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Fuels reduction can directly improve spotted owl foraging habitat in the Sierra Nevada

Marilyn E. Wright[a,b], M. Zachariah Peery[b], Jessalyn Ayars[a,c], Brian P. Dotters[d], Kevin N. Roberts[d], Gavin M. Jones[a,*]

[a] USDA Forest Service, Rocky Mountain Research Station, Albuquerque, NM, USA
[b] Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA
[c] Biology Department, University of New Mexico, Albuquerque, NM, USA
[d] Sierra Pacific Industries, Anderson, CA, USA

A R T I C L E I N F O

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A B S T R A C T

Wildfire has been an important force in shaping biological diversity in forests of western North America. Patterns of reburning helped to maintain heterogenous landscapes with low tree densities that naturally limited the extent of severe stand-replacing fires. However, anthropogenic impacts over the past two centuries have dramatically altered fire activity and its ecological function, creating conditions that promote large and intense fires with no historical analog. Fuels reduction treatments represent proven methods to mitigate extreme fire events, but there is controversy over their potential effects to sensitive wildlife species. The California spotted owl (*Strix occidentalis occidentalis*) is a forest species that evolved under a frequent-fire regime. Controversy over how spotted owls may be impacted by fuels reduction is one of numerous contributing factors that has limited the pace and scale of implementation. To examine the relationships between spotted owls and fuels reduction treatments, we studied breeding season nocturnal foraging habitat selection related to fuel structural metrics of 159 GPS-tagged California spotted owls across the Sierra Nevada bioregion. Spotted owls selected for higher canopy base height, lower ladder fuel density, and lower canopy bulk density, which represent synergies between fuels reduction treatments and owl space use. Spotted owls also selected for higher surface fuels and higher canopy layer counts, representing potential trade-offs between fuels reduction goals and spotted owl space use. We overlaid the probability of space use by foraging spotted owls with relative stand density index (SDI), a measure of forest resilience, to classify Sierra Nevada landscapes into four groups: low management priority (low owl use/high forest resilience), fuels reduction priority (low owl use/low forest resilience), potential conflict zones (high owl use/low forest resilience), and habitat retention priority (high owl use/high forest resilience). Fuels reduction priority (34.4%) was the largest category, suggesting that potential impacts of fuels reduction on spotted owl foraging habitat may be less widespread in the Sierra Nevada than previously believed. Our results suggest that fuels reduction treatments, especially those focused on mutually beneficial goals such as increasing canopy base height, reducing ladder fuels, and reducing canopy bulk density may directly improve spotted owl foraging habitat while also mitigating the effects of large and severe wildfires on forest species and forest ecosystems.

1. Introduction

Wildfire has shaped the western forests of North America for thousands of years, driving the evolution of both ecosystems and the species inhabiting them (Kelly et al., 2020). Prior to Euro-American settlement, many western forests were characterized by frequent low- to moderate-severity wildfires (Arno and Allison-Bunnell, 2013; Hessburg et al., 2005; Stephens et al., 2012) that varied in size, duration, and seasonality (Hessburg et al., 2016; Perry et al., 2011). Frequent fires created mosaics of forest and non-forest vegetation, with forest patches containing

Abbreviations: RSF, resource selection function; SSF, step selection function; GPS, global positioning system; VHF, very high frequency; DOP, dilution of precision; CFO, California Forest Observatory; SDI, stand density index; ACCEL, for accelerating the pace and scale of treatments; ROC, receiver operating characteristic curve; TSS, true skill statistic; USDA, United States Department of Agriculture.

* Corresponding author.
E-mail address: gavin.jones@usda.gov (G.M. Jones).

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mature fire-tolerant tree species as small understory trees were naturally thinned (North et al., 2016; van Wagtendonk et al., 2018). Fire dynamics also played a significant role in influencing other ecological processes including carbon and nutrient cycling, hydrology, and primary productivity, which in turn influenced the persistence and distribution of organisms (Bowman et al., 2009; Turner, 1989). The patterns of burning and reburning across the landscape reduced the quantity and connectivity of live and dead forest fuels (Agee and Skinner, 2005) and maintained low tree densities (Safford and Stevens, 2017). The resulting heterogenous landscape helped to naturally limit the extent of severe and stand replacing fire events (Hagmann et al., 2021; Nigro and Molinari, 2019; Prichard et al., 2017).

Over the past two centuries, western forests have undergone a significant shift in fire activity and ecological function, primarily due to anthropogenic influence. Fire regimes were significantly altered through the exclusion of indigenous burning (Kay, 2000; Stewart, 2002) and wildfire suppression (Hagmann et al., 2021; Hessburg et al., 2005), as well as the selective harvesting of large, mature trees which contributed to losses of fire-adapted forest structure (Hessburg and Agee, 2003; Lydersen et al., 2013). These practices homogenized forest landscapes (Raphael et al., 2001; Wisdom et al., 2000) with decreased average tree size, increased stand density and canopy cover, higher densities of fire-intolerant species, and increased fuel loads and connectivity (Battaglia et al., 2018; Collins et al., 2011; Hagmann et al., 2021; Knapp et al., 2013; Savage et al., 2013; Scholl and Taylor, 2010; van Mantgem et al., 2018). Contemporary forest conditions promote large and intense fires that are uncharacteristic of historical ranges (Hann, 1997; Haugo et al., 2019; Holsinger et al., 2014; Keane et al., 2009; Loehman et al., 2017; Stockdale et al., 2019), and changes to forest and fuels structures have left these systems increasingly vulnerable to the direct and indirect effects of climate warming and drought (Allen et al., 2002; Bryant et al., 2019; Hessburg et al., 2019; Keane et al., 2018; Noss et al., 2006). Warming climate trends are contributing to the lengthening of fire seasons and increased likelihood of extreme fire weather, leading to fire effects increasing in severity and magnitude (North et al., 2015; Parks and Abatzoglou, 2020). Climate change predictions suggest that burned area in western North America is likely to at least double or triple by mid-century (McKenzie et al., 2004; Westerling et al., 2011).

