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Habitat selection by spotted owls after a megafire in Yosemite National park

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ABSTRACT

As fires in the western United States have become larger and more severe over recent decades, understanding how the changing fire regime affects wildlife has become a key issue for conservation. Spotted owls (*Strix occidentalis*) associate with late-successional forest characteristics and therefore may be particularly sensitive to structural changes in habitat that result from fire. Previous studies have found varying responses of the owls to forest fire. We investigated the effects of the 2013 Rim Fire on territory selection by California spotted owls within Yosemite National Park, which, unlike the surrounding landscape, has been managed with no commercial logging since the early 1900s and minimal fire suppression since the 1970s. We examined specific habitat characteristics associated with spotted owl presence before and after the fire to understand how fire-induced changes in habitat structure may influence spotted owl territory selection. Spotted owls persisted and nested within the fire perimeter throughout the four post-fire years of our study at rates similar to what we observed in areas of Yosemite that were unaffected by the fire. However, within the fire perimeter, spotted owls avoided areas characterized by > 30% percent high severity fire. Prior to the fire, spotted owls selected for areas of high canopy cover relative to the rest of the landscape; after the fire, even though territory centers shifted substantially from pre-fire locations, pre-fire canopy cover remained a stronger predictor of spotted owl presence than post-fire canopy cover, or any other pre- or post-fire habitat variables we assessed. The importance of pre-fire forest structure in predicting owl presence after fire suggests that reported variation in spotted owl population response to different fires across the Sierra Nevada may in part reflect variation in pre-fire forest characteristics, and perhaps different forest management regimes that shaped those characteristics. Pre-fire forest characteristics may impart a legacy of post-fire habitat conditions important to owls that commonly used forest and fire metrics do not effectively describe. Further study of owl response to fire in forests with a broader spectrum of pre-fire forest structure and management regimes is needed to better predict and manage effects of the changing fire regime on spotted owls.

1. Introduction

Spotted owls (*Strix occidentalis*) are often considered vulnerable to habitat disturbances like stand-altering fire (Ganey et al., 2017), although their sensitivity to such disturbance may not be as severe as once assumed (Seamans and Gutiérrez, 2007, Gutiérrez et al., 2017). Spotted owls generally favor late seral forests (Gutiérrez et al., 1995, 2017), but the California subspecies (*S. o. occidentalis*) evolved in a landscape that was frequently disturbed by wildfire (Caprio and Swetnam, 1995; Scholl and Taylor, 2010). The historic fire regime under which California spotted owls evolved was characterized by a short fire return interval and fires that burned large areas at low severities, interspersed with small areas of higher severity in a relatively heterogeneous mosaic (Jeronimo et al., 2019). Driven in large part by climate change (Miller et al., 2009b; Diffenbaugh et al., 2015; Holden et al., 2018) and a century of fire suppression (Arno et al., 2000; Calkin et al., 2005; Scholl and Taylor, 2010; Stephens et al., 2014), this type of heterogenous mixed-severity wildfire has become less common across California spotted owls' range while large, more homogenous fires with extensive areas of high severity burn have become more common (Arno et al., 2000; Miller et al., 2009b; Miller and Safford, 2012; Westerling, 2016; Stevens et al., 2017), including so-called 'megafires' that burn > 10,000 ha at high severity (Stephens et al., 2014). Megafires are anticipated to dramatically alter existing habitat during the coming decades (Miller et al., 2009b; Stephens et al., 2016; Wan et al., 2019). Increasing prevalence of large, high severity fire has been identified as

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one of the most important conservation threats for spotted owls (USDA Forest Service, 2019), making understanding how and why fire affects the owls critically important for their conservation.

The impact of fire on forested landscapes is often characterized by classifying the burned area into discrete areas of low, moderate, and high severity using the relative differenced normalized burn ratio (RdNBR; a measurement based on satellite imagery taken before and after a fire), calibrated by the composite burn index (CBI; a measurement based on direct observations of changes in vegetation at individual plots) (Miller and Thode, 2007; Miller et al., 2009b; Morgan et al., 2014). These burn severity metrics are useful because they succinctly describe fire severity by integrating multiple kinds of information about fire-induced vegetation changes (Miller et al., 2009a), but this integration introduces challenges in identifying the specific effects of fire on habitat that contribute most to changes in occupancy by wildlife species like spotted owls. Morgan et al., (2014) therefore suggested that, in addition to composite indices, assessments of fire effects on habitat should also individually address relevant habitat attributes changed by the fire that are encompassed by composite metrics.

Spotted owls' response to habitat disturbance may depend on numerous inter-related factors including the cause, severity, frequency, relative size, and spatial configuration of the disturbance (Jones et al., 2016; Collins et al., 2017; Ganey et al., 2017). Low to moderate severity fire may only minimally affect California spotted owl occupancy and productivity (Lee, 2018), because the density of large, tall trees and extent of high canopy cover are often not substantially reduced unless fire burns at high severity (Bias and Gutiérrez, 1992; North et al., 2017). Moderate understory burns may even enhance foraging opportunities for spotted owls (Bond et al., 2010; Ganey et al., 2017). The response of spotted owls to high severity fire appears to vary among fires (Ganey et al., 2017; Lee, 2018; Jones et al., 2019). For example, within the King Fire, which burned nearly 395 km^2 in the central Sierra Nevada in 2014, nesting spotted owl numbers were significantly reduced during the early post-fire years and owls were not observed at all within the extensive areas of high severity fire (Jones et al., 2016). When tracked via GPS, persisting owls were found to continue to avoid large patches of high severity burn several years after the fire (Jones et al., 2019). In contrast, spotted owls were observed even within high severity burned areas in the year immediately after the 2013 Rim Fire in the Stanislaus National Forest (Lee and Bond, 2015). What proportion of those detections represent true occupancy by territorial individuals is unknown (Berigan et al., 2019).

