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Note

Spotted Owl Foraging Patterns Following Fuels Treatments, Sierra Nevada, California

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ABSTRACT Western dry conifer forests continue to experience increased severe, stand-replacing wildfire that is outside of historical precedent. Fuels treatments, landscape-scale modifications of forest fuels and structure, are likely to remain a management tool to modify fire behavior and restore ecological resilience. The impacts of fuels treatments to listed species such as spotted owls (*Strix occidentalis*) remain uncertain and are contested because of limited available information. To evaluate spotted owl foraging habitat selection in a landscape recently modified by forest fuels-reduction treatments, we radio-marked and tracked 10 California spotted owls (*S. o. occidentalis*) for 2 years immediately following fuels treatment installation in the northern Sierra Nevada, California, USA. We categorized fuels treatments into 3 types: mechanical thin, installed within the study area as landscape-scale fire breaks characterized by even tree spacing, open understory, and low canopy cover, or group selections; understory thin, a hand-removal of small trees and shrubs; and understory thin followed by underburn, a controlled surface-fuel burn that left the overstory intact. We described post-treatment habitat using forest structural metrics derived from a Light Detection and Ranging (LiDAR) dataset that was collected 1 year after fuels treatments were completed. We collected 436 spotted owl foraging locations during 2 breeding seasons and evaluated breeding season home range size and composition using a resource selection function. We assessed possible contributors to owl foraging patterns by comparing *a priori* hypotheses in an information-theoretic approach and using randomly generated points that estimated available habitat. Spotted owl breeding season home ranges contained fuels treatments in proportion to their availability on the landscape and averaged 17.1% treated area. Within the home range, owl foraging locations in the post-treatment landscape were best predicted by lower proportions of gaps than anticipated at random, steeper slopes, and minimized distance from the owl's site center. Our results suggest that moderate to high proportions of gaps, typically a feature of forest fuels reduction and restoration treatments, may reduce the probability of spotted owl foraging.

KEY WORDS California spotted owl, foraging, forest restoration, fuels management, fuels treatment, habitat use, home range, LiDAR, Sierra Nevada, *Strix occidentalis occidentalis*.

Ecosystem restoration of historically mixed-severity fire regime forests is a primary concern and management goal across western North America, particularly amidst increasing trends in the size and severity of wildfire and insect mortality disturbances (Westerling et al. 2006, North et al. 2009, Safford et al. 2009, Hessburg et al. 2016). In the Sierra Nevada of California, USA, a century of fire suppression, timber harvest, and grazing practices have fundamentally changed forest structure, composition, and function, resulting in forests with a reduced large tree component and increased homogeneity, fuel loads, and vulnerability to high-severity wildfire compared with historical records (Miller et al. 2009, North 2012, Stephens et al. 2012, Knapp et al. 2013, Dolanc et al. 2014). These changes have affected forest resilience and rendered these forests vulnerable to stand-replacing wildfire and insect mortality, both of which are projected to increase in size and severity under future climate predictions (Westerling et al. 2006, Millar et al. 2007, Liu et al. 2013, Hessburg et al. 2016). Methods to mediate severe wildfire events and restore Sierra Nevada forests in the face of climate change have been controversial (North 2012); current management guidelines for the United States Forest Service (USFS) lands in the Sierra Nevada adopt landscape-scale fire and fuels treatments (e.g., forest thinning) as an approach to reduce higher fuel loads, modify fire behavior,

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promote stand resilience, restore forest ecosystems, and protect civic and economic interests (USFS 2004, Stephens and Moghaddas 2005, North et al. 2009, Safford et al. 2009). The potential benefits of fire and fuels treatments (i.e., fuels treatments) to both ecosystem improvement and reduction of catastrophic fire risk has led federal land management agencies to invest in fuels treatments as a forest management strategy (Kalies and Kent 2016).

Fuels treatments, which include mechanical thin, understory manual thin, pile burning, and prescribed fire, are currently the primary management activities affecting forest ecosystems and species of concern, such as California spotted owls (*Strix occidentalis occidentalis*), on USFS lands in the Sierra Nevada (USFS 2004, Keane 2017, North et al. 2017*b*). The general prescription for fuels treatments is to reduce stand-replacing wildfire risk and create an open forest structure using a reduction of forest canopy cover to ≤40%, retention of trees ≥76 cm diameter at breast height (dbh), and a reduction of tree density, ladder fuels, and surface fuels (USFS 2004), prescribed according to site conditions and topography. Although resulting modifications in fire behavior are documented (Stephens and Moghaddas 2005, Schmidt et al. 2008, Stephens et al. 2009), broader ecological implications of fuels treatments are less clear, particularly for reductions in structure and diversity in late seral forests and effects on associated species such as spotted owls (Kalies and Kent 2016). In the case of the spotted owl, this is an important information need because long-term demographic monitoring indicates California spotted owl populations have declined over the last 20 years on USFS lands (Blakesley et al. 2010, Tempel and Gutiérrez 2013, Tempel 2014, Conner et al. 2016).