Current conditions and the continued practice of fire exclusion threaten fire-dependent biodiversity as well as forests' capacity to resist and recover from large disturbances (Franklin et al., 2000; Krawchuk et al., 2020; Reilly et al., 2019). Under these circumstances, high severity wildfires can have lasting impacts including the loss of social and ecological resources, ecosystem type conversion, and reduced options for future adaptation (Coop et al., 2020; Kemp et al., 2019; Norgaard, 2014; Sowerwine et al., 2019; Stephens et al., 2020; Stevens-Rumann and Morgan, 2019). In this context, proactive management, including scientifically informed and appropriately designed thinning, burning, and wildfire treatments, are likely to adapt landscapes for future wildfire activity (Hagmann et al., 2021; Prichard et al., 2021). Fuels reduction treatments are proven methods to influence the ecological impacts of wildfire and mitigate extreme events (Prichard et al., 2021; Taylor et al., 2016) by encouraging the proliferation of fire-adapted biological communities (Hessburg et al., 2021; Prichard et al., 2021). The purpose of fuels reduction treatments is to significantly alter the fuel complex, including reducing surface fuels, ladder fuels, and crown density (Agee and Skinner, 2005), thereby modifying future fire behavior and minimizing the impacts of wildfires on ecosystem goods and services, cultural resources, and human communities (Hoffman et al., 2018). Fuels reduction treatments increase the likelihood that future fires will burn at low- to moderate-severity by creating more heterogenous structural conditions (Churchill et al., 2013; Knapp et al., 2017) and increase forest resilience or the capacity to respond favorably to future disturbances (Stephens et al., 2020).

Though proactive management through fuels reduction is the dominant adaptation strategy for preventing uncharacteristically severe fires (Allen et al., 2002; Fulé et al., 2012; Hessburg et al., 2015; Moore et al., 1999; Underhill et al., 2014), the scale and pace of current fuels reduction treatments is much less than that of fuels reduction from pre-European fire regimes (Brown et al., 2019; Kane et al., 2019; Mueller et al., 2020; North et al., 2012; Parks et al., 2014; Stevens-Rumann et al., 2016; Vaillant and Reinhardt, 2017; Walker et al., 2018). Projected increases in warming due to climate change continue to dramatically increase the probability of large, severe wildfires for many western forests (Hurteau et al., 2019; Littell et al., 2018), increasing the necessity for intentional management focused on adapting forests to this rapidly changing environment (Prichard et al., 2021). Fuels reduction treatments implemented at large regional scales are likely to promote forest health (Coop et al., 2020; Moritz et al., 2013), foster native biodiversity (Bisson et al., 2003; Isaak et al., 2010; Raphael et al., 2001; Rieman et al., 2010), and maintain essential ecosystem services and processes (Dale et al., 2001; Hurteau et al., 2014; Millar et al., 2007). Despite efforts to form multi-entity, cross-jurisdictional partnerships to increase proactive management and forest restorative treatments to promote landscape-scale resilience, perceived uncertainty in the science of fuels reduction treatments and adaptive management coupled with socio-economic challenges continue to limit implementation of fuels reduction treatments to a small percentage of western North American forested lands (Franklin and Johnson, 2012; Hessburg et al., 2020; Kolden, 2019; Long, 2009; North et al., 2012; Prichard et al., 2021).

One area of uncertainty and disagreement is in understanding the impacts that fuels reduction treatments may have on wildlife, especially sensitive and threatened species (Laband et al., 2008, 2006; Pilliod et al., 2006; Runge, 2011). This dynamic is particularly prevalent in the Sierra Nevada, California, a biologically diverse region facing an unprecedented threat of severe and intense wildfire (Gutierrez et al., 2021; Lenihan et al., 2008; Murphy and Stine, 2004). While the need for fuels reduction treatments and restoration of some degree of natural fire within the Sierra Nevada is particularly acute (Stephens et al., 2021; Wood and Jones, 2019), uncertainty and disagreement over wildlife responses to such treatments has led to contention over how and where these treatments should be permitted (Jones et al., 2022; Wood and Jones, 2019). The California spotted owl (*Strix occidentalis occidentalis*) has been at the center of much of this debate, with disagreement over how fuels reduction treatments may impact this forest species (Gallagher et al., 2019; Kramer et al., 2021b; Lee and Irwin, 2005; Peery et al., 2019; Stephens et al., 2014; Tempel et al., 2014a, 2015; Wood and Jones, 2019).

To address concerns over the potential impacts of fuels reduction treatments on California spotted owls, it is imperative to understand the nuanced relationship that owls have with forest structures that will be altered by treatments. Previous research suggests that California spotted owls are threatened by extensive severe wildfire (Jones et al., 2016a, 2016b, 2020; Miller et al., 2018; Tempel et al., 2014a, 2015) and may benefit from fuels reduction treatments (Jones et al., 2021; Tempel et al., 2015; Zulla et al., 2022). Many of the goals inherent in fuels reduction treatments such as retaining fire-resistant large, mature trees (Agee and Skinner, 2005; Hessburg et al., 2021; Spies et al., 2019; Spies et al., 2018) and restoring successionally and spatially heterogenous forests with openings between patches (Addington et al., 2018; Churchill et al., 2013, 2013; Franklin and Johnson, 2012; Larson and Churchill, 2012; LeFevre et al., 2020; North et al., 2009; Perry et al., 2011; Reynolds et al., 2013; Stine et al., 2014) are goals that align well with the habitat needs of spotted owls, especially when considering the potential long-term benefits of fuels reduction treatments for the species (Jones et al., 2021, 2019; Tempel et al., 2015; Wood et al., 2018; Wood and Jones, 2019). However, the current understanding of the relationships between fuels reduction and spotted owl foraging habitat use are still reliant primarily on secondary inference from studies seeking to parse out habitat relationships with other goals (Dow et al., 2016; Hobart et al., 2019; Stephens et al., 2014; Tempel et al., 2014a; Wood et al., 2018; Wood and Jones, 2019).

To examine the relationship between fuels reduction treatments and California spotted owl foraging habitat, we considered the direct relationship between forest structural characteristics targeted as part of fuels reduction treatments and California spotted owl space use. We used mixed-effects habitat selection functions (resource selection functions (RSFs) and step selection functions (SSFs) to examine both individual- and population-level habitat selection (Muff et al., 2020) based on information from a large sample of GPS-tagged California spotted owls (n = 159) in the Sierra Nevada between 2015 and 2020. We examined the relationship between foraging habitat use and fuel characteristics (canopy base height, canopy bulk density, canopy layer count, ladder fuel density, and surface fuels; Table 1) to elucidate patterns of owl space use and selection directly related to these metrics and developed a suite of predictions indicating expected relationships based on our current understanding of spotted owl ecology (Table 2).