Differences in spotted owl persistence and territory selection after different fires likely arise from differences in the characteristics of each fire and the pre-fire landscape that it burned (Jones et al., 2020). Jones et al. (2020) found that spotted owls favored areas of high severity when high severity patches represented only a small portion of their total territory (< 5%), but avoided areas of high severity when a larger overall portion of their territory was burned at high severity. Fire size and overall severity may be relatively poor predictors of a fire's effects on spotted owls (Lee, 2018), whose response may also depend on factors such as the heterogeneity of the fire area, size and extent of stand-replacing burn patches, the structure and composition of the forest prior to the fire, or a combination thereof. Perhaps even fairly subtle or fine-scale variation in post-fire vegetation may allow or prevent owl persistence after fire.

The 2013 Rim Fire was the largest forest fire on record in the Sierra Nevada and burned over 1041 km^2 across the Stanislaus National Forest, private lands within the perimeter of the Stanislaus National Forest, and Yosemite National Park (Lydersen et al., 2017). Yosemite, which includes about 1/3 of the area burned by the Rim Fire (316 km^2), provides an opportunity to investigate effects of pre-fire and post-fire forest conditions on post-fire spotted owl occurrence in the context of an extensive area of contiguous suitable spotted owl habitat that approximates the historic Sierra Nevada ecosystem (Jeronimo et al., 2019). The park has been managed distinctly from adjacent National Forests and private lands, with no commercial logging since the early 1900s and minimal fire suppression since the 1970s (Miller et al., 2012; Kane et al., 2013; Jeronimo et al., 2019). The park's fire management plan emphasizes the "restoration of fire to its natural role in park ecosystems" as being among the higher priorities (Martin, 2009), and this is being achieved through a combination of managed wildfire and prescribed burning. Within the park, naturally occurring fires are allowed to burn to achieve management goals if they do not threaten developed, populated, or culturally important areas (Martin, 2009).

This strategy resulted in the Rim Fire creating a landscape with a more heterogeneous mosaic of mixed severity burn than the adjacent Stanislaus National Forest (Lydersen et al., 2017). In fact, within Yosemite National Park, the Rim Fire yielded a landscape that is considered to represent a restored fire regime that resembles the forest structure and composition found in the Sierra Nevada prior to European settlement (Miller et al., 2012; Jeronimo et al., 2019). This is the only area in the Sierra Nevada that has been identified as being returned to historic conditions (Jeronimo et al., 2019) and it provides a unique opportunity to examine how wildlife species respond to forest fires when they are within the conditions they initially evolved with.

We anticipated that owls would persist within the perimeter of the Rim Fire in Yosemite, as they did in the western portion of the fire footprint on Stanislaus National Forest (Lee and Bond 2015), and perhaps fare even better given the restored fire regime in our study area as suggested by Kramer et al. (in press). We sought to understand how habitat selection changed between the pre-and post-fire eras within this restored system. Spotted owls in low quality habitat or after reproductive failure often disperse to higher-quality habitat (Zimmerman et al., 2003; Blakesley et al., 2006); therefore, we expected that after the fire, spotted owls territories within the Rim Fire perimeter in Yosemite would shift to the best available post-fire habitat, which we predicted would be areas with the least severe fire effects and/or the greatest retention of pre-fire habitat characteristics known to be important to the owls, including canopy height, canopy cover, and overall vegetation greenness as measured by the Normalized Difference Vegetation Index (NDVI; Seamans and Gutiérrez, 2007; Gutiérrez et al., 2017; North et al., 2017; Tempel et al., 2017). We further hypothesized that habitat characteristics in territories found before or after the fire would be distinguishable from the surrounding landscape, but that the differences would be greater after the fire, when more of the habitat would likely have been rendered less suitable.

2. Methods

2.1. Study area

We studied California spotted owls within Yosemite National Park in the central Sierra Nevada of California. The study area comprised all areas within the park that met minimum characteristics of appropriate spotted owl habitat (Gutiérrez et al., 2017; Tempel et al., 2017; USDA Forest Service, 2019; Fig. 1) prior to the 2013 Rim Fire. We considered appropriate spotted owl habitat to be areas of montane forest below 2500 m in elevation with canopy cover $\geq$40% and dominant trees > 28 cm diameter at breast height (USDA Forest Service, 2019). We assessed these characteristics using data from the California Department of Forestry and Fire Protection's CALFIRE Fire and Resource Assessment Program (Vegetation fveg, FRAP 2015; https://frap.fire.ca.gov/). Using these criteria for suitable habitat, we found the Rim Fire to have affected 210 km^2 of the 717 km^2 (29%) of the total available spotted owl habitat in the park.

2.2. Field methods

We surveyed spotted owl territories in Yosemite National Park between 2015 and 2017 (hereafter referred to as the 'recent era') to determine post-fire occupancy and reproductive status. Surveys were

