Forest Ecology and Management 479 (2021) 118576

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

California spotted owl habitat selection in a fire-managed landscape suggests conservation benefit of restoring historical fire regimes

Anu Kramer[a,*], Gavin M. Jones[a,b,1], Sheila A. Whitmore[a], John J. Keane[c], Fidelis A. Atuo[a,d], Brian P. Dotters[e], Sarah C. Sawyer[f], Sarah L. Stock[g], R.J. Gutiérrez[h], M. Zachariah Peery[a]

[a] Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA
[b] USDA Forest Service, Rocky Mountain Research Station, Albuquerque, NM, USA
[c] USDA Forest Service, Pacific Southwest Research Station, Davis, CA, USA
[d] Department of Biology, Southeast Missouri State University, Cape Girardeau, MO, USA
[e] Sierra Pacific Industries, PO Box 496014, Redding, CA, USA
[f] USDA Forest Service, Pacific Southwest Region, Vallejo, CA, USA
[g] Yosemite National Park, El Portal, CA, USA
[h] Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul, MN, USA

ARTICLE INFO

Keywords:
California spotted owl
Foraging habitat selection
Fire use
Sierra Nevada
Strix occidentalis occidentalis
Wildland fire

ABSTRACT

Wildland fire is a disturbance that shapes frequent-fire forest ecosystems and the life-histories of wildlife species that inhabit them. The California spotted owl (*Strix occidentalis occidentalis*) is an iconic old-forest species that evolved under a frequent-fire regime in western North America. While recent studies have focused on owl response to large, severe fire events, relatively little is known about how owls might respond to prescribed fires and wildfires managed for resource benefit. Therefore, understanding how owls use landscapes that are managed using fire may offer insight into how owls respond to fire management. We studied the breeding season nocturnal foraging habitat selection of 22 GPS-tagged California spotted owls in three national parks (Yosemite, Sequoia, and Kings Canyon) in the Sierra Nevada, California, USA where natural fires have largely been allowed to burn during the past 50 years and controlled burning has been used to target additional areas. Consistent with other studies of this species, owls selected forests dominated by medium and large trees and avoided areas with smaller trees within their home ranges based on step selection analysis. Owls neither selected nor avoided forests burned by low- and moderate-severity, or high-severity fires, yet avoided larger patches of severely-burned forest (odds of selection decreased by 20% for every 10 ha increase in severely-burned patch area). These results indicated the importance of patch characteristics, suggesting that larger patches reflected either lower quality foraging habitat or increased predation risk, even in these frequent-fire landscapes where "large" severely-burned patches were small compared to those common after megafires. Additionally, selection strength increased for areas burned recently by lower-severity fire and, to a lesser extent, by older fires (largely of lower severity) as the extent of these burned areas increased within individual home ranges. These results suggested that lower-severity fire benefitted spotted owls and that these benefits declined over time. Thus, our findings are consistent with the hypothesis that California spotted owls are adapted to historical frequent-fire regimes of overall lower-severity with small high-severity patches. We hypothesize that fire management, coupled with medium- and large-tree retention, likely maintains high quality spotted owl habitat and may contribute to the observed owl population stability in Sequoia and Kings Canyon National Parks, compared to declining populations on three national forests. Finally, our results indicated that fire management, as practiced in these national parks, could benefit owl conservation elsewhere if challenges to the reintroduction of frequent-fire regimes can be overcome.

Abbreviations: HRV, historical range of variability; DOP, dilution of precision; FRAP, CAL FIRE's Fire and Resource Assessment Program; GNN, gradient nearest neighbor; GPS, global positioning system; SSF, step selection function; KDE, kernel density estimate; LEMMA Lab, Landscape Ecology, Modeling, Mapping, and Analysis Lab, Oregon State University; MTBS, Monitoring Trends in Burn Severity; VHF, very high frequency; VEGCLASS, vegetation class

* Corresponding author.
E-mail address: hakramer@wisc.edu (A. Kramer).

[1] Author made equal contributions as first author.

https://doi.org/10.1016/j.foreco.2020.118576
Received 26 June 2020; Received in revised form 31 August 2020; Accepted 1 September 2020

1. Introduction

Wildland fire, ignited both naturally and intentionally by humans, has shaped ecosystems and the ecology of species living in them for millions of years (Clark, 1989; Bond and Keeley, 2005; Shakesby and Doerr, 2006; Johnstone et al., 2016). Despite the importance of wildland fires as a natural process, they can impact natural resources (e.g., trees, water) and environments (e.g., rural and urban areas) to such an extent that people have attempted to suppress them for many years and across many systems (Moritz et al., 2014; Kramer et al., 2019; Wood and Jones, 2019). Consequently, fire suppression has led to unnaturally high densities of vegetation in some areas (Parsons and DeBenedetti, 1979; Sugihara et al., 2006; Collins et al., 2011, 2017a). This situation is particularly true of dry forests in the western United States, such as those in California's Sierra Nevada forest ecosystems, where unnatural increases in vegetation density, warming and drying associated with climate change, and increasing human populations in the wildland-urban interface have increased both the size and severity of wildland fires (Gill et al., 2013; Abatzoglou and Williams, 2016; Westerling, 2016; Schoennagel et al., 2017; Stevens et al., 2017). Although many "fuels management" techniques are available to land managers to reduce the risk of large, severe fires in natural landscapes, some techniques (e.g., tree thinning and fire use) have been controversial partly because of their potential negative effects on sensitive wildlife species (Hanson et al., 2009; Collins et al., 2010; Stephens et al., 2019; Kuchinke et al., 2020). Thus, understanding wildlife responses to thinning and fire use intended to reduce high-severity wildfires, as well as wildlife responses to those severe fires themselves, will inform management decisions.

Managing dry forests with fire is considered an effective and economical method of mimicking historical fire regimes to restore forest resilience and reduce the risk of future severe fire (Hardy and Arno, 1996; Sugihara et al., 2006; van Wagtendonk, 2007; North et al., 2015; Stephens et al., 2019; Hiers et al., 2020). Both prescribed fire and managed wildfire are methods of fire use: prescribed fire refers to fires that are planned, ignited, and managed from start to finish (Stephens and Moghaddas, 2005; Stephens and Ruth, 2005; North et al., 2007; Hiers et al., 2020) and managed wildfires are naturally ignited fires that are allowed to burn if they are deemed to pose little or no threat to humans or ecosystems (Christensen et al., 1987; Parsons and van Wagtendonk, 1996; Parsons and Landres, 1998; van Wagtendonk and Lutz, 2007). Despite the benefits of fire use, this technique is not always compatible with management objectives, which differ among private landowners, non-profit organizations, and public land management agencies (Young et al., 2020). As a result, different groups often use different approaches to reduce the risk of severe fire. For example, mechanical "treatments" (thinning or harvesting trees and/or manually thinning the understory) may be used instead of or in combination with fire in order to offset the cost of fuel reduction treatments, to increase precision of treatment outcomes (by choosing the spatial pattern or altering species composition), or to avoid the liability and smoke associated with burning (Stephens and Moghaddas, 2005). Wildland fire size, severity, and frequency, as well as its socio-ecological impact, also vary across the western United States because of variation in management approaches, local climate, and ecosystems (Parsons and Landres, 1998).

The U.S. National Park Service has pursued a policy of encouraging the use of fire since the 1960 s to restore or maintain natural ecosystem processes across the large, often remote landscapes of national parks. In these settings, fire is a relatively cost-effective management tool. In Yosemite, as well as Sequoia and Kings Canyon (the latter two parks are under joint management and hereafter referred to as Sequoia-Kings Canyon), National Parks located in the Sierra Nevada, fire policy allows not only prescribed fire, but also managed wildfire (Christensen et al., 1987; Parsons and van Wagtendonk, 1996; Parsons and Landres, 1998; van Wagtendonk and Lutz, 2007). Thus, compared to other forest lands in this region managed under different guiding objectives, this policy has resulted in some national park landscapes that more closely resemble historical conditions and processes: more frequent fires burning at low- to moderate-severity with fewer and smaller patches of high-severity fire (Collins and Stephens, 2007; Collins et al., 2008; Stevens et al., 2017; Kane et al., 2019).

Within the seasonal dry forests of the western United States, some management-sensitive species like the spotted owl (*Strix occidentalis*) use forest conditions typical of both historical and fire-suppressed forests for nesting, roosting, and foraging if they contain large trees and dense canopies with available prey (Bias and Gutiérrez, 1992; Call et al., 1992; Jones et al., 2018; Atuo et al., 2019; Blakey et al., 2019). However, spotted owls can be negatively impacted by both large high-severity fires (Jones et al., 2016, 2020; Rockweit et al., 2017) and fuel reduction treatments, at least in the short term, that are designed to reduce fire risk (Stephens et al., 2014a; Tempel et al., 2014; Gallagher et al., 2019). Therefore, it is essential to understand the impacts and tradeoffs of wildfire, prescribed fire, and mechanical fuels treatments on spotted owls and other sensitive species to facilitate their conservation in the short and long term. How best to manage habitat for spotted owls, given the potential threat of "megafires" (fires with an area of at least ~ 40,500 ha; Stephens et al., 2014b), is complicated by research suggesting opposite effects of severe fire on spotted owls. Whereas some studies have reported negative effects of high-severity fire on spotted owls (e.g. Jones et al., 2016, 2019, 2020; Eyes et al., 2017; Rockweit et al., 2017; Lommler, 2019), others have reported no negative effects of high-severity fire on this species (e.g. Lee and Bond, 2015; Bond et al., 2016). Thus, the resolution of these different findings will require studies of owl response to prescribed, managed, and wildland fire to answer the following questions: what types and configurations of high-severity fire negatively impact owls and their habitats, and what types and configurations might not convey these negative consequences? Given such information, how can prescribed fire, managed wildfire, or even other vegetation management techniques be used to mitigate potential threats without also harming owls (Jones, 2019; Peery et al., 2019; Jones et al., 2020)?

California spotted owls (*S. o. occidentalis*) have been studied intensively for many years throughout the dry forests of the Sierra Nevada in California and only one of four populations studied on public lands (located in Sequoia-Kings Canyon National Parks) has shown a stable population trend (Franklin et al., 2004; Blakesley et al., 2010; Tempel et al., 2016). Although it is not known why this owl population has been stable while the three others on national forests have declined, it has been hypothesized that the presence of higher densities of large trees, differing prey resources, and the restoration of fire to this system through prescribed and managed wildfire may be contributing factors (Franklin et al., 2004; Blakesley et al., 2010; Jones et al., 2018). Additionally, and perhaps because of these differences in burning between these landscapes, prey type consumed by owls also differs between national parks and national forests, with the diet of spotted owls in national parks consisting of a higher proportion of (high-calorie) woodrats and pocket gophers compared to national forests (Hobart et al., 2019a). Therefore, the forest conditions that are maintained through restorative fire management in Yosemite and Sequoia-Kings Canyon National Parks provide a unique opportunity to understand owl habitat selection when prescribed and managed fire are used extensively within their home ranges. Indeed, a recent study in Yosemite National Park revealed neutral owl selection of recently burned territories when < 30% of the core area had burned at high-severity, indicating compatibility between owl occupancy and lower-severity fire (Schofield et al., In press). One explicit goal of restorative fire management is to reduce high-severity fire that has the potential to kill larger trees that are key features of both old-growth forests and owl habitat (Jones et al., 2018). The benefits of restorative fire also include a reduction in the size of patches of forest that burn at high-severity (Collins et al., 2008; Kane et al., 2014). Hence, conserving larger trees and reducing the size of high-severity fire patches are two outcomes of restorative fire management that we predict will benefit spotted owls.