Our goal was to identify potential synergies and trade-offs between forest fuels reduction treatments and spotted owl use of habitat. We predicted that owls would prefer higher canopy base height consistent with their need for tall trees (North et al., 2017), especially to facilitate prey capture (Zulla et al., 2022), and that this would be a synergistic goal for fuels reduction treatments seeking to increase canopy base height. We also predicted that owls would prefer higher surface fuels as surface fuels can create habitat for important prey species like woodrats (Fraik et al., 2023; Innes et al., 2007); however, preference for higher surface fuels would indicate an area of trade-off between owl preferences and fuels reduction goals as surface fuels reduction is an important component of fuels reduction treatments. We predicted that owls could either prefer or avoid higher canopy bulk density and ladder fuels. Selection for higher canopy bulk density and ladder fuels could suggest that these structures provide important habitat for prey species (Zulla et al., 2022), but avoidance could also be possible as owls have been documented avoiding lower strata cover (North et al., 2017). Selection for higher canopy bulk density and ladder fuels would indicate a trade-off between owl preferences and fuels reduction goals whereas avoidance of these structures would indicate synergistic goals. Finally, we predicted that owls would avoid areas with higher canopy layer count as increased distinct layers, especially in dense forests, might indicate the presence of younger and smaller trees (Jones et al., 2020; Zulla et al., 2022). Avoidance of higher canopy layer count would be a synergistic with fuels reduction goals that aim to decrease ladder fuels in the lower strata (Table 2).

Table 1
California Forest Observatory (CFO) covariates used to model California spotted owl habitat selection across the Sierra Nevada, including variable description, unit of measurement, and range of values. All variables were centered and scaled (z-standardized) so that mean values were approximately 0 and the standard deviations were approximately 1.

Variable	Description	Unit	Range
Canopy base height	Distance between the ground and the lowest branches in the canopy	m	0 – 29
Canopy bulk density	Mass of the available fuel that burns in a canopy fire divided by the volume of the crown	kg/m^3	0 – 0.45
Canopy layer count	Number of distinct vertical canopy layers	count	0 – 9
Ladder fuel density	Proportion of surface fuels in the understory	%	0 – 100
Surface fuels	Model describing vegetation fuel type, size class, depth, moisture content, and heat content	spread rate	91 – 202

Table 2
Predicted owl response (positive or negative) and whether this response would represent a synergy or trade-off with fuel reduction goals.

Variable	Owl response	Synergy or trade-off
Canopy base height	+	Synergy
Canopy bulk density	− / +	Synergy / trade-off
Canopy layer count	−	Trade-off
Ladder fuel density	− / +	Synergy / trade-off
Surface fuels	+	Trade-off

After determining the selection preferences for spotted owls, we mapped the probability of use for all landscapes falling within a California spotted owl range map within the Sierra Nevada bioregion. We also related this probability of use map to a region-wide map of stand density index (SDI), which is a general representation of forest resilience to many stresses including drought, bark beetles, and fire (North et al., 2022). We then classified owl foraging habitat in the Sierra Nevada as falling into one of four categories: 'low management priority' (low probability of use/low fire risk), 'fuels reduction priority' (low probability of use/high fire risk), 'potential conflict zones' (high probability of use/high fire risk), and 'habitat retention priority' (high probability of use/low fire risk; Fig. 1).

2. Materials and methods

2.1. Study site

We studied California spotted owl nocturnal foraging habitat selection during the breeding seasons in the Sierra Nevada from 2015 to 2020. The landscape encompassed in our study represented a mosaic of mixed ownership, including national parks (Yosemite and Sequoia-Kings Canyon), national forests (Tahoe, Eldorado, Plumas, and Stanislaus), privately-owned forests managed for commercial timber production (primarily Sierra Pacific Industries), and other small privately-owned allotments managed for other uses. The climate is Mediterranean, with cool, wet winters and warm, dry summers. Elevations range from 590 to 2200 m. Forest vegetation in the Sierra Nevada is diverse, with high variation in density and vertical structure due to management history, fire, topography, soil, elevation, and latitude (North et al., 2016). Oak

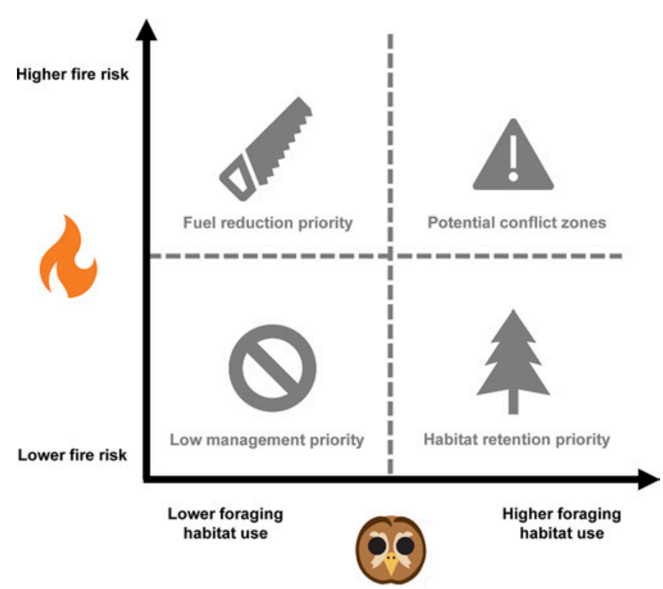

Fig. 1. Conceptual relationship between California spotted owl foraging habitat use and fire risk in association to forest fuel measurements.

woodlands and chaparral are predominant at lower elevations, gradually shifting to mixed-conifer forests at mid-elevations, and subalpine forests at higher elevations (Mayer and Laudenslayer, 1988; Sugihara et al., 2006).

2.2. Owl space use data

From 2015 through 2020, we captured adult spotted owls (males and non-nesting females) before or early in the breeding season as part of a longer-term demographic and space use study of spotted owls in the Sierra Nevada (Atuo et al., 2019; Jones et al., 2020; Kramer et al., 2021b, 2021a; Zulla et al., 2022). Territorial breeding spotted owls were located during routine monitoring surveys, which are conducted annually in the Sierra Nevada (e.g., Hobart et al., 2019; Roberts et al., 2017). Call-based surveys were used to locate owls briefly at night, and then dawn/dusk surveys the following day were completed to determine their reproductive status and locate nests (Franklin et al., 1996). Owls were captured using hand-grab techniques, pan traps, bal-chatri traps, or snare poles (Bull, 1987; Franklin et al., 1996). We then fitted owls with either a backpack- or tail-mounted dual GPS/VHF unit or a GPS unit with remote downloading capabilities (Biotrack Ltd., Wareham, UK; Lotek Wireless, model Pinpoint VHF 120, Newmarket, Ontario, Canada; Alle-300, Ecotone, Poland; hereafter "GPS tag"). GPS tags and harnesses weighed 7–10 g (less than 2% of average spotted owl body weight).

