Journal of Mammalogy, 103(1):111–123, 2022
https://doi.org/10.1093/jmammal/gyab129
Published online November 24, 2021

Bats in the megafire: assessing species' site use in a postfire landscape in the Sierra Nevada

Haley E. Mirts,[1] John P. McLaughlin,[2] Theodore J. Weller,[3] Angela M. White,[4] Hillary S. Young,[5] and Rahel Sollmann[1,6,*]

[1]*Department of Wildlife, Fish, and Conservation Biology, University of California Davis, Davis, CA, USA*
[2]*Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA, USA*
[3]*USDA Forest Service, Pacific Southwest Research Station, Arcata, CA, USA*
[4]*USDA Forest Service, Pacific Southwest Research Station, Davis, CA, USA*
[5]*Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, CA, USA*
[6]*Department of Ecological Dynamics, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany*

**To whom correspondence should be addressed: rsollmann@ucdavis.edu*

Large high-severity fires are increasing in frequency in many parts of the world, including the coniferous forests of the Sierra Nevada mountains. These "megafires" alter vegetation and environmental conditions in forests, yet their impacts on native wildlife remain poorly understood. Bats play an important role in forest ecosystems, but their responses to megafires likewise are understudied. We investigated bat responses to the King Fire, a megafire that burned nearly 40,000 ha within the Eldorado National Forest in 2014, half of it at high severity. From June to September 2017, we used remote acoustic recorders to survey bats at 26 sites with varying fire severity (unburned, mixed, and high severity). We analyzed data with Royle–Nichols occupancy models to investigate how bat space use was influenced by megafires, and whether this response was driven by prey availability, fire severity, or fire-altered habitat conditions. We calculated prey species richness, biomass, and abundance, from moths sampled with blacklight surveys. Vegetation covariates included tree density, canopy cover, and shrub density, measured along vegetation transects. To capture general effects of fire, we also included fire severity and the percentage of dead trees as potential covariates on space use. Prey variables were highest in unburned forests, were the most common predictors of, and generally had positive effects on bat space use. Responses to tree density and canopy cover varied by species; the most common vegetation covariate, shrub density, had weak positive effects on bat space use. In spite of the varying prey and vegetation conditions across fire severity categories, most bats showed weak to no response in space use to fire severity and tree mortality. We attribute this to the highly mobile nature of bats, which reduces the impact of potentially negative local conditions.

Key words: bats, coniferous forests, megafire, moths, occupancy modeling, Sierra Nevada, space use, wildfire

Humans are dramatically changing fire regimes globally, by changing fuel loads, altering the climate, and changing the timing and frequency of ignition events, among other causes (Bowman et al. 2011). Particularly in the Mediterranean basin, Western United States, and Eastern Australia, a common signature of these changes has been the increase in large (> 10,000 ha), high-severity fires (i.e., crown fires that cause high rates of tree death, consume most understory vegetation, and penetrate deep into the soil), also called "megafires" (Stephens et al. 2014). Changes in fire regime are well established to have strong effects on vegetation structure and composition (Jayen et al. 2006; Hollingsworth et al. 2013) as well as downstream effects on functioning of ecosystems (Knelman et al. 2015; Butler et al. 2019). Yet we still have relatively little knowledge of the effects of megafires on many vertebrate communities, including bats.

Bats play important roles in the ecosystems that they inhabit. In forests, they are critical as top-down regulators of potentially damaging insect populations (e.g., Charbonnier et al. 2014). They also consume mosquitoes and other insect vectors that can cause disease to humans and wildlife species (Wray et al. 2018). In addition, bats are prey for a wide

© The Author(s) 2021. Published by Oxford University Press on behalf of the American Society of Mammalogists, www.mammalogy.org.

variety of avian and mammalian carnivores, thus serving both as predators and prey in food webs (Hutson et al. 2001). Indeed, they often are considered indicator species of ecosystem health (Jones et al. 2009).

Despite their ecological importance, the effects of fire on bats remain unclear. Most studies on this topic have focused on the effects of prescribed fires on bat habitat use and found that these were mostly positive or neutral (Inkster-Draper et al. 2013; Law et al. 2019; Loeb 2020). Prescribed fires, however, generally are small in scale and low in severity. Nevertheless, bats may be more able to escape direct mortality from large and high-severity wildfires than most mammals and likely experience fewer barriers to recolonization (Dickinson et al. 2009). Owing to their mobility, they should be able to exploit fire-induced pulses in food resources (e.g., Malison and Baxter 2010) and at the same time have access to resources associated with unburned habitat. As such, they may be particularly resilient to wildfires. Indeed, several studies globally show no or even positive changes in bat activity or occupancy following wildfire (Malison and Baxter 2010; Buchalski et al. 2013; Doty et al. 2016; Steel et al. 2019; Ancillotto et al. 2021), although effects tended to be species-specific and dependent on other factors such as time since fire or the landscape context (Steel et al. 2019; Ancillotto et al. 2021).

Fire likely affects bats in many ways, including changes in food resources and habitat structure. Several studies have made use of remote sensing data to investigate the relationships between wildfire, habitat structure, and bat activity or occurrence. These studies suggest that by decreasing "clutter" (mid- and overstory vegetation) in the forest, fire can increase foraging opportunities for open-adapted species (Buchalski et al. 2013; Blakey et al. 2019), whereas clutter or edge-adapted bats may reduce their activity in the more open landscapes created by large, high-severity burns (Broken-Brow et al. 2020; Starbuck et al. 2020). In contrast, the relationships among fire, prey, and bats have received much less attention. Fire can increase prey availability because it encourages the emergence of pyrophilic insects (Pausas and Parr 2018) and aquatic invertebrates (Swengel 2001; Malison and Baxter 2010). Terrestrial invertebrates, however (which include larval stages of the nocturnal flying insects that dominate the diet of most species of insectivorous bats), may decline after fire (Swengel 2001; Malison and Baxter 2010). Two studies that have investigated the relationship among fire, prey availability, and bat activity suggest that these latter increase after high-severity fire (Malison and Baxter 2010; Doty et al. 2016), albeit at different intervals following fire (months vs. 5–10 years postfire). Clearly, the relationship among fire, prey, and bats requires further study.

The coniferous forests of the Sierra Nevada mountains in California are used by 17 species of bats. Prior to Euro-American settlement, mid-elevation conifer forests of the region experienced fire return intervals of 12–25 years (McKelvey et al. 1996; North et al. 2012). These historic fires largely were of low-to-moderate severity, with patches of high-severity fire, and created forest landscapes heterogeneous both in age structure and species composition (Stephenson et al. 1991; Dodson and Peterson 2010). Wide-scale logging and fire suppression in the 20th century contributed to the denser, even-aged forests with high fuel loads seen today (Laudenslayer and Darr 1990; Savage and Swetnam 1990; McKelvey et al. 1996). Elevated fuel levels, prolonged drought and rising temperatures due to climate change, and increasing human encroachment have created ideal conditions for widespread, high-severity wildfires throughout the region (Westerling et al. 2006). Studies have shown that fire frequency (McKelvey et al. 1996) and burn area have been increasing since the 1970s (Miller et al. 2009; Miller and Safford 2012). Indeed, the hottest, largest, and most destructive fires in the state's history all have occurred in recent years. These megafires produce large, homogeneous landscapes with high tree mortality (Miller and Safford 2012). Native plant species adapted to frequent low- to moderate-severity fire often fail to reestablish due to loss of seed banks or changing microclimates (Stephens et al. 2014). Under these conditions, coniferous forests are replaced by shrubland (van Wagtendonk et al. 2012). Depending on damage to seed banks and local conditions, tree succession could take as few as 30 years, or as long as a century (McGinnis et al. 2010). Previous studies in the Sierra Nevada suggest that activity and occurrence of forest-dwelling bats are resilient to wildfire (Buchalski et al. 2013) and that some species may, in fact, benefit from the diversity of conditions created by variable fire history on the landscape scale (i.e., pyrodiversity, Steel et al. 2019) or postfire habitat conditions (Blakey et al. 2019). But only Blakey et al. (2019) considered habitat structural variables (such as tree diameter and basal area) and none of these studies considered prey availability as potential drivers of postfire habitat use by bats.