It is against this background and existing knowledge gaps that we studied California spotted owls in forests where fire is regularly used as a management tool. We formulated our study based on the hypothesis that owls evolved in forests characterized by frequent-fire regimes, including a patchy burn pattern with small areas of high-severity fire (Safford and Stevens, 2017), and that they would respond in predicable ways to the occurrence of fire in their home ranges. We predicted that in fire-restored landscapes, where high-severity patch size and characteristics are likely to be more closely aligned with the historical range of variability (HRV), (1) owls would show neutral or positive overall response to high-severity fire and higher levels of pyrodiversity (a mix of different burn severities and unburned area in close proximity), (2) owls would show no selection for or against high-severity patch characteristics, such as patch size, and they would equally forage along edges and far into larger patches of high-severity fire, and (3) owls would show neutral or positive response to low- and moderate-severity fire. These predictions were based on the assumption that in this landscape, high-severity patches created by a frequent-fire regime would fall within the HRV and therefore not adversely affect owl populations. Nevertheless, we acknowledge that severe fire even within the HRV could render some areas unsuitable for foraging by individual owls without adversely impacting populations. In addition, we tested whether habitat selection changed as a function of habitat availability within the home range (i.e., functional response) (Holbrook et al., 2019; Matthiopoulos et al., 2011; Mysterud and Ims, 1998). Our intent in testing these predictions was to help answer critical questions about the potential effects of fire to inform spotted owl conservation efforts.

2. Methods

2.1. Study site

We studied California spotted owl nocturnal habitat selection during the breeding season within three national parks: Yosemite and Sequoia-Kings Canyon. All three parks are located in the southern Sierra Nevada, California, and have experienced 50 years of active fire management (Fig. 1). Although fire restoration is still relatively recent in national parks, and "restored" areas encompass only 0.3% of the Sierra Nevada, Jeronimo et al., (2019) found that nearly 80% of these areas "restored" to the HRV fell within Yosemite and Sequoia-Kings Canyon National Parks, covering 3.7% of the area within these parks. Our study area encompassed these three parks, which spanned approximately 652,000 ha from the foothills (~500 m elevation) to the crest of the Sierra Nevada (> 4000 m elevation). The climate was Mediterranean, with cool, wet winters and warm, dry summers. Vegetation varied by elevation with oak woodlands and chaparral predominant at lower elevations, grading to mixed-conifer forests at middle elevations, and subalpine forests at higher elevations (Mayer and Laudenslayer, 1988; Sugihara et al., 2006). Logging is prohibited in national parks, which has resulted in the preservation of large, old trees (Beesley, 1996). Fire suppression began in the region during the late 19th century and continued until the late 1960 s when new fire policies for national parks allowed the use of fire as a restoration tool (van Wagtendonk, 1991, 2007; Sugihara et al., 2006). Beginning in 1968 in Sequoia-Kings Canyon National Parks, and 1972 in Yosemite National Park, both prescribed and managed fire were used to facilitate restoration of historical fire regimes and to increase forest resilience within the parks (van Wagtendonk, 1991; Parsons and Botti, 1996).

2.2. Owl space use data

We captured 27 owls (males and non-nesting females) in the breeding season of 2018 (April and May) either by hand, pan trap, or using snare poles (Bull, 1987; Franklin et al., 1996). We then fitted owls with small (7–10 g) tail-mounted dual GPS/VHF (very high frequency) tags (Lotek Pinpoint VHF 120, Newmarket, Ontario, Canada; GPS/VHF tags hereafter as "GPS tags") that allowed remote downloading of onboard data. We recaptured owls to remove GPS tags when possible and expected tail-mounted tags of owls that we did not recapture to be shed during the next tail molt. We used the VHF capabilities to relocate tagged owls for recapture and GPS data retrieval, but in our habitat selection analyses, we used only the GPS locations. Accordingly, we programmed GPS tags to collect five hourly GPS locations per night (2200 to 0200), which we assumed primarily represented foraging activities because owls are nocturnal predators. However, owls engage in territory defense, resting, and returns to the nest at night that may also be reflected in these GPS locations (Forsman et al., 1984; Delaney et al., 1999).

2.3. Fire history and severity

We compiled fire history from CAL FIRE's Fire and Resource Assessment Program (FRAP) database, where we downloaded perimeters of all fires in our study area that were at least 10 acres in size (http://frap.fire.ca.gov/, accessed May 2, 2018). This dataset also included information on whether a fire was a wildfire or a prescribed fire. We compiled fire severity data using the Monitoring Trends in Burn Severity (MTBS) database and additional data maintained by each national park. MTBS severity data (http://www.mtbs.gov/, accessed February 14, 2018) accounted for all fires in our study area over 1,000 acres (405 ha) in size that burned between 1984 and 2017 (Eidenshink et al., 2007). However, for smaller fires (100–1,000 acres) including wildfires and prescribed burns, we used spatially explicit severity data provided by Yosemite (personal communication, K. van Wagtendonk; Lutz et al., 2011) and Sequoia-Kings Canyon (personal communication, K. Folger) National Parks that used the same methodology as MTBS. Although these additional datasets included fires that burned before 2003, many older wildfires in the smaller size class (100–1,000 acres) lacked data on severity. Therefore, we used 2003 as the oldest date to include fire severity in our analyses.

We used the FRAP database of fire perimeters to check that our fire severity dataset included all wildland fires that burned over 100 acres between 2003 and 2017, with at least 30 acres of that burned area within an owl's home range. We defined home range as the 95% kernel density estimate (KDE) from all filtered nocturnal GPS locations (see Habitat Selection Analysis section below for filtering methods) for each individual owl. However, a significant amount of fire severity data was missing for two owls, so we removed them from analysis. Four of 21 prescribed fires were missing information on fire severity, yet we found that only 1% of the area of the 17 prescribed fires in our dataset burned at high-severity. Thus, we assumed that these four prescribed fires only burned at low- and moderate-severity and that all fires smaller than 100 acres (for which we did not have information on fire severity) also burned at low- and moderate-severity. For fires that burned < 30 acres (12 ha) of an owl's home range (home ranges were 750 – 3,000 ha), we included severity information, where available, and assumed that the area burned at low- and moderate-severity in cases when this information was not available.

We classified each burn location as follows: (a) burned 41 to 65 years prior (1953–1977), (b) burned 16 to 40 years prior (1978–2002), (c) burned at low- and moderate-severity (up to 75% overstory mortality) up to 15 years prior (2003–2017), and (d) burned at high-severity (over 75% overstory mortality) up to 15 years prior (2003–2017; Table 1). We grouped low- and moderate-severity fire (henceforth "lower-severity") because others have shown that owl selection was similar between these areas (Bond et al., 2002; Eyes et al., 2017). We also used the definition of high-severity commonly used in other papers on spotted owls and wildfire (Jones et al., 2016; Eyes et al., 2017; Hobart et al., 2020), although we note that other thresholds for high-severity wildfire have been used (Bond et al., 2002;

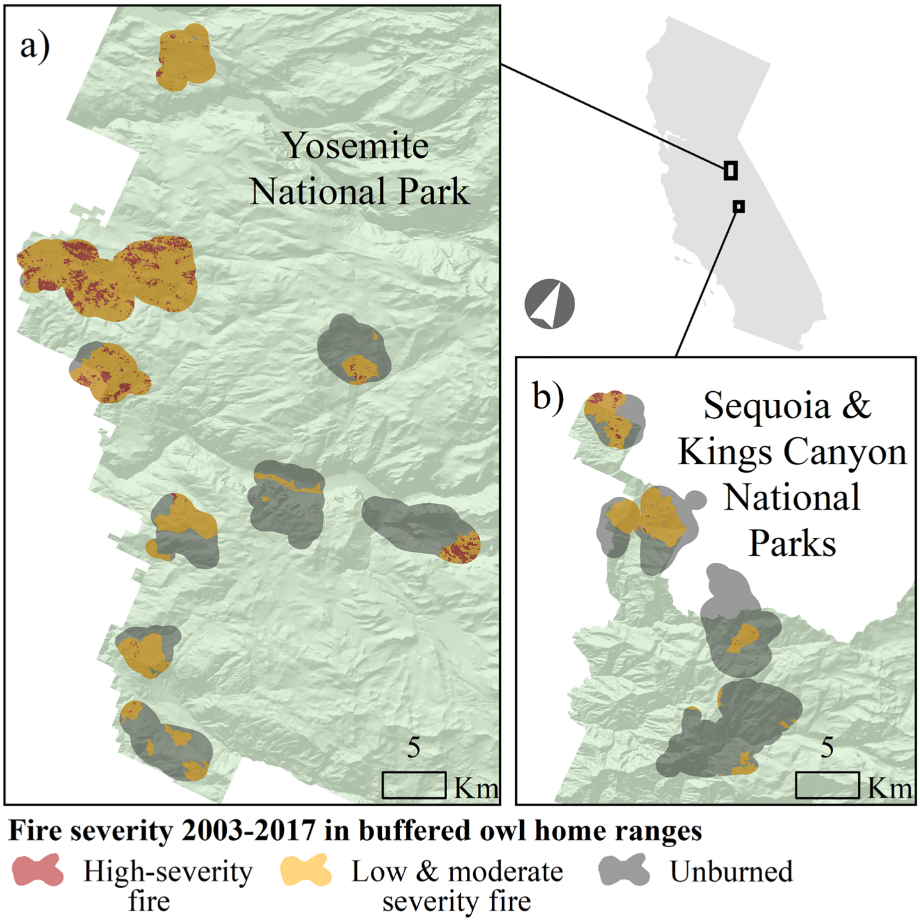

Fig. 1. Map of our California spotted owl study area in the Sierra Nevada, California, showing fire severity within buffered owl home ranges in (a) Yosemite National Park (n = 13 owls), and (b) Sequoia & Kings Canyon (n = 9 owls) National Parks. Home ranges represent the 95% kernel density estimate of all owl nocturnal GPS locations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Lydersen et al., 2016; Collins et al., 2017b). If an area burned more than once between 2003 and 2017 (0.6% of assessment points in our analysis), we used the highest burn severity for that location for the classification because we expected high-severity fire to represent the predominant fire effects at that location. However, areas that burned in older fires were noted separately, such that an area could be coded as having burned during as many as three time periods, corresponding to the three time periods described above (e.g. an area that burned in 1967 and 1976, but not more recently would be coded as Burned $_{1953\text{-}1977}$ = 1, Burned $_{1978\text{-}2002}$ = 0, Lower-severity = 0, and High-severity = 0; Table 1).