Most owls were recaptured to remove the GPS tags, but owls that were not recaptured were fitted with tail-mounted GPS tags, which we expected to be shed in the subsequent molt. VHF locations were used only to relocate tagged owls for recapture and GPS data retrieval and were not used in any analyses. GPS tags were programmed to retrieve location data at different intervals to characterize spotted owl nocturnal movements at different scales. From 2015 to 2017, 23 owls were fitted with GPS tags that were programmed to record 1–3 locations per night, separated by at least two hours to reduce spatial autocorrelation. From 2017 to 2018, 98 owls were fitted with GPS tags that were programmed to record five hourly locations per night (22:00–02:00 or 23:00–0:300) and one diurnal location. Finally, from 2019 to 2020, 46 owls were fitted with GPS tags that were programmed to record locations at 2-min intervals (22:00–02:00). We removed all locations with a DOP (dilution of precision) score > 5, resulting from poor satellite signals to avoid potential erroneous inference about space use. While owls engage in a variety of nocturnal activities including territory defense, resting, and trips to the nest that may be captured in our GPS locations (Delaney et al., 1999; Forsman et al., 1984), we assumed that our location data primarily represented foraging space use activities because owls are nocturnal predators.

2.3. Forest fuel structure variables

We obtained forest fuel structure measurements from the California Forest Observatory (CFO) (https://forestobservatory.com/). CFO links airborne lidar to remotely sensed imagery from the Sentinel satellite program to map statewide forest structure. We used the Python application programming interface provided by CFO (https://github.com/forestobservatory/cfo-api, accessed October 6, 2022) to download 10-meter resolution raster layers for canopy base height, canopy bulk density, canopy layer count, ladder fuel density, and surface fuels for all years corresponding to spotted owl GPS data collection years 2016 to 2020 (Table 1). Where assessments are available, accuracy of forest structure layers that we selected for our analyses ranges from 0.59 to 0.71. Because CFO data only dates back to 2016, we determined that there were no major landscape disturbances in the area covered by our 2015 GPS points. There were no major disturbances between 2015 and 2016, so we paired 2016 CFO data with 2015 owl GPS points. Table 1.

2.4. Foraging habitat selection analyses

We analyzed habitat selection and space use relative to fuel metrics at three different temporal scales (nightly, hourly, and minute-to-minute) using locations derived from GPS-tagged spotted owls. We analyzed our nightly data using mixed-effects resource selection functions (RSFs) (logistic regression) with slopes and intercepts that varied by individual, and we analyzed our hourly and minute-to-minute data using mixed-effects step selection functions (SSFs) with slopes and intercepts that varied by individual, where available habitat is conditional on the previous location and turn angle to the subsequent location (Avgar et al., 2016; Duchesne et al., 2010; Muff et al., 2020). Including coefficients that vary by individual reduces the biases in estimated population-level (fixed) effects (Duchesne et al., 2010; Gillies et al., 2006; Harrison et al., 2018). For step selection functions, we generated 20 random steps for each observed step, randomly sampled from the empirical distributions of step lengths and turn angles (Avgar et al., 2016; Duchesne et al., 2010). Due to collinearity among some of the fuel structural metrics, we fit all models as univariate models and made inference on individual effects rather than attempting to develop a single, optimal model structure. In all models, we fixed the variance term for individual-specific intercepts to a large value ($\sigma^2 = 1000$) to avoid shrinkage toward zero and available points were assigned weight $W = 5000$ to facilitate approximate convergence to the inhomogeneous Poisson process likelihood (Muff et al., 2020).

Available area for each individual owl in the RSF framework was defined by the 95% autocorrelated kernel density estimate of the breeding season home range (Fleming et al., 2015). To increase the sample size, spatial coverage, and temporal duration of our nightly GPS locations, we randomly sampled one location per night for each unique combination of individual and year from the hourly GPS locations, however, we did not subsample hourly locations for owls with less than 20 total GPS locations. We generated three times as many available points as used points for each owl within the RSF framework (Muff et al., 2020) and 20 times as many available points as used points for each owl in the SSF framework (Hooten et al., 2017).

All analyses were conducted in R version 4.2.2. We used the R package *amt* v. 0.1.7 to draw home ranges and tracks, create available points, and extract covariate values. All models were fit using the R package *glmmTMB* v. 1.1.5. We made inferences about the statistical importance of fixed effects from their direction (positive/negative), effect size (magnitude), and uncertainty (95% confidence intervals), but avoided interpreting significance of results through arbitrary p-value thresholds (Muff et al., 2022). We used odds ratios to further aid in the interpretation of the effects of forest fuel structure metrics on spotted owl foraging habitat selection (Lele et al., 2013).

2.5. Classifying landscape into management objectives based on probability of use and fire risk

To classify California spotted owl foraging habitat into management objectives (Fig. 1), we combined a probability of use and stand density index (SDI) for areas within the California spotted owl range in the Sierra Nevada. For each forest fuel structural variable, we used the 2020 CFO raster data to create a data frame of unique values. We used the unique values to predict the probability of habitat use based on the univariate models, and then created a reclassification matrix relating the original raster values to the probability of habitat use. After completing these steps for each of the 2020 data, we then multiplied all the probability rasters together to create a composite probability of habitat use map covering the Sierra Nevada study area.

We obtained a 30-m raster of proportion of maximum SDI from the ACCEL (for accelerating pace and scale of treatments) program (Young-Hart et al., 2023) for the year 2020. The proportion of maximum SDI raster was created based on the Zeide (1983) calculations. Maximum SDI represents the approximate species- and site-specific upper limit on potential SDI that a site has before tree growth begins to be limited by competition, and therefore has been interpreted as an operational measure of forest resilience (North et al. 2022). Competition benchmarks in previous studies have described the onset of site competition (25% of maximum SDI), lower limit of full site occupancy (35% maximum SDI), and the maximum competition or the 'zone of imminent mortality' (≥60% maximum SDI). We used 35% maximum SDI as our threshold for forest resilience and proxy for fire risk, where any values ≤ 35% maximum SDI across the landscape were coded as a high resilience/low fire risk and any values > 35% maximum SDI were coded as low resilience/high fire risk.