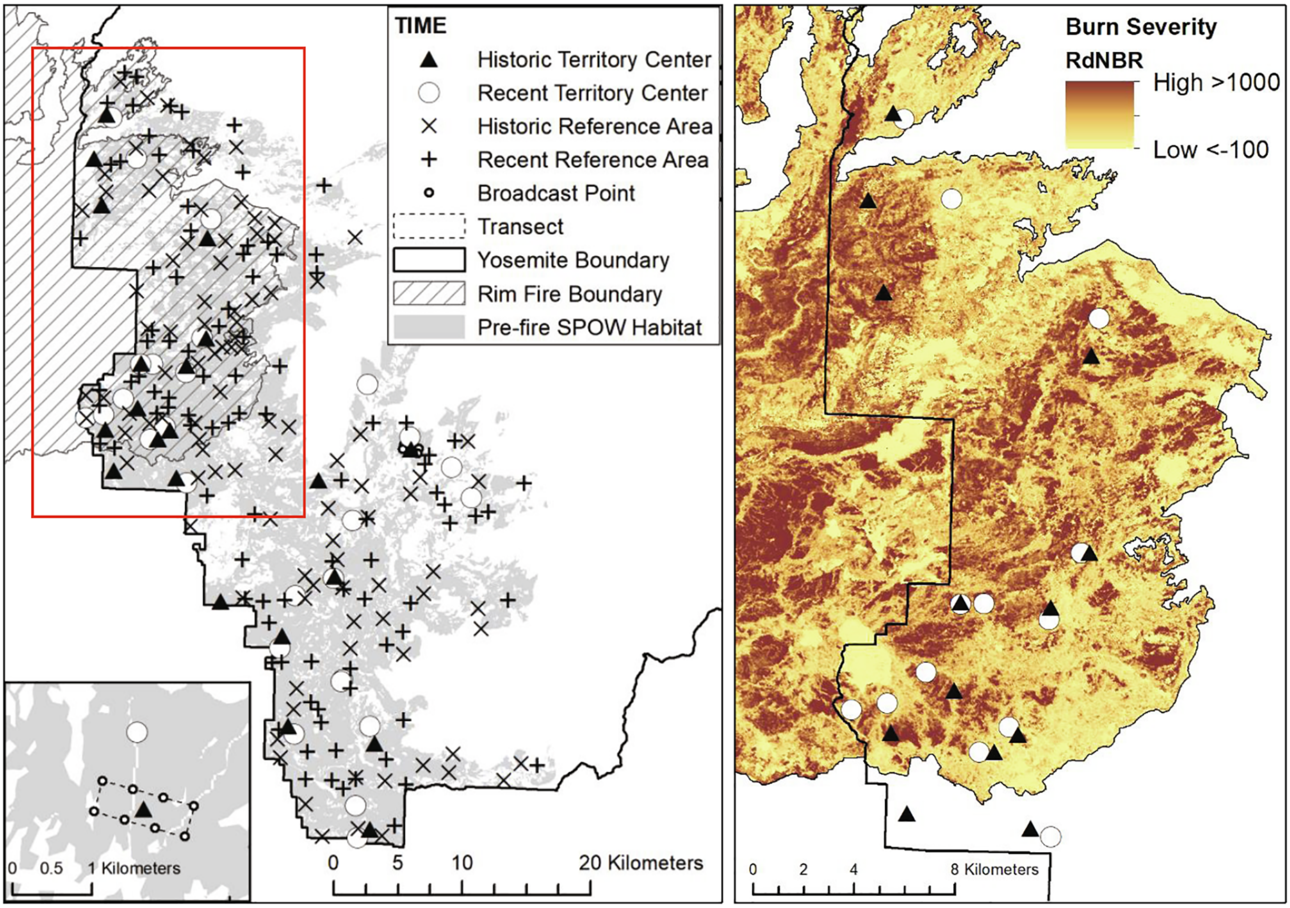

Fig. 1. Left: Locations of historical spotted owl territory centers (triangles; occupied prior to the 2013 Rim Fire), recent spotted owl territories (circles; occupied after the Rim Fire), and randomly generated reference points (crosses and plusses) in Yosemite National Park (Inset: an example of a transect surrounding a historical territory center where broadcast surveys were conducted after the fire). Gray shading indicates appropriate spotted owl habitat prior to the fire, based on the presence of montane forest with > 40% canopy cover and a diameter at breast height > 28 cm. Right: Magnified view of fire severity (RdNBR) across the Rim Fire study area in Yosemite National Park; symbols are as indicated in left panel.

conducted at the location of 36 historical spotted owl territories made between 2004 and 2013 (hereafter referred to as the 'historical era') by USGS and NPS personnel either during formal, park-wide surveys or incidentally (Fig. 1; Roberts et al., 2011). Given their density, these historical territories likely represent a sizable proportion of spotted owls within the park. During both historical and recent survey efforts, surveyors used standard methods to find spotted owls, determine reproductive status, and identify nest and roost locations (Forsman, 1983; USFWS, 2012).

We conducted recent era surveys by broadcasting conspecific vocalizations along a 1200 m × 400 m rectangular transect centered on the historical territory center, which we defined as either the nest location or, if no nest had been found during the historical surveys, the most frequently used roost site. Each transect comprised eight call stations distributed at least 400 m apart (Fig. 1, inset). At each call station, we vocally imitated spotted owl vocalizations for 10 min to elicit a response from nearby owls. We visited each transect three times per year and surveyed all stations along each transect during each visit unless we detected an owl, at which point we stopped surveying that transect that year. All visits were conducted between April 1 and August 31 at least 10 days apart and two visits occurred before June 30 each year (USFWS, 2012). Broadcast surveys began no earlier than a half hour before dusk and ended no later than a half hour after dawn. If surveyors detected one or more spotted owls from a transect at any distance, we conducted an active follow-up survey either immediately after the detection or the following day, depending on conditions. We used follow-up surveys to locate owl nests, roosts, or young by walking through the area of the response, vocally imitating the owl, listening for responses, and looking for owl sign (e.g. pellets, whitewash). If an owl was located, live prey was offered to confirm nesting status using established protocols (USFWS, 2012). If no nest was located during a follow-up survey, we repeated the follow-up protocol at least three more times that year. In subsequent years, transect surveys were re-initiated only if an owl could not be located using active searching methods within a previously identified territory.

2.3. Habitat characteristics

We assessed habitat conditions within a 700-m radius (153 ha) 'core area' centered on the nest or most used roost tree associated with each historical and recent territory. The core area is intended to approximate an area which a pair of spotted owls would actively defend from conspecifics (USDA Forest Service, 2019). The 700-m radius defined an average area consistent in size with previously reported areas defended by territorial California spotted owls (Bingham and Noon 1997; Roberts et al., 2017; USDA Forest Service, 2019). This distance is also consistent with the observed distance from California spotted owl nest sites where the canopy structure remains distinct from the surrounding forest (North et al., 2017). The resulting 153 ha circle also aligned closely with the minimum size of a California spotted owl protected activity center (PAC; typically at least 121 ha), established by the USDA Forest Service (Verner et al., 1992; Gutiérrez et al., 2017; USDA Forest Service, 2019), although PACs are not established within the National Park.