Here, we use acoustic surveys to study how bat space use is affected by fire severity, fire-induced changes in vegetation structure, and prey availability 3 years after a megafire in the lower montane coniferous forest of the central Sierra Nevada. We expected prey availability to have a positive effect on bat space use for all species. The expected relationship between fire and prey availability, however, is less clear: because postfire conifers are replaced by *Ceanothus* and other shrubs, specialist prey species may be lost, possibly decreasing overall prey volume and/or richness. Conversely, increasing shrub abundance may increase food availability for generalist insect species, or attract shrub specialist species. Bat space use also could be influenced by structural habitat characteristics. In line with previous studies, we expect positive impacts on space use by open habitat-adapted species that use low-frequency echolocation calls, and negative impacts on closed forest-adapted species that use high-frequency calls. Combined, these mechanisms (prey and habitat) will lead to divergent responses of different bat species to fire severity. By focusing on prey and vegetation structure, we can begin to understand the underlying mechanisms that shape bat space use in a postfire forest.

Materials and Methods

Study area.—This study was conducted in the Eldorado National Forest (ENF; 38°45′N, 120°20′W) in the central

Sierra Nevada mountain range of California. The ENF consists primarily of lower montane forest, which ranges in elevation from 910 to 2,130 m. At these elevations, the vegetation community is a mixed-conifer forest consisting primarily of yellow pines (*Pinus ponderosa* and *Pinus jeffreyi*), white fir (*Abies concolor*), red fir (*Abies magnifica*), and California incense cedar (*Calocedrus decurrens*), with shrubs in the understory. Ownership of the land is split between the US Forest Service and private landowners, creating a mosaic of public and private management. The region receives an average of 1,422 mm of rainfall annually, largely in the form of snowfall that melts during the dry Mediterranean summers. During summer, the ENF can reach temperatures of 37.7°C, with winter lows of −17.7°C (USDA Forest Service 2020).

The King Fire burned 39,500 ha of the ENF during September 2014, with most of the impact occurring within 5 days (Fig. 1). Fifty percent of the affected area suffered high-severity fire, most of this with tree mortality > 90% (USDA Forest Service 2015). We stratified sampling by fire severity, with nine sites in the unburned forest outside the fire perimeter, nine in areas of low- to moderate-severity fire (henceforth, mixed severity), and nine in high-severity fire areas (Fig. 1), all within the lower montane forest elevation band. We selected potential sampling sites based on predicted fire severity from the differenced Normalized Burn Ratio derived from Landsat imagery (Miller et al. 2009). Areas in which estimated tree mortality exceeded 75% were defined as high severity, areas with estimated tree mortality of 25–75% were denoted as mixed severity. Unburned sites were placed between 0.1 and 4.7 km from the edge of the fire perimeter (mean = 1.5 km, *SD* = 1.66 km). All sites were on public land with no postfire treatments such as salvage logging, replanting, or mechanical mastication, and at least 50 m away from roadways, trails, and flowing water to minimize impacts from these features. Sites were relocated if in situ severity conditions varied significantly from remote-sensed estimates or slopes were too steep (> 30 degrees) to sample safely. At each sampling site we established a 200 × 200 m plot in which were measured vegetation, bats, and prey (see protocols below). Plots were established such that fire severity conditions within a plot were consistent. We sampled from 27 June 2017 to 1 September 2017, the warmest months of the year in the ENF and the most active period for North American bats (O'Shea and Vaughan 1977).

Bat surveys.—At each site, we placed a Wildlife Acoustics Songmeter SM4BAT FS echolocation detector (Maynard, Massachusetts) for a minimum of three consecutive nights, recording from 30 min prior to sunset to 30 min after sunrise. We simultaneously sampled a set of one unburned, one mixed, and one high-severity site. The detectors were set to begin a 3-s recording when triggered by an 8-kHz or greater sound within the environment. We placed detectors close to the center of each sampling plot. We chose points in open areas to minimize signal attenuation from nearby vegetation and placed the microphones 2.5 m above the ground. We analyzed audio recordings using SonoBat 4.2 (sonobat.com) software. Sonobat selects high signal–noise ratio calls within each file and assigns a suggested species identification when possible. The software also outputs the number of calls within the recording that match characteristics for a particular species. We used this information to prioritize recordings for manual verification of suggested species identifications as well as to assign recordings to frequency groups without inspection when software indicated uncertainty as to species identity. We only include manually identified recordings in our analyses.

Prey sampling.—On the third sampling night at each site, we placed a modified, self-collecting blacklight trap, powered by a 12-V battery, in the vicinity of the bat detector to collect night-flying insects. The blacklights were hung approximately 1.5 m off the ground in open spaces between trees. A fan running below the light blew insects from the hood into a weighted mesh bag. We collected samples the following morning. We froze lepidoptera in airtight freezer bags, and stored beetles, wasps, and flies in 70% ethanol.

We used moths as a proxy for overall prey because they accounted for 85% of specimens collected and are an important component of the diet of insectivorous bats (Whitaker 1972; Long et al. 1998). Bat diet can vary in space and time and to our knowledge, community-wide diet studies for the Sierra Nevada bats are not available. A diet study in forests in Oregon including 11 of the 14 species from our study found lepidoptera to be an important prey item across bat species, occurring in 77–100% of all analyzed fecal samples (Ober and Hayes 2008). Lacki et al. (2007) in forests in Idaho found lepidoptera to be the dominant prey for four out of five bat species, all of which also are represented in our study community. We identified all undamaged moths to species or morphospecies using dichotomous keys and reference collections. Identification followed the keys to taxonomic family in Triplehorn et al. (2005) and further identification was undertaken in conjunction with the Bohart Museum of Entomology (University of California, Davis). Macrolepidoptera (wingspans > 20 mm in length) were identified based on their wing size, shape, and pattern. Species-level identification for microlepidoptera is difficult and these moths were grouped into morphospecies based on their size, shape, color, and other distinguishing characteristics.

We calculated three measures of prey availability for each site: moth abundance (total count regardless of identification), species richness (number of unique morphospecies, excluding specimens for which no morphospecies could be determined), and prey biomass based on estimated mean weight of each morphospecies, multiplied by its abundance. We estimated mean weight volumetrically, by measuring the length (tip of abdomen to tip of head), width (maximum width of body excluding wings), and depth (maximum depth of body excluding appendages) of individual moths and converting them into volume using an approximate shape (e.g., ellipsoid, cylinder, hemisphere, etc., Siemann et al. 1996; Haddad et al. 2000). For each morphospecies, we measured 10 specimens (unless we had < 10 specimens, in which case we measured all individuals), then estimated mass by multiplying average volume by a tissue density of 1.1 g/ml (Peters 1986; Hechinger et al. 2011).

