for all parameter and model estimations.

In spring (April to July) 2004 and 2005, we live-trapped at 10 burned sites for a total of 15 299 trap nights. We captured a total of 614 unique individuals, with 245 deer mice, 30 brush mice, 152 chipmunks, and 27 California ground squirrels representing the four most common species (Table 2). The rest of the small mammal assemblage we captured included one or two individuals of the following species: California pocket mouse (Chaetodipus californicus), northern flying squirrel (Glaucomys sabrinus), long-tailed vole (Microtus longicaudus), mountain vole

Table 1. Vegetation and fire severity patch characteristics at 10 small mammal trapping areas in Yosemite National Park, California.

Site number	Canopy cover (%) ^a	Shrub cover (%) ^a	Oak tree cover (%) ^a	Fire severity index ^b	Total severity patch perimeter (m) ^c	Severity patch squareness index ^d	Distance to nearest unburned edge (m)
1	80	26	0.3	1.41	30 660	0.84	228.5
2	65	6	9.3	1.68	26 220	0.81	173.3
3	57	0	1.8	1.76	29 580	0.81	228.3
4	79	3	1.8	2.07	21 360	0.72	876.0
5	79	2	0.0	2.10	18 240	0.67	917.4
6	52	0	4.1	2.20	20 820	0.77	302.6
7	76	2	0.0	2.73	22 260	0.75	4436.2
8	47	7	3.7	2.97	15 600	0.48	729.5
9	50	6	0.0	3.13	23 400	0.76	683.6
10	36	7	3.6	3.46	16 380	0.61	571.2

^a Vegetation characteristics ocularly estimated using aerial photographs and stereoscope; canopy cover refers to total cover of all tree species.

^b Fire severity index = amount of area within the boundary of a fire × that area's estimated fire severity code (Miller and Thode 2007), where each polygon was assigned one of the following: 1 = unchanged, 2 = low severity, 3 = moderate severity, and 4 = high severity.

^c Total severity patch perimeter = sum of the perimeter of all of the fire severity polygons within the trapping area.

d Patch squareness is an index representing how square the patches are for a trapping area, 0 = square, 1 = least square-like.

Table 2. The mean capture rate for the 4 most common species (>5 individuals captured at each area) for all 10 burned areas trapped each week April - July 2004 and 2005 in Yosemite National Park, California.

	Mean capture rate ^a						
	Low fire severity ^b		Moderate fire severity ^b		High fire severity ^b		
Species	Mean	SE	Mean	SE	Mean	SE	
Deer mouse	40.0	15.5	25.3	6.5	15.5	7.4	
Brush mouse	5.6	5.1	0.3	0.3	4.6	4.1	
Chipmunk species	14.3	7.3	10.8	4.6	4.7	4.4	
California ground squirrel	5.8	7.6	4.3	0.7	0.0	0.0	

^a Capture rate calculated as $CR = I \times 1000/(T - S/2)$ (Nelson and Clark 1973) where I = number individuals captured, T = number of traps multiplied by number of nights traps were open, and S = number of traps sprung by all causes (or frozen open due to extreme weather).

(M. montanus), large-eared woodrat (Neotoma macrotus), western gray squirrel (Sciurus griseus), golden-mantled ground squirrel (S. lateralis), and Douglas squirrel (Tamiasciurus To summarize the mammal douglasii). trapping data across the fire severity levels for the four most common species, we categorized mammal trapping sites as low, moderate, or high severity sites based on the FSI calculated for each site (Table 2). As all of these sites were burned to some extent in this study, there were no unchanged trapping areas. With the sites categorized into these fire severity levels, the mean capture rates of chipmunks, deer mice, and California ground squirrels all decreased as fire severity at a site increased. and we captured no California ground squirrels in any of the high severity areas.

The model that best represented deer mouse abundance was the fire severity model (abundance = $63.24 - 15.8 \times FSI + \varepsilon_i$, where ε_i is the error term; $\Delta AIC_c = 0$, $w_i = 0.25$) (Table 3). The evidence ratio between the two models tied for second best compared to the best model was 1.68, suggesting that these were suitable alternative models for predicting deer mice response to fire. These alternatives included the oak tree model (abundance = $34.3 - 3.3 \times oak$ tree cover $+ \varepsilon_i$; $\Delta AIC_c = 1.04$, $w_i = 0.15$) and the patch perimeter model (abundance = $-15.6 + 0.02 \times patch perimeter + \varepsilon_i$; $\Delta AIC_c = 1.04$, $w_i = 0.15$).

Brush mouse abundance was best supported using the oak cover model (abundance = $-0.71 + 1.57 \times$ oak tree cover + ε_i ; $\Delta AIC_c = 0$, $w_i = 0.73$) (Table 4). No other model was supported (minimum $\Delta AIC_c = 3.89$, $w_i = 0.10$).