Spotted owl foraging patterns have been shown to be correlated with the spatial characteristics of high-severity patches (Jones et al., 2020). Thus, we calculated the size of each high-severity fire patch, the "permeation distance" of each point (the distance from the point to the patch edge, conditional on the point occurring within a high-severity patch), and the patch complexity (perimeter-area ratio of the patch; Table 1). We also computed a pyrodiversity index using data from fires

Table 1
Covariates used to model California spotted owl habitat selection in Sequoia, Kings Canyon, and Yosemite National Parks California, including the variable description, class, type, and values. Continuous variables were scaled so that values fell between 0 and 1.The class of each variable links it to the three stages of analyses, where stage I corresponds to landscape and disturbance covariates tested in a step selection function (SSF), stage II uses only high-severity patch covariates in an SSF, and stage III utilizes disturbance and patch covariates to test for functional response. Acronyms used in the table include digital elevation model (DEM), gradient nearest neighbor vegetation estimates (GNN), quadratic mean diameter (QMD), and monitoring trends in burn severity (MTBS).

Variable	Description	Class	Type	Range of values
Elevation	Elevation (m) based on a DEM	Landscape	Continuous	1000–2800
Medium-large trees	Proportion of area where dominant trees have medium and large diameters (as determined by 2016 GNN; QMD ≥ 25 cm) within 100 m radius (0–100%)	Landscape	Continuous	0–1
Small trees	Proportion of area where dominant trees have small diameters (as determined by 2016 GNN; QMD < 25 cm) within 100 m radius (0–100%)	Landscape	Continuous	0–1
Lower-severity	The point burned at low- and moderate-severity in 2003–2017	Disturbance	Categorical	0 or 1
High-severity	The point burned at high-severity in 2003–2017	Disturbance	Categorical	0 or 1
Burned$_{1978–2002}$	The point burned from 1978 to 2002	Disturbance	Categorical	0 or 1
Burned$_{1953–1977}$	The point burned from 1953 to 1977	Disturbance	Categorical	0 or 1
Pyrodiversity	Shannon diversity of 3-class (unburned; low/mod -severity; high-severity) MTBS classification within 100 m buffer for fires in 2003–2017	Disturbance	Continuous	0–1.09
Patch area	Area (ha) of severe fire patch[1] that point falls in for fires in 2003–2017	Patch	Continuous	0–225
Patch complexity	Perimeter-to-area ratio of the severe fire patch[1] that a point falls in for fires in 2003–2017	Patch	Continuous	0–0.133
Permeation distance	Distance (m) from point within severe fire patch to edge for fires in 2003–2017	Patch	Continuous	0–265

[1] High-severity patches were smoothed to remove patches under 4 pixels (0.36 ha)

that burned between 2003 and 2017, where we calculated the Shannon diversity of unburned, lower-severity, and high-severity fire within a 100-m radius of each point (Table 1). Thus, an area composed entirely of a single class (unburned, lower-severity, or high-severity) would yield a pyrodiversity index equal to 0, whereas an area composed of multiple classes would yield a pyrodiversity index > 0.

2.4. Environmental variables

We determined the elevation at each point, which is related to spotted owl habitat preferences (Kramer et al., in revision). We also used Gradient Nearest Neighbor (GNN) maps of forest structure to classify the 2016 landscape into vegetation classes as follows: (i) forests where dominant trees were small in diameter (henceforth small trees), where canopy cover was at least 40% and the quadratic mean diameter of dominant trees was under 25 cm, (ii) forests where dominant trees were medium and large in diameter (henceforth medium-large trees), where canopy cover was at least 40% and the quadratic mean diameter of dominant trees was at least 25 cm, and (iii) open areas where canopy cover was under 40% (LEMMA Lab, Oregon State University, Corvallis, OR; using their *VEGCLASS* variable; Ohmann and Gregory, 2002). Note that we combined medium and large tree categories, given uncertainties in the accuracy of the GNN-based vegetation cover type classifications at fine scales. While there were two years between GNN habitat classification and bird tagging, there were minimal changes in forest structure to owl home ranges in our study area besides a few small fires (all under 10 acres between 2016 and when owl GPS data was collected in 2018), so we assumed these habitat classifications provided an acceptable representation of general forest structure.

2.5. Three stages of analysis

We used a three-part analysis to explore the effects of fire on spotted owl foraging habitat selection. In stage I of our analyses, we modeled selection relative to landscape and fire-related disturbance variables (Table 1) to examine how this broad range of environmental covariates shaped selection. In stage II of our analyses, we examined whether covariates related to the spatial characteristics of severely-burned areas could further explain patterns of selection related to the simple categorical severe fire effect from stage I. Therefore, we tested whether the spatial pattern and configuration of high-severity patches (area, complexity, and permeation distance; Table 1) influenced selection by owls. The third and final stage of analysis tested for a functional response in habitat selection to determine whether differing individual levels of exposure to the fire disturbance- and high-severity patch-related covariates (Table 1) also influenced habitat selection (see below) (Holbrook et al., 2019; Matthiopoulos et al., 2011; Mysterud and Ims, 1998). We examined these three stages of questions by developing models in each stage that allowed us to test and evaluate these questions.

2.5.1. Habitat selection analyses: Stages I and II

The analyses performed for stages I and II were similar, with the exception of the covariates used in the models. We examined patterns of habitat selection using a use-availability framework that compared habitat attributes at used locations to those at randomly generated available locations (Manly et al., 2002; Hooten et al., 2017). To improve spatial accuracy (to achieve median error of ~20 m) we only used GPS location points that had a dilution of precision (DOP) below five and whose coordinates were estimated by at least four satellites (Kramer et al., in revision). As a result, we excluded three individuals from analysis that had < 100 usable GPS points and two individuals that lacked sufficient fire severity data, which yielded an analysis sample of 22 individuals (13 from Yosemite and nine from Sequoia-Kings Canyon National Parks). Our sample owls had an average of 4.6 GPS points per night and 47 nights per individual. Because we eliminated an average of only 0.4 points per night per owl, we were confident that our data filtering process did not result in substantive bias, even though it was possible that more points under dense canopy were elimated due to fewer satellite hits (but see Frair et al., 2004).

We used a step selection function (SSF) to test for patterns in habitat selection (Duchesne et al., 2010; Fortin et al., 2005; Muff et al., 2020), where available habitat associated with a given owl location was conditional on where the individual occurred at the time of the previous GPS location during the same night (i.e. a “step”). While a “used” point refers to an owl GPS location, “available” points refer to 10 locations that were theoretically available for selection by that individual during that time period. For this reason, we calculated the position of these 10 available points by selecting random points that fit the spatial distribution of step lengths and step time intervals for any movement an owl made, while accounting for differences among individuals. Since some step intervals were 2–3 h long (because some GPS points were eliminated from analysis as described above), we created distributions of hourly, bi-hourly, and tri-hourly step lengths. All random points were located within a 400 m buffered 95% KDE. We used this buffer to avoid restricting the directionality of available steps near the edge of the owl’s home range. Thus, turn angles were random and represented a uniform distribution, corresponding to non-directional random walks (Fortin et al., 2005).

We used mixed conditional Poisson regression models with stratum-specific intercepts, which are likelihood-equivalent to mixed conditional logistic regression models that yield equivalent parameter estimates and standard errors (Duchesne et al., 2010; Muff et al., 2020). We fitted the SSF using the Poisson formulation where the stratum-specific random intercept variance was fixed to a large value to avoid shrinkage, following Muff et al. (2020). By using conditional Poisson regression we were able to compare observed and available locations representing temporally correlated “matched pairs,” as was the case with our data.

Our response variable was binary (1 = used, 0 = available). In the stage I analysis that examined landscape characteristics and fire-related disturbance, we fitted a model that included elevation, pyrodiversity (2003-2017), small trees, and medium-large trees as continuous fixed effects and burned$_{1953\text{-}1977}$, burned$_{1978\text{-}2002}$, lower-severity burn (2003-2017), and high-severity burn (2003-2017) as categorical fixed effects. In the stage II analysis that focused on high-severity patch characteristics, we added to the stage I model continuous variables related to features of high-severity fire patches: patch size (2003-2017), permeation distance (2003-2017), and patch complexity (2003-2017). Since these variables were moderately- to highly-collinear with one another, we did not include them in the same model, but ran three separate SSF models. Because a SSF matches available points in close proximity to each used point, we did not include a variable for the distance from the nest or activity center of these central place foragers (Rosenberg and McKelvey, 1999). We tested for correlation among all continuous predictor variables and none were highly correlated (correlation coefficient > 0.7). We rescaled all continuous variables so that they would range between 0 and 1. Although we did not formally test for variability among individuals, we adopted the advice of Duchesne et al. (2010) that individual (random) coefficients should be included to avoid bias in the population-level (fixed) effects, allowing for more robust population-level habitat selection estimates, given individual heterogeneity. We used the R package glmmTMB version 0.2.0 to conduct the step selection analysis (Magnusson et al., 2017).

2.5.2. Functional response analysis: Stage III

A functional response to an available resource by an animal is indicated by an estimate for selection of that resource that changes as that resource also becomes more abundant (available) to the animal in its home range (Hebblewhite and Merrill, 2008; Holbrook et al., 2019; Jones et al., 2020; Mysterud and Ims, 1998). We tested for functional responses in habitat selection in our stage III analysis by including an interaction term between the habitat covariate of interest and a term representing its availability within a given individual's home range,

Table 2
Coefficient estimates from a mixed-effect step selection analysis from stage I (estimating California spotted owl selection relative to disturbance and land cover in the Sierra Nevada) and stage II (estimating California spotted owl selection relative to high-severity fire patch-related covariates). Column abbreviations correspond to: β, population-level (fixed) coefficient; SE, standard error of the mean; LCL, lower 95% confidence limit; UCL, upper 95% confidence limit; p, p-value for the effect of the population-level coefficient; σ^2, variance of individual-level (random) effects for each parameter.

variable	β	SE	LCL	UCL	p	σ^2
stage I						
elevation	−0.46	0.71	−1.84	0.93	0.52	10.69
small trees	−2.43	0.93	−4.25	−0.61	0.01	13.94
medium-large trees	1.16	0.26	0.65	1.66	< 0.01	1.19
burned $_{1953\text{-}1977}$	−0.25	0.37	−0.97	0.48	0.51	1.47
burned $_{1978\text{-}2002}$	−0.30	0.17	−0.64	0.03	0.08	0.49
lower-severity	0.47	0.33	−0.17	1.11	0.15	1.59
high-severity	−0.50	0.41	−1.30	0.29	0.22	< 0.01
pyrodiversity	−0.91	0.35	−1.58	−0.23	< 0.01	1.65
stage II						
patch size	−4.52	2.15	−8.73	−0.31	0.04	12.18
permeation distance	−3.45	2.26	−7.89	0.99	0.13	9.64
patch complexity	1.18	0.92	−0.63	2.99	0.20	1.40

where availability was constant for each individual owl and represented the proportion of that resource among all available locations generated for the SSF within each individual's home range (Matthiopoulos et al., 2011; Aarts et al., 2013). We ln-transformed availability because functional responses are assumed to be non-linear (Mysterud and Ims, 1998; Beyer et al., 2010). In all three analyses, we gauged the importance of fixed effects based upon their direction, effect size, and uncertainty (using 95% confidence intervals). We used R version 3.6.0 for analyses.