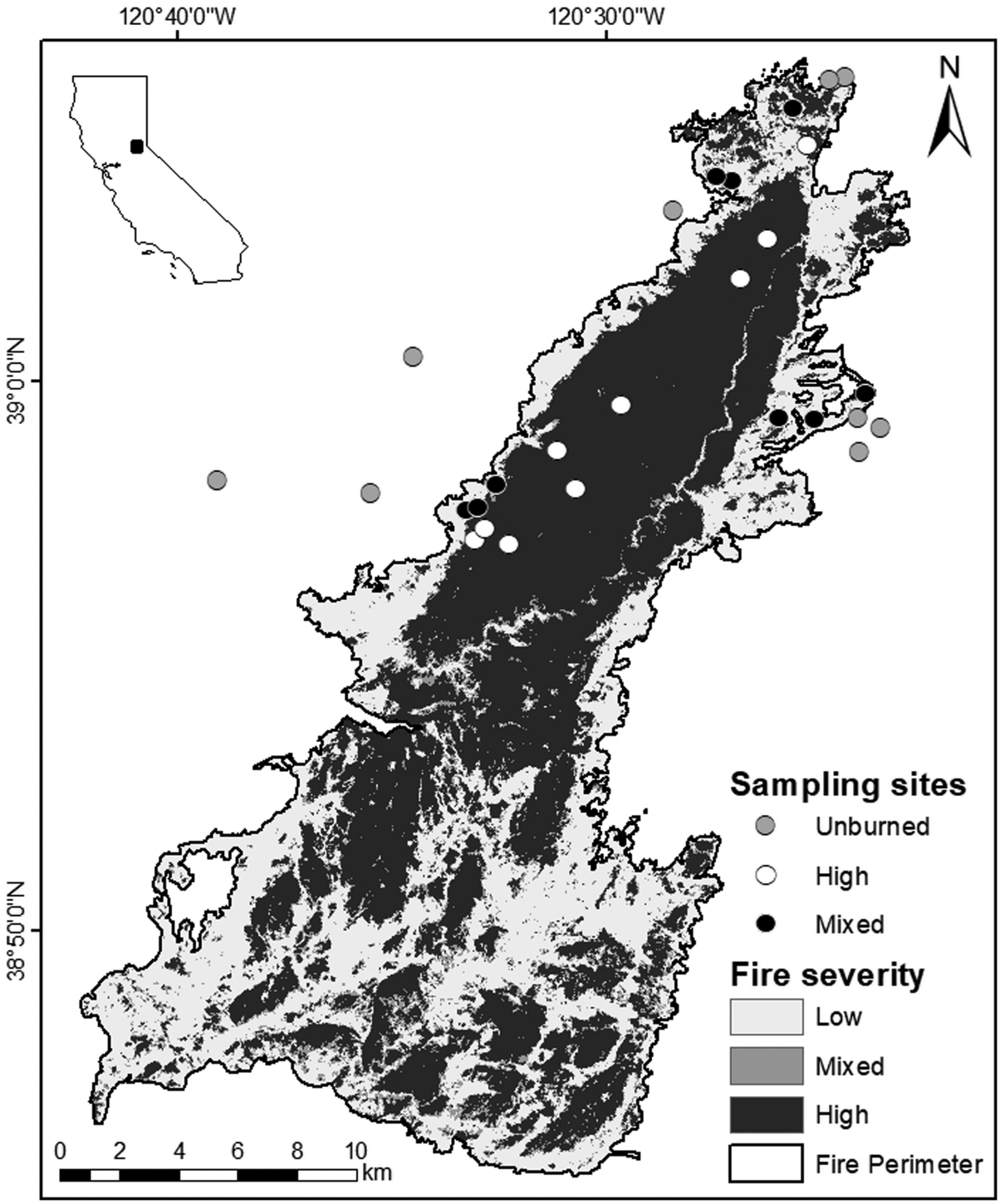

Fig. 1.—Map of the 2014 King Fire (Placer and El Dorado county, California, United States), with sampling units for the present study, color-coded for their respective fire severity category. The shading from light to dark gray indicates fire severity categories based on the percentage of tree mortality (> 75% tree mortality = high severity; 25–75% tree mortality = mixed severity, < 25% tree mortality = low severity).

Vegetation sampling.—To investigate the effect of vegetation structure on bat space use and detection, we measured canopy cover, tree density (trees ha^{-1}) and shrub density (shrubs ha^{-1}) along line transects. We surveyed two 50-m transects per site, on opposite edges of the 200 × 200 m sampling plot. Along each transect, we measured all trees > 15 cm diameter at breast height (DBH) rooted within 7.5 m and all shrubs at least one dimension (height, width, depth) > 50 cm rooted within 2.5 m of the transect centerline. To calculate shrub and tree density, we divided counts by the transect area. We classified all trees within a transect as alive (< 75% needles discolored/missing) or dead (> 75% needles discolored/missing) to calculate the percentage of dead trees. We estimated canopy cover by recording the percentage of a 0.5 × 0.5 m quadrat with direct

overhead canopy at 5-m intervals along each transect. For each covariate, we averaged multiple measurements collected at a site to obtain a single site-level value. Covariate summaries are compiled in Table 1.

Data analysis.—Imperfect detection is a pervasive challenge in wildlife surveys, and while detection of a species indicates certain presence at a site, assuming nondetection means species absence can result in the underestimation of site occupancy. This holds true for bats, because species behavior and call characteristics make certain species more identifiable and thus more detectable by acoustic monitoring than others. Particularly for quiet or high-flying species, an individual may be present at a site but go undetected (Szewczak et al. 2018). We used occupancy models (MacKenzie et al. 2002) to account for differences in detectability among species of bats and treatments. By integrating site-specific covariates within the model, this approach can inform drivers of species occurrence (Ball et al. 2005). Occupancy modeling requires repeated species-level detection/nondetection data, and acoustic monitoring data of bats collected over multiple nights can be condensed to this binary format (i.e., 1 if the species was detected at least once at a given night and survey location, 0 otherwise) and analyzed within this framework. In this study, we applied the Royle–Nichols occupancy (RN) model (Royle and Nichols 2003). Like regular occupancy models, the RN model uses repeated binary species detection/nondetection data, y_{jk}, but takes into account that the probability of detecting a species at site j on occasion k, p_{jk}, is related to how many individuals of the species are present at that site (i.e., the species' local abundance), N_j. The model exploits this relationship between p and N to estimate local abundance from binary detection data. Variation in expected local abundance λ_j can be modeled, on the log scale, as a function of site-level covariates $\mathbf{X}$ and their coefficients $\boldsymbol{\beta}$. Individual detection probability (r_{jk}) can be modeled on the logit scale as a function of site and visit specific covariates $\mathbf{Z}_{jk}$ and their coefficients $\boldsymbol{\alpha}$.

$$y_{jk} \sim \text{Bernoulli}(p_j)$$

$$p_{jk} = 1 - (1 - r_{jk})^{N_j}$$

$$\text{logit}(r_{jk}) = \alpha \mathbf{Z}_{jk}$$

$$N_j \sim \text{Poisson}(\lambda_j)$$

$$\log(\lambda_j) = \boldsymbol{\beta} \mathbf{X}_j$$

Estimates of local abundance are difficult to interpret for point-based sampling methods such as acoustic detectors, particularly for wide-ranging species like bats, because it is unclear to which area these estimates refer (Sollmann 2018). We do not interpret estimates of λ as actual local abundance, but rather, we view it as an index of space use, and we focus on the relationships of λ with site-level covariates. The RN framework was especially suited for this data set, because it allowed for the inclusion of five species that were detected at (nearly) all sites, for which we would not have been able to model variation in occupancy (Royle and Nichols 2003).

Occupancy modeling assumes a closed population, that is, no change in occupancy or local abundance (here, site use) during the sampling period (MacKenzie et al. 2002). Because each site was sampled on usually three, but in some cases five, consecutive nights, the assumption of closure seems reasonable. Occupancy models also assume independence between sampling sites, an assumption that likely is violated due to the highly mobile nature of forest bats. Due to the scale of the King Fire, the coupling of our acoustic and invertebrate data collection with the collecting of other data (this study was part of a larger ecological study of postfire conditions), and the uncertainty of home range size for the species in question, ensuring site independence for bat surveys was unfeasible. We acknowledge that as a result, standard errors of parameter estimates may be too low, but expect estimated relationships between predictor variables and site use to be valid nevertheless.

To fit RN models, we created nightly binary detection/nondetection data for each species at each site from the species' vetted call record. With these data, we fitted a series of models to estimate site use (λ) and individual detection (r) as functions of environmental covariates for each bat species. We scaled all continuous covariates for analysis. As measures of prey availability, we included moth abundance, biomass, and richness as predictors of λ. Biomass accounts for potential bat preference for larger moths, which provide higher energetic return, whereas the richness indicator serves to investigate the effect of a more diverse prey base.

Percent canopy cover, tree density, and shrub density were included to assess the impact of vegetation structure on λ. By

Table 1.—Summary (mean and standard deviation) of covariates used to model bat space use for each of the three fire severity categories, measured in 2017 in the area affected by the 2014 King Fire (Sierra Nevada mountains, California).

Covariate type	Covariate name	Unburned	Mixed severity	High severity
Moth covariates	Abundance (# of individuals)	143.78 (±223.80)	39.56 (±21.01)	65.11 (±78.39)
	Biomass (g)	6.74 (±6.48)	2.44 (±1.78)	2.56 (±2.78)
	Richness (# of species)	21.33 (±11.42)	14.67 (±6.02)	13.56 (±8.20)
Burn condition	Dead trees (%)	19.36 (±15.00)	55.63 (±26.71)	100 (±0.00)
Vegetation covariates	Canopy cover (%)	44.47 (±9.32)	33.10 (±11.87)	8.07 (±5.44)
	Shrub density (ha^{-1})	440 (±551.18)	984.44 (±1173.2)	5120 (±4852.41)
	Tree density (ha^{-1})	401.48 (±136.86)	331.11 (±148.17)	362.22 (±157.30)

incorporating tree density as a covariate, we attempted to account for general heterogeneity in forest conditions among sites. We included shrub density as a site use covariate to reflect change in vegetation structure due to fire, but also as a measure potentially related to prey availability, because many of the common moth species captured feed on *Ceanothus* shrubs as caterpillars (Miller 1995).