The oak cover and patch perimeter combined model (abundance = -4.9 - 2.3 × oak tree cover + 0.001 × patch perimeter + ε_i) showed the greatest support for chipmunk abundance ($\Delta AIC_c = 0$, $w_i = 0.42$) (Table 5). There was substantial support for the alternative model using just oak cover to predict chipmunk abundance (abundance = -15.9 - 2.4 × oak tree cover; $\Delta AIC_c = 0.99$, $w_i = 0.26$).

The patch perimeter model (abundance = $-23.4 + 0.001 \times \text{patch perimeter} + \varepsilon_i$) showed the best support for the abundance of California ground squirrels ($\Delta \text{AIC}_c = 0$, $w_i = 0.61$) (Table 6). No other model was informative (minimum $\Delta \text{AIC}_c = 4.37$, $w_i = 0.07$).

Heuristic application of linear regression demonstrated that deer mouse abundance declined with fire severity (Figure 4a) and oak tree cover (Figure 4b), but increased with patch perimeter (Figure 4c). Brush mouse abundance increased with oak tree cover (Figure 5). In contrast, chipmunk abundance decreased with increasing oak tree cover (Figure 6a) and increased with increasing sum of all of the perimeters of the fire severity patches in the

b Mean capture rates were calculated for fire severity levels by grouping each site according to its total fire severity index; 1-1.9 = low severity, 2-2.9 = moderate severity, and 3-4 = high severity.

Table 3. Summary of model statistics^a from regression analysis of fire severity effects^b on deer mouse (*Peromyscus maniculatus*) abundance in Yosemite National Park, California, 2004 and 2005 (n = 10). Models are listed from best to poorest fit.

Model description	K	AIC	ΔAIC_{c}	W_{i}
Abundance {fire severity}	3	62.96	0.00	0.25
Abundance {oak cover}	3	64.00	1.04	0.15
Abundance {patch perimeter}	3	64.01	1.04	0.15
Abundance {canopy cover}	3	65.09	2.13	0.08
Abundance {shrub cover}	3	65.71	2.74	0.06
Abundance {oak cover + patch perimeter}	4	65.80	2.84	0.06
Abundance {patch squareness}	3	66.15	3.19	0.03
Abundance {edge distance}	3	66.94	3.97	0.03
Abundance{trap week}	3	67.06	4.01	0.03
Abundance {trap year}	3	67.10	4.14	0.03
Abundance {edge distance + oak cover}	4	67.71	4.75	0.02
Abundance{fire severity + patch perimeter}	4	68.68	5.71	0.01
Abundance{oak cover + patch squareness}	4	68.74	5.78	0.01
Abundance{fire severity + patch squareness}	4	68.76	5.79	0.01
Abundance {edge distance + fire severity}	4	68.96	5.99	0.01
Abundance {canopy cover + patch perimeter}	4	69.14	6.17	0.01
Abundance{canopy cover + edge distance}	4	69.88	6.92	0.01
Abundance {edge distance + patch perimeter}	4	69.94	6.98	0.01
Abundance {canopy cover + patch squareness}	4	70.89	7.92	0.00
Abundance {edge distance + patch squareness}	4	71.94	8.97	0.00

a Statistics include: number of parameters (K) in the model, Akaike's Information Criterion corrected for small sample size (AIC_c), relative AIC_c (ΔAIC_c), and Akaike weights (w_i).
 b Model effects were measured on individual trapping area level and include: total fire severity index (fire severity),

trapping area (Figure 6b). California ground squirrel abundance increased as the sum of the perimeters of all of the fire severity polygons contained within the trapping area increased (Figure 7).

DISCUSSION

Fire plays a vital role in shaping the forests of the Sierra Nevada, influencing structure, composition, and spatial characteristics such as patch size and shape, connectivity, and juxtaposition (Cooperrider *et al.* 2000, Shaffer and Laudenslayer 2006). Due to these dynamic

influences of fire, the forests of Yosemite are a matrix of variable burn severities, including unburned patches within burns. Our NMDS ordination of trapping sites showed little clustering along the first two composite gradient axes, indicating that the sites were dissimilar in habitat structure (Figure 3). The trapping sites with the lowest fire severity index (FSI) had higher overstory canopy closure and higher spatial complexity, with less patch squareness and higher total patch perimeters (Figure 3). Overall, the FSI was low to moderate for the trapping areas, with no sites being completely burned at high severity

^b Model effects were measured on individual trapping area level and include: total fire severity index (fire severity), sum of the perimeter of all fire severity patches (patch perimeter), patch squareness of fire severity patches (squareness), distance to nearest unburned edge (edge distance), total overstory canopy cover (canopy cover), shrub cover, and oak cover (oak tree cover).

Table 4. Summary of model statistics from regression analysis of fire severity effects on brush mouse (*Peromyscus boylii*) abundance in Yosemite National Park, California, 2004 and 2005 (n = 10). Models are listed from best to poorest fit.