3. Results

We obtained 4,815 usable nocturnal GPS locations for the 22 GPS-tagged owls we monitored in 2018 that was composed of four females (all paired, but not nesting), and 18 males (all paired, with nine nesting and nine not nesting). These GPS locations provided data for 3,765 used steps (i.e., the first GPS point on any given night was the reference for subsequent steps and was not treated as a step itself) ranging from 118 to 188 used steps per owl (Table 1). We generated 37,650 available step locations corresponding to the 10 available steps generated for each used step. Owl home ranges were composed of 59.8% medium-large tree forest, 5.6% small tree forest, and 34.6% bare area (Fig. S1). Among all owls, 47.6% of used locations (steps) were in areas that had burned in the previous 15 years (between 2003 and 2017), with 46.2% of all used points having burned at lower-severity and 1.4% at high-severity (Fig. S1). The distribution of available locations (steps) was similar, with 44.1% falling in burned areas but with fewer available points in lower-severity burned areas (40.3%) and more in severely burned areas (3.9%). Among high-severity patches used, patch size ranged between 0.36 and 225 ha with a median of 18 ha (Table 1; Fig. S2). The overall distribution of high-severity patches within owl home ranges was skewed toward smaller patch sizes, with a maximum patch size of 225 ha (Fig. S2).

3.1. Landscape and disturbance selection analysis: Stage I

Spotted owls in our study areas selected forests with medium and large-sized dominant trees ($\beta_{\text{medium-large trees}}$ = 1.16, 95% confidence interval [0.65, 1.66]) and avoided forests where dominant trees were small ($\beta_{\text{small trees}}$ = − 2.43 [−4.25, −0.61]; Table 2; Fig. 2). There was no apparent selection relative to whether an area had burned in older fires ($\beta_{\text{burned 1953-1977}}$ = − 0.25 [−0.97, 0.48]; $\beta_{\text{burned 1978-}}$

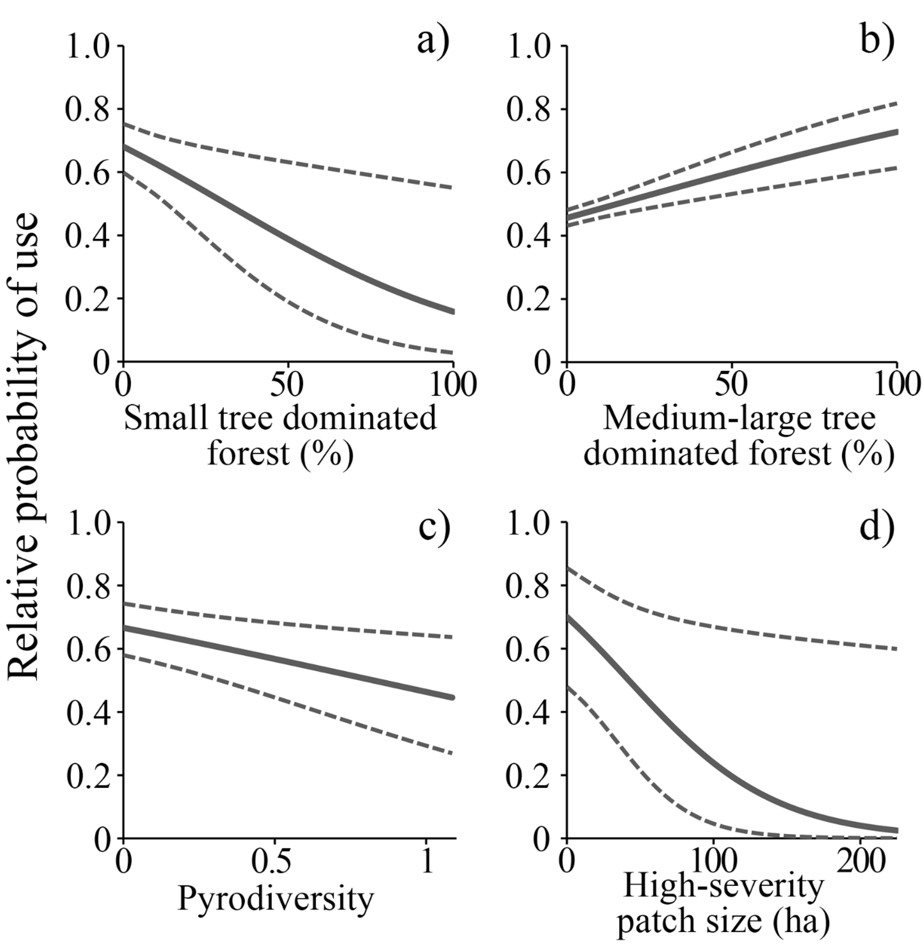

Fig. 2. Relative probability of use by California spotted owls in Sequoia, Kings Canyon, and Yosemite National Parks plotted against (a) the proportion of small tree dominated forest within 100 m, (b) the proportion of medium-large tree dominated forest within 100 m, (c) the pyrodiversity of fires that burned between 2003 and 2017 within 100 m, and (d) the size of a given high-severity fire patch (that burned between 2003 and 2017). The probability of use is shown as a solid line and the 95% confidence interval is bounded by dashed lines.

$_{2002}$ = − 0.30 [−0.64, 0.03]). There was also no apparent selection relative to the categorical effect of high fire severity ($\beta_{\text{high-severity}}$ = − 0.50 [−1.30, 0.29]) or lower-severity fire ($\beta_{\text{lower-severity}}$ = 0.47 [−0.17, 1.11]) in more recent fires (Table 2). Owls selected areas that had lower pyrodiversity suggesting that, opposite to our prediction, they avoided areas that experienced a higher diversity of burn severities ($\beta_{\text{pyrodiversity}}$ = − 0.91 [−1.58, −0.23]; Table 2; Fig. 2).

3.2. High-severity patch selection: Stage II

When we compared selection or avoidance of patch characteristics by owls within severely-burned areas, owls showed avoidance of larger patches ($\beta_{\text{patch size}}$ = − 4.52 [−8.73, −0.31]) indicating that the odds of selection decreased by 20% for every 10 ha increase in severe fire patch size based on odds ratio and covariate scaling (Table 2; Fig. 2). Owls appeared to avoid traveling farther into severe fire patches ($\beta_{\text{permeation distance}}$ = − 3.45 [−7.89, 0.99]) and appeared to select more convoluted patches ($\beta_{\text{patch complexity}}$ = 1.18 [−0.63, 2.99]), although the 95% CIs for both of these effects overlapped zero (Table 2).

3.3. Functional response analysis: Stage III

Owls selected areas that had burned in the past 16–40 years when this type of area was more abundant within their home range ($\beta_{\text{burned 1978-2002-FR}}$ = 0.48 [0.09, 0.87]; Table S1; Fig. 3A). Similarly, owl selection for areas that burned at lower-severity in recent fires (up to 15 years old) increased as this type of burned area became more abundant within their home range ($\beta_{\text{lower-severityFR}}$ = 0.55 [0.04, 1.05]; Table S1; Fig. 3B). There was no evidence for a functional response in the other six variables considered (see Table S1 and Fig. S3). Although Table S1 indicates weak evidence for a functional response to severe fire patch size (p = 0.06), inspection of the response curve indicates this effect was driven by a single owl that showed no change in selection based on patch size, while all other individuals showed relatively strong avoidance as patch size grew larger (Table S1; Fig. S3).

apparent in our stage I analysis in which only a categorical effect of severe fire was explored. This demonstrated the importance of including high-severity patch size in analyses of spotted owl habitat selection, even in these landscapes with partially restored fire regimes and relatively small severely-burned patches (Jones et al., 2020). Second, although owls neither preferentially selected nor avoided areas burned recently at lower-severity and areas burned by older fires, their strength of selection for these areas became stronger as their prevalence within home ranges increased – this functional response in habitat selection was a finding novel to studies of spotted owls in burned landscapes. Collectively, these two results suggested that owls were resilient, and likely adapted, to the patchwork of fire effects that characterize these landscapes with frequent-fire regimes (primarily low- and moderate-severity intermixed with small high-severity patches). Our findings support the hypothesis that spotted owls are adapted to frequent-fire regimes and when coupled with the retention of medium-large trees, may explain in part why spotted owl populations were stable in Sequoia-Kings Canyon National Parks (Franklin et al., 2004; Blakesley et al., 2010). Our results also suggest that spotted owl habitat can benefit from the restoration of frequent fires.

3.5. Selection for forest type

Spotted owls avoided forests dominated by small trees and selected for forests dominated by medium- to large-sized trees, a finding that was consistent with previous studies of both California (Call et al., 1992; Gutiérrez et al., 1992; Roberts, 2017) and northern spotted owls (Solis and Gutiérrez, 1990; Gutiérrez et al., 1995). Thus, despite our broad characterization of medium-large forest (QMD ≥ 25 cm) that covered 59.8% of owl home ranges (Fig. S1), our results emphasize that this forest type constitutes important foraging habitat for spotted owls in fire-managed landscapes, as is the case in other forested landscapes. Although we did not evaluate specific structures likely important to owls such as large trees and dense large-tree canopies (Bias and Gutiérrez, 1992; North et al., 2017), higher resolution representations of forest type and structure (e.g., with LiDAR) and prey studies would further improve our understanding of the specific features used by owls for foraging in forests with frequent fire regimes.