The 700-m radius core areas are not intended to represent the true area of use, because areas of use are often complexly shaped, vary widely in size, and can only be inferred through intensive tracking efforts (Blakey et al., 2019). We did not attempt to exclude less favorable habitat surrounding the nests and roost sites from our core areas, as is done when delineating protected activity centers (PACs) for management purposes, because that would require making a priori assumptions about what is the most appropriate habitat. We assume that even if spotted owls do not spend a significant amount of time within some portion of the core area, forest characteristics in that core area still influence nest and roost site favorability and selection. Our core areas represent the habitat surrounding nest and roost sites, to yield insight into owl habitat preferences relevant to where they center their territories, without presuming to describe the entirety of their territory. When we detected one or more owls at night but never found an associated nest or roost tree during the day, we excluded the observation from analyses because we could not establish a center of a core area, as spotted owls regularly make forays of over 10 km from their territory centers during the breeding season which can create overestimates of occupancy (Berigan et al., 2019; Blakey et al., 2019).

To compare characteristics of historical and recent core areas with unoccupied habitat available across the landscape, we randomly selected reference areas (700-m radius circles) in appropriate but assumed unoccupied spotted owl habitat throughout Yosemite National Park for each era. A distinct set of 100 reference areas was selected for each era, as we wanted to ensure that the center of each reference area was > 700 m from any core area center in the corresponding era. We calculated the mean value for habitat characteristics at core and reference areas both before and after the Rim Fire (hereafter pre-fire and post-fire characteristics) using data derived from LANDSAT imagery. When spotted owls changed their territory center between years within an era but remained within the same core area (i.e. the center shifted < 700 m), we preferentially selected nest sites over roost sites to represent the territory center. In cases where the territory center changed between years and no nest site was identified in either year, we assessed habitat characteristics surrounding each year's territory center each year and averaged them to avoid pseudoreplication.

We assessed habitat within historical and recent core areas, both before and after the fire, by considering four characteristics: mean normalized difference vegetation index (NDVI), percent canopy cover, mean canopy height, and mean relative difference normalized burn ratio (RdNBR; assessed only for core areas within the fire perimeter). We chose these characteristics because they represent habitat features influenced by forest fire that are known to be important to spotted owls and were quantifiable from remotely sensed data available for the entirety of the study area from both before and after the Rim Fire. We chose RdNBR to quantify burn severity because it is designed to reduce bias in fire severity estimations caused by variation in pre-fire conditions and because it is more accurate than change in canopy cover at correctly classifying moderate severity burns (Miller and Thode, 2007; Miller et al., 2009a). We obtained canopy cover and canopy height from the USFS's LANDFIRE database (LANDFIRE 2018; https://www.landfire.gov/) and derived NDVI and RdNBR values using surface reflectance imagery data from LANDSAT (https://www.usgs.gov/land-resources/nli/landsat). All habitat metrics were calculated at a 30 × 30 m pixel resolution. To capture average breeding season conditions, we calculated NDVI as mean values from June 15 to July 15 from 2004 to 2006 for pre-fire conditions and in 2015–2017 for post-fire conditions. We quantified canopy cover and height, using LANDFIRE data from 2012 for pre-fire conditions and 2014 for post-fire conditions, as these values change negligibly over the timescale of this project except in response to stand-altering events such as the Rim Fire. After initial data collection, we ultimately excluded canopy height from further analysis because it was excessively correlated with canopy cover ($r^2 = 0.93$) and resulted in top-ranked models with excessive collinearity (variance inflation factor [VIF] > 10). AIC_c is able to handle correlated variables to some extent, but it has the potential to suffer from multicollinearity and inflate the importance of a weakly influential variable when paired with a highly influential and correlated variable (Freckleton, 2011). For this reason, we still chose to include other correlated variables, but did so with caution. This includes three pairs of variables with correlation coefficients > 0.6: pre-fire NDVI and pre-fire canopy cover ($r^2 = 0.79$), post-fire NDVI and post-fire canopy cover ($r^2 = 0.73$), and pre-fire canopy cover and post-fire canopy cover ($r^2 = 0.65$). To assure that top-ranked models found through AIC_c did not inflate the importance of one or more variables, we assessed the variance inflation factor (VIF) to determine whether models created using these data displayed excessive multicollinearity from the inclusion of correlated variables.

2.4. Analytical methods

To verify our assumption that the Rim Fire created quantifiable landscape-level changes in the habitat characteristics of interest that did not occur in suitable spotted owl habitat in portions of Yosemite that were unaffected by the Rim Fire, we used Welch's *t*-tests to compare habitat change between the recent and historical reference areas within the Rim Fire with habitat changes at reference sites outside of the Rim Fire. We also used Welch's *t*-tests to compare changes in habitat before and after the Rim Fire at occupied core areas within and outside of the fire perimeter.

We used a chi-squared test to determine if the fire displaced owls by comparing the number of owl territories within the fire perimeter between recent and historical eras, relative to the number outside of the fire's perimeter during these periods. Because only a single nest/roost site was < 1500 m from the edge of the fire (at 429 m), we assume that all territory centers found within the fire perimeter are substantially influenced by the fire and those outside of the fire are not appreciably influenced by the fire even if owls could hypothetically move across that perimeter. We also used a chi-square test to assess whether the fire reduced the likelihood of breeding, by comparing the proportion of territories with confirmed nests within the fire perimeter between recent and historical eras. To determine if owl density in Yosemite was higher within or outside the Rim Fire perimeter, we compared the proportion of owl territories found in the fire perimeter with the proportion of potentially suitable habitat that was burned using a chi-squared test for both eras.

We used Welch's *t*-tests to ascertain whether the percent of high severity burn within recent occupied core areas in the fire perimeter differed from recent-era reference areas. We also used this test to compare the percent of historical core areas that burned at high severity with the historical-era reference areas.