We further used fire severity (unburned/mixed/high) as a categorical covariate on λ. This created a coarse measure of the effect of fire severity in general, incorporating postfire prey and vegetation conditions as well as aspects of the fire that we did not explicitly measure. Alternatively, we used the percentage of dead trees as a continuous predictor quantifying fire severity. Tree death is a naturally occurring process outside of fire; however, tree mortality outside the fire perimeter (due to other causes, such as insect infestation and drought) was low (Table 1).

Finally, we used shrub and tree density as covariates on bat detection (*r*), because of their potential to interfere with the effectiveness of the acoustic detectors. As many of the *Ceanothus* shrubs found in the study area regularly grew to heights of 1–1.5 m, they create a raised surface near the microphone that can result in call dampening or echoes in the recorded files, thereby making the calls difficult to identify (Chenger 2017). While the detectors were placed in canopy gaps, dense stands of trees surrounding the microphone likewise could result in echoes, or sound interference.

We built single species occupancy models for each bat species with 10 or more detections. We chose this cutoff because models for more rarely detected species did not converge. We created nine models for site use (λ), including the null model (i.e., no covariates) and eight single-covariate models using all above-described covariates. We combined these site use models with three detection (*r*) models: a null model, a model that included shrub density, and a model that included tree density as a covariate on *r*, for a total of 27 models per species. Simplifying models to a single site use covariate was warranted given the relatively low number of spatial sampling units, as well as the level of correlation among some of the predictor variables (Supplementary Data SD1). We used Akaike's information criterion (AIC) to determine the most parsimonious model for each species (Burnham and Anderson 2002). Models that were within 2 ΔAIC of the top model were considered as having comparable support. Within a set of top models, we only considered a covariate to be a relevant predictor of species detection or site use when its inclusion improved on (i.e., led to a lower AIC than) the null model. Because many species had several models within 2 ΔAIC of the top model, we employed model averaging (Burnham and Anderson 2002). Specifically, for species with multiple models within 2 ΔAIC of the null model, we calculated model-averaged parameters using all top models, and we consider covariate effects as statistically significant when conditional 95% confidence intervals (*CI*s) of the model-averaged coefficients did not overlap zero. For consistency, we used the same *CI*-based criterion to determine significance of coefficients for cases with a single top model. We interpret statistically significant covariates as having strong effects, and conversely, covariates present in the top model set and improving on the null model but having 95% *CI*s overlapping 0 as having weak effects.

Models were fit using the unmarked package (Fiske and Chandler 2011) version 0.12-3, using the R statistical programming language version 3.4.3 (R Core Team 2018). We used the MuMIn package v.1.43.6 (Bartoń 2019) for model averaging. To assess model fit, we used the parboot function in unmarked, which contrasts the sum of squared residuals (SSR) of the original data and model with the distribution of SSR from data simulated under, then analyzed with, the model in question; we implemented this test for the top model for each species and found no evidence of lack of fit (i.e., the original SSR was always centrally located in the distribution of simulated SSR).

Results

Bat detections.—Due to equipment failure, we lost all data from one unburned site. Out of 23,902 total recordings from the remaining 26 sites, Sonobat 4.0 identified 22,534 bat records collected over 81 recording nights (Table 2). Of these, 7,348 records were assigned to individual species. California myotis (*Myotis californicus*) was the most commonly recorded species with over 3,700 records, while the rarest species, western mastiff bat (*Eumops perotis*) and spotted bat (*Euderma maculatum*), were recorded < 3 times. Due to sparse data, we discarded western mastiff bat, spotted bat, and canyon bat (*Parastrellus hesperus*) from the analysis (Table 2). Unburned sites had the most bat records, with 9,016 recordings, of which 3,179 (35%) were identified to species. High-severity sites were the second most active with 8,230 total records (2,411, or 29%, identified to species), while moderate-severity sites had 5,288 records total (1,758, or 33%, identified to species). Sixteen of the 17 bat species were detected in unburned and moderate-severity sites, while 15 also were recorded in high-severity burns.

Moth detections.—We collected 2,236 moths from the blacklight traps, encompassing 163 morphospecies from 10 families. The average abundance of moths at unburned sites was more than twice as high as at high-severity sites, and over 3.5 times as high as at mixed-severity sites (Table 1). Similarly, average moth biomass was highest in unburned sites, but very similar in mixed- and high-severity sites (Table 1). We were able to identify 91.3% of all moths to morphospecies, and 50% to genus or species. Most specimens not identified to genus/species-level were microlepidoptera; most of the macrolepidoptera were in the families Noctuidae or Geometridae. *Drepanulatrix carnearia* (Geometridae), *D. unicalcaria* (Geometridae), *Eudrepanulatrix rectifascia* (Geometridae), and *Epinotia signiferana* (Erebidae) were the most common species, each captured over 60 times. Species richness was highest across unburned sites at 110 (average site richness 21.33 ± 11.42) compared to 83 in mixed-severity burns (14.67 ± 6.02) and 75 (13.56 ± 8.2) in high-severity burn sites.

Occupancy model results.—For two species, silver-haired bat (*Lasionycteris noctivagans*) and western small-footed

Table 2.—Common name, scientific code, Latin name, call records, and foraging strategy for 17 bat species detected using acoustic recorders across 26 sites in and around the 2014 King Fire (Sierra Nevada mountains, California) 3 years postfire. For each bat, the total number of records collected (# Records), and the number of records (and sites with detections, out of nine for high- and mixed-severity sites, eight for unburned sites) in each fire severity category is given.

Common name	Code	Latin name	# Records	Unburned	Mixed severity	High severity	Foraging strategy[a]
Pallid bat	ANPA	*Antrozous pallidus*	51	14 (5)	18 (7)	19 (4)	Clutter
Townsend's big-eared bat	COTO	*Corynorhinus townsendii*	15	4 (3)	4 (3)	7 (4)	Clutter
Big brown bat	EPFU	*Eptesicus fuscus*	899	414 (7)	84 (9)	401 (8)	Edge
Spotted bat[b]	EUMA	*Euderma maculatum*	2	2 (1)	0 (0)	0 (0)	Clutter
Western mastiff bat[b]	EUPE	*Eumops perotis*	1	1 (1)	0 (0)	0 (0)	Open
Western red bat	LABL	*Lasiurus blossevillii teliotis*	22	8 (3)	7 (4)	7 (5)	Edge
Hoary bat	LACI	*Lasiurus cinereus*	90	27 (8)	20 (6)	43 (9)	Open
Silver-haired bat	LANO	*Lasionycteris noctivagans*	708	118 (7)	274 (9)	316 (9)	Edge
California myotis	MYCA	*Myotis californicus*	3716	1950 (8)	729 (9)	1037 (9)	Edge
Western small-footed myotis	MYCI	*Myotis ciliolabrum*	72	41 (5)	17 (7)	14 (7)	Edge
Long-eared myotis	MYEV	*Myotis evotis*	377	126 (8)	144 (9)	107 (9)	Clutter
Little brown myotis	MYLU	*Myotis lucifugus*	243	106 (7)	94 (8)	43 (7)	Edge
Fringed myotis	MYTH	*Myotis thysanodes*	190	66 (6)	86 (8)	38 (9)	Clutter
Long-legged myotis	MYVO	*Myotis volans*	278	114 (8)	114 (9)	50 (8)	Edge
Yuma myotis	MYYU	*Myotis yumanensis*	345	115 (8)	91 (9)	139 (9)	Edge
Canyon bat[b]	PAHE	*Parastrellus hesperus*	9	0 (0)	1 (1)	8 (2)	Edge
Mexican free-tailed bat	TABR	*Tadarida brasiliensis*	330	73 (6)	75 (6)	182 (9)	Open

[a]Categories taken from Blakey et al. (2019).
[b]Species not included in analysis due to sparse data.

myotis (*Myotis ciliolabrum*), none of the covariates of interest on occupancy and detection were included in the top model set. Nine species had at least one occupancy covariate in the top model set; covariates in top models varied (Fig. 2). Seven bat species included at least one of the prey covariates in their top models, with four species incorporating all three. For a given species, effects of different prey covariates always had the same direction, but contrary to our expectations, effects were not always positive. The most prevalent prey covariate was moth biomass, which was included in the top models of six species: Yuma myotis (*Myotis yumanensis*), long-legged myotis (*Myotis volans*), long-eared myotis (*Myotis evotis*), hoary bat (*Lasiurus cinereus*), Western red bat (*Lasiurus blossevillii teliotis*), and big brown bat (*Eptesicus fuscus*; Fig. 2A). Moth biomass had a positive effect on five of these species, and was statistically significant for hoary bat and long-eared myotis. One species, Western red bat, displayed nonsignificant negative effects. Moth abundance was included in the top model for four species (big brown bat, Western red bat, hoary bat, and Yuma myotis), was positive except for Western red bat, and was significant for big brown bat and hoary bat (Fig. 2A). Moth species richness (Fig. 2A) was included in top models for Yuma myotis, hoary bat, Western red bat, big brown bat, and Townsend's big-eared bat (*Corynorhinus townsendii*). The effect was negative for Townsend's big-eared bat and Western red bat, and significant only for the latter.