We used a receiver operating characteristic (ROC) curve to assess the sensitivity and specificity of our data and determine a true skill statistic (TSS; Allouche et al., 2006). We used the TSS value (0.399) as a threshold to define low probability of habitat use as ≤ 0.399 and high probability of habitat use as > 0.399. We then divided our reclassified proportion of maximum SDI raster by our reclassified probability of use raster to obtain a composite raster with four distinct groups corresponding with the four quadrants in Fig. 1: "habitat retention areas" with low proportion maximum SDI and high probability of use; "fuel reduction areas" with high proportion maximum SDI and low probability of use; "conflict zones" with high proportion maximum SDI and high probability of use; and "low priority landscapes" with low proportion maximum SDI and low probability of use. We clipped the final raster to extent of the California spotted owl range (https://data.ca.gov/dataset/spotted-owl-range-cwhr-b270-ds897) within the Sierra Nevada bioregion. There were 108,018,160 total pixels across the Sierra Nevada bioregion and 49,633,640 within the California spotted owl range. For computational efficiency, we examined the mean SDI and TSS classification values as well as the distribution of pixels across ownership types by taking a 5,000-pixel subsample.

We examined the proportion of the California spotted owl range that fell into each category both across the entire region and by ownership type (national parks, national forests, and private land). We also highlighted and summarized the predicted distribution of classification categories within two high-risk firesheds in the Sierra Nevada, the Stanislaus and North Yuba, that have been selected as two of the ten Initial Landscape Investments to receive funding for fuels reduction treatments as part of an effort by the USDA Forest Service to protect communities and improve forest resilience. Funding for these projects began in 2022 and will continue through 2024 (USDA Forest Service, 2022).

3. Results

We obtained usable nocturnal GPS locations from 159 GPS-tagged owls monitored in the breeding seasons from 2015 to 2020, composed of 104 males and 55 females. Of the total locations, 3,837 were used for conducting the nightly RSFs, composed of 77 total owls (56 male and 21 female). We were able to use 14,315 locations from 86 owls (59 male and 27 female) for the hourly step selection functions, and we were able to use 32,380 locations from 46 owls (29 male and 17 female) for the minute-to-minute step selection functions.

3.1. *Foraging habitat selection analyses*

Spotted owls in our study selected for higher canopy base height (RSF $\beta_{CanopyBaseHeight} = 0.275$, 95% confidence interval [0.196, 0.353], odds ratio = 1.317) and avoided higher canopy bulk density (RSF $\beta_{CanopyBulkDensity} = -0.071$, 95% confidence interval [−0.154, 0.011], odds ratio = 0.931) and higher ladder fuel density (RSF $\beta_{LadderFuelDensity} = -0.071$, 95% confidence interval [−0.153, 0.010], odds ratio = 0.931) (Fig. 2). These relationships held across all RSF and SSF analyses, except for ladder fuel density, which switched to a positive relationship in the minute-to-minute SSF. However, the effect size of ladder fuel density in the minute-to-minute SSF was small (SSF_{minute} $\beta_{LadderFuelDensity} = 0.003$, 95% confidence interval [−0.010, 0.017], odds ratio = 1.003). Spotted owls in our study selected for higher surface fuels (RSF $\beta_{SurfaceFuels} = 0.306$, 95% confidence interval [0.243, 0.369], odds ratio = 1.358) and higher canopy layer count (RSF $\beta_{CanopyLayerCount} = 0.331$, 95% confidence interval [0.268, 0.394], odds ratio = 1.392; Fig. 2). The directional (positive/negative) relationships held across all RSF and SSF analyses, but the effect size was greatest for the nightly RSFs. Because of the robustness of results across all RSF and SSF analyses (nightly, hourly, and minute-to-minute scales), we discuss in detail only the RSF analyses moving forward for simplicity.

3.2. *Classifying landscape into management objectives based on probability of use and fire risk*

Across the California spotted owl range within the Sierra Nevada, most of the landscape could be classified as "fuel reduction" areas (34.4%), followed by potential "conflict zones" (31.5%), "low priority" areas (28.0%) and "habitat retention areas" (6.0%). Density plots of each ownership type suggest each ownership type has a varied landscape with the highest local densities of points in the "low priority" and "conflict zone" classifications (Fig. 3). When owl foraging habitat was further broken down into distinct ownership types, there was variation in the classification of landscape. For national forests, the majority of the landscape could be classified into potential "conflict zones" (37.1%), followed by "fuel reduction" areas (34.3%), "low priority" areas

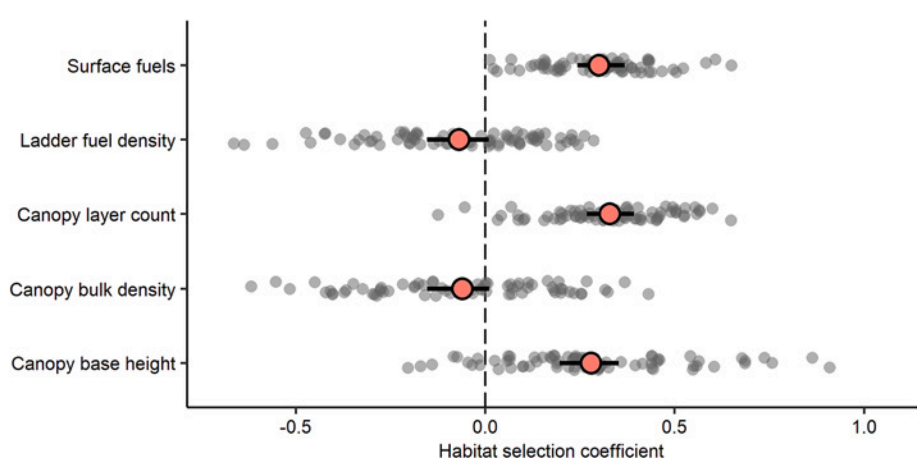

Fig. 2. Coefficient values for the nightly data RSFs. Red circles represent population (fixed-effects) mean with 95% confidence interval shown in the black error bars. Grey circles represent the individual coefficients for each owl in the mixed-effects RSF. The vertical dashed line indicates that selection for a given covariate is equal to availability.