Although federal land management in the Sierra Nevada incorporates standards to manage for spotted owl habitat, little empirical information is available that assesses the effects of the structural modifications of fuels treatments on spotted owls or their habitat (Stephens et al. 2014, Tempel et al. 2014, Kalies and Kent 2016). Studies using habitat quality to model northern spotted owl (*S.o. caurina*) response to fuels treatments have reported reductions in habitat suitability, accompanied by positive long-term effects from reduction of nesting habitat loss to high-severity and stand-replacing fire (Gaines et al. 2010, Ager et al. 2012, Roloff et al. 2012). Similarly, effects of fuels treatments on California spotted owl demographics and territory quality have suggested that treatments may reduce the effects of high-severity fire but, in the absence of fire, can result in long-term reductions in habitat quality (Tempel et al. 2015). In an empirical study in the northern Sierra Nevada, the number of California spotted owl territories declined following implementation of a landscape fuels treatment strategy, although this was a single, observational case study (Stephens et al. 2014).

California spotted owl habitat selection at nest and roost sites is documented as favoring multi-layered understories with high canopy closure, dominated by large-diameter trees (Gutiérrez et al. 1995, LaHaye et al. 1997, Moen and Gutiérrez 1997, Bond et al. 2004). California spotted owl foraging habitat use has received less research attention (Keane 2014); available studies report foraging habitat as occurring close to nest trees, with more open canopies and greater structural and compositional heterogeneity compared with nesting habitat, including late seral forest, broadleaf forest, and post-burn areas (Call et al. 1992, Irwin et al. 2007, Bond et al. 2009, Williams et al. 2011, Eyes et al. 2017). Analyses of spotted owl foraging habitat use have previously been limited by coarse-resolution habitat data that categorizes vegetation into broad categories based on tree species composition, size classes, and canopy-cover classes, precluding opportunities to describe finer-resolution habitat use patterns at the patch-scale used by owls (Kramer et al. 2016*a*). However, recent availability of vegetation data from remotely sensed Light Detection and Ranging (LiDAR) provides high-resolution imaging of forest structure and pattern, and holds promise for improved understanding of spotted owl habitat use (García-Feced et al. 2011, Ackers et al. 2015, Kramer et al. 2016*a*, North et al. 2017*a*).

Information on the effects of fuels treatments on California spotted owls is needed to inform forest management in the Sierra Nevada and contributes to broader discussions of the direction of fire and fuels management in Sierra Nevada forests. Our objective was to assess the foraging patterns of California spotted owls in a post-treatment landscape, by characterizing individual owl breeding season home range (i.e., home range) configuration and foraging site selection immediately following fuels treatment installation. We hypothesized that spotted owls would forage less frequently within fuels treatments because of structural modification of habitat components that are important to the owls' mammalian prey. We also hypothesized that spotted owls would forage close to their site center in areas with large-diameter trees (≥76 cm dbh), >40% canopy cover, and a mosaic of small gaps, where small-mammal abundance at early seral forest edges is combined with increased protection and movement offered by mature forest.

STUDY AREA

We conducted our study within the 23,823-ha Meadow Valley Project (MVP) area located on the Plumas National Forest in the northern Sierra Nevada Mountains, California, USA (Fig. 1) from 2007 to 2008. Elevation ranged 950–2,150 m in mountainous terrain, with dominant vegetation types of Sierra mixed conifer (35%) and montane hardwood-conifer (20%), consisting primarily of ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), Jeffrey pine (*P. jeffreyi*), Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), California black oak (*Quercus kelloggii*), dogwood (*Cornus* spp.), and willow (*Salix* spp.). Pockets of white fir and red fir (*A. magnifica*) forest occurred at higher elevations. The Mediterranean climate consisted of warm, dry summers and cool, wet winters; precipitation (105 cm/year) occurred as snow and rain primarily during winter and spring months. Average daily low and high temperatures were 9 °C to 31 °C during summer and −3 °C to 7 °C during winter. Dominant fauna included mule deer (*Odocoileus hemionus*),