As expected, the effects of the three vegetation covariates varied among species. Shrub density was the most prevalent, with four species, Mexican free-tailed bat (*Tadarida brasiliensis*), Fringed myotis (*Myotis thysanodes*), hoary bat, and Townsend's big-eared bat, showing nonsignificant positive relationships between shrub density and site use (Fig. 2B). Canopy cover was included in the top models for Mexican free-tailed bat and long-legged myotis, showing a weak negative and a weak positive relationship between canopy cover and site use, respectively (Fig. 2B). Tree density was included in the top models for two species, having a nonsignificant negative effect on site use of pallid bats (*Antrozous pallidus*) and a significant positive effect on long-legged myotis (Fig. 2B).

The two burn covariates were included in the fewest species' top model sets. As expected, effects of fire severity were variable. The percentage of dead trees was included in the top model for the Mexican free-tailed bat and California myotis, having a nonsignificant negative effect on the latter, and a significant positive effect on the former (Fig. 2C). Fire severity category was included in the top models for Mexican free-tailed bats; high-severity burns had weak positive effects on site use relative to unburned sites, while mixed-severity burns had a weak negative effect (Fig. 2C).

Shrub and/or tree density occurred in the detection component of top models for 11 species. Effects more often were positive than negative; when both were present, their direction usually differed. With one exception (shrub for hoary bats), however, effects always were nonsignificant (Fig. 2D).

Discussion

We found that site use of bats in the coniferous forests of the Sierra Nevada seemed largely resilient to fire impacts 3 years after a megafire. Prey availability was the most important predictor of space use. As expected, biomass, richness, and abundance of moths had mostly positive, though often weak, impacts on bat space use, suggesting the importance of prey availability in habitat selection. Effects of habitat structure were less common, and as expected, were inconsistent in their direction and strength across species, showing some correlation with open versus clutter adaptation, as has been observed in previous studies (e.g., Blakey et al. 2019; Starbuck et al. 2020).

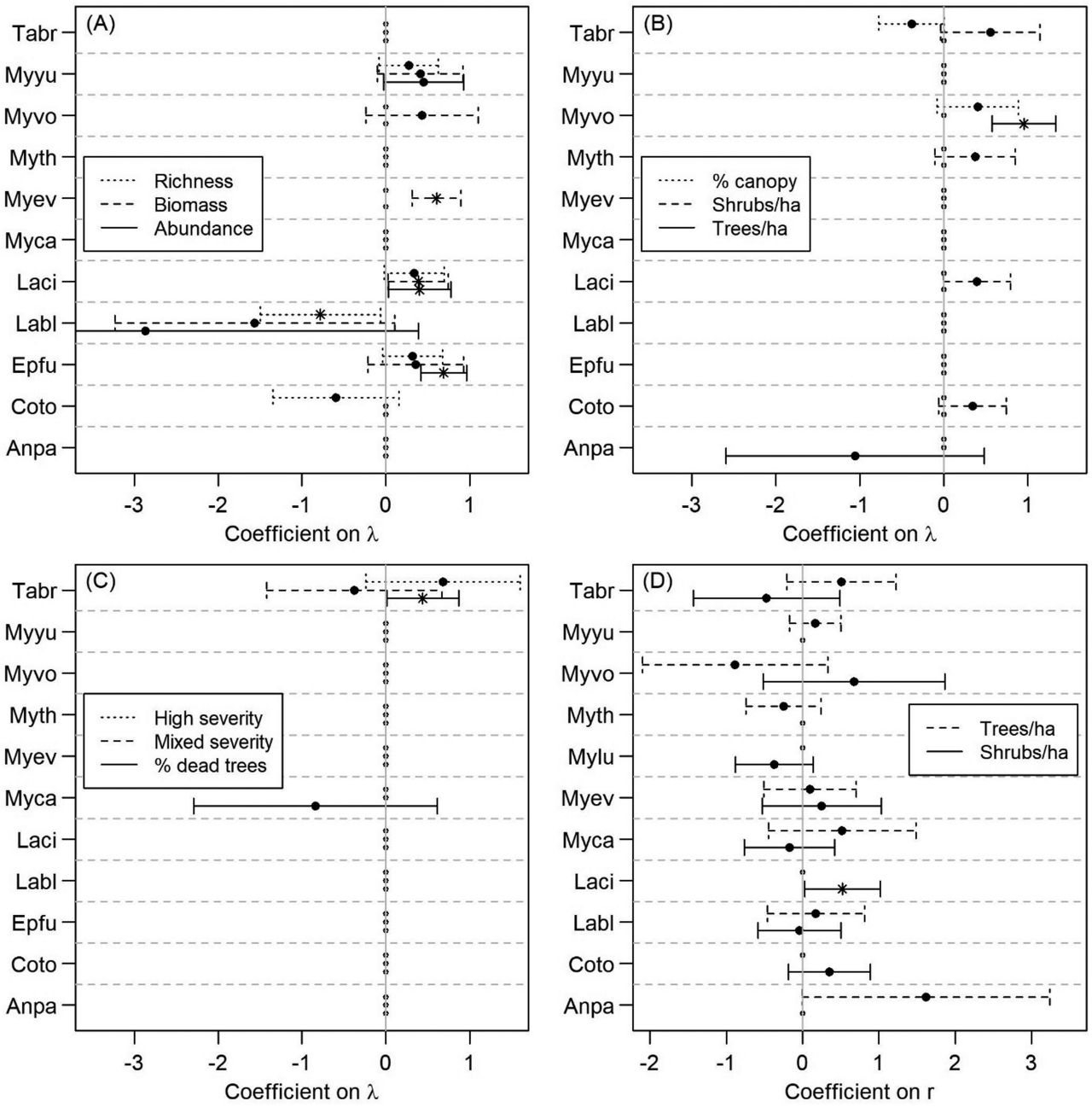

Fig. 2.—Model-averaged covariate effects (with conditional 95% confidence intervals; cutoff error bar in plot A would extend to –6.12) on space use λ (A–C) and detection *r* (D) estimated with Royle–Nichols occupancy models for a community of bat species from the Sierra Nevada mountains, California, sampled with acoustic recorders in/around the King Fire 3 years postfire. Covariate effects on space use are grouped into measures of prey availability (A), habitat structure (B), and fire severity (C). Asterisks represent statistically significant effects; dots represent effects present in the top model set that were not significant; open circles without error bars represent effects that were not in the top model set. Plots A–C omit species that had no covariates on space use in their top model set (LANO, MYCI, MYLU); plot D omits species that had no covariates on detection in their top model set (EPFU, LANO, MYCI); full species names in Table 2.

Even though both prey and habitat condition differed along the fire severity gradient of our study area, measures of fire severity largely were unimportant for bat space use. Our study thus contributes further evidence that forest bats appear to be largely resilient even to high-severity wildfire in their space use, occupancy, or activity (Buchalski et al. 2013; Blakey et al. 2019; Steel et al. 2019; Starbuck et al. 2020; Ancillotto et al. 2021).