Model description	K	AIC _c	ΔAIC_{c}	W_{i}
Abundance {oak cover}	3	35.25	0.00	0.73
Abundance {oak cover + patch squareness}	4	39.13	3.89	0.10
Abundance {oak cover + edge distance}	4	41.07	5.83	0.04
Abundance {oak cover + patch perimeter}	4	41.09	5.85	0.04
Abundance{trap week}	3	41.28	6.04	0.04
Abundance {patch squareness}	3	43.48	8.24	0.01
Abundance {edge distance}	3	43.93	8.68	0.01
Abundance {patch perimeter}	3	44.32	9.08	0.01
Abundance {fire severity}	3	44.39	9.15	0.01
Abundance{shrub cover}	3	44.41	9.16	0.01
Abundance{trap year}	3	44.44	9.19	0.01
Abundance{fire severity + patch squareness}	4	47.75	12.50	0.00
Abundance {edge distance + patch squareness }	4	48.83	13.58	0.00
Abundance{shrub cover + patch squareness}	4	49.33	14.08	0.00
Abundance {edge distance + patch perimeter}	4	49.69	14.44	0.00
Abundance{fire severity + patch perimeter}	4	49.79	14.54	0.00
Abundance{shrub cover + edge distance}	4	49.93	14.68	0.00
Abundance {edge distance + fire severity}	4	49.93	14.68	0.00
Abundance {shrub cover + patch perimeter}	4	50.19	14.94	0.00

^aStatistics include: number of parameters (K) in the model, Akaike's Information Criterion corrected for small sample

and every site having >1 low severity patch (Table 1); thus, these heterogeneous sites represent the result of fires burning within the historic fire regimes in this region (Skinner and Chang 1996).

Fire severity was the most important habitat characteristic influencing deer mouse abundance (Table 3); additionally, fire severity is the principal force affecting the other variables we measured. Deer mice are habitat generalists and appear to distribute themselves according to the pattern imprinted on the landscape by fire severity. Although other studies have demonstrated positive effects of fire on deer mouse population size (Kaufman

et al. 1990, Jones 1992, Fisher and Wilkinson 2005, Converse et al. 2006), we documented substantial variation in the response of deer mice to burns, and deer mouse abundance decreased with increasing fire severity (Figure 4a). We trapped in the spring when deer mice rely heavily on conifer seeds (Jameson 1952). Conifer mortality increases with fire severity (Schwilk et al. 2006); therefore, lower fire severity could result in higher quality foraging habitat for deer mice via increased tree survival and subsequent elevated seed availability throughout the year.

The ΔAIC_c (Table 3) shows that oak cover and the sum of the perimeter of all fire severity

size (AIC), relative AIC (Δ AIC), and Akaike weights (w_i).

^b Model effects were measured on individual trapping area level and include: total fire severity index (fire severity), sum of the perimeter of all fire severity patches (patch perimeter), patch squareness of fire severity patches (squareness), distance to nearest unburned edge (edge distance), total overstory canopy cover (canopy cover), shrub cover, and oak cover (oak tree cover).

Table 5. Summary of model statistics^a from regression analysis of fire severity effects^b on chipmunks (*Neotamias* spp.) abundance in Yosemite National Park, California, 2004 and 2005 (n = 10). Models are listed from best to poorest fit.

Model description	K	AIC	ΔAIC_c	w_{i}
Abundance {oak cover + patch perimeter}	4	45.84	0.00	0.42
Abundance {oak cover}	3	46.83	0.99	0.26
Abundance {oak cover + patch squareness}	4	47.98	2.14	0.14
Abundance {canopy cover}	3	50.87	5.03	0.03
Abundance {patch perimeter}	3	51.00	5.16	0.03
Abundance {patch squareness}	3	51.86	6.02	0.02
Abundance {edge distance + oak cover}	4	51.98	6.14	0.02
Abundance{fire severity}	3	52.23	6.39	0.02
Abundance {shrub cover}	3	53.10	7.26	0.01
Abundance {trap week}	3	53.58	7.74	0.01
Abundance {edge distance}	3	54.08	8.24	0.01
Abundance {trap year}	3	54.16	8.33	0.01
Abundance {canopy cover + patch perimeter}	4	55.14	9.31	0.00
Abundance {canopy cover + patch squareness}	4	56.05	10.21	0.00
Abundance {edge distance + patch perimeter}	4	56.51	10.67	0.00
Abundance {shrub cover + patch perimeter}	4	56.78	10.94	0.00
Abundance {canopy cover + edge distance}	4	56.80	10.96	0.00
Abundance {fire severity + patch perimeter}	4	56.96	11.12	0.00
Abundance{shrub cover + patch squareness}	4	57.09	11.25	0.00
Abundance {edge distance + fire severity}	4	57.56	11.72	0.00
Abundance{fire severity + patch squareness }	4	57.56	11.72	0.00
Abundance {edge distance + patch squareness}	4	57.67	11.83	0.00
Abundance {shrub cover + edge distance}	4	58.72	12.88	0.00