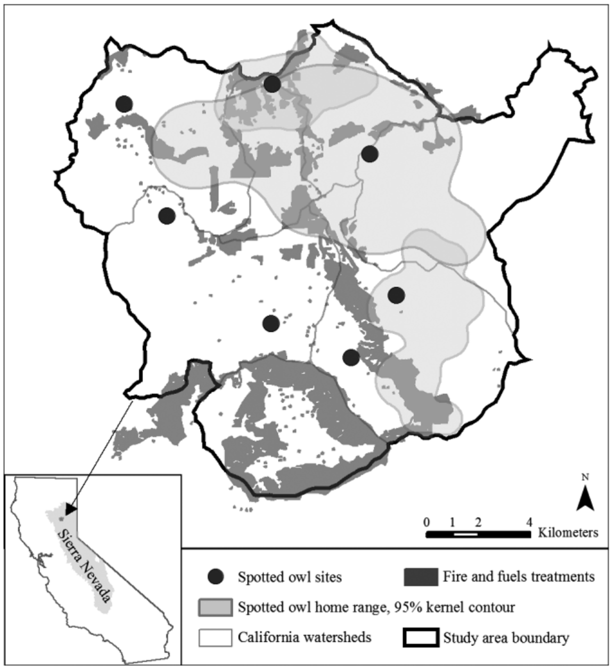

Figure 1. The 238-km^2 spotted owl study area located in the Plumas National Forest, in the northern Sierra Nevada of California, USA, 2007–2008. For clarity, we show 3 spotted owl home ranges illustrating the minimum (northernmost), maximum (center), and an intermediately sized home range (southernmost).

American marten (*Martes americana*), mountain lion (*Puma concolor*), American black bear (*Ursus americanus*), Humboldt's flying squirrel (*Glaucomys oregonensis*), dusky-footed woodrat (*Neotoma fuscipes*), and northern goshawk (*Accipiter gentilis*). The historical fire regime for the study area was a return of low to moderate severity fires every 7–19 years, prior to fire suppression (Moody et al. 2006).

Forest management during the study was guided by the Herger-Feinstein Quincy Library Group Forest Recovery Act of 1998 (HFQLG Act), which mandated a landscape-scale fuels management strategy consisting of Defensible Fuel Profile Zone (DFPZ) and group selection timber harvests; DFPZs are landscape-scale (400–800 m wide) linear fuel thins strategically located to function as wildfire breaks and characterized by a reduction of ground and ladder fuels, even tree spacing, and ≤40% canopy cover. Group selections are ≤0.8-ha patch cuts in which all trees <76 cm diameter are harvested, to create vegetation heterogeneity and generate revenue. The HFQLG Act prohibited fuels and timber harvest treatments within spotted owl Protected Activity Centers (PACs), 121-ha units of late seral forest delineated by forest biologists around spotted owl nests and roosts; other areas of spotted owl home ranges were treated.

The Meadow Valley Project was the only landscape-level HFQLG Act forest treatment suite fully implemented in an area containing suitable spotted owl habitat. Under HFQLG Act guidelines, contracting parties had ≤5 years from the date of sale to complete fuels treatments. The MVP treatment and harvest operations began in 2003 and were 80% complete by January 2007; all project treatments and harvests were completed by October 2008.

We created a perimeter for the study area by overlaying the MVP area with the California Watershed Map (CALWATER version 2.2, California Interagency Watershed Mapping Committee) in a geographic information system (GIS). Seven watersheds contained most of the MVP treatments, and had been surveyed for spotted owls for 5 years prior to this study. We delineated the perimeter of these 7 watersheds as the perimeter of the study (Fig. 1). The resulting 23,823-ha study area encompassed 4,160 ha of fuels treatments. We collected spotted owl foraging data during the breeding seasons of 2007 and 2008. The breeding season was 1 April to 30 September, based on the expected return of territorial birds from wintering grounds, and the juvenile fledging period extending into August and September (Gutiérrez et al. 1995). These *a priori* dates were later supported by winter habits of the radio-tagged owls, which remained on territory through early November, and returned to territories in mid-March of the following year.

METHODS

We grouped treatments into 3 broad categories: large-scale mechanical thin and biomass removal implemented across the study area as DFPZs and group selections; understory thins, prescribed as a non-commercial removal of shrubs and trees <25 cm dbh; and understory thin followed by prescribed underburn, a controlled surface-fuel burn that did not affect the forest overstory. The MVP area contained 1,784 ha of DFPZ treatments and 272 ha of group selections, which were typically located near or embedded within DFPZs. The MVP area also contained 1,440 ha of understory thin and 665 ha of underburn.

Spotted owl sites within the study area boundary were identified by annual surveys conducted by the Pacific Southwest Research Station, USFS. For site selection, we constrained sites to those that had been occupied for >1 year prior to this study and were occupied by pairs at the time of the study. This limited our site selection to 6 sites in the first post-treatment year (2007) and a different configuration of 6 sites in the second post-treatment year (2008).

We radio-marked owls at these sites with backpack radio-transmitters (Holohil Systems, Model RI-2C, Ontario, Canada) fitted to each owl with Teflon®-coated Kevlar® ribbon (Bally Ribbon Mills, Bally, PA, USA). Total mass of the radio-transmitters was 14 g, or 2.5% of the body mass of an average spotted owl male (Gutiérrez et al. 1995). We radio-tagged females in June, after young fledged from the nest; we removed radio-transmitters from all owls at the conclusion of the study.