We assessed the importance of additional separate variables indicative of the fire's effects on the landscape; pre- and post-fire canopy cover and NDVI, and mean burn severity as measured by RdNBR on spotted owl presence within the Rim Fire using logistic regression models in the 'stats' package in R (R Core Team, 2017). One additional variable we intended to include in the models, percent high severity burn, was excluded because, as a composite index, it was excessively multicollinear with the other variables considered and resulted in top models with a VIF of > 10. We retained mean burn severity rather than percent high severity burn within this analyses of individual variables because we address the role of percent high severity in the previous analysis and the inclusion of mean burn severity helps to answer the separate question of whether burn at other severities has an impact of Spotted Owl presence that is not otherwise addressed. We created three model sets, comparing historically occupied core areas with reference areas during the pre-fire era, recent core areas with reference areas during the post-fire era, and historical versus recent core areas during the era in which they were occupied. We determined which models differentiated these areas using Akaike's Information Criterion corrected for small sample size (AIC_c). All results are presented as mean ± standard deviation and considered significant at an α-level of

0.05. We calculated the variance inflation factor (VIF) for the top-ranked models if they included more than one covariate to assure that these models were not affected by excessive collinearity. We also compared single-variable models post-hoc when highly ranked models (with a delta $AIC_c < 2$) included these closely correlated variables to better assess whether the influence of one variable is similar to that of another correlated variable.

3. Results

We found 27 distinct territory centers during recent survey efforts, 12 (44%) of which were within the fire perimeter. This was similar to the share of historical territories (10 of 21 historical territories; 48%) that were found within the same area prior to the fire ($\chi^2 > 0.99$, $df = 1$, $p > 0.99$), indicating that the fire did not change the numbers of spotted owl nest and roost sites within its perimeter relative to the number in surrounding National Park land. The proportion of recent ($\chi^2 = 0.802$, $df = 1$, $p = 0.370$) and historical ($\chi^2 = 1.51$, $df = 1$, $p = 0.219$) spotted owl territories within the Rim Fire in both eras was greater than, but not statistically different from, the proportion of total spotted owl habitat in the park that was within the fire perimeter (20,787 ha of 71,708 ha across the park; 29%).

Across the whole park, nesting was confirmed at 13 historical and 16 recent territories at least once during the relevant survey period. The proportion of total nests within the Rim Fire did not significantly differ between historical (8/13, 62%) and recent (8/16, 50%) eras ($\chi^2 = 0.060$, $df = 1$, $p = 0.806$). Nearly all recent nests were found in 2017, with eight pairs found nesting within the Rim Fire perimeter and eight outside, although two of these nests were also found during the previous years of the study. One pair within the Rim Fire perimeter nested in both 2015 and 2016 and was the only pair confirmed to nest during those years within the park. For analyses, we treated those nests as being from the same territory, as they were located within 700 m of one another.

Pooling data from the entire park, historical and recent core areas were spatially distinct, with mean distance between recent territory centers and the nearest historical territory center > 2 km ($\bar{x}$ = 2001 m, ± 1878 m). Recent territory centers within the Rim Fire were on average 1111 m (± 1058 m) from the nearest historical territory center; recent territory centers outside the fire perimeter averaged 2890 m (± 2086 m) from the nearest historical territory center. During the 2015–2017 survey period, territory centers identified as being part of the same core area (i.e. < 700 m apart) moved an average of 285 m (SD 217 m) between years.

Habitat measurements did not significantly differ between historical and recent core areas or historical and recent reference areas outside the fire perimeter, but within the perimeter both canopy cover and NDVI decreased significantly after the fire at core areas as well as reference areas (Table 1). We found no significant difference in RdNBR within the fire between recent core ($\bar{x}$ = 402.71, ± 170.12) and reference areas ($\bar{x}$ = 368.83, ± 217.03; $t = 0.65$, $df = 18$, $p = 0.53$).

Within the fire perimeter, the average percent of high severity fire within recent core areas ($\bar{x}$ = 10.1, ± 11.3) was significantly less than in reference areas ($\bar{x}$ = 26.6, ± 29.7; t = 3.031, df = 54.70, p = 0.004; Fig. 2), but mean values were similar in historical core areas ($\bar{x}$ = 32.6, ± 34.5) versus reference areas ($\bar{x}$ = 26.8, ± 28.3; t = −0.5217, df = 13.41, p = 0.610; Fig. 2). The maximum percent of high severity burn within recent core areas was 27.2 while the maximum within reference areas was 87.6.

Within the perimeter of the Rim Fire, the model that best differentiated historical core areas from reference areas included only pre-fire canopy cover (Table 2), which was significantly greater in historical core areas ($\bar{x}$ = 53.01, ± 11.92) than reference areas ($\bar{x}$ = 39.87, ± 14.9; estimate = −0.089, SE = 0.037, $Z = -2.408$, $p = 0.016$; Fig. 3). All other variables except change in canopy cover were included in highly ranked models.

Table 1
Comparison of habitat characteristics within 700-m radius circles representing historical (2004–2014) and recent (2015–2017) spotted owl core areas and reference areas within and outside the perimeter of the 2013 Rim Fire in Yosemite National Park.