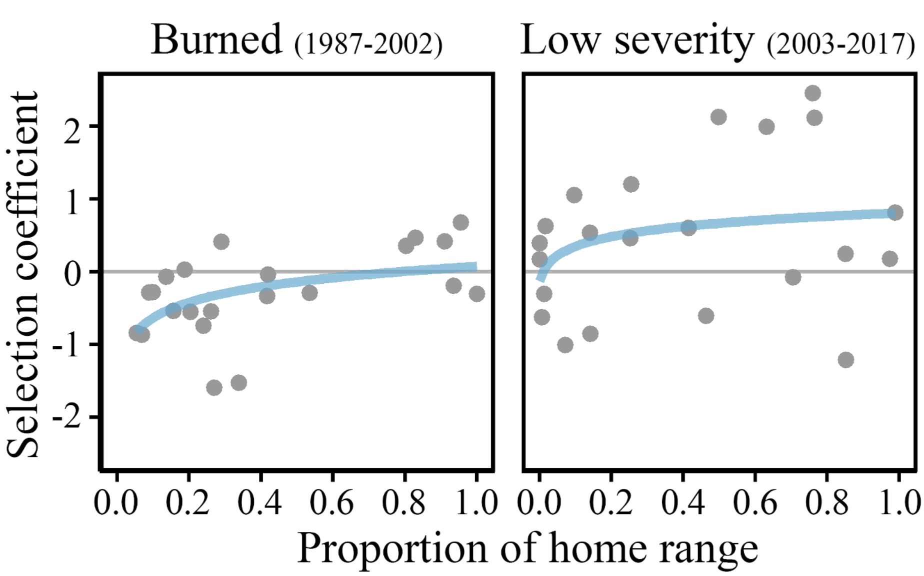

Fig. 3. Functional responses by California spotted owls in Sequoia, Kings Canyon, and Yosemite National Parks when selecting areas burned within their home ranges that were significantly different from zero, including the proportion of owl territory (a) burned at any severity between 1978 and 2002 and (b) burned at lower-severity between 2003 and 2017, with each dot representing an individual owl, and blue lines indicating significant trends. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Discussion

We made two key discoveries about the way California spotted owls used burned forests in national parks that have significant implications for the conservation of this species in the Sierra Nevada and other frequent-fire forest ecosystems where they occur. First, spotted owls avoided larger patches of high-severity fire, a trend that was not

3.6. Selection for burn severity class and patch characteristics

Owls avoided larger patches of severely-burned forest, suggesting that spotted owl selection/avoidance of forests burned at high-severity could only be adequately interpreted in light of severe fire patch size. We expected that the largest high-severity patches on these fire-managed landscapes would be relatively small in comparison to previous studies and would thus not be avoided by owls. Indeed, high-severity patches within owl home ranges in this study were heavily skewed toward smaller patches, with a median of 18 ha and the largest patch measuring 225 ha and highly convoluted in shape (Fig. S2; Fig. S3). This pattern was consistent with the HRV for Sierra Nevada yellow pine mixed-conifer forests, where high-severity patches rarely exceeded 100 ha (Safford and Stevens, 2017). In comparison, in the 2014 King fire (a megafire), where Jones et al. (2020) found that owls avoided larger patches and patch interiors, the largest high-severity burned patch was 8,818 ha. Severe fire patches in this study were smaller and more complex than the patches within the King Fire (Collins et al., 2017b; Stevens et al., 2017) (Fig. S4). Therefore, although owls may use smaller severely burned patches, owls tended to avoid larger patches within their home range (but see Fig. S3), even in landscapes where patches of this type remain relatively small and often highly convoluted (Jones et al., 2016, 2019, 2020; Eyes et al., 2017). Although these patches were recently burned, their age ranged between one and 15 years old, with varying amounts of vegetative ingrowth. Despite this variation, owls may have avoided large patches of high-severity fire for several potential reasons such as predator avoidance, low prey availability (little vegetation on recently burned areas may decrease prey abundance, and dense shrub ingrowth longer after a fire may hinder prey capture by owls, even if prey abundance is high), and insufficient perches to support their hunting strategy (Forsman et al., 1984; Gutiérrez, 1985). Consistent with our finding that spotted owls avoided large patches of severe fire, Schofield et al. (in press) found that owls were less likely to occupy territories in Yosemite National Park that experienced high severity fire across $>$ 30% of their core area. Thus, while owl populations may be relatively stable in landscapes with partially restored fire regimes, larger areas of high severity fire that make habitat less suitable for foraging also appear to have emergent effects that render territories less suitable for occupancy by owls in these landscapes.

Although confidence intervals for effects of permeation distance and patch complexity overlapped zero, our results suggested that owls may have selected more complex severe fire patches and may have avoided traveling further into severe fire patches (Table 2). The direction of the selection coefficient estimates were consistent with Eyes et al. (2017), who found that owls frequently foraged along the edges of severely burned patches, as well as Jones et al. (2020), who showed that spotted owls rarely traveled over 100 m into a severely-burned patch. Similarly, the maximum distance traveled into severely burned patches in our study was 169 m, and only 6% of locations that occurred within severely burned patches (0.08% of all locations) were farther than 100 m from the patch edge. Thus, our ability to detect significant effects may have been constrained by the small patches in this study. Even though we did not detect a significant effect of permeation distance, owls appeared to avoid making deep forays into larger patches of severe fire, regardless of tree size, in areas burned by both megafires (in the case of the King fire referenced above) and fires resembling historical regimes (reflected by our results for this study).

There has been disagreement in the literature about the effect of high-severity fire on spotted owls (Peery et al., 2019) because some studies have detected positive effects while others have detected negative effects (Ganey et al., 2017; Lee, 2018; Jones et al. In press). However, mounting evidence suggests these contrasting results could be explained in part by the spatial pattern and configuration of severely burned areas (Jones et al., 2020; this study). Our results indicated that owls avoided larger high-severity patches, even in a landscape where larger high-severity patches were relatively small, suggesting the importance of these characteristics to owl selection. Additionally, recent work on the King fire showed that while owls used some areas that burned at high-severity, they avoided both larger patches of severe fire and avoided traveling deep into those patch interiors, even after accounting for the potential effects of salvage logging (Jones et al., 2019, 2020). Thus, the size and configuration of high-severity patches may determine the direction and strength of owl habitat selection. The absence of these high-severity patch characteristics in earlier studies (e.g., Bond et al., 2009, 2002) may potentially explain why adverse effects of high-severity fire were not detected, which would be similar to our results of neutral selection in our stage I analysis where we did not consider the characteristics of high-severity patches.

Questions have also lingered about the potentially confounding effects that salvage logging of severely burned areas could have on spotted owl response to high-severity fire. Although salvage logging was explicitly accounted for by Jones et al. (2020), who found avoidance by spotted owls of both salvage logging and large patches of severe fire after the King fire, there is strong interest in studies of owl response to severe fire in areas where salvage logging operations have not occurred at all (Bond et al., 2009; Lee and Bond, 2015). Our study in national park landscapes (also see Roberts et al., 2011, Eyes et al., 2017, and Schofield et al., in press) provided such an opportunity to formally examine the response of owls to severe fire in the absence of salvage logging while also accounting for patch characteristics that were not considered in many previous studies (e.g. Bond et al., 2009, 2016; Lee and Bond, 2015). Thus, our results suggested that in the absence of salvage logging (though we note the possibility of the occurrence of small areas of hazard tree removal along roads and other areas where hazard trees could endanger park visitors) spotted owls avoided larger patches of severely-burned forest, yet this relationship was only apparent when high-severity patch size was included in the analysis.

3.7. Selection for lower-severity burned areas

Our results supported our prediction that spotted owls are resilient to lower-severity fire, as well as older burned areas, the majority of which were likely of lower-severity (similar to trends in more recent fires). Owls in this study neither selected for nor against areas burned by recent lower-severity fire (within 15 years) or older fire (that burned 16–40 years before), each of which covered about 40% (with overlap) of owl home ranges in our study. Our results were supported by other studies that have shown spotted owls to be resilient to low- and moderate-severity fires (Bond et al., 2002; Ganey et al., 2017), perhaps partially due to their broader range of habitat use when foraging (Verner et al., 1992; Williams et al., 2011; Eyes et al., 2017; Hobart et al., 2019b).

Although owls exhibited neutral overall selection for recent lower-severity fire, the strength of selection for these conditions increased as the area of lower-severity fire increased within owl home ranges (Fig. 3). Indeed, a heterogeneous landscape of lower-severity burned and unburned areas likely promotes small mammal community diversity (Roberts et al., 2015) and could increase the abundance and availability of key prey species such as woodrats, pocket gophers, and flying squirrels – with emergent benefits to spotted owl populations (Hobart et al., 2019a, 2020). However, it could be that prey using lower-severity burned areas require larger areas of habitat to persist and maintain stable populations, especially as owls deplete those populations, making these areas beneficial to owls only if they cover a sufficiently large portion of an owl's home range. Alternately, small pockets of prey created by less overall burned area within an owl's home range may be less energetically efficient for an owl to find and utilize. Our functional response analysis also revealed a significant effect of the amount of older burned areas (which likely burned primarily at lower-severity) within an owl's home range on selection of those areas. Owls with little older burned area available to them avoided these older burned areas, whereas owls with greater amounts of older burned area showed neutral selection for those areas (Fig. 3). Together, these results suggest that the benefits of lower-severity fire may attenuate over time, and that frequent, low-severity fire events might benefit owl populations and perhaps their prey.

The owl's use of lower-severity burned areas could also explain why owls avoided more pyrodiverse areas. Avoidance of pyrodiverse areas was in contrast to our prediction that owls foraging in heterogeneous landscapes shaped by fire would exhibit neutral or positive selection for areas with high pyrodiversity (Franklin et al., 2000; Franklin and Gutiérrez, 2002). Indeed, the most pyrodiverse locations were those containing a mix of burn severity classes (unburned, lower-severity, and high-severity fire), whereas areas of low pyrodiversity were those composed entirely of a single class of these three categories. Therefore, the composition of areas with low pyrodiversity becomes important for determining the direction and magnitude of owl selection. For instance, owls appeared to show weak selection for areas with high pyrodiversity in the King fire (Jones et al., 2016, 2020). However, areas of low pyrodiversity in the King fire predominately occurred in the large high-severity patch that owls avoided (and would have driven selection for greater pyrodiversity). In comparison, areas with low pyrodiversity in this study were most often composed of lower-severity or unburned area. Thus, neutral selection for lower-severity and unburned areas in our study may have resulted in an apparent avoidance of pyrodiversity unlike the owls in the King fire study (Jones et al., 2020; Fig. S5). Furthermore, the diversity of forest structure in unburned areas also may play a role in selection for pyrodiversity. Selection for more pyrodiverse areas may be more pronounced if pre-fire forest conditions are homogeneous, such that increased pyrodiversity might create structural heterogeneity preferred by owls, as may be the case on national forests and areas burned by the King fire (Jones et al., 2020). Regardless of the specific mechanism, our results suggest the importance of characterizing both pyrodiversity and structural diversity of unburned areas, especially when comparing selection for or against pyrodiversity among fires with different patterns of severity.