Radio-Telemetry

Two observers, working together, derived owl locations using standard radio-telemetry triangulation techniques (White and Garrott 1990, Kenward 2001, Millspaugh and Marzluff 2001). We separated sequential locations for each owl by ≥24 hours to reduce temporal autocorrelation; this resulted in a maximum sampling regime of 5 locations per bird every 2 weeks, or 10 locations per bird per month. We continuously varied the owl tracking sequence to sample across the full nocturnal activity period for each owl, and gathered all owl locations between 1 hour after sunset and 1 hour before sunrise. We followed protocols in accordance with the Guidelines for the Use of Wild Birds in Research (Fair et al. 2010), and all procedures were part of a study plan approved by the USFS.

Observers gathered bearings as close together in time as possible to reduce the probability of bird movement; once near the owl, mean elapsed time of the triangulation process was 16 ± 0.5 (SE) minutes ($n = 465$). After collecting ≥ 3 bearings, observers checked data in the field using Palm LOCATE (Pacer Computing, Nova Scotia, Canada). We accepted locations when the 95% confidence ellipse was <1.5 ha; similar spotted owl telemetry studies have used a 95% confidence ellipse of 2 ha (Clark 2007) or 5 ha (Glenn et al. 2004, Williams et al. 2011). If the owl was $\leq$200 m from the surveyors, surveyors attempted to observe the bird and verify location; surveyors abandoned this effort if they detected a signal change indicating bird movement.

We used LOAS 4.0b software (Ecological Software Solutions, Urnäsch, Switzerland) to calculate the 95% confidence ellipse of each owl location with the maximum likelihood estimator. We assessed accuracy of triangulation estimates using daytime owl locations; working individually while owls were roosting, observers triangulated on the owl and then moved in on the signal to directly observe the bird. Surveyors recorded the owl's true location with a global positioning system unit accurate to $\leq$5 m and noted the difference between the estimated location and true location. We rejected the datum if, upon observing the owl, the owl appeared disturbed or awake, or if we detected changes in the radio-signal indicating bird movement while the observer approached. Mean bearing error between estimated and true locations was 7.25 ± 0.85 degrees and mean distance error was 68.5 ± 38 m. Similar studies on spotted owls report accuracy estimates of 7.2–9.6 degrees bearing error and mean distance errors of 68–164 m (Carey et al. 1992, Glenn et al. 2004, Forsman et al. 2005, Williams et al. 2011).

Habitat and Fuels Treatment Mapping

To create a study-wide map of fuels treatments (MVP map), we combined the 2009 USFS Region 5 Remote Sensing Laboratory map for the Meadow Valley Project area, derived from aerial photographs and satellite data captured in August 2009, with Plumas National Forest harvest records. The resolution of the MVP map was 5 m, based on the remote sensing imagery used in its creation (C. M. Ramirez, USFS Remote Sensing Laboratory, personal communication).

Watershed Sciences (Corvallis, OR, USA) collected aerial LiDAR imagery for the MVP area in July and August 2009. The imagery was captured with an average point density of 4.68 points/m^2, and an average vertical and horizontal accuracy of 2.6 cm and 7.2 cm, respectively. We extracted 21 LiDAR metrics that we thought could be biologically important to spotted owls (Table 1) using LasTools (Isenburg 2011) and Fusion (McGaughey 2012). Metrics included topography, direct forest structural metrics such as

Table 1. Post-treatment landscape metrics derived from Light Detection and Range (LiDAR) for spotted owl foraging locations and random locations within owl breeding season home ranges, Meadow Valley Project area, northern Sierra Nevada, California, USA, 2007–2008.