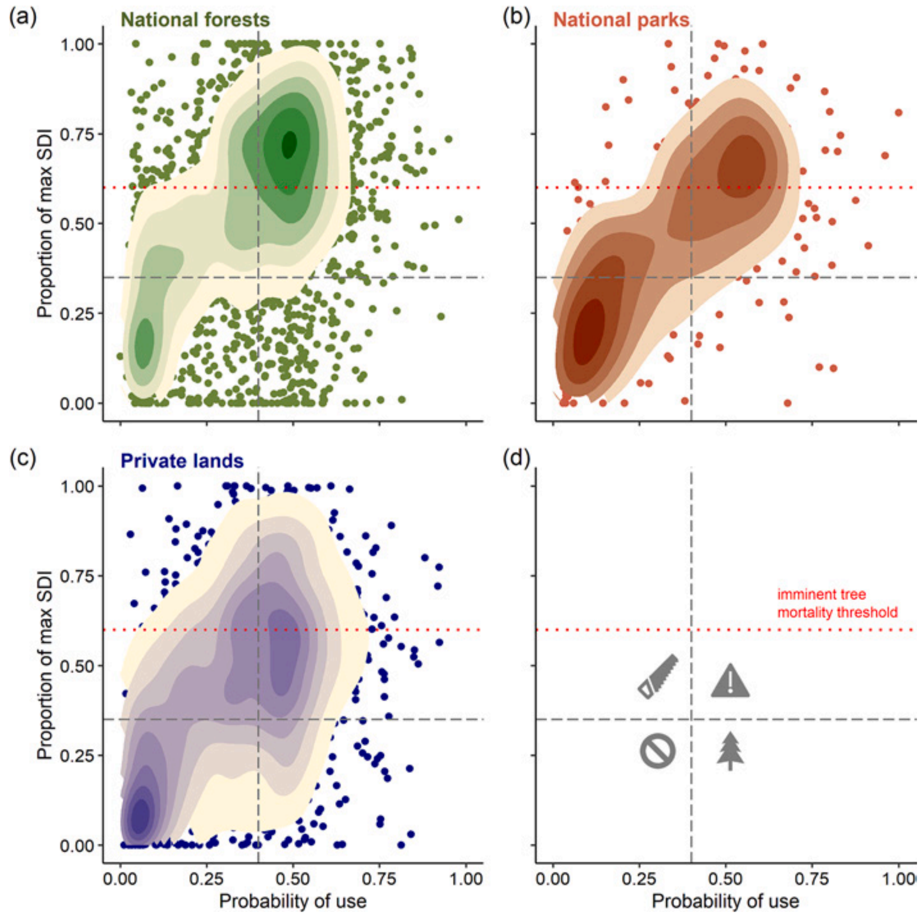

Fig. 3. Average values of proportion of maximum stand density index (SDI) and probability of site use from a 5000-point sample across the California spotted owl range in the Sierra Nevada bioregion for three ownership types: (a) national forest, (b) national park, and (c) private land. Panel (d) reminds readers of how to interpret the four quadrants: fuels reduction (upper left), potential conflict (upper right), low priority (lower left), and habitat retention (lower right). The threshold for high likelihood of site use by GPS-tagged spotted owls was set at 0.399 based on sensitivity and specificity (grey vertical line), and the threshold for proportion of maximum SDI was set at 0.35, corresponding to full site occupancy (grey horizontal line). The point of imminent tree mortality at SDI = 0.60 (red horizontal dashed line) represents where forests are considered least resilient. The relative density of points falling within each landscape classification quadrant is shown for each ownership type.

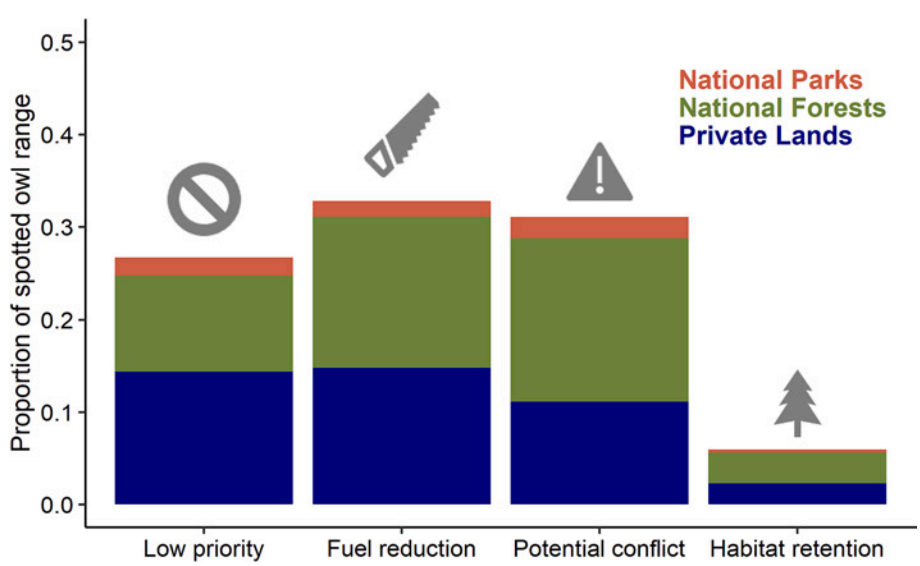

Fig. 4. The proportion of landscape across the Sierra Nevada bioregion that falls into each classification (low priority, fuel reduction, potential conflict, and habitat retention). Proportions are further separated by ownership type.

(21.7%), and “habitat retention” areas (6.9%). For national parks, the majority of the landscape fell into potential “conflict zones” (36.5%), followed by “low priority” areas (31.1%), “fuel reduction” areas (27.0%), and “habitat retention” areas (5.4%). For private land, the majority of the landscape fell into “fuel reduction” areas (34.7%), followed by “low priority” areas (33.8%), potential “conflict zones” (26.1%), and “habitat retention” areas (5.4%; Fig. 4).

Within the Stanislaus high priority fireshed, most of the landscape is classified as “fuel reduction” (53.8%) followed by “conflict zones” (32.6%), “low priority” (12.1%), and “habitat retention” (1.5%). Within the North Yuba high priority fireshed, most of the landscape is classified as “conflict zones” (66.6%), followed by “fuel reduction” (23.0%), “low priority” (8.9%), and “habitat retention” (1.4%; Fig. 5).

4. Discussion

We found that California spotted owls select for some habitat characteristics that reflect conditions consistent with fuel reduction treatment goals such as increasing canopy base height, decreasing ladder fuel density, and decreasing canopy bulk density, making prioritizing these goals mutually beneficial for owls and fuels management. California spotted owls also selected for higher amounts of surface fuels and greater canopy layer counts across the Sierra Nevada, which are preferences that may present potential challenges to managers attempting to balance preserving important owl habitat and reducing fuel loads, especially in denser forest conditions.