4. Conclusions and implications for using fire for owl conservation

Our study supports the long-held hypothesis that spotted owls are adapted to frequent-fire regimes, characterized by low- to moderate-severity fire with small patches of severe fire, such as those that have been reintroduced to the national parks that comprised our study area (Verner et al., 1992; Gutiérrez et al., 2017). Conversely, natural fire regimes on Sierra Nevada national forests have been altered by fire suppression, which has resulted in very different forest structures between the national parks we studied and other public lands in the Sierra Nevada. Hence, our study supports earlier speculation that the difference in management between these two general landscapes (fire managed and fire suppressed) may account for the difference in owl population trajectories – stable in Sequoia-Kings Canyon National Parks and declining on national forests (Franklin et al., 2004; Blakesley et al., 2010; Tempel et al., 2016). We do not know the mechanism(s) that confer higher fitness in fire-managed landscapes, but we propose that the benefit is conferred by (1) a positive influence of frequent low- and moderate-severity fire on prey habitat, (2) the change in forest structure that reduces the impact or spread of high-severity fires, and (3) the interaction of large trees and fire because large trees are relatively fire resistant and have helped facilitate the reintroduction of frequent lower-severity fire regimes. Therefore, we conclude that the effect of a natural fire regime is complex with positive benefits conferred on owls, the maintenance of forest systems, and reduction in high severity fire.

The habitat selection patterns revealed by owls in our study suggest that prudent use of fire, as practiced in the Sierra Nevada national parks we studied, could benefit spotted owl conservation in fire-suppressed landscapes such as national forests as previously proposed (Bond et al., 2002; Roberts et al., 2011; Eyes et al., 2017). However, the positive functional response owls exhibited to low-severity fire and the apparent attenuating benefits of lower-severity fire over time that we found suggest that restoration of frequent fire regimes, rather than discrete (nonrepeating) fire treatments, will be needed to continue achieving benefits for owl foraging habitat. Hence, increasing the amount and frequency of lower-severity fire would serve a dual purpose of (1) reducing surface and ladder fuels that contribute to the large, high-severity fires that negatively affect owls and (2) promoting prey habitat for owls (Jones et al., 2016; Hobart et al., 2019a).

The extensive reintroduction of frequent lower-severity fire on national forests and other fire-suppressed areas within the range of spotted owls is constrained by social (e.g., air pollution, fear of escaped fire), economic (e.g., high cost), and ecological (e.g., escaped fire, unintended negative impacts on wildlife habitat) considerations (Collins et al., 2010; Young et al., 2020). In areas lacking frequent, lower-severity fire, mechanical treatments intended to remove surface and ladder fuels may serve as an intermediate step to the restoration of fire regimes, although they are also constrained by concerns of stakeholders – that logging to remove smaller trees may also have negative effects on spotted owls and other wildlife (Wood and Jones, 2019). Note that our study was limited to national parks, where such treatments do not occur, and so our results cannot provide direct insight on mechanical treatments. Nevertheless, if mechanical treatments are applied with rigorous guidelines designed to maintain key habitat features (e.g., retention of large trees and dense canopy of tall trees) of old forest ecosystems and sensitive species like spotted owls, fishers (*Pekania pennanti*), and others, the benefits of reducing severe fire through mechanical thinning may outweigh the adverse effect on spotted owl habitat, yet these areas need to be closely monitored because of high scientific uncertainty (Verner et al., 1992; Schwilk et al., 2009; Tempel et al., 2015; Jones, 2019). Increasing the use of fire as a management tool in fire-suppressed forests may increase the feasibility and spatial extent of restoration efforts compared to mechanical treatments alone (North et al., 2012). However, fire used in combination with mechanical treatments (e.g., removal of small and medium-sized trees) may be more effective in restoring vegetation structure with lower fuel loads than currently present, particularly in forests where the risks from prescribed or managed fire are now high (Schwilk et al., 2009). Thus, while much uncertainty and many obstacles remain, our study reinforces previous findings that owl conservation may benefit from restoration of frequent fire regimes in dry forests (Roberts et al., 2011; Jones et al., 2016, 2020; Eyes et al., 2017; Stephens et al., 2019).

5. Ethics approval and consent to participate

University of Wisconsin Institutional Animal Care and Use Protocol # A005367

6. Consent for publication

Not applicable.

7. Availability of data and materials

General data is available on request, but because of the sensitive status of these owls, specific owl locations will not be released.

Funding

Funding was provided by Region 5, USDA Forest Service (CS Agreement: 14-CS-11052007-015)

CRediT authorship contribution statement

Anu Kramer: Conceptualization, Methodology, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Gavin M. Jones:** Conceptualization, Methodology, Formal analysis, Visualization, Writing - original draft, Writing - review & editing.

Sheila A. Whitmore: Data curation, Writing - review & editing. **John J. Keane:** Writing - review & editing, Project administration. **Fidelis A. Atuo:** Conceptualization, Methodology, Writing - review & editing. **Brian P. Dotters:** Data curation, Writing - review & editing. **Sarah C. Sawyer:** Project administration. **Sarah L. Stock:** Writing - review & editing, Project administration. **R.J. Gutiérrez:** Writing - original draft, Writing - review & editing. **M. Zachariah Peery:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Region 5 of the USDA Forest Service for funding this work. We also thank Ceeanna Zulla, Daniel Hofstadter, Zachary Wilkinson, Mike McDonald, and Tim Demers, who collected the data, and staff at Yosemite, as well as Sequoia-Kings Canyon National Parks, who assisted with locating the owls used for this work. We are grateful to Kent van Wagtendonk and Karen Folger at Yosemite and Sequoia and Kings Canyon National Parks, respectively, for sharing data on fire severity for historical fires within each park. We gratefully acknowledge the Lemma Lab at Oregon State University for sharing the most recent version of GNN data corresponding to imagery from 2016. We thank Kevin Roberts and Ed Murphy for constructive comments on earlier versions of the manuscript. We also thank Jens Stevens for sharing data and expertise on stand decay coefficients and Sean Jeronimo for sharing data on restored areas in the Sierra Nevada.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118576.

References

Aarts, G., Fieberg, J., Brasseur, S., Matthiopoulos, J., 2013. Quantifying the effect of habitat availability on species distributions. J. Anim. Ecol. 82 (6), 1135–1145.
Abatzoglou, J.T., Williams, A.P., 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proc. Natl. Acad. Sci. 113 (42), 11770–11775.
Atuo, F.A., Roberts, K., Whitmore, S., Dotters, B.P., Raphael, M.G., Sawyer, S.C., Keane, J.J., Gutiérrez, R., Peery, M.Z., 2019. Resource selection by GPS-tagged California spotted owls in mixed-ownership forests. For. Ecol. Manage. 433, 295–304.
Beesley D (1996) Reconstructing the landscape: an environmental history, 1820-1960.
Beyer, H.L., Haydon, D.T., Morales, J.M., Frair, J.L., Hebblewhite, M., Mitchell, M., Matthiopoulos, J., 2010. The interpretation of habitat preference metrics under use–availability designs. Philos. Trans. Royal Soc. Biolog. Sci. 365 (1550), 2245–2254.
Bias, M.A., Gutiérrez, R., 1992. Habitat associations of California spotted owls in the central Sierra Nevada. J. Wildl. Manag. 56 (3), 584–595.
Blakesley, J.A., Seamans, M.E., Conner, M.M., Franklin, A.B., White, G.C., Gutiérrez, R., Hines, J.E., Nichols, J.D., Munton, T.E., Shaw, D.W., 2010. Population dynamics of spotted owls in the Sierra Nevada California. Wildlife Monographs 174 (1), 1–36.
Blakey, R.V., Siegel, R.B., Webb, E.B., Dillingham, C.P., Bauer, R.L., Johnson, M., Kesler, D.C., 2019. Space use, forays, and habitat selection by California Spotted Owls (Strix occidentalis occidentalis) during the breeding season: New insights from high resolution GPS tracking. For. Ecol. Manage. 432, 912–922.
Bond, M.L., Bradley, C., Lee, D.E., 2016. Foraging habitat selection by California spotted owls after fire. J. Wildl. Manage. 80 (7), 1290–1300.
Bond, M.L., Gutierrez, R.J., Franklin, A.B., LaHaye, W.S., May, C.A., Seamans, M.E., 2002. Short-term effects of wildfires on spotted owl survival, site fidelity, mate fidelity, and reproductive success. Wildlife Soc. Bulletin 1022–1028.
Bond, M.L., Lee, D.E., Siegel, R.B., Ward Jr, J.P., 2009. Habitat use and selection by California spotted owls in a postfire landscape. J. Wildl. Manag. 73 (7), 1116–1124.
Bond, W.J., Keeley, J.E., 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol. Evol. 20 (7), 387–394.
Bull E, 1987, Capture techniques for owls. Biology and conservation of northern forest owls USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO USA:291-293.
Call, D.R., Gutierrez, R.J., Verner, J., 1992. Foraging habitat and home-range characteristics of California spotted owls in the Sierra Nevada. The Condor 94 (4), 880–888.
Christensen, N.L., Cotton, L., Harvey, T., Martin, R., McBride, J., Rundel, P., Wakimoto, R., 1987. Review of fire management program for sequoia-mixed conifer forests of Yosemite. Sequoia and Kings Canyon National Parks, Final Report to the National Park Service, Washington, DC.
Clark JS, 1989, Ecological disturbance as a renewal process: theory and application to fire history. Oikos:17-30.
Collins, B.M., Everett, R.G., Stephens, S.L., 2011. Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. Ecosphere 2 (4), 1–14.
Collins, B.M., Fry, D.L., Lydersen, J.M., Everett, R., Stephens, S.L., 2017a. Impacts of different land management histories on forest change. Ecol. Appl. 27 (8), 2475–2486.
Collins, B.M., Miller, J.D., Thode, A.E., Kelly, M., van Wagtendonk, J.W., Stephens, S.L., 2008. Interactions Among Wildland Fires in a Long-Established Sierra Nevada Natural Fire Area. Ecosystems 12 (1), 114–128. https://doi.org/10.1007/s10021-008-9211-7.
Collins, B.M., Stephens, S.L., 2007. Managing natural wildfires in Sierra Nevada wilderness areas. Front. Ecol. Environ. 5 (10), 523–527.
Collins, B.M., Stephens, S.L., Moghaddas, J.J., Battles, J., 2010. Challenges and approaches in planning fuel treatments across fire-excluded forested landscapes. J. Forest. 108 (1), 24–31.
Collins, B.M., Stevens, J.T., Miller, J.D., Stephens, S.L., Brown, P.M., North, M.P., 2017b. Alternative characterization of forest fire regimes: incorporating spatial patterns. Landscape Ecol. 32 (8), 1543–1552.
Delaney, D.K., Grubb, T.G., Beier, P., 1999. Activity patterns of nesting Mexican spotted owls. The Condor 101 (1), 42–49.
Duchesne, T., Fortin, D., Courbin, N., 2010. Mixed conditional logistic regression for habitat selection studies. J. Anim. Ecol. 79 (3), 548–555.
Eidenshink, J., Schwind, B., Brewer, K., Zhu, Z.-L., Quayle, B., Howard, S., 2007. A project for monitoring trends in burn severity. Fire ecology 3 (1), 3–21.
Eyes, S.A., Roberts, S.L., Johnson, M.D., 2017. California Spotted Owl (Strix occidentalis occidentalis) habitat use patterns in a burned landscape. The Condor 119 (3), 375–388.
Forsman ED, Meslow EC, Wight HM, 1984, Distribution and biology of the spotted owl in Oregon. Wildlife Monographs:3-64.
Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T., Mao, J.S., 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86 (5), 1320–1330.
Frair, J.L., Nielsen, S.E., Merrill, E.H., Lele, S.R., Boyce, M.S., Munro, R.H., Stenhouse, G.B., Beyer, H.L., 2004. Removing GPS collar bias in habitat selection studies. J. Appl. Ecol. 41 (2), 201–212.
Franklin, A.B., Anderson, D.R., Forsman, E.D., Burnham, K., Wagner, F., 1996. Methods for collecting and analyzing demographic data on the northern spotted owl. Studies Avian Biol. 17, 12–20.
Franklin, A.B., Anderson, D.R., Gutiérrez, R., Burnham, K.P., 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecol. Monogr. 70 (4), 539–590.
Franklin, A.B., Gutiérrez, R., 2002. Spotted owls, forest fragmentation, and forest heterogeneity. Studies Avian Biol. 25, 203–220.
Franklin, A.B., Gutierrez, R.J., Nichols, J.D., Seamans, M.E., White, G.C., Zimmerman, G.S., Hines, J.E., Munton, T.E., LaHaye, W.S., Blakesley, J.A., 2004. Population dynamics of the California spotted owl (Strix occidentalis occidentalis): a meta-analysis. Ornitholog. Monographs 1–54.
Gallagher, C.V., Keane, J.J., Shaklee, P.A., Kramer, H.A., Gerrard, R., 2019. Spotted owl foraging patterns following fuels treatments, Sierra Nevada California. J. Wildlife Manage. 83 (2), 487–501.
Ganey, J.L., Wan, H.Y., Cushman, S.A., Vojta, C.D., 2017. Conflicting perspectives on spotted owls, wildfire, and forest restoration. Fire Ecol. 13 (3), 146–165.
Gill, A.M., Stephens, S.L., Cary, G.J., 2013. The worldwide "wildfire" problem. Ecol. Appl. 23 (2), 438–454.
Gutiérrez R, 1985, Ecology and management of the spotted owl in the Pacific Northwest. 115.
Gutiérrez R, Franklin A, LaHaye W, 1995, Spotted owl (Strix occidentalis). In: Poole A, Gill F (eds) The Birds of North America No. 179: Life Histories for the 21st Century. The Philadelphia Academy of Sciences and The American Ornithologists' Union, Washington, D. C.
Gutiérrez R, Manley PN, Stine PA, 2017, The California spotted owl: current state of knowledge. Gen Tech Rep PSW-GTR-254 Albany, CA: US Department of Agriculture, Forest Service, Pacific Southwest Research Station 254.
Gutiérrez R, McKelvey K, Noon B, Steger G, Call D, LaHaye W, Bingham B, Senser J, 1992, Habitat relations of the California spotted owl. Pages 79-98 in J Verner, K S McKelvey, B R Noon, R J Gutiérrez, G I Gould Jr, and T W Beck [tech coordinators] The California Spotted Owl: a tech-nical assessment of its current status PSW-GTR-133 USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.
Hanson, C.T., Odion, D.C., DellaSala, D.A., Baker, W.L., 2009. Overestimation of fire risk in the northern spotted owl recovery plan. Conserv. Biol. 23 (5), 1314–1319. https://