			Owl foraging ($n = 413$)		Random ($n = 2,100$)	
Abbreviation	Description	Resolution (m)	($\bar{x}$)	SE	($\bar{x}$)	SE
Slope	Slope at point location	10	20.36	0.45	17.49	0.19
Aspect	Aspect at point location	10	169.68	5.59	162.80	2.36
CH_{max}	Maximum canopy height (m) across ellipse, mean	1	13.73	0.37	11.74	0.12
CH1	Canopy height class 1 (0–2 m; proportion in ellipse)	1	0.24	0.01	0.27	0.00
CH2	Canopy height class 2 (2–8 m; proportion in ellipse)	1	0.16	0.01	0.15	0.00
CH3	Canopy height class 3 (8–16 m; proportion in ellipse)	1	0.17	0.01	0.19	0.00
CH4	Canopy height class 4 (16–32 m; proportion in ellipse)	1	0.29	0.01	0.27	0.00
CH5	Canopy height class 5 (32–48 m; proportion in ellipse)	1	0.10	0.01	0.06	0.00
CH6	Canopy height class 6 (>48 m; proportion in ellipse)	1	0.01	0.00	0.00	0.00
LargeTree	Density of large trees (>76 cm dbh), trees/ha	10	29.77	1.80	20.10	0.71
$Cover_{>70\%}$	Proportion of ellipse that is >70% total cover	30	0.64	0.02	0.55	0.01
$Cover_{40–70\%}$	Proportion of ellipse that is 40–70% total cover	30	0.27	0.02	0.30	0.01
$Cover_{>70\%,\ 16m}$	Above 16 m minimum canopy height, proportion of ellipse that is >70% cover	30	0.11	0.01	0.09	0.00
$Cover_{40–70\%,\ 16m}$	Above 16 m minimum canopy height, proportion of ellipse that is 40–70% cover	30	0.38	0.02	0.30	0.01
$Cover_{>70\%,\ 32m}$	Above 32 m minimum canopy height, proportion of ellipse that is >70% cover	30	0.002	0.001	0.001	0.000
$Cover_{40–70\%.\ 32m}$	Above 32 m minimum canopy height, proportion of ellipse that is 40–70% cover	30	0.04	0.01	0.03	0.00
H'_{Cover}	Shannon diversity index (H') of cover across 6 canopy strata	10	1.35	0.01	1.39	0.00
Edge	Edge at intersection of forest (>2 m canopy height) and gap ($\leq$2 m maximum canopy height), calculated as total edge/ellipse area	2	0.14	0.01	0.15	0.00
Gap_{prop}	Gap ($\leq$2 m maximum canopy height) area, as proportion of ellipse	2	0.22	0.01	0.28	0.00
Gap_{size}	Mean gap size across ellipse	2	50.02	7.06	105.61	13.10
Edge:Area	Ratio of total gap edge to total gap area within the ellipse	2	0.86	0.03	0.75	0.01

canopy height and cover (Kramer et al. 2016*a*), and derived metrics such as a Shannon diversity index of cover across 5 height strata to describe canopy complexity (Table 1). Although we desired to explore the components of shrubs, downed woody debris, and herbaceous layers, MVP LiDAR data in the 0–2-m height strata suffered from signal degradation in areas of dense upper canopy, such as those found in owl core areas. We therefore excluded the 0–2-m height strata from analyses except when the maximum canopy height was <2 m.

An advantage of aerial LiDAR is exceptional spatial resolution; base LiDAR data for the MVP area has a 1-m pixel size with sub-meter accuracy. We did not extract LiDAR variables directly from 1-m raster cells that overlapped an owl use location; given the mean telemetry distance error of 68.5 m, extraction of a LiDAR value at an estimated location had potential to introduce substantial spatial error and misinterpretation. For this reason, we calculated LiDAR metrics across the entire error ellipse of owl locations, thus describing the overall habitat conditions within the ellipse. Similarly, for random points that approximated available foraging habitat, we used the mean telemetry error to create a 68.5-m radius circle around each random point, and calculated LiDAR metrics across the entire circle. Our choice of an aggregation method was likely more robust than alternatives, although still susceptible to spatial autocorrelation of neighboring pixels and smoothing of spatial heterogeneity, which would be more pronounced for dissimilar than similar pixel values (Gotway and Young 2002).

We considered owl and random locations to be within treatment if the location fell within a treatment polygon in the MVP map, or within the 5-m error buffer of the treatment polygon boundary. Additionally, we visited all owl locations within or near treatment areas during daytime hours to ground-truth the treatment status indicated by the map. We did not consider ground-truthed owl locations 5.0–68.5 m from a treatment boundary to be within treatment because it was unclear if the animals were associated with the treatment, the area adjacent to treatment, or the treatment edge; our dataset included 31 such locations. To minimize complications of this uncertainty, we avoided statistical methods requiring a categorical response of owl locations within treatment.

Home Range Estimation and Fuels Treatment Composition

We estimated spotted owl home ranges using fixed kernel density estimator methods and 100% minimum convex polygons (MCPs). Following Williams et al. (2011), we used the MCP method strictly for comparison purposes because it is the only home range size metric included in all previous California spotted owl home range studies.

We chose fixed kernel density estimators as the home range model for this dataset because adaptive kernel estimators tend to undersmooth data at outer contour levels and overemphasize outliers (Seaman et al. 1999). To objectively assess the choice of estimator, we tested the fit of the fixed kernel density estimator against the fit of the adaptive-kernel density estimator by applying information-theoretic model selection using the relative Kullback-Leibler (KL) distance in Animal Space Use 1.2 (Horne and Garton 2006). The relative KL distances supported fixed kernel density estimators as an appropriate choice for this dataset. We chose the likelihood-cross-validation (CVh) smoothing parameter to calculate bandwidth for fixed kernel estimators. We calculated breeding season home ranges for owls with a minimum of 30 locations, following Seaman et al. (1999), and used owl locations with 95% confidence ellipses $\leq$1.5 ha for home range derivation.