Statistics include: number of parameters (K) in the model, Akaike's Information Criterion corrected for small sample size (AIC), relative AIC (ΔAIC), and Akaike weights (w).
 Model effects were measured on individual trapping area level and include: total fire severity index (fire sever-

patches (patch perimeters) substantially poorer models for explaining deer mouse abundance. We believe this can be attributed to variability in deer mouse capture data across the trapping areas and the close correlation among these three variables. The alternate models showed deer mouse abundance decreasing with increasing oak tree cover or deer mouse abundance increasing with patch perimeter. This contrasts with our a priori hypotheses that oak tree cover would have a positive influence on deer mice due to the increased availability of acorns, as documented in the eastern USA (Wolff 1996). However, acorn production in Sierra Nevada forests is highly variable (van Mantgem *et al.* 2006), such that either or both years of our study could have been poor acorn years (thereby diluting the influence of this parameter). High oak tree cover may co-opt space from conifer trees and, at our study sites, overstory canopy cover, which is associated

b Model effects were measured on individual trapping area level and include: total fire severity index (fire severity), sum of the perimeter of all fire severity patches (patch perimeter), patch squareness of fire severity patches (squareness), distance to nearest unburned edge (edge distance), total overstory canopy cover (canopy cover), shrub cover, and oak cover (oak tree cover).

Table 6. Summary of model statistics from regression analysis of fire severity effects on California ground squirrel (*Spermophilus beecheyi*) abundance in Yosemite National Park, California, 2004 and 2005 (n = 10). Models are listed from best to poorest fit.

Model description	K	AIC	ΔAIC_{c}	W_{i}
Abundance {patch perimeter}	3	44.69	0.00	0.61
Abundance{fire severity}	3	49.07	4.37	0.07
Abundance {oak cover + patch perimeter}	4	49.48	4.78	0.06
Abundance {patch squareness}	3	49.83	5.13	0.05
Abundance {canopy cover + patch perimeter}	4	50.15	5.45	0.04
Abundance{shrub cover + patch perimeter}	4	50.52	5.83	0.03
Abundance{fire severity + patch perimeter}	4	50.69	6.00	0.03
Abundance{trap week}	3	50.98	6.29	0.03
Abundance {oak cover}	3	51.75	7.06	0.02
Abundance{shrub cover}	3	52.03	7.33	0.02
Abundance {edge distance}	3	52.15	7.46	0.02
Abundance{canopy cover}	3	52.23	7.53	0.01
Abundance {trap year}	3	52.28	7.59	0.01
Abundance{fire severity + patch squareness}	4	54.70	10.01	0.00
Abundance{oak cover + patch squareness}	4	55.03	10.33	0.00
Abundance{shrub cover + patch squareness}	4	55.63	10.94	0.00
Abundance{canopy cover + patch squareness}	4	55.75	11.05	0.00

^a Statistics include: number of parameters (K) in the model, Akaike's Information Criterion corrected for small sample size (AIC), relative AIC (ΛAIC), and Akaike weights (w).

predominantly with the conifers, was lowest at sites with the higher oak tree cover (Table 1). Because we trapped in spring, however, acorns generally would not be available due to a high number of large animals preferentially ingesting acorns during the previous fall (e.g., bears; Graber and White 1983) and deer mice would be consuming a higher proportion of conifer seeds (Jameson 1952).

The positive influence of patch perimeter on deer mouse abundance suggests that increased habitat complexity provides more diversity in vegetation structure and composition. As the sum of the perimeters of all of the patches caused by various fire severities increases, the number of patches increases, reflecting an increase in habitat heterogeneity and, therefore, an increase in

diversity of available forage for generalists such as deer mice. While increased forage diversity does not imply increased forage abundance, areas with higher diversity may provide more stable food availability throughout the year when preferred items are limited.

Total patch perimeter is inherently linked to fire severity because it was variation in fire severity that created the patches, and as fire severity increases to moderate and high severity levels, the patches tend to be larger. Within a fixed area, such as a trapping site, larger patch size is correlated with fewer total patches, such that the sum of patch perimeter and the habitat heterogeneity both are constrained to be lower. The fire severity index alone is a good indicator of deer mouse

size (AIC), relative AIC (AAIC), and Akaike weights (w).

b Model effects were measured on individual trapping area level and include: total fire severity index (fire severity), sum of the perimeter of all fire severity patches (patch perimeter), patch squareness of fire severity patches (squareness), distance to nearest unburned edge (edge distance), total overstory canopy cover (canopy cover), shrub cover, and oak cover (oak tree cover).