Moths are an important component of the diet of insectivorous bats, but the interactions between wildfire, moths, and bats are little studied. Doty et al. (2016) found much lower numbers of moths 2 years after a high-severity fire compared to 4 months postfire but made no comparison with unburned sites, while Lacki et al. (2009) found that prescribed fire had no short-term effect on moth abundance. In both studies, changes in bat activity mirrored changes in insect availability. In general, flying

insects are thought to be resilient to fire owing to their mobility (Perry 2011). The availability of live vegetation several years postfire potentially provides resources to both larval (woody vegetation) and adult (flowering plants for those species feeding as adults) moth life stages (Perry 2011). Nonetheless, we found that average moth abundance, richness, and particularly biomass were higher in unburned forests. Among-site variability, however, was high even within a given fire severity category including unburned forest, suggesting that factors other than those measured may drive these metrics, such as local plant community composition or type of ground cover. The most common moth species found in mixed- and high-severity fire sites, such as *Epinotia signiferana* and *Drepanulatrix carnearia*, are wide-ranging and feed on members of the shrub genus *Ceanothus* as larva, making them highly suited to burned Sierra Nevada forests where *Ceanothus* shrubs are common (Miller 1995; Powell and Opler 2009). Generalists, such as the black cutworm (*Agrotis ipsilon*) or *Abagrotis* species, were less common within the burn perimeter, while some conifer specialists, such as the silver-spotted tiger moth (*Lophocampa argentata*), were entirely absent from high-severity burn sites. Although species composition of these night-flying insect communities varied drastically among burn categories and even sites (Supplementary Data SD2), community composition is less likely than abundance to influence space use in bats which are thought to cue in on prey size, flight speed, and other characteristics, rather than species (Clare et al. 2014).

Given their prominent role in the diet of many insectivorous bats, we predicted moth availability covariates to have a positive effect on space use for all bat species. Indeed, prey covariates were the most common predictors of space use in our study and were the only significant predictors for hoary bats, big brown bats, and long-eared myotis. The diets of the first two species are known to include large numbers of lepidoptera (Valdez and Cryan 2009, 2013; Clare et al. 2014), although coleoptera have been shown to be the dominant prey for big brown bats in some studies (Lacki et al. 2007; Ober and Hayes 2008). The fact that we did not consider other potential prey species might explain why effects for remaining species were weak or absent. Pallid bats, for example, frequently glean invertebrates from the ground (Johnston and Fenton 2001), and fringed myotis may glean prey from vegetation (Ober and Hayes 2008). In addition, our single-night sampling of moths may not fully capture spatial variation in moth availability. Finally, bats have been found to change their diet composition following prescribed fire to make use of abundant invertebrate groups (Lacki et al. 2009). Testing whether that occurs among Sierra Nevada bats postfire would require both diet data and information on other potential prey species.

Changes in vegetation structure constitute an important pathway by means of which fire affects wildlife. For bats, the removal of "clutter" is thought to affect activity and occurrence depending on a species' ecomorphology and associated foraging strategy (Blakey et al. 2019; Steel et al. 2019; Broken-Brow et al. 2020; Starbuck et al. 2020). Consequently, we expected effects of vegetation covariates to vary among species. We found that canopy cover and tree density, both proxies for "clutter," were unimportant for most species. The few effects we did find mostly agreed with expected patterns based on foraging strategy. Specifically, the open-space adapted Mexican free-tailed bat was weakly negatively associated with canopy cover, whereas the edge-adapted long-legged myotis showed a weak positive relationship with canopy cover and a strong positive relationship with tree density. An exception was the weak negative association of the clutter-adapted pallid bat with higher tree density. Tree density may not be an important predictor in this study because it does not account for tree size, alive status, or other characteristics that may be more important to bats (e.g., burned trees contribute little to clutter and thus their density may not be relevant to bat space use), or because it showed less variability across and within fire severity categories than other covariates considered.

Shrub density was the habitat covariate most commonly found in top models for bat space use, but the reasons for this are unclear. Shrubs < 1.5 m tall are unlikely to contribute to the type of structural clutter that would impact bat movements, but in burned habitat, shrubs can grow beyond that height. Four species, both open- (hoary bat, Mexican free-tailed bat) and clutter-adapted (Townsend's big-eared bat, fringed myotis), showed positive, though weak, relationships between shrub density and site use. Woody vegetation density has been shown elsewhere to positively affect moth abundance and richness (Dodd et al. 2008) and we speculated that increased shrub density could increase prey abundance or biomass; instead, we found weak, negative correlations among these variables. Shrub density may represent the availability of other shrub-associated prey species such as planthoppers that are known to contribute to the diets of several bat species (e.g., Whitaker 1972). In the Sierra Nevada, shrubs can become the dominant vegetation in the understory postfire due to their fire-dependent germination and ability to crowd out other plants for light and moisture (Nagel and Taylor 2005). Indeed, shrub density was highest in high-severity burned sites, but among-site variability was high. Thus, the positive association with shrub density could also indicate a positive association with certain conditions in burned habitat. In the long term, if shrubs prevent reestablishment of trees, they may affect bat space use negatively because most bats in the study community rely on trees for roosting.

Several studies from around the globe have shown that bats generally are resilient even to large and severe wildfires (Buchalski et al. 2013; Law et al. 2018; Starbuck et al. 2020; Ancillotto et al. 2021), and that owing to fire-mediated changes in vegetation structure, species responses to fire depend on foraging strategy. Specifically, Blakey et al. (2019) found that in the Sierra Nevada, occurrence probability of open-adapted species was positively related with areas of higher fire severity or a history of more frequent fire, while the opposite was true for clutter-adapted species. More comparable in scope to our study, Starbuck et al. (2020) showed that in Arizona, forest bat activity 3 years postfire increased with fire severity for open-adapted species and decreased for clutter-adapted species. In Italy, Ancillotto et al. (2021) reported bats associated with

forest habitat showed a negative response in activity 1 year after a high-severity fire, but for most species, that effect disappeared or reversed 2 years postfire. We expected variable effects of fire severity on bat space use, mediated by their response to prey and habitat structure. Some of our findings agreed with previous studies: California myotis, a small species that forages in and around tree canopy (Krutzsch 1954), displayed a negative (though weak) response to increasing fire severity; one open-adapted species, the Mexican free-tailed bat, had a strong positive relationship with fire severity. But even though fire severity clearly affected habitat and prey conditions in our study, fire severity variables were the least important predictors of space use for the bat community (appearing in top models for only two species). This is consistent with other studies that found attributes of forest structure (Blakey et al. 2019), elevation, and distance to water (Starbuck et al. 2020) to be more important predictors of bat occupancy/activity than fire severity. Given the amount of variation in environmental conditions within categories of fire severity, the most likely explanation is that fire severity indicators alone are insufficient to describe aspects of the postfire landscape that are influential on bat space use.

Vegetation density affected the detection probability of the majority of bat species studied. Contrary to our expectations, shrub or tree density showed both positive and negative relationships with detection probability, depending on the species. These relationships followed no discernable pattern with respect to species foraging strategy, and species often had opposite responses to the two variables. Steel et al. (2019) similarly observed both (expected) negative and (unexpected) positive relationships of detection probability with canopy cover and suggested that bats may change their echolocation behavior in more cluttered environments.

While this study makes an important contribution to our understanding of the relationship between fire, habitat, prey, and bat space use, it is limited by its spatial and temporal scope. Sampling occurred during a single season 3 years postfire and thus only represents one snapshot in the succession of a postfire forest. Habitat structure postfire changes over time as understory plants—and eventually, trees—regenerate, consumers recolonize, and snags collapse. The effect of fire on bat space use is thus likely to change over time, as well. Indeed, time since fire was an important predictor of bat occupancy and activity in several studies (Blakey et al. 2019; Ancillotto et al. 2021). Our study also took place over a small area relative to the mobility of bats and thus potentially misses important fire-related predictors of bat space use that act on a larger (i.e., landscape) scale, such as pyrodiversity (Steel et al. 2019). Further, different bat species appear to respond to different predictors at different spatial scales (Starbuck et al. 2020). Due to the smaller spatial scale, sampling locations almost certainly were not spatially independent because multiple sites could be visited by the same bat in a single evening. This behavior can effectively "homogenize" apparent space use, especially when recordings are reduced to binary detection data for occupancy modeling, and likely contributed to the weakness or absence of effects for several covariates. While modeling the number of bat records (i.e., activity) provides higher resolution to investigate effects of fire on space use, condensing records to binary detection data circumvents several potential problems with record counts, such as the inability to distinguish between absence and nondetection at a site, and the need to determine a (almost always arbitrary) threshold beyond which subsequent records are deemed independent. Moreover, the adoption of the RN occupancy model allowed us to estimate site-level abundance (which we interpreted as an index of space use), which can be any nonnegative real number and thus is a more flexible quantity than occupancy probability, which cannot exceed 1. As a result, for example, a bat that has been detected at all sites will have perfect occupancy but still may exhibit variation in space use (in the RN model, the information for this variation comes from variation in encounter histories). Finally, our study was limited to a small number of survey locations, which constrained the complexity of models we were able to explore. For example, we did not explore interaction effects or quadratic effects of predictor variables, both of which are ecologically plausible (e.g., canopy cover may not be important in unburned habitat where it is consistently high but may be important in burned habitat). The small sample size, combined with large variability in environmental conditions within fire severity categories, also may preclude our ability to detect ecologically important effects because we lack the necessary statistical power, although use of AIC, which does not rely on statistical significance to determine effect importance, addresses this problem to a degree.