We used a simplified resource selection function (Manly et al. 2002) to evaluate the fuels treatment composition of owl home ranges relative to the study area. The area contained within the 95% fixed kernel volume contour defined spotted owl home range use area, whereas the study area described the available area. We quantified fuels treatments for each owl's home range by overlaying the 95% fixed kernel contour with the MVP map.

We compared the proportion of fuels treatments in each home range with the total proportion available in the study area using resource selection ratios (w_i'). We estimated selection ratios, variances, and confidence limits, following Design II Sampling Protocol A in Manly et al. (2002). We used Bonferroni-corrected 90% confidence limits to define whether use of each treatment type was disproportionately abundant ($w_i' > 1$) or absent ($w_i' < 1$) in owl home ranges compared to its availability on the landscape.

Owl Use of Treatment Areas: Foraging Locations

To explore owl habitat selection within the home range, we developed *a priori* models comparing owl use locations and randomly generated locations (available locations), and evaluated these models using mixed-model logistic regression (Keating and Cherry 2004), Akaike's Information Criterion corrected for small sample sizes (AIC_c), and Akaike weights (w_i; Burnham and Anderson 2002). We used GIS to create 5 times as many random points as owl locations within each owl's 95% home range contour and used these randomly generated points to approximate the available habitat within the home range (Johnson et al. 2006). We modeled owl identity as a random effect and all other variables as fixed effects. Because our study area is the only instance that we know of within the range of the California spotted owl to have overlapping areas of LiDAR and telemetry, and we were interested in forest structural characteristics that may be key components of owl foraging habitat and altered during fuels reduction, our analysis was exploratory and contained 68 *a priori* models.

We used a step-wise approach to build our model set. The first set of models compared distance to the owl's site center (nest tree, or primary roost for non-nesting owls), physiographic features, study year, and a null model (Table S1, available online in Supporting Information). Because spotted owls are central-place foragers, the distance to site center metric assumes that owls will not travel more than necessary to forage, and land cover types near the nest or roost will have greater probability of use simply as a result of minimizing distance traveled (Rosenberg and McKelvey 1999, Glenn et al. 2004, Irwin et al. 2007). Given spotted owls preference for mature forest (Gutiérrez et al. 1995), we anticipated that the prevalence of large trees (>76 cm dbh) in steep, north-facing slopes in the study area would result in owl selection for steep or north-facing slopes. We did not include elevation in models because owl home ranges in our study area contained similar elevations. We included year as a nuisance variable, anticipating possible differences between the first year of study, which was an average reproductive year, and the second year of study, which was an exceptionally poor reproductive year. We predicted that owls would forage more widely and explore novel areas during the second study year, without the need to return regularly to a nest. Finally, we included a model of owl identity as a null model because of variation in owl home ranges.

Our second step of model selection compared LiDAR-derived forest structural metrics (Tables 1 and S1). To narrow down a large list of potential LiDAR metrics, we selected forest variables that were important to spotted owl nesting and foraging habitat in prior studies.

Throughout their range, spotted owls have been documented to prefer mature forest with large-diameter trees for nesting and roosting (Bias and Gutiérrez 1992, Verner et al. 1992, Moen and Gutiérrez 1997), including late seral forests interspersed with alternate forest types and edges (Franklin et al. 2000). Large-diameter trees are important to spotted owl foraging habitat, perhaps because of their relevance to an important prey species, Humboldt's flying squirrel (Carey et al. 1992, Waters and Zabel 1995, Meyer et al. 2007). We estimated the presence of large trees using 2 methods: proportion of large trees within the ellipse, a simple measure of the presence of large trees in any configuration, and large tree density, a measure sensitive to clustering of large trees.

Following Kramer et al. (2016*b*) and North et al. (1999), we estimated the proportion of large trees by first calculating the maximum canopy height across the landscape in 1 × 1-m pixels and distributing the maximum heights into 6 classes: 0 to 2, >2 to 8, >8 to 16, >16 to 32, >32 to 48, and >48 m. We predicted that owls would preferentially select for higher proportions of 32–48-m trees (class 5), considered nesting habitat, and 16–32-m trees (class 4), which are often considered suitable foraging habitat (Verner et al. 1992). We were unable to include the tallest size class, >48 m, because of its rarity within the study area (0.3% of all LiDAR-derived pixels).

Tree size, as measured by tree diameter, is not directly estimated by LiDAR and is typically inferred using individual tree segmentation algorithms or statistical modeling (García-Feced et al. 2011, Jakubowski et al. 2013). Tree segmentation algorithms require extensive tree stem maps as training data, and can be prone to decreased accuracy when stems are close to each other, such as areas of dense canopy cover (Kaartinen et al. 2012). Following Kramer et al. (2016*a*), we opted for a regression approach to estimate the density of large trees (>76 cm dbh) as trees/ha, using an algorithm created from MVP data that could also be easily adapted to other studies. To estimate large tree density, we used the equation:

$$\sqrt{\frac{Trees}{ha}} = 2.37 + 0.786\left(\sqrt{CHM32}\right) - 0.909\left(log(VAR) + 1\right), \quad (1)$$

where CHM32 is the proportion of area with >32 m maximum canopy height, an equivalent for trees >76 cm dbh, and VAR is the variance of point heights above 2 m (Kramer et al. 2016*a*). This large tree density model had a cross-validation error of less than a single tree, and an adjusted R^2 value of 0.77 for the MVP area, which is comparable to other tree segmentation and statistical modeling methods. We predicted that spotted owls would preferentially forage in areas with high density of large trees.