doi.org/10.1111/j.1523-1739.2009.01265.x.
Hardy CC, Arno SF, 1996. The use of fire in forest restoration. Gen Tech Rep INT-GTR-341 Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Research Station 86 p 341.
Hebblewhite, M., Merrill, E., 2008. Modelling wildlife–human relationships for social species with mixed-effects resource selection models. J. Appl. Ecol. 45 (3), 834–844.
Hiers, J.K., O'Brien, J.J., Varner, J.M., Butler, B.W., Dickinson, M., Furman, J., Gallagher, M., Godwin, D., Goodrick, S.L., Hood, S.M., 2020. Prescribed fire science: the case for a refined research agenda. Fire Ecol. 16 (1), 1–15.
Hobart, B.K., Jones, G.M., Roberts, K.N., Dotters, B.P., Whitmore, S.A., Berigan, W.J., Raphael, M.G., Keane, J.J., Gutiérrez, R., Peery, M.Z., 2019a. Trophic interactions mediate the response of predator populations to habitat change. Biol. Conserv. 238, 108217.
Hobart, B.K., Kramer, H.A., Jones, G.M., Dotters, B.P., Whitmore, S.A., Keane, J.J., Peery, M.Z., 2020. Stable isotopes reveal unexpected relationships between fire history and the diet of Spotted Owls. Ibis. https://doi.org/10.1111/ibi.12832.
Hobart, B.K., Roberts, K.N., Dotters, B.P., Berigan, W.J., Whitmore, S.A., Raphael, M.G., Keane, J.J., Gutiérrez, R., Peery, M.Z., 2019b. Site occupancy and reproductive dynamics of California spotted owls in a mixed-ownership landscape. For. Ecol. Manage. 437, 188–200.
Holbrook, Joseph D., Olson, Lucretia E., DeCesare, Nicholas J., Hebblewhite, Mark, Squires, John R., Steenweg, Robin, 2019. Functional responses in habitat selection: clarifying hypotheses and interpretations. Ecol. Appl. 29 (3).
Hooten, M.B., Johnson, D.S., McClintock, B.T., Morales, J.M., 2017. Animal movement: statistical models for telemetry data. CRC Press.
Jeronimo, S.M., Kane, V.R., Churchill, D.J., Lutz, J.A., North, M.P., Asner, G.P., Franklin, J.F., 2019. Forest structure and pattern vary by climate and landform across active-fire landscapes in the montane Sierra Nevada. For. Ecol. Manage. 437, 70–86.
Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L., 2016. Changing disturbance regimes, ecological memory, and forest resilience. Front. Ecol. Environ. 14 (7), 369–378.
Jones, G.M., 2019. Fire, forest restoration, and spotted owl conservation in the Sierra Nevada. The University of Wisconsin-Madison, CA.
Jones GM, Gutiérrez R, Kramer HA, Tempel DJ, Berigan WJ, Whitmore SA, Peery MZ (2019) Megafire effects on spotted owls: elucidation of a growing threat and a response to Hanson et al., 2018, Nature Conservation 37:31.
Jones, G.M., Gutiérrez, R., Tempel, D.J., Whitmore, S.A., Berigan, W.J., Peery, M.Z., 2016. Megafires: an emerging threat to old-forest species. Front. Ecol. Environ. 14 (6), 300–306.
Jones GM, Gutiérrez RJ, Block WM, Carlson PC, Comfort EJ, Cushman SA, Davis RJ, Eyes SA, Franklin AB, Ganey JL, Hedwall S, Keane JJ, Kelsey R, Lesmeister DB, North MP, Roberts SL, Rockweit JT, Sanderlin JS, Sawyer SC, Solvesky B, Tempel DJ, Wan HY, Westerling AL, White GC, Peery MZ (In press) Spotted owls and forest fire: Comment.
Jones, G.M., Keane, J.J., Gutiérrez, R., Peery, M.Z., 2018. Declining old-forest species as a legacy of large trees lost. Divers. Distrib. 24 (3), 341–351.
Jones, G.M., Kramer, H.A., Whitmore, S., Berigan, W., Tempel, D.J., Wood, C.M., Hobart, B.K., Erker, T., Atuo, F.A., Pietrunti, N.R., Kelsey, R., Gutierrez, R.J., Peery, M.Z., 2020. Habitat selection by spotted owls after a megafire reflects their adaptation to historical frequent-fire regimes. Landscape Ecol. https://doi.org/10.1007/s10980-020-01010-y.
Kane, V.R., Bartl-Geller, B.N., North, M.P., Kane, J.T., Lydersen, J.M., Jeronimo, S.M., Collins, B.M., Moskal, L.M., 2019. First-entry wildfires can create opening and tree clump patterns characteristic of resilient forests. For. Ecol. Manage. 454, 117659.
Kane, V.R., North, M.P., Lutz, J.A., Churchill, D.J., Roberts, S.L., Smith, D.F., McGaughey, R.J., Kane, J.T., Brooks, M.L., 2014. Assessing fire effects on forest spatial structure using a fusion of Landsat and airborne LiDAR data in Yosemite National Park. Remote Sens. Environ. 151, 89–101.
Kramer HA, Jones GM, Kane VR, Bartl-Geller BN, Kane JT, Whitmore S, Berigan W, Dotters BP, Roberts KN, Sawyer SC, Keane JJ, North MP, Gutiérrez RJ, Peery MZ (In revision) Elevational gradients strongly mediate habitat selection patterns in a nocturnal predator. Ecosphere.
Kramer, H.A., Mockrin, M.H., Alexandre, P.M., Radeloff, V.C., 2019. High wildfire damage in interface communities in California. Int. J. Wildland Fire 28 (9), 641–650.
Kuchinke, D., di Stefano, J., Sitters, H., Loyn, R., Gell, P., Palmer, G., 2020. Prescribed burn severity has minimal effect on common bird species in a fire-prone forest ecosystem. For. Ecol. Manage. 475, 118437.
Lee, D.E., 2018. Spotted Owls and forest fire: A systematic review and meta-analysis of the evidence. Ecosphere 9 (7), e02354.
Lee, D.E., Bond, M.L., 2015. Occupancy of California Spotted Owl sites following a large fire in the Sierra Nevada California. Condor. Ornitholog. Appl. 117 (2), 228–236.
Lommler MA, 2019, Mexican Spotted Owl Breeding Population, Site Occupancy, and Habitat Selection 13–15 Years after the Rodeo-Chediski Fire in East-Central Arizona. Northern Arizona University.
Lutz, J.A., Key, C.H., Kolden, C.A., Kane, J.T., van Wagtendonk, J.W., 2011. Fire frequency, area burned, and severity: a quantitative approach to defining a normal fire year. Fire Ecol. 7 (2), 51–65.
Lydersen, J.M., Collins, B.M., Miller, J.D., Fry, D.L., Stephens, S.L., 2016. Relating fire-caused change in forest structure to remotely sensed estimates of fire severity. Fire Ecol. 12 (3).
Magnusson A, Skaug H, Nielsen A, Berg C, Kristensen K, Maechler M, van Bentham K, Bolker B, Brooks M (2017) glmmTMB: generalized linear mixed models using template model builder. R package version 0.1, vol 3.
Manly, B., McDonald, L., Thomas, D., McDonald, T., Erickson, W., 2002. Resource Selection by Animals, Statistical Design and Analysis for Field Studies, second edn. Dordrecht, Netherlands, Kluwer Academic Publishers.
Matthiopoulos, J., Hebblewhite, M., Aarts, G., Fieberg, J., 2011. Generalized functional responses for species distributions. Ecology 92 (3), 583–589.
Mayer, K.E., Laudenslayer, W.F., 1988. A guide to wildlife habitats of California. The Dept.
Moritz, M.A., Batllori, E., Bradstock, R.A., Gill, A.M., Handmer, J., Hessburg, P.F., Leonard, J., McCaffrey, S., Odion, D.C., Schoennagel, T., 2014. Learning to coexist with wildfire. Nature 515 (7525), 58–66.
Muff, S., Signer, J., Fieberg, J., 2020. Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. J. Anim. Ecol. https://doi.org/10.1111/jane.13087:411801. doi.org/10.1101/411801.
Mysterud, A., Ims, R.A., 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology 79 (4), 1435–1441.
North, M., Collins, B.M., Stephens, S., 2012. Using fire to increase the scale, benefits, and future maintenance of fuels treatments. J. Forest. 110 (7), 392–401.
North, M., Innes, J., Zald, H., 2007. Comparison of thinning and prescribed fire restoration treatments to Sierran mixed-conifer historic conditions. Can. J. For. Res. 37 (2), 331–342.
North, M., Stephens, S., Collins, B., Agee, J., Aplet, G., Franklin, J., Fulé, P., 2015. Reform forest fire management. Science 349 (6254), 1280–1281.
North, M.P., Kane, J.T., Kane, V.R., Asner, G.P., Berigan, W., Churchill, D.J., Conway, S., Gutiérrez, R., Jeronimo, S., Keane, J., 2017. Cover of tall trees best predicts California spotted owl habitat. For. Ecol. Manage. 405, 166–178.
Ohmann, J.L., Gregory, M.J., 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, USA. Can. J. For. Res. 32 (4), 725–741.
Parsons DJ, Botti SJ (1996) Restoration of fire in National Parks. In: Hardy, Colin C; Arno, Stephen F, eds The use of fire in forest restoration Gen Tech Rep INT-GTR-341 Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Research Station p 29-31 341.
Parsons, D.J., DeBenedetti, S.H., 1979. Impact of fire suppression on a mixed-conifer forest. For. Ecol. Manage. 2, 21–33.
Parsons, D.J., Landres, P.B., 1998. Restoring natural fire to wilderness: how are we doing. Tall Timbers Fire Ecol. Conference Proc. 366–373.
Parsons, D.J., van Wagtendonk, J.W., 1996. Fire research and management in the Sierra Nevada National Parks. Science and ecosystem management in the national parks. University of Arizona Press, Tucson, Arizona, USA:25–48.
Peery, M.Z., Jones, G.M., Gutierrez, R., Redpath, S.M., Franklin, A.B., Simberloff, D., Turner, M.G., Radeloff, V.C., White, G.C., 2019. The conundrum of agenda-driven science in conservation. Front. Ecol. Environ. 17 (2), 80–82. https://doi.org/10.1002/fee.2006.
Roberts, S.L., 2017. California spotted owl habitat characteristics and use. Gen Tech Rep PSW-GTR-254 Albany, CA: US Department of Agriculture, Forest Service. Pacific Southwest Research Station 49–73 254, 49–73.
Roberts, S.L., Kelt, D.A., van Wagtendonk, J.W., Miles, A.K., Meyer, M.D., 2015. Effects of fire on small mammal communities in frequent-fire forests in California. J. Mammal. 96 (1), 107–119.
Roberts, S.L., van Wagtendonk, J.W., Miles, A.K., Kelt, D.A., 2011. Effects of fire on spotted owl site occupancy in a late-successional forest. Biol. Conserv. 144 (1), 610–619.
Rockweit, J.T., Franklin, A.B., Carlson, P.C., 2017. Differential impacts of wildfire on the population dynamics of an old-forest species. Ecology 98 (6), 1574–1582.
Rosenberg, D.K., McKelvey, K.S., 1999. Estimation of habitat selection for central-place foraging animals. J. Wildlife Manage. 1028–1038.
Safford HD, Stevens JT, 2017, Natural range of variation for yellow pine and mixed-conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. Gen Tech Rep PSW-GTR-256 Albany, CA: US Department of Agriculture, Forest Service, Pacific Southwest Research Station 229 p 256.
Schoennagel, T., Balch, J.K., Brenkert-Smith, H., Dennison, P.E., Harvey, B.J., Krawchuk, M.A., Mietkiewicz, N., Morgan, P., Moritz, M.A., Rasker, R., 2017. Adapt to more wildfire in western North American forests as climate changes. Proc. Natl. Acad. Sci. 114 (18), 4582–4590.
Schofield LN, Eyes SA, Siegel RB, Stock SL (In press) Habitat selection by Spotted Owls after a megafire in Yosemite National Park. Forest Ecology and Management.
Schwilk, D.W., Keeley, J.E., Knapp, E.E., McIver, J., Bailey, J.D., Fettig, C.J., Fiedler, C.E., Harrod, R.J., Moghaddas, J.J., Outcalt, K.W., 2009. The national Fire and Fire Surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. Ecol. Appl. 19 (2), 285–304.
Shakesby, R., Doerr, S., 2006. Wildfire as a hydrological and geomorphological agent. Earth Sci. Rev. 74 (3–4), 269–307.
Solis, D.M., Gutiérrez, R., 1990. Summer habitat ecology of northern spotted owls in northwestern California. The Condor 92 (3), 739–748.
Stephens, S.L., Bigelow, S.W., Burnett, R.D., Collins, B.M., Gallagher, C.V., Keane, J., Kelt, D.A., North, M.P., Roberts, L.J., Stine, P.A., 2014a. California spotted owl, songbird, and small mammal responses to landscape fuel treatments. Bioscience 64 (10), 893–906.
Stephens, S.L., Burrows, N., Buyantuyev, A., Gray, R.W., Keane, R.E., Kubian, R., Liu, S., Seijo, F., Shu, L., Tolhurst, K.G., Van Wagtendonk, J.W., 2014b. Temperate and boreal forest mega-fires: characteristics and challenges. Front. Ecol. Environ. 12 (2), 115–122.
Stephens, S.L., Kobziar, L.N., Collins, B.M., Davis, R., Fulé, P.Z., Gaines, W., Ganey, J., Guldin, J.M., Hessburg, P.F., Hiers, K., Hoagland, S., Keane, J.J., Masters, R.E., McKellar, A.E., Montague, W., North, M., Spies, T.A., 2019. Is fire "for the birds"? How two rare species influence fire management across the US. Front. Ecol. Environ. 17 (7), 391–399. https://doi.org/10.1002/fee.2076.
Stephens, S.L., Moghaddas, J.J., 2005. Experimental fuel treatment impacts on forest