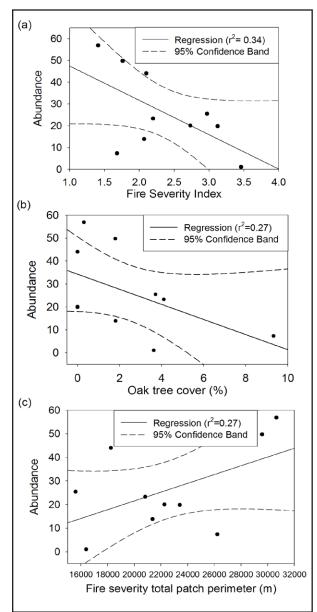


Figure 4. Linear regressions and corresponding coefficient of determination for the variables in the three best models (according to AIC_c values) for describing deer mouse abundance given the habitat characteristics at 10 burned sites in Yosemite National Park, California (2004-2005). The best model is: Y_{deer mouse abundance} = 63.24 – 15.77 × (fire severity index). (a) deer mouse abundance regressed on fire severity index, best model chosen by AIC; (b) deer mouse abundance regressed on oak tree cover (%), tied for the second best model chosen by AIC; (c) deer mouse abundance regressed on patch perimeter, tied for the second best model chosen by AIC.

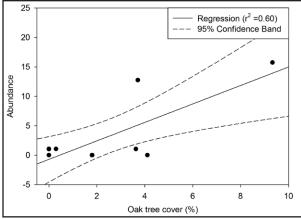


Figure 5. Linear regression and corresponding coefficient of determination for the best model (according to AIC values) for describing brush mouse abundance given the habitat characteristics at 10 burned sites in Yosemite National Park, California (2004-2005). Model: $Y_{brush\ mouse\ abundance} = -0.71 + 1.57 \times (oak\ tree\ cover)$.

abundance when considering an area of fixed size, but the sum of all of the fire severity patch perimeters may be more important when attempting to extrapolate to a landscape scale or across multiple fires.

Jameson (1952) found brush mouse abundance to be tightly related to shrub cover. However, our best model for brush mice involved only oak tree cover, and the evidence ratio when compared with the second best model was 6.99, indicating substantially less evidence to support any subordinate models. While acorns are important in brush mouse diets (Jameson 1952), we have no information on local mast crops for the trapping period (2004 to 2005). Trapping sites with higher oak tree cover tended to have more open overstory canopy (Table 1), allowing for more shrub and herbaceous plant growth in the understory. Our method of estimating shrub cover using remote sensing data may have been inadequate due to the difficulty of observing shrubs through the canopy. Therefore, the oak tree cover may be acting as a surrogate for shrub cover by representing an area that is more open in the canopy, allowing shrub growth.

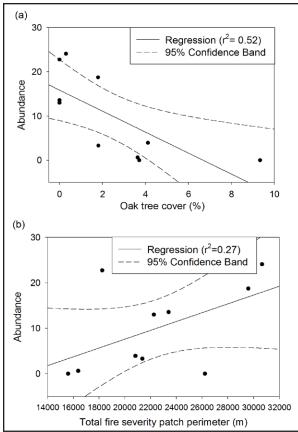


Figure 6. Linear regressions and corresponding coefficient of determination for the two variables in the best model (according to AIC_c values) for describing chipmunk abundance given the habitat characteristics at 10 burned sites in Yosemite National Park, California (2004-2005). Model: $Y_{\text{chipmunk abundance}} = -4.84 - 2.30 \times \text{(oak tree cover)} + 0.001 \times \text{(total fire severity patch perimeter).}$ (a) Chipmunk abundance regressed on oak tree cover. (b) Chipmunk abundance regressed on total fire severity patch perimeter.

The best model for chipmunk abundance included a combination of oak tree cover and the sum of the perimeters of the fire severity patches (patch perimeter) (Table 5). To visualize the influence of these variables individually we applied heuristic linear regressions separately for each variable and chipmunk abundance (Figure 6). As shown by the model coefficients (Figure 6), oak tree cover was approximately two times more important than patch perimeter in influencing chipmunk abundance. Oak tree cover (%) was

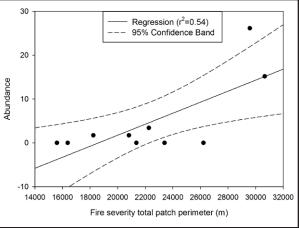


Figure 7. Linear regression and corresponding coefficient of determination for the best model (according to AIC_c values) for describing California ground squirrel abundance given the habitat characteristics at 10 burned sites in Yosemite National Park, California (2004-2005). Model: $Y_{CA \text{ ground squirrel abundance}} = -23.40 + 0.001 \times \text{(total fire severity patch perimeter)}$.

associated negatively with chipmunk abundance (Figure 6a), presumably because chipmunks rely heavily on conifer seeds in the spring (Travis 1952, Vander Wall 1993). The inclusion of patch perimeter is not only related to increased habitat heterogeneity, but possibly to truffle, hypogeous, and epigeous fungi abundance. Chipmunks in the Sierra Nevada also consume various species of fungi (Meyer et al. 2005), especially in wet spring conditions, which are correlated with high fungi abundance (Travis 1953). Wet spring conditions characterized our sites in both years of trapping. Truffle biomass was significantly lower in oak woodlands when compared to pine, fir, and mixed-conifer forests in the southern Sierra Nevada (North 2002). Therefore, as oak cover increased, truffle abundance likely decreased. Chipmunk abundance increased with patch perimeter (Figure 6b) indicating the importance of greater habitat heterogeneity to chipmunks. Habitat heterogeneity leads to more diverse options with various foraging shrubs interspersed with forested areas for chipmunks

who also consume a large amount of fruits from various shrub species (Travis 1953).