Spotted owl management guidelines regularly divide canopy cover into 2 activity-based functional categories: high (>70%) cover, considered to be optimal nesting habitat, and medium (40–70%) cover, considered to be suitable foraging habitat. Given the importance of high canopy cover areas to spotted owls in recent studies (Tempel et al. 2014, 2015; North et al. 2017*a*), we calculated the proportion of high (>70%) canopy area within each ellipse. We chose a 30-m pixel size for this calculation, based on Program Fusion guidelines (McGaughey 2012). We estimated canopy cover using 900 1-m × 1-m cells, and calculated percent cover area as the number of cells within the 900-cell grid that were considered canopy (min. height ≥2 m) divided by the total number of cells (900). Given the importance of cover at height strata created by large trees (North et al. 2017*a*), we also estimated the cover contribution of co-dominant and large trees by repeating the above method and using minimum canopy heights of 16 m and 32 m.

We included the proportion of high (>70%) canopy cover in models because of its importance to survival, reproduction, and site occupancy in prior spotted owl studies (Franklin et al. 2000, Blakesley et al. 2005, Seamans and Gutiérrez 2007, Tempel et al. 2014). Further, we included the proportion of medium (40–70%) canopy cover in models because management guidelines define medium canopy cover as suitable foraging habitat based on the findings of early foraging studies (Call et al. 1992, Zabel et al. 1992). Additionally, Williams et al. (2011) described spotted owl preference for areas of both high and medium canopy cover, particularly in mature forests, for foraging. We estimated medium (40–70%) and high (>70%) cover at 3 height strata: ≥2 m to represent the overall canopy, ≥16 m to address cover contribution of co-dominant trees, and ≥32 m for cover created by large trees.

We predicted that owl foraging would positively correlate with both high (>70%) and medium (40–70%) canopy cover classes, regardless of the minimum canopy height used in cover calculations. Further, we predicted owl selection of high and medium cover would follow 1 of 2 possible trends: linear, in which areas with greater proportions of high or medium canopy cover are used preferentially; and quadratic, in which the likelihood of owls selecting an area for foraging increases to a maximum probability at an ideal contribution of high or medium cover, then either declines as the proportion of the cover class increases, or holds at a threshold. Our model set thus included linear and quadratic trends for medium and high cover categories. We did not create candidate models containing both high and medium cover classes because the classes are mutually exclusive by definition and thus correlated.

To estimate vertical canopy complexity, we generated a Shannon diversity index (Equation 2) for canopy cover. Following North et al. (1999) and Kramer et al. (2016*b*), we divided the vertical canopy into 5 horizontal bands at >2 to 8-m, >8 to 16-m, >16 to 32-m, >32 to 48-m, and >48-m height strata, and estimated LiDAR-derived canopy cover within each band. We then calculated the Shannon diversity index (H') for cover across the telemetry error ellipse as

$$H\prime = -\sum\nolimits_{i=1}^{S} P_i ln P_i \qquad (2)$$

where S is the number of horizontal canopy strata (5) and P_i is the mean canopy cover for each strata within the ellipse. We predicted that owls would prefer foraging areas with greater vertical structure or denser canopy throughout the vertical stand, which would correspond to lower diversity values.

We were interested in exploring owl foraging preference for forest gaps and edges, given their importance to owl survivorship and reproductive fitness (Franklin et al. 2000), and their foraging preferences (Williams et al. 2011). We defined a gap in this study as any area, 2-m × 2-m pixel or greater, in which the maximum canopy height is ≤2 m; a 4-m^2 pixel size was the smallest resolution available to us because of computational limitations. We defined edge as the hard edge between forest (>2-m canopy height) and gap (≤2-m canopy height). We predicted that owls would prefer areas with intermediate proportions of gaps and edges, where increases of small-mammal abundance at early seral forest edges balance with protective cover of mature forest (Zabel et al. 1995, Ward et al. 1998, Franklin et al. 2000). We also anticipated that owls would prefer smaller gaps, represented in the data as small mean gap size because smaller gap size offers increased protection from predators and more contiguous surrounding forest for movement. Lastly, we predicted that owls would prefer gaps with maximum edge per exposed area, to increase the availability of forest edge preferred by small mammals without compromising protective cover from predators.