	Historical	Recent	*t*	*df*	*p*
Reference Areas Outside the Fire Perimeter					
Canopy Cover	43% ± 11%	44% ± 11%	−0.34	272	0.73
NDVI	0.55 ± 0.10	0.55 ± 0.08	−0.35	260	0.73
Reference Areas Within the Fire Perimeter					
Canopy Cover	44% ± 14%	33% ± 11%	6.84	208	< 0.0001
NDVI	0.57 ± 0.10	0.43 ± 0.07	12.22	199	< 0.0001
Core Areas Outside the Fire Perimeter					
Canopy Cover	52% ± 9%	48% ± 11%	1.04	22.08	0.31
NDVI	0.61 ± 0.09	0.58 ± 0.09	0.77	19.88	0.45
Core Areas Within the Fire Perimeter					
Canopy Cover	53% ± 12%	40% ± 9%	3.13	17.77	0.006
NDVI	0.62 ± 0.05	0.44 ± 0.06	8.11	21.622	< 0.0001

The model that best differentiated recent core areas from reference areas in the Rim Fire also included only pre-fire canopy cover (Table 3), with the pre-fire canopy cover having been significantly greater in recent core areas ($\bar{x}$ = 55.21, ± 11.98) than reference areas ($\bar{x}$ = 43.55, ± 12.38; estimate = −0.094, SE = 0.037, $Z = -2.543$, $p = 0.001$; Fig. 3). Other top-ranked models included post-fire canopy cover, pre-fire NDVI, post-fire NDVI and change in NDVI. Change in canopy cover and mean RdNBR were not included in the top models for differentiating recent core areas from reference areas.

A null model was best differentiated recent and historical core areas, although post-fire canopy cover, change in canopy cover, and mean RdNBR were also selected in high ranking models (Table 4).

4. Discussion

In Yosemite National Park, the Rim Fire burned nearly 1/3 of potential spotted owl habitat, significantly lowering the affected area's mean NDVI and canopy cover, two variables reported to be strongly associated with spotted owl occupancy and habitat quality in other studies (Carroll, 1998; Seamans and Gutiérrez, 2007; Garcia-Feced et al., 2011; Gutiérrez et al., 2017; North et al., 2017; Tempel et al., 2017). However, spotted owl numbers did not change appreciably after the fire. Although nesting rates appeared quite low in 2015 and 2016, they were relatively high in 2017 and were generally comparable to nesting rates in areas of the park unaffected by the fire across all 3 years.

Multiple studies have reported spotted owls persisting after forest fires, even in areas with substantial high severity fire effects (Lee and Bond, 2015; Stephens et al., 2016; Rockweit et al., 2017; Lee, 2018), although the occupancy estimates of these studies may be inflated (Berigan et al., 2019). In other instances, even where similar methodologies were used, owls appear to have been largely displaced by fire (Jones et al., 2016, 2019; Ganey et al., 2017; Rockweit et al., 2017). Jones et al. (2016) observed the local spotted owl population to decline dramatically immediately after the 2014 King Fire in Eldorado National Forest in California, and to continue avoiding patches burned at high severity in subsequent years (Jones et al., 2019).

Spotted owls in our study area persisted and nested after the Rim Fire in numbers similar to before the fire, even though canopy cover and NDVI were lower in modern core areas within the Rim Fire perimeter than they were in historical core areas in the fire's perimeter. Although the owls were apparently robust to declines in those metrics of habitat suitability, we found that the percent of high severity burn within postfire core areas and reference areas was significantly different. All of the postfire core areas had less than 30% of the area burned at high severity. This is consistent with the findings of a GPS tracking study conducted in Yosemite that found that spotted owls were

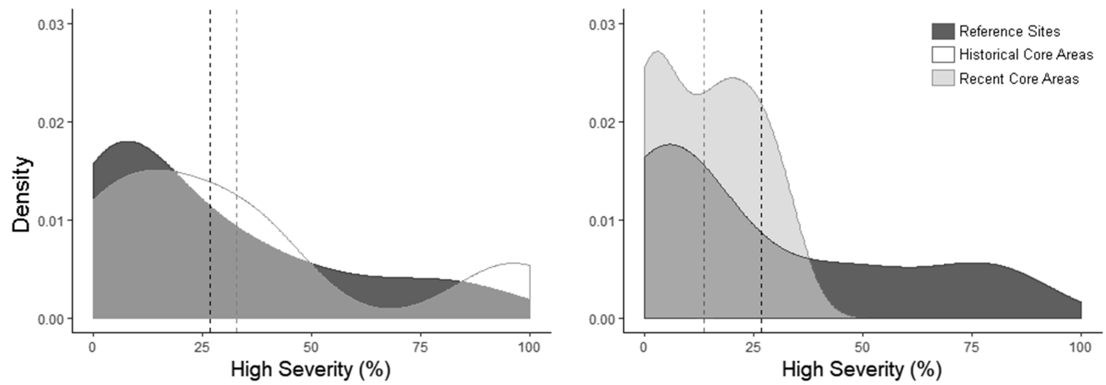

Fig. 2. Comparison of percent area burned at high severity in historical (white) and recent (light gray) spotted owl core areas, and reference sites (dark gray) within the perimeter of the 2013 Rim Fire in Yosemite National Park. Dotted lines represent the mean values of each variable for reference and core areas.

Table 2
Top ranked models (delta AICc < 2) for differentiating historical spotted owl core area from reference areas within the Rim Fire perimeter.

Model	df	logLik	AICc	delta	Wt
Pre-fire Canopy Cover	2	−24.016	52.3	0	0.170
Pre-fire NDVI	2	−24.840	53.9	1.65	0.075
Post-fire Canopy Cover + Mean RdNBR	3	−23.777	54.0	1.75	0.071
Pre-fire Canopy Cover + Post-fire NDVI	3	−23.816	54.1	1.83	0.068
Pre-fire Canopy Cover + Mean RdNBR	3	−23.816	54.2	1.94	0.064
Pre-fire Canopy Cover + Pre-fire NDVI	3	−23.873	54.2	1.98	0.063

neither selecting for nor avoiding areas of high severity burn except in the case where patches of high severity burn was extensive (Kramer et al., in press).

Despite the overall differences in population-level effects on owls between the Rim and King fires, our finding of an apparent threshold of tolerable high severity burn at the scale of the core area within the Rim fire is consistent with findings from the King Fire. Jones et al. (2016) reported that the percent of area burned at high severity by that fire was strongly related to local extinction probability, which was near zero at low percentages of high severity burn, but was extremely high where > 50% of the spotted owl core area burned at high severity. Owls at both fires thus appear to have been displaced from areas where high severity burn was extensive.