Across all ownership types, over 34% of spotted owl foraging habitat fell into “fuel reduction”, suggesting that a large portion of the landscape could be treated without negatively impacting the species. Yet even in the 31.5% of spotted owl foraging habitat within the Sierra Nevada bioregion falling into what we term “conflict zones”, fuels reduction treatments can likely occur with minimal impacts to owls, so long as treatments focus on promoting the fuels characteristics that we found owls are likely to select: increased canopy base height and decreased ladder fuels and canopy bulk density. Notable was the rarity of ‘habitat retention’ zones (higher resilience, higher foraging habitat quality), constituting only 6% of the California spotted owl range (Fig. 5). We think one reason for this rarity is the fact that such a large percentage of the landscape is classified as not resilient (~65%), but through fuels reduction and forest restoration, could be transitioned into more suitable habitat for spotted owls.

Our study took a novel approach of looking at the direct relationships between California spotted owl space use and measurements of fuel characteristics across the Sierra Nevada. Gallagher et al. (2019) examined the relationship between space use and forest fuels and suggested that treatments may have negative effects on owl foraging. The study

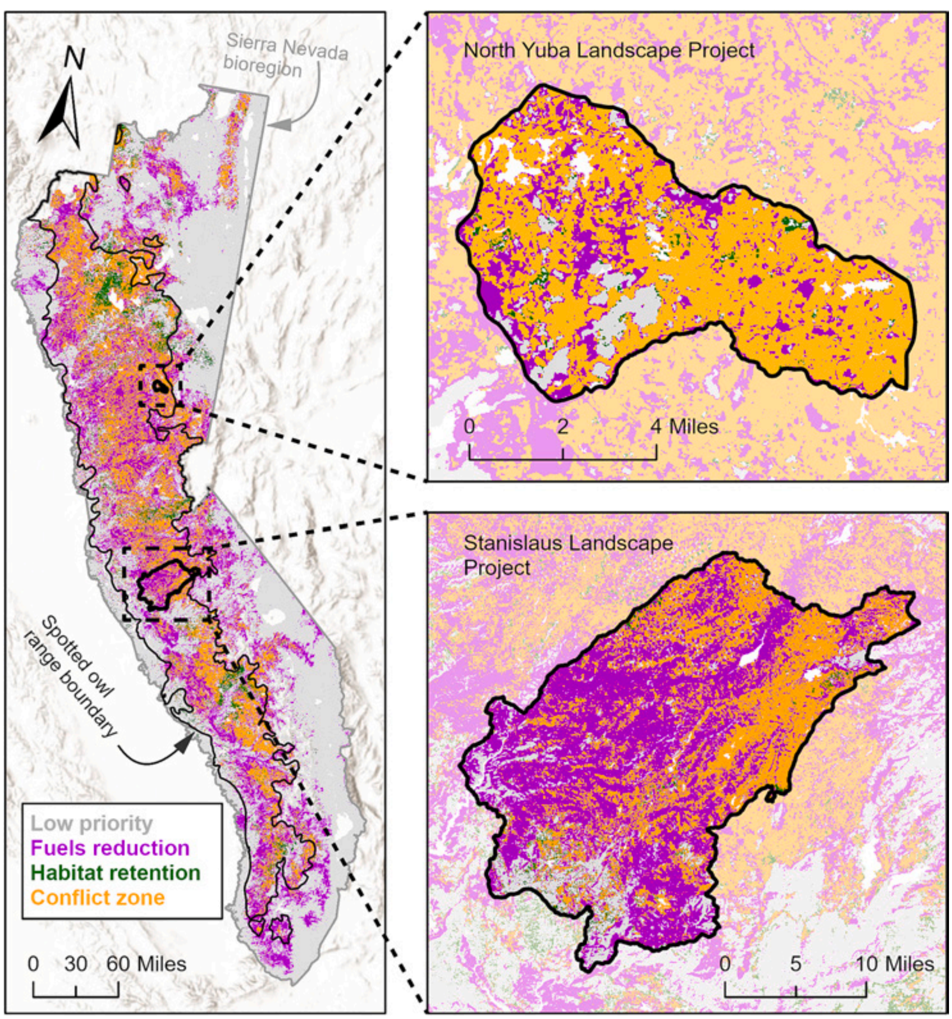

Fig. 5. The distribution of landscape classifications across the Sierra Nevada (left) and in the North Yuba (top right) and Stanislaus (bottom right) high priority firesheds. Across the Sierra Nevada bioregion, most of the landscape is “low priority” (52%) or “fuel reduction” (26%). The North Yuba fireshed represents an area with a majority of conflict zones (66.6%) while the Stanislaus fireshed represents an area with a majority of “fuel reduction” areas (53.8%). The varying distributions of categories across these two landscapes indicates different types of strategies may need to be implemented to achieve fuels reduction and owl conservation objectives.

relied on VHF telemetry and was limited to inference from only ten owls restricted to the Plumas National Forest in the northern Sierra Nevada. Fuels reduction treatments were grouped into three broad categories and treated as binary categorical variables, making it difficult to examine the nuances of different fuels reduction treatment targets or gradient effects.

Our study addresses these issues directly. Using three different levels of movement data (nightly, hourly, and minute-to-minute) from 159 owls, we were able to capture a large space use sample that covered the entire range of California spotted owls in the Sierra Nevada and demonstrate that the relationships between owl space use and fuel characteristics held across habitat types and temporal scales. By considering the relationships between space use and fuel characteristics prior to fuels reduction management, we were also able to examine the more nuanced relationships that owls have with fuel structures, suggesting that fuels reduction treatments which focus on reducing understory fuel loads through increasing canopy base height and decreasing ladder fuels and canopy bulk density may directly improve foraging habitat for spotted owls.