California ground squirrels were the largest and most mobile mammal species we studied. The best model for describing California ground squirrel abundance included patch perimeter (Table 6). The evidence ratio >8 indicated that the best model is by far the most reasonable model. The diet of California ground squirrels in the central Sierra Nevada is dominated by herbaceous leaves and seeds (Schitoskey and Woodmansee 1978). Habitat heterogeneity is extremely important to these mobile species. Higher herbaceous plant abundance in open areas provides greater opportunities, foraging and adjacent interspersed areas of thick undergrowth or coarse woody debris provide refuge from predators.

Fire severity may play a different role for each species. Aside from structural diversity, habitat heterogeneity can promote higher plant diversity and offer greater food availability throughout the year, thereby reducing the effect of competition for food. A matrix of diverse fire severity patches and burn history including a few high severity patches produces a heterogeneous landscape.

Restoring the process of fire to fire-adapted systems is an important management and policy issue for many public lands across the Understanding how fire United States. behavior affects the inhabitants of ecosystem is imperative for establishing sustainable management plans. Small mammals are critical components to many ecosystems because they disperse seeds and fungal spores and are important prey for other species. Managers need to know how to plan for the conservation of these faunal assemblages. We suggest that managers can influence habitat complexity and quality by creating a mosaic of fire severity. Wagtendonk and Lutz (2007) showed that prescribed fires burn at lower severities and smaller spatial extent than contemporary

wildfires in Yosemite. We propose that more aggressive and widespread use of prescribed fire can reduce the probability of catastrophic, stand replacing fires in fire-adapted systems while improving and maintaining habitat complexity and quality.

CONCLUSIONS

There are many components to fire regimes beyond a simple delineation of a fire perimeter. Fire severity determines not only direct mortality rates to the resident flora and fauna, but also structures the habitat in which they live. Variability in fire severity increases postfire spatial heterogeneity, both structurally and compositionally. Our study showed that small mammal abundance was directly related to fire severity and variables affected by severity such as vegetation canopy cover, distance to unburned edge, and patch size and shape. Each small mammal species responded to different variables that influenced abundance. Deer mice decreased with increasing fire severity, although at a landscape scale, the sum of the patch perimeters formed by the variability in fire severity may be more important. The sum of the perimeter of all of the patches formed by varying fire severities was important to deer mice, chipmunks, and California ground squirrels, with the abundance of all three species increasing with total patch perimeter. Brush mice responded positively to increasing oak tree cover. Fire management strategies need to incorporate fire behavior and to predict how severely specific areas will Information on how small mammal burn. species respond to fire regime attributes can be important in the conservation and persistence of that species or other taxa that rely on it (e. g., predators). As catastrophic wildfire is one of the largest threats to the persistence of the California spotted owl, understanding how fire mediates the distribution and abundance of species is imperative prey conservation.

ACKNOWLEDGEMENTS

We thank M. Meyer for his invaluable advice and field support, E. Berlow and University of California, Merced, for housing and office support, and Yosemite National Park for funding the project. S. Thompson was critical for obtaining the funding and providing logistical support. J. Miller and A. Thode graciously provided satellite imagery with fire severity classifications. We are forever grateful to R. Anthony for loaning us the Tomahawk traps. The project would not have been possible without the incredibly dedicated efforts of the field crews: S. Evans, S. Eyes, A. Farris, J. Felis, D. Giordano, C. Grattan, Z. Hambleton, N. Hatch, L. Illingworth, M. Kaufman, E. Kolden, J. Lane, R. Lechalk, M. Masten, M. McDonald, C. Morcos, G. Palmer, K. Schlimme, P. Segre, and E. Williams. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

LITERATURE CITED

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 in: B.N. Petrov, and F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.
- Anderson, D.R., K.P. Burnham, and W.L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64: 912-923.
- Anderson, D.R., K.P. Burnham, W.R. Gould, and S. Cherry. 2001. Concerns about finding effects that are actually spurious. Wildlife Society Bulletin 29: 311-316.
- Bray, J.R., and J.T. Curtis. 1957. An ordination of the upland forest communities in southern Wisconsin. Ecological Monographs 27: 325-349.
- Brazner, J.C., and E.W. Beals. 1997. Patterns in fish assemblages from coastal wetland and beach habitats in Green Bay, Lake Michigan: a multivariate analysis of abiotic and biotic forcing factors. Canadian Journal of Aquatic Science 54: 1743-1761.
- Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information—theoretic approach. Second edition. Springer Science+Business Media, New York, New York, USA.
- Carey, A.B., and M.L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. Ecological Applications 5: 336-352.
- Chang, C. 1996. Ecosystem responses to fire and variations in fire regime. Pages 1071-1099 in: D.C. Erman, editor. Sierra Nevada Ecosystem Project: Final report to Congress, Volume 2. University of California, Davis, Wildland Resources Center Report 37.
- Converse, S.J., G.C. White, and W.M. Block. 2006. Small mammal responses to thinning and wildfire in ponderosa pine-dominated forests of the southwestern United States. Journal of Wildlife Management 70: 1711-1722.
- Cooperrider, A., R.F. Noss, H.H. Welsh, Jr., C. Carroll, W. Zielinski, D. Olson, S.K. Nelson, and B.G. Marcot. 2000. Terrestrial fauna of redwood forests. Pages 119-164 in: R.F. Noss, editor. The redwood forest: history, ecology, and conservation of the coast redwoods. Save the Redwood League and Island Press, Washington, D.C., USA.
- Fisher, J.T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Review 35: 51-81.
- Forsman, E.D., E.C. Meslow, and H.M. Wright. 1984. Distribution and biology of the spotted owl in Oregon. Wildlife Monographs 87: 1-64.