Owls in our study, however, appeared to have a lower threshold for high severity burn within their territories than has been found elsewhere. Jones et al. (2016) reported owls occupying territories with up to 50% of the area burned at high severity within the King Fire, and Lee and Bond (2015) observed owls within activity centers with 100% of the area burned at high severity within portions of the Rim Fire on Stanislaus National Forest. However, it is unclear whether observations within these extensive areas of high severity represent occupancy by territorial individuals rather than transient birds (Berigan et al., 2019).

The avoidance of areas with > 30% high severity burn we observed does not necessarily demonstrate that the owls cannot persist in such conditions, but it indicates that Spotted Owls preferentially selected area with less high severity fire when they are available. The King Fire and the portion of the Rim Fire that burned on the Stanislaus National Forest are characterized by notably more extensive, homogeneous areas of high severity burn than what we observed in Yosemite National Park (Kane et al., 2015; Jones et al., 2016; Povak et al., 2019). These homogenous landscapes likely offered fewer options to owls that may have otherwise preferred to shift their territories to encompass less high severity burn.

We further suspect that the spatial distribution of high severity burn, rather than just the total proportion of an area burned at high severity, may affect owls' predilection or ability to persist in burned landscapes. Despite differences in the size of high severity patches found between the Yosemite and Stanislaus portions of the Rim Fire, the overall percentage of the Rim Fire area burned at high severity was relatively similar between those portions of the Rim Fire (27% and 32% respectively). Within occupied core areas we assessed, the mean burn severity was similar to that within reference areas, even as the proportion of high severity burn differed.

Our results are less consistent with findings from an analysis of post-fire spotted owl persistence across six Sierra Nevada fires (Lee et al., 2012). In that study, an average of 32% of suitable habitat within spotted owl territories burned at high severity, yet rates of colonization and local extinction of established territories and activity centers were not significantly different from those at unburned sites. Spotted owls in that study did not appear to move their territories in response to fire. Heterogeneity in owls' response to the extent of high severity fire between our study area and the six fires studied by Lee et al. suggests that additional habitat variables may be important in mediating the consequences of high severity fire on owl persistence. Although the differences may also be influenced by methodological differences as Lee et al. included spotted owl detections that could have represented transient owls whereas we only included birds found at confirmed nest and roost sites (Berigan et al., 2019).

The variable we examined, especially canopy cover, effectively differentiate historical spotted owl territories from historical reference areas in our study area. However, our prediction that spotted owls remaining in the Rim Fire perimeter would relocate their territory centers to areas with lower mean burn severity and higher available canopy cover and NDVI than the burned landscape at large was partially incorrect.

Spotted owl core areas shifted substantially from historical sites after the Rim Fire, but except for avoidance of areas with > 30% high severity fire effects, we found little distinction between recent territories and the surrounding landscape. Indeed, pre-fire habitat characteristics better predicted spotted owls' post-fire habitat selection patterns, and recent spotted owl core areas were best differentiated from reference areas by their pre-fire canopy cover. Aside from burning with a greater overall percentage of high severity, the habitat characteristics of recent core areas were also not distinct from the characteristics of historical core areas. That is to say, the pre-fire conditions of recent territories matched the pre-fire conditions of historical territories, and post-fire conditions of recent territories matched the post-fire condition of historical territories. The locations of historical and recent territories also experienced a similar mean burn severity. The recent spotted owl core areas in our study were better predicted by pre-fire habitat characteristics than by the habitat characteristics present at the time of occupancy after the fire. Spotted owls actively select productive habitat and, given that spotted owls were nesting up to four years after the fire, it seems reasonable to assume that the habitat they selected was indeed favorable, but it remains unclear why pre-fire