In conclusion, our data suggest that space use by bats in the Sierra Nevada may be largely resilient to megafire impacts, although variation in bat response to fire poses the possibility that community composition may change with increasing incidents of large and high-severity fire (Blakey et al. 2019). Despite sampling in a relatively small geographic area, our sampling efforts revealed an identical community assemblage to other studies in the Sierra Nevada with much larger spatial extent (Blakey et al. 2019; Steel et al. 2019), indicating that no species were locally extirpated due to the fire. This resilience, which also has been observed in other fire-prone ecosystems in Australia and Europe (Law et al. 2018; Ancillotto et al. 2021), likely stems from bats' mobility and resulting ability to exploit different habitat conditions over large spatial scales, evade immediate effects of fire, and recolonize burned landscapes. Even though moth prey—the strongest driver for bat space use in our study—were less abundant in burned forests, all but one bat species used burned forest as much as, or more, than unburned forest. Given our limited sampling scope (spatial, temporal, and, for prey, taxonomic), the relationship among wildfire, prey, and bat space use deserves further research. Many other questions remain related to how fire affects bats, for example, through changes in availability of roosting structures (e.g., Goldingay 2009). Developing a clear understanding of how megafires affect bats and their resources will help us protect these species and the ecosystem services they provide in a changing fire regime.

Acknowledgements

This work is part of the California Agricultural Station Hatch Project CA-D-WFB-2400-H. Invertebrate collection took place

under California Department of Fish and Wildlife Permit #SC-3638. We thank Christen Long (Bat Conservation International) for helping with bat species identification from call recordings. We thank the entire 13-person field team without whom data collection would not have been possible; and Kate Faber for helping with reference formatting and figure preparation. Finally, we thank two anonymous reviewers and the editor for their constructive feedback on earlier drafts of this manuscript. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the US Government.

Funding

This work received funding from the University of California Office of the President Catalyst Award (#CA-17-451736) and a Joint Venture Agreement (identification number: 17-JV-11272138-054) between the USDA Forest Service and UC Davis.

Supplementary Material

Supplementary data are available at Journal of Mammalogy online.

Supplementary Data SD1.—Spearman rank correlation between predictor variables used to model bat space use.

Supplementary Data SD2.—Moth community similarity among 27 sampling sites and the three burn categories.

Literature Cited

Ancillotto L., Bosso L., Conti P., Russo D. 2021. Resilient responses by bats to a severe wildfire: conservation implications. Animal Conservation 24:470–481.

Ball L.C., Doherty P.F., McDonald M.W. 2005. An occupancy modeling approach to evaluating a Palm Springs ground squirrel habitat model. Journal of Wildlife Management 69:894–904.

Bartoń K. 2019. MuMIn: multi-model inference. R package version 1.43.6. https://CRAN.R-project.org/package=MuMIn. Accessed 2019 Aug 1.

Blakey R.V., Webb E.B., Kesler D.C., Siegel R.B., Corcoran D., Johnson M. 2019. Bats in a changing landscape: linking occupancy and traits of a diverse montane bat community to fire regime. Ecology and Evolution 9:5324–5337.

Bowman D.M., Balch J., Artaxo P., Bond W.J., Cochrane M.A., D'Antonio C.M., Defries R., Johnston F.H., Keeley J.E., Krawchuk M.A., et al. 2011. The human dimension of fire regimes on Earth. Journal of Biogeography 38:2223–2236.

Broken-Brow J., Hitch A.T., Armstrong K.N., Leung L.K.-P. 2020. Effect of fire on insectivorous bat activity in northern Australia: does fire intensity matter on a local scale? Australian Journal of Zoology 67:260–268.

Buchalski M.R., Fontaine J.B., Heady P.A., 3rd, Hayes J.P., Frick W.F. 2013. Bat response to differing fire severity in mixed-conifer forest California, USA. PLoS One 8:e57884.

Burnham K.P., Anderson D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer Science & Business Media.

Butler O.M., Lewis T., Rezaei Rashti M., Maunsell S.C., Elser J.J., Chen C. 2019. The stoichiometric legacy of fire regime regulates the roles of micro-organisms and invertebrates in decomposition. Ecology 100:e02732.

Charbonnier Y., Barbaro L., Theillout A., Jactel H. 2014. Numerical and functional responses of forest bats to a major insect pest in pine plantations. PLoS One 9:e109488.

Chenger J. 2017. Tips for siting bat detectors. Bat Conservation and Management, Inc. https://batmanagement.com/blogs/acoustic-monitoring/tips-for-siting-bat-detectors. Accessed 2020 Sep 10.

Clare E.L., Symondson W.O., Fenton M.B. 2014. An inordinate fondness for beetles? Variation in seasonal dietary preferences of night-roosting big brown bats (*Eptesicus fuscus*). Molecular Ecology 23:3633–3647.

Dickinson M.B., Lacki M.J., Cox D.R. 2009. A review of fire effects on bats and bat habitat in the Eastern Oak region. In: Hutchinson T.F., editor. Proceedings of the 3rd Fire in Eastern Oak Forests Conference. General Technical Report NRS-P-46. Newtown Square (PA): US Department of Agriculture, Forest Service, Northern Research Station; p. 51–75.

Dodd L.E., Lacki M.J., Rieske L.K. 2008. Variation in moth occurrence and implications for foraging habitat of Ozark big-eared bats. Forest Ecology and Management 255:3866–3872.

Dodson E.K., Peterson D.W. 2010. Dry coniferous forest restoration and understory plant diversity: the importance of community heterogeneity and the scale of observation. Forest Ecology and Management 260:1702–1707.

Doty A.C., Stawski C., Law B.S., Geiser F. 2016. Post-wildfire physiological ecology of an Australian microbat. Journal of Comparative Physiology, B. Biochemical, Systemic, and Environmental Physiology 186:937–946.

Fiske I., Chandler R. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Goldingay R.L. 2009. Characteristics of tree hollows used by Australian birds and bats. Wildlife Research 36:394–409.

Haddad N.M., Haarstad J., Tilman D. 2000. The effects of long-term nitrogen loading on grassland insect communities. Oecologia 124:73–84.

Hechinger R.F., Lafferty K.D., Dobson A.P., Brown J.H., Kuris A.M. 2011. A common scaling rule for abundance, energetics, and production of parasitic and free-living species. Science 333:445–448.

Hollingsworth T.N., Johnstone J.F., Bernhardt E.L., Chapin F.S., 3rd. 2013. Fire severity filters regeneration traits to shape community assembly in Alaska's boreal forest. PLoS One 8:e56033.

Hutson A.M., Mickleburgh S.P., Racey P.A. 2001. Microchiropteran bats: global status survey and conservation action plan. Gland (Switzerland): IUCN.

Inkster-Draper T.E., Sheaves M., Johnson C.N., Robson S.K. 2013. Prescribed fire in eucalypt woodlands: immediate effects on a microbat community of northern Australia. Wildlife Research 40:70–76.

Jayen K., Leduc A., Bergeron Y. 2006. Effect of fire severity on regeneration success in the boreal forest of northwest Québec, Canada. Écoscience 13:143–151.

Johnston D.S., Fenton M.B. 2001. Individual and population-level variability in diets of pallid bats (*Antrozous pallidus*). Journal of Mammalogy 82:362–373.

Jones G., Jacobs D.S., Kunz T.H., Willig M.R., Racey P.A. 2009. Carpe noctem: the importance of bats as bioindicators. Endangered Species Research 8:93–115.