- Frohn, R.C. 1998. Remote sensing for landscape ecology: new metric indicators for monitoring, modeling and assessment of ecosystems. CRC Press, Boca Raton, Florida, USA.
- Gannon, W.L., R.S. Sikes, and The Animal Care and Use Committee. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88: 809-823.
- Graber, D.M., and M. White. 1983. Black bear food habits in Yosemite National Park. International conference on bear research and management 5: 1-10.
- Graber, D.M. 1996. Status of terrestrial vertebrates. Pages 709-734 in: D.C. Erman, editor. Sierra Nevada Ecosystem Project: Final report to Congress, Volume 2. University of California, Davis, Wildland Resources Center Report 37.
- Hurvich, C.M., and C.L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76: 297-307.
- Jameson, E.W., Jr. 1952. Food of deer mice, *Peromyscus maniculatus* and *P. boylii*, in the northern Sierra Nevada, California. Journal of Mammalogy 33: 50-60.
- Jones, C.A. 1992. Review of the effects of fire on *Peromyscus* and *Podomys*. Florida Scientist 55: 75-84.
- Kaufman, D.W., E.J. Finck, and G.A. Kaufman. 1990. Small mammals and grassland fires. Pages 46-80 in: S.L. Collins, and L.L. Wallace, editors. Fire in the north American tallgrass prairies. University of Oklahoma Press, Norman, USA.
- Kelt, D.A., and D. Van Vuren. 1999. Energetic constraints and the relationship between body size and home range area in mammals. Ecology 80: 337-340.
- Key, C.H. 2006. Ecological and sampling constraints on defining landscape fire severity. Fire Ecology 2(2): 34-59. doi: 10.4996/fireecology.0202034
- Kokaly, R.F., B.W. Rockwell, S.L. Hiare, and T.V.V. King. 2007. Characterization of post-fire surface cover, soils, and burn severity at the Cerro Grande Fire, New Mexico, using hyperspectral and mulitspectral remote sensing. Remote Sensing of the Environment 106: 305-325.
- Legendre, L., and P. Legendre. 1983. Numerical ecology. Elsevier, Amsterdam, Netherlands.
- Manning, J.A., and W.D. Edge. 2004. Small mammal survival and downed wood at multiple scales in managed forests. Journal of Mammalogy 85: 87-96.
- Maser, C., and Z. Maser. 1988. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. Great Basin Naturalist 48: 358-369.
- McCune, B., and J.B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, USA.
- McGarigal, K., S.A. Cushman, M.C. Neel, and E. Ene. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst. http://www.umass.edu/landeco/research/fragstats/fragstats.html. Accessed 6 July 2007.
- McShea, W.J. 2000. The influence of acorn crops on annual variation in rodent and bird populations. Ecology 81: 228-238.
- Meyer, M.D., M.P. North, and D.A. Kelt. 2005. Fungi in the diets of northern flying squirrels and lodgepole chipmunks in the Sierra Nevada. Canadian Journal of Zoology 83: 1581-1589.
- Miller, J.D., and A.E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta normalized burn ratio (dNBR). Remote Sensing of Environment 109: 66-80.