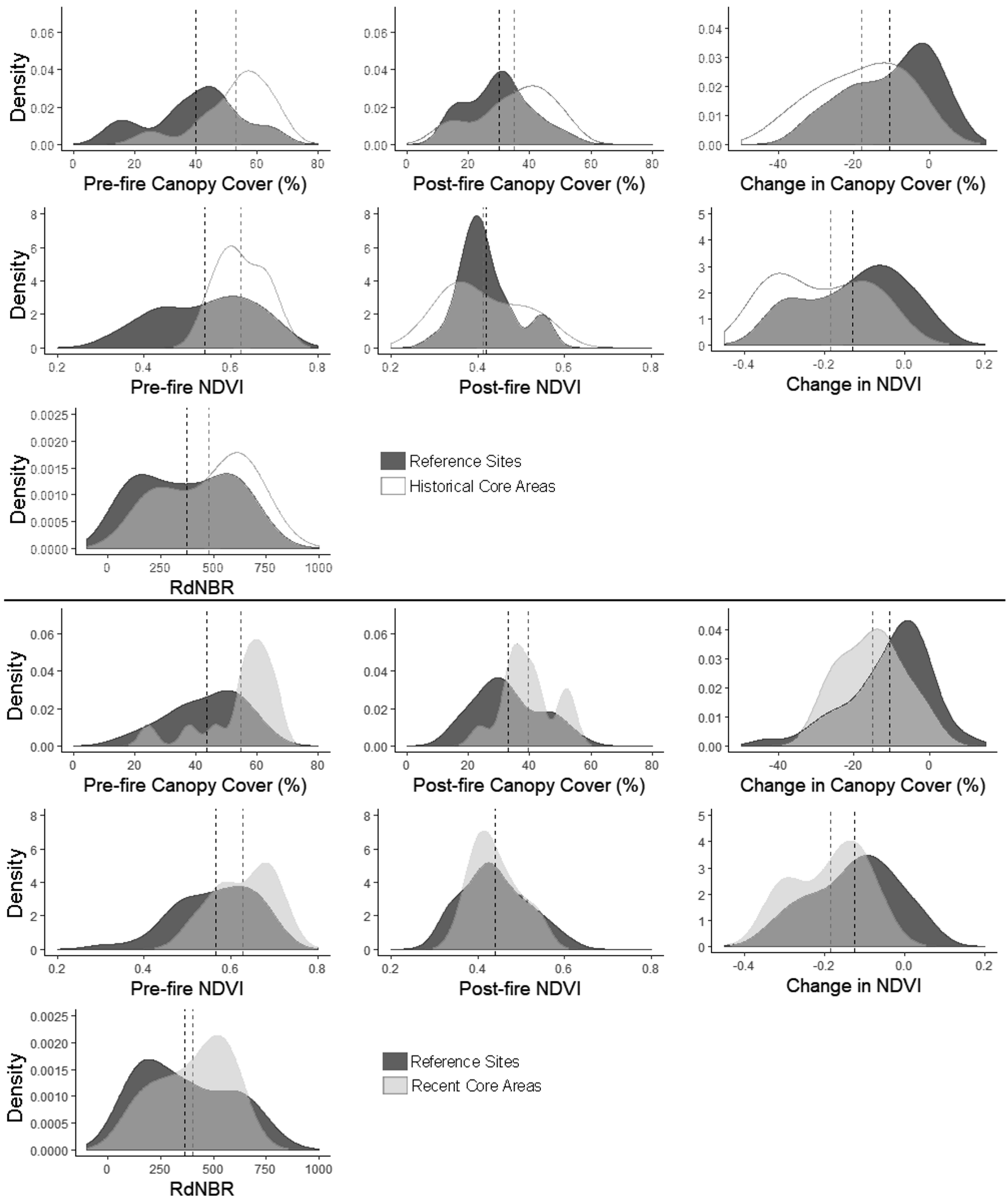

Fig. 3. Comparison of habitat characteristics between historical (white) and recent (light gray) spotted owl core areas and reference sites (dark gray; a distinct set of reference sites was evaluated for each era) within the perimeter of the 2013 Rim Fire in Yosemite National Park. Dotted lines represent the mean values of each variable for reference and core areas.

conditions were more strongly associated with post-fire owl presence than post-fire canopy cover or NDVI.

Forest structure influences how fire affects the landscape (Agee, 1996). Povak et al. (2019) found that the characteristics of the Rim Fire were influenced by the landscape's history and variability in forest structure prior to the fire. The differences in pre-fire forest structure we observed between occupied core areas and reference areas prior to the fire may have resulted in different post-fire conditions that were not quantified by the available satellite data. A complex suite of factors including, but not limited to, forest management, previous fire history,

Table 3
Top ranked models (delta AICc < 2) for differentiating recent spotted owl core areas from reference areas within the Rim Fire perimeter.

Model	df	logLik	AICc	delta	Wt
Pre-fire Canopy Cover	2	−25.667	55.6	0.00	0.167
Post-fire Canopy Cover Post-fire NDVI	3	−25.111	56.7	1.13	0.095
Pre-fire Canopy Cover + Post-fire NDVI	3	−23.726	57.5	1.98	0.062

Table 4
Top ranked models (delta AICc < 2) for differentiating historical versus recent spotted owl territories within the Rim Fire perimeter.

Model	df	logLik	AICc	delta	wt
Null	1	−16.552	35.3	0.00	0.196
Post-fire Canopy Cover	2	−15.950	36.5	1.18	0.108
Mean RdNBR	2	−16.058	36.7	1.40	0.097
Post-fire NDVI	2	−16.084	36.7	1.45	0.095

topography, tree species composition and geophysical characteristics can all contribute to forest structure, and many of these features may play some role in habitat selection by Spotted Owls after fire. Although spotted owls in the recent era would not have direct knowledge of conditions prior to the fire, the habitat characteristics measured prior to the fire may be related to some hold-over effect caused by pre-fire conditions. For example, high pre-fire canopy cover could be linked to availability of remnant stands of large trees that could continue to provide suitable nest and roost sites after a fire. Pre-fire conditions may also play a role in future prey abundance. Pre-fire conditions influence how a forest regenerates after a fire (Agee, 1996; Broncano and Retana, 2004; Beaty and Taylor, 2007; Crotteau et al., 2013; Young et al., 2019), so perhaps spotted owls prefer certain early-stage characteristics in disturbed habitats. More comprehensive habitat data such as park-wide LiDAR data will be valuable in identifying which habitat features drive post-fire habitat selection.

Regardless of the exact mechanism, if pre-fire conditions are strongly predictive of spotted owl nest and roost site selection after a fire, pre-fire forest management also seems likely to affect spotted owls' response to fire. Indeed, differences in pre-fire management may be related to spotted owls' heterogeneous response to forest fires. Within Yosemite, minimal fire suppression for many decades and prohibitions on logging for over a century have created a landscape characterized by larger areas of forest with old growth characteristics (Collins et al., 2011; Miller et al., 2012; Jeronimo et al., 2019) and more structural diversity than what is currently found across much of the California spotted owl's range (Jeronimo et al., 2019). To the extent that the largely restored fire regime approximates historical conditions (Jeronimo et al., 2019), the Rim Fire in Yosemite may suggest how spotted owls historically responded to forest fires. Yosemite's post-fire landscape likely provides spotted owls different opportunities when selecting territories than are available in burned areas outside of the park. A better understanding of how pre-fire forest management and pre-fire forest conditions influence spotted owl response to fire will require assessing owl response to pre- and post- fire forest conditions across a broader range of forest landscapes with differing pre-fire management regimes. Doing so may help to resolve enduring questions about the implications of changing fire regimes on California spotted owls.

CRediT authorship contribution statement

Lynn N. Schofield: Conceptualization, Formal analysis, Data curation, Writing - original draft, Visualization. **Stephanie A. Eyes:** Conceptualization, Methodology, Investigation, Data curation, Writing - review & editing, Supervision. **Rodney B. Siegel:** Conceptualization, Writing - original draft, Project administration, Funding acquisition. **Sarah L. Stock:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision, Project administration, 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.

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