Other studies that have examined the relationship between California spotted owls and fuels reduction treatments have done so at broader level such as examining treatment effects on occupancy and demography. Stephens et al. (2014) found a decrease in the number of territorial spotted owls following implementation of fuels reduction treatments, but their inference was limited by small sample size (decrease from 7 to 4 owls), the potential influence of colonizing barred owls (*Strix varia*), and the fact that similar declines were occurring across the broader study area. Others have used simulations to examine impacts of fuels reduction on populations (e.g., Tempel et al., 2022, 2015), disentangling effects of fuels reduction treatment effects from other potential background pressures such as wildfire and region-wide declines in spotted owl populations. Yet because of limited overlap between actual fuels reduction treatments and spotted owl demographic studies, most population-level inferences must pool broad ranges of treatment types into a single category (Tempel et al., 2014a), thus making it difficult to provide insight into particular management actions. Looking at the direct relationship to measurements of fuel characteristics allows us to circumvent these potentially confounding effects and help guide management practices before they occur. We were able to tease apart the more nuanced relationships that California spotted owls have with forest structure and complexity (as opposed to simply assuming fuels reduction will decrease canopy cover).

The findings of this study help to further address the longstanding contention between forest management goals for fuels reduction and California spotted owl conservation (Peery et al., 2017). Implementation of landscape-scale fuels reduction treatments in the Sierra Nevada (USFS, 2004) have been contentious, due in part to a perception held by some that fuels reduction treatments will negatively impact spotted owls by altering their habitats (nesting, roosting and/or foraging). Planning documents protecting forest and sensitive species have constrained the placement and extent of fuel treatments (Collins et al., 2010; Tempel et al., 2014a) and have resulted in forest plans that separate landscapes into restoration zones, managed to reduce fuels and stand density, and owl habitat zones that are managed to preserve and increase canopy cover (Ager et al., 2007; Carroll and Johnson, 2008; North et al., 2017). This risk-averse approach is consistent with the viewpoint that fuels reduction treatments may pose a risk to spotted owls, especially through habitat loss in the short term (Irwin and Thomas, 2002). High canopy cover and a higher density of larger trees are considered preferred spotted owl habitat (Jones et al., 2018) and a widespread perception is that actions such as reducing ladder and canopy bulk density fuels to improve a forest's fire and drought resilience would be in direct conflict with preserving owl habitat (Jones et al., 2016a; North, 1999; North et al., 2017; Stephens et al., 2016, 2014; Zabel et al., 1995). However, our study suggests that fuels reduction treatments may have the potential to directly improve habitat, both in the short- and long-term, through the reduction of ladder fuels and canopy bulk density and increase in canopy base height.

Landscape-scale fuels reduction treatments can substantially reduce the risk of large and severe fires (Ager et al., 2007; Collins et al., 2013; Stephens et al., 2014) as well as increase habitat heterogeneity (North et al., 2009). High severity wildfire has been identified as one of the leading threats to California spotted owl occupancy and population persistence across the Sierra Nevada (Jones et al., 2022, 2021, 2016a; Tempel et al., 2022). Partially due to the uncertainty surrounding the response of forest species like the spotted owl, fuels reduction treatments and forest restoration currently occur below the pace and scale needed to significantly alter fire activity and behavior (Agee et al., 2000; Collins et al., 2010; Jones et al., 2021; North et al., 2015). Warming climate trends are likely to increase fire severity and magnitude throughout the Sierra Nevada, further exacerbating wildfire as a threat to spotted owl population persistence (Jones et al., 2020; McKenzie et al., 2004; North et al., 2015; Tempel et al., 2022; Westerling et al., 2011).

Balancing the need for fuels reduction treatments in the Sierra Nevada with spotted owl conservation will be achieved by focusing on goals that are mutually beneficial for both objectives. In addition to providing clear treatment guidance on the trade-offs and synergies of fuels reduction treatment objectives for spotted owls, we also identified most of spotted owl foraging habitat within the Sierra Nevada landscape as falling in “fuel reduction” zones (34.4%), which have a low probability of foraging use by spotted owls. The prevalence of “fuel reduction” zones suggests that increasing pace and scale of treatments, particularly when focused in these areas, are not likely to have adverse effects on spotted owl space use. Moreover, implementation of treatments in “conflict zones” may also have minimal impacts on owls, and may directly benefit owls, when focused on increasing canopy base height, reducing ladder fuels, and reducing canopy bulk density. Promoting spatial heterogeneity in fuels reduction treatments and retaining large trees is likely to benefit both spotted owls and increase forest resilience (Gallagher et al., 2019; Jones et al., 2020; Kramer et al., 2021; Stephens et al., 2014) and focusing on reducing fuel load in the mid-canopy strata should be viewed as a mutually beneficial goal that is likely to retain the necessary canopy cover associated with spotted owl foraging habitat preferences while also reducing potential fire intensity and drought stress (North et al., 2017; Tempel et al., 2014a, 2022).

It should be noted that, in our classification of probability of habitat use, we only considered foraging patterns of owls and did not account for habitat needs associated with nesting and roosting, as these have been previously documented by many other studies (Franklin et al., 2000; Jones et al., 2018; Tempel et al., 2014b). Nevertheless, assuming the continued conservation of large, old trees that are used for nesting, recent work has reinforced that high-quality foraging habitat (characterized by the metrics used in this paper, and forest heterogeneity more generally) can lead to increased reproductive output at spotted owl nest sites (Wilkinson et al. 2023, Zulla et al. 2023). Retention of patches with large trees and snags where they currently exist are likely to be beneficial for spotted owls (both as foraging and nesting/roosting habitat) and other sensitive species such as the fisher (*Pekania pennanti*), northern goshawk (*Accipiter gentilis*), and American marten (*Martes americana*) (Jones et al., 2021, 2018; North et al., 2017). It is also possible that, due to our use of proportion of maximum SDI as a proxy for fire risk and resilience, areas where large, severe fires have burned in recent years may have been classified as ‘low priority’ areas, even though these areas could have heightened fire risk and might be amenable to post-fire fuels management.

5. Conclusions

The results of our study suggest that fuels reduction treatments, especially those focusing on reducing ladder fuels and canopy bulk density as well as increasing canopy base height may directly benefit California spotted owls by improving foraging habitat. Space use by spotted owls along with the distribution of fuels across the landscape indicates that there may be far less landscape-scale conflict between fuels reduction and spotted owl habitat conservation than previously thought. With the increased threat of large and severe wildfire, this information is critical for managers to help move the scale and pace of fuels reduction treatments forward in a way that will minimally impact spotted owls.

Ethics approval and consent to participate

This study received approval from the University of Wisconsin Institutional Animal Care and Use Committee.

Consent for publication

Not applicable

Availability of data and materials

General data is available upon request, but because of the sensitive status of this species, GPS locations will not be released. Code for this project can be found at the following GitHub repository https://github.com/MarilynEWright/CSO-Fuels.

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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.

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121430.

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