- Minnich, R.A., M.G. Barbour, J.H. Burk, and J. Sosa-Ramirez. 2000. Californian mixed-conifer forests under unmanaged fire regimes in the Sierra San Pedro Martir, Baja California, Mexico. Journal of Biogeography 27: 105-129.
- Monroe, M.E., and S.J. Converse. 2006. The effects of early season and late season prescribed fires on small mammals in a Sierra Nevada mixed conifer forest. Forest Ecology and Management 236: 229-240.
- National Park Service. 1997. Vegetation map of Yosemite National Park and vicinity, [computer optical disk]. El Portal, CA: National Park Service, 1997.
- Nelson, L., Jr., and F.W. Clark. 1973. Correction for sprung traps in catch/effort calculations of trapping results. Journal of Mammalogy 54: 295-298.
- North, M.P. 2002. Seasonality and abundance of truffles from oak woodlands to red fir forests. USDA Forest Service General Technical Report PSW-GTR-183.
- Pearson, D.E., and L.F. Ruggiero. 2003. Transect versus grid trapping arrangements for sampling small-mammal communities. Wildlife Bulletin 31: 454-459.
- Pyare, S., and W. Longland. 2001. Patterns of ectomycorrhizal fungi consumption by small mammals in remnant old growth forests of the Sierra Nevada. Journal of Mammalogy 82: 681-689.
- Schitoskey, F., Jr., and S.R. Woodmansee. 1978. Energy requirements and the diet of the California ground squirrel. Journal of Wildlife Management 42: 373-382.
- Schwilk, D.W., E.E. Knapp, S.M. Ferrenberg, J.E. Keeley, and A.C. Caprio. 2006. Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. Forest Ecology and Management 232: 36-45.
- Schwilk, D.W., and J.E. Keeley. 1998. Rodent populations after a large wildfire in California chaparral and coastal sage scrub. Southwestern Naturalist 43: 480-483.
- Shaffer, K.E., and W.F. Laudenslayer, Jr. 2006. Fire and animal interactions. Pages 118-144 in: N.G. Sugihara, J.W. van Wagtendonk, K.E. Shaffer, J. Fites-Kaufman, and A.E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, California, USA.
- Skinner, C.N., and C. Chang. 1996. Fire regimes: past and present. Pages 1041-1067 in: D.C. Erman, editor. Sierra Nevada ecosystem project: Final report to Congress, Volume 2. University of California, Davis, Wildland Resources Center Report 37.
- Sørenson, T.A. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. Biologiske Skrifter Kongelige Dankse Videnskabernes Selskab 5: 1-34.
- Stebbins, R.C. 2003. A field guide to western reptiles and amphibians, third edition. Houghton Mifflin Company, Boston, Massachusetts, USA.
- Sugihara, N.G., and M.G. Barbour. 2006. Fire and California vegetation. Pages 1-9 in: N.G. Sugihara, J.W. van Wagtendonk, K.E. Shaffer, J. Fites-Kaufman, and A.E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, California, USA.
- Summers, R.W., and R. Proctor. 2005. Timing and shedding of seeds and cones, and production in different stands of Scots pines at Abernathy Forest, Scotland. Forestry 87: 541-549.
- Thode, A.E. 2005. Quantifying the fire regime attributes of severity and spatial complexity using field and imagery data. Dissertation, University of California, Davis, USA.
- Travis, L., Jr. 1953. Stomach contents of chipmunks and mantled squirrels in northeastern California. Journal of Mammalogy 34: 316-324.

Page 104

- Travis, L., Jr. 1952. Autumn foods of chipmunks and golden-mantled ground squirrels in the northern Sierra Nevada. Journal of Mammalogy 33: 198-205.
- van Mantgem, P.J., N.L. Stephenson, and J.E. Keeley. 2006. Forest reproduction along a climatic gradient in the Sierra Nevada, California. Forest Ecology and Management 225: 391-399.
- van Wagtendonk, J.W., and J.A. Lutz. 2007. Fire regime attributes of wildland fires in Yosemite National Park, USA. Fire Ecology 3(2): 34-52. doi: 10.4996/fireecology.0302034
- van Wagtendonk, J.W. 2006. Fire as a physical process. Pages 38-57 in: N.G. Sugihara, J.W. van Wagtendonk, K.E. Shaffer, J. Fites-Kaufman, and A.E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, California, USA.
- van Wagtendonk, J.W., and J. Fites-Kaufman. 2006. Sierra Nevada bioregion. Pages 264-294 in: N.G. Sugihara, J.W. van Wagtendonk, K.E. Shaffer, J. Fites-Kaufman, and A.E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, California, USA.
- van Wagtendonk, J.W., K.A. van Wagtendonk, J.B. Meyer, and K.J. Paintner. 2002. The use of geographic information for fire management planning in Yosemite National Park. The George Wright Forum 19: 19-39.
- Vander Wall, S.B. 1993. Cache site selection by chipmunks (*Tamias* spp.) and its influence on the effectiveness of seed dispersal in Jeffery pine (*Pinus jeffreyi*). Oecologia 96: 246-252.
- Vander Wall, S.B., T.C. Thayer, S.B. Hodge, M.J. Beck, and J.K. Roth. 2001. Scatter-hoarding behavior of deer mice (*Peromyscus maniculatus*). Western North American Naturalist 61: 109-113.
- Wolff, J.O. 1996. Population fluctuations of mast-eating rodents are correlated with the production of acorns. Journal of Mammalogy 77: 850-885.
- Wright, H.A., and A.W. Bailey. 1982. Fire ecology, United States and southern Canada. John Wiley and Sons, New York, New York, USA.
- Zielinski, W.J., W.D. Spencer, and R.H. Barrett. 1983. Relationship between food habits and activity patterns in pine martens. Journal of Mammalogy 64: 387-396.