structure, potential fire behavior, and predicted tree mortality in a California mixed conifer forest. For. Ecol. Manage. 215 (1–3), 21–36. https://doi.org/10.1016/j.foreco.2005.03.070.

Stephens, S.L., Ruth, L.W., 2005. Federal forest-fire policy in the United States. Ecol. Appl. 15 (2), 532–542.

Stevens, J.T., Collins, B.M., Miller, J.D., North, M.P., Stephens, S.L., 2017. Changing spatial patterns of stand-replacing fire in California conifer forests. For. Ecol. Manage. 406, 28–36.

Sugihara, N.G., van Wagtendonk, J., Fites-Kaufman, J., Shaffer, K., Thode, A., 2006. Fire in California's ecosystems. University of California Press, Oakland, CA.

Tempel, D.J., Gutierrez, R.J., Battles, J.J., Fry, D.L., Su, Y., Guo, Q., Reetz, M.J., Whitmore, S.A., Jones, G.M., Collins, B.M., 2015. Evaluating short-and long-term impacts of fuels treatments and simulated wildfire on an old-forest species. Ecosphere 6 (12), 1–18.

Tempel, D.J., Gutiérrez, R.J., Sa, W., Reetz, M.J., Stoelting, R.E., Berigan, W., Seamans, M.E., Peery, M.Z., 2014. Effects of Forest Management on California Spotted Owls: Implications for Reducing Wildfire Risk in Fire-prone Forests. Ecol. Appl. 24 (8), 2089–2106. https://doi.org/10.1890/13-2192.1.

Tempel, D.J., Keane, J.J., Gutiérrez, R., Wolfe, J.D., Jones, G.M., Koltunov, A., Ramirez, C.M., Berigan, W.J., Gallagher, C.V., Munton, T.E., 2016. Meta-analysis of California Spotted Owl (Strix occidentalis occidentalis) territory occupancy in the Sierra Nevada: Habitat associations and their implications for forest management. The Condor 118 (4), 747–765.

van Wagtendonk, J.W., 1991. The evolution of National Park Service fire policy. Fire Management Notes 52 (4), 10–15.

van Wagtendonk, J.W., 2007. The history and evolution of wildland fire use. Fire Ecology 3 (2), 3–17.

van Wagtendonk, J.W., Lutz, J.A., 2007. Fire regime attributes of wildland fires in Yosemite National Park, USA. Fire Ecology 3 (2), 34–52.

Verner J, Gutiérrez R, Gould GJ (1992) The California spotted owl: general biology and ecological relations. Chapter 4 in: Verner, Jared McKelvey, Kevin S, Noon, Barry R, Gutierrez, RJ, Gould, Gordon I Jr, Beck, Thomas W, Technical Coordinators The California spotted owl: a technical assessment of its current status Gen Tech Rep PSW-GTR-133 Albany, CA: Pacific Southwest Research Station, Forest Service, US Department of Agriculture 133:55-77.

Westerling, A.L., 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Phil Trans R Soc B 371 (1696), 20150178.

Williams, P.J., Gutierrez, R.J., Whitmore, S.A., 2011. Home range and habitat selection of spotted owls in the central Sierra Nevada. J. Wildl. Manag. 75 (2), 333–343.

Wood, C.M., Jones, G.M., 2019. Framing management of social-ecological systems in terms of the cost of failure: the Sierra Nevada, USA as a case study. Environ. Res. Lett. 14 (10), 105004.

Young, J.D., Evans, A.M., Iniguez, J.M., Thode, A., Meyer, M.D., Hedwall, S.J., McCaffrey, S., Shin, P., Huang, C.-H., 2020. Effects of policy change on wildland fire management strategies: evidence for a paradigm shift in the western US? Int. J. Wildland Fire. https://doi.org/10.1071/WF19189.