We modeled each of the LiDAR variables above, as stand-alone models. In addition, we created simple additive models containing 2 or 3 variables in the general configuration of large trees + cover + gaps or edge (Table S1).

Our third step of model selection explored associations of owl foraging locations with fuels treatments, alone and additively with the top models from the first 2 modeling steps (Table S1). Although mechanical thin treatments were distributed throughout the study area, understory thin and underburn treatments were not; understory thins were implemented only in the southern half of the study area and underburns were only conducted in the northern half. To preserve power, we pooled all fuels treatment types together. Given the presence of mechanical thin treatments in all owl home ranges, we were able to specifically address mechanically thinned treatments. We predicted that owl use of an area for foraging would decline as the proportion of mechanical thin or total treated area increased. We also considered that above a certain threshold of treatment area, owls would move elsewhere to forage, and included a quadratic trend of mechanical thin and fuels treatments in the model set.

We searched for any correlation of variables prior to running all models and excluded models that would contain collinear components. We used the pROC package in Program R to estimate an area under the receiver operating characteristic (ROC) curve, an assessment of the goodness of fit of the top model(s); we defined the top model(s) as that with the lowest AIC_c value or within 2 AIC_c of the lowest value. Given the small sample sizes typical of radio-telemetry studies and our study, our last modeling step was to test the robustness and sensitivity of our modeling results to influential observations by removing one individual at a time from the dataset and re-evaluating all models using the same methods as described above.

RESULTS

We tracked 10 spotted owls (6 females, 4 males) during the study; we tracked 6 owls continuously throughout the first and second post-treatment years. We radio-marked 8 owls (3 males, 5 females) in 2007, including both members of 2 pairs. We found 2 of these birds deceased the following winter: a male was depredated and necropsy results for a female indicated nematode parasitism. We radio-marked 2 additional owls in 2008, bringing the sample size again to 8 owls: 3 males and 5 females, including 2 pairs. One female moved outside of the study area during the study period and was excluded from analyses. We collected 446 nocturnal use locations, with 4 of 236 locations (1.7%) occurring within fuels treatments in 2007, and 32 of 210 locations (15.2%) occurring within fuels treatments in 2008.

Home Range Size and Placement

We estimated home ranges for 9 owls using 30–60 foraging locations per bird (Seaman et al. 1999). Home ranges estimated with the 95% fixed kernel estimator averaged 2,494 ± 405.1 ha during 2007 and 3,386 ± 625.6 ha during 2008. Average MCP home range sizes for this study were 1,281 ± 208.4 ha and 2,026 ± 336.2 ha for 2007 and 2008, respectively.

Of the 3 treatment types, owl home ranges contained primarily mechanical thin areas ($\bar{x} = 271 \pm 60.2$ ha, $n = 9$), which were composed of DFPZs ($\bar{x} = 234 \pm 51.8$ ha, $n = 9$) and group selections ($\bar{x} = 36.8 \pm 8.8$ ha, $n = 9$). The amount of each treatment type within home ranges varied widely among owls, especially for underburn ($\bar{x} = 236 \pm 70.6$ ha, $n = 4$), and understory thin ($\bar{x} = 222 \pm 70.1$ ha, $n = 5$), which were not available within all owl home ranges. Spotted owl home ranges contained an average of 17.1 ± 3.3% ($n = 9$) total fuels treatments (Table 2). Selection ratios (w_i')

Table 2. Proportion of area treated and resource selection function for 4 fuels treatment types in 9 spotted owl home ranges and overall study area, Meadow Valley Project area, northern Sierra Nevada, California, USA, 2007–2008.

					Bonferroni confidence limits	
	Study area	Owl $\bar{x}$	w_i'[a]	SE(w_i')	Lower	Upper
DFPZ[b]	0.07	0.08	1.018	0.176	0.598	1.438
Group selection	0.01	0.01	1.043	0.199	0.566	1.520
Understory thin	0.06	0.04	0.663	0.347	0.000	1.495
Underburn	0.03	0.03	1.125	0.638	0.000	2.652
All treatments	0.17	0.16	0.914	0.189	0.462	1.366

[a] Selection ratio.
[b] Defensible Fuel Profile Zone.

suggested that proportions of treated areas within owl home ranges were similar to proportions of treatments available on the landscape (Table 2). All 90% Bonferroni confidence intervals for fuels treatments overlapped 1, indicating no difference between the composition of fuels treatments within home ranges and that available within the study area.

Owl Use of Treatment Areas: Foraging Locations

At the foraging-location scale, individual owl use of fuels treatments varied widely, and independently of the percentage of the home range that had been treated. Across all birds and both study years, 36 owl locations (8%) were within fuels treatments; all fuels treatment categories were used by an owl on at least 1 occasion. Locations within fuels treatments comprised 3–13% of the nocturnal use locations for 4 owls and 4 owls were never located within