Knelman J.E., Graham E.B., Trahan N.A., Schmidt S.K., Nemergut D.R. 2015. Fire severity shapes plant colonization

effects on bacterial community structure, microbial biomass, and soil enzyme activity in secondary succession of a burned forest. Soil Biology and Biochemistry 90:161–168.

Krutzsch P.H. 1954. Notes on the habits of the bat, *Myotis californicus*. Journal of Mammalogy 35:539–545.

Lacki M.J., Cox D.R., Dodd L.E., Dickinson M.B. 2009. Response of northern bats (*Myotis septentrionalis*) to prescribed fires in eastern Kentucky forests. Journal of Mammalogy 90:1165–1175.

Lacki M.J., Johnson J.S., Dodd L.E., Baker M.D. 2007. Prey consumption of insectivorous bats in coniferous forests of north-central Idaho. Northwest Science 81:199–205.

Laudenslayer W.F., Darr H.H. 1990. Historical effects of logging on forests of the Cascade and Sierra Nevada ranges of California. Transactions of the Western Section of the Wildlife Society 26:12–23.

Law B., Doty A., Chidel M., Brassil T. 2018. Bat activity before and after a severe wildfire in Pilliga forests: resilience influenced by fire extent and landscape mobility? Austral Ecology 43:706–718.

Law B., Kathuria A., Chidel M., Brassil T. 2019. Long-term effects of repeated fuel-reduction burning and logging on bats in south-eastern Australia. Austral Ecology 44:1013–1024.

Loeb S.C. 2020. Qualitative synthesis of temperate bat responses to silvicultural treatments—where do we go from here? Journal of Mammalogy 101:1513–1525.

Long R., Simpson T., Ding T., Heydon S., Reil W. 1998. Bats feed on crop pests in Sacramento Valley. California Agriculture 52:8–10.

MacKenzie D.I., Nichols J.D., Lachman G.B., Droege S., Royle J.A., Langtimm C.A. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

Malison R.L., Baxter C.V. 2010. The fire pulse: wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers. Canadian Journal of Fisheries and Aquatic Sciences 67:570–579.

McGinnis T.W., Keeley J.E., Stephens S.L., Roller G.B. 2010. Fuel buildup and potential fire behavior after stand-replacing fires, logging fire-killed trees and herbicide shrub removal in Sierra Nevada forests. Forest Ecology and Management 260:22–35.

McKelvey K.S., Skinner C.N., Chang C., Et-man D.C., Husari S.J., Parson D.J., van Wagtendonk J.W., Weatherspoon C.P. 1996. An overview of fire in the Sierra Nevada. In: Centers for Water and Wildland Resources, editor. Sierra Nevada ecosystem project: final report to Congress, vol. II, assessments and scientific basis for management options. Davis (CA): University of California; p. 1033–1040.

Miller J.C. 1995. Caterpillars of Pacific Northwest forests and woodlands. Morgantown (WV): USDA Forest Service National Center of Forest Health Management.

Miller J.D., Knapp E.E., Key C.H., Skinner C.N., Isbell C.J., Creasy R.M., Sherlock J.W. 2009. Calibration and validation of the relative differenced Normalized Burn Ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. Remote Sensing of Environment 113:645–656.

Miller J.D., Safford H. 2012. Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, Modoc Plateau, and Southern Cascades, California, USA. Fire Ecology 8:41–57.

Nagel T.A., Taylor A.H. 2005. Fire and persistence of montane chaparral in mixed conifer forest landscapes in the northern Sierra Nevada, Lake Tahoe Basin, California, USA. Journal of the Torrey Botanical Society 132:442–457.

North M., Collins B.M., Stephens S. 2012. Using fire to increase the scale, benefits, and future maintenance of fuels treatments. Journal of Forestry 110:392–401.

Ober H.K., Hayes J.P. 2008. Prey selection by bats in forests of western Oregon. Journal of Mammalogy 89:1191–1200.

O'Shea T.J., Vaughan T.A. 1977. Nocturnal and seasonal activities of the pallid bat, *Antrozous pallidus*. Journal of Mammalogy 58:269–284.

Pausas J.G., Parr C.L. 2018. Towards an understanding of the evolutionary role of fire in animals. Evolutionary Ecology 32:113–125.

Perry R.W. 2011. A review of fire effects on bats and bat habitat in the Eastern Oak region. In: Dey D.C., Stambaugh M.C., Clark S.L., Schweitzer C.J., editors. Proceedings of the 4th Fire in Eastern Oak Forests Conference. General Technical Report NRS-P-102. Newtown Square (PA): US Department of Agriculture, Forest Service, Northern Research Station; p. 170–191.

Peters R.H. 1986. The ecological implications of body size. Cambridge University Press.

Powell J.A., Opler P.A. 2009. Moths of western North America. Oakland (CA): University of California Press.

R Core Team. 2018. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing; [accessed 2018 Feb 15]. www.R-project.org/.

Royle J.A., Nichols J.D. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84:777–790.

Savage M., Swetnam T.W. 1990. Early 19th-century fire decline following sheep pasturing in a Navajo Ponderosa pine forest. Ecology 71:2374–2378.

Siemann E., Tilman D., Haarstad J. 1996. Insect species diversity, abundance and body size relationships. Nature 380:704–706.

Sollmann R. 2018. A gentle introduction to camera-trap data analysis. African Journal of Ecology 56:740–749.

Starbuck C.A., Considine E.S., Chambers C.L. 2020. Water and elevation are more important than burn severity in predicting bat activity at multiple scales in a post-wildfire landscape. PLoS One 15:e0231170.

Steel Z.L., Campos B., Frick W.F., Burnett R., Safford H.D. 2019. The effects of wildfire severity and pyrodiversity on bat occupancy and diversity in fire-suppressed forests. Scientific Reports 9:16300.

Stephens S.L., Burrows N., Buyantuyev A., Gray A.W., Keane R.E., Kubian R., Liu S., Seijo F., Shu L., Tolhurst K.G., ET AL. 2014. Temperate and boreal forest mega-fires: characteristics and challenges. Frontiers in Ecology and the Environment 12:115–122.

Stephenson N.L., Parsons D.J., Swetnam T.W. 1991. Restoring natural fire to the sequoia-mixed conifer forest: should intense fire play a role. In: Sherman S.H., editor. Proceedings of the 17th Tall Timbers Fire Ecology Conference, May 18–21, 1989: High Intensity Fire in Wildlands: Management Challenges and Options. Tallahassee (FL): Tall Timbers Research Station; p. 321–337.

Swengel A.B. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. Biodiversity and Conservation 10:1141–1169.

Szewczak J.M., Morrison M.L., Harris L.S. 2018. Townsend's big-eared bat statewide assessment. Sacramento (CA): State of California, Natural Resources Agency, Department of Fish and Wildlife, Wildlife Branch.

Triplehorn C.A., Johnson N.F., Borror D.J. 2005. Borror and DeLong's introduction to the study of insects. Belmont (CA): Thompson Brooks/Cole.

USDA Forest Service. 2015. Environmental impact statement: King Fire restoration project volume 1. El Dorado and Placer Counties (CA): Eldorado National Forest.

USDA Forest Service. 2020. Eldorado—about the forest. https://www.fs.usda.gov/main/eldorado/about-forest. Accessed 2020 Sep 11.

Valdez E.W., Cryan P.M. 2009. Food habits of the hoary bat (*Lasiurus cinereus*) during spring migration through New Mexico. Southwestern Naturalist 54:195–200.

Valdez E.W., Cryan P.M. 2013. Insect prey eaten by hoary bats (*Lasiurus cinereus*) prior to fatal collisions with wind turbines. Western North American Naturalist 73:516–524.

van Wagtendonk J.W., van Wagtendonk K.A., Thode A.E. 2012. Factors associated with the severity of intersecting fires in Yosemite National Park, California, USA. Fire Ecology 8:11–31.

Westerling A.L., Hidalgo H.G., Cayan D.R., Swetnam T.W. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science 313:940–943.

Whitaker J.O. 1972. Food habits of bats from Indiana. Canadian Journal of Zoology 50:877–883.

Wray A.K., Jusino M.A., Banik M.T., Palmer J.M., Kaarakka H., White J.P., Lindner D.L., Gratton C., Peery M.Z. 2018. Incidence and taxonomic richness of mosquitoes in the diets of little brown and big brown bats. Journal of Mammalogy 99:668–674.

Submitted 25 September 2020. Accepted 23 October 2021.

Associate Editor was Chris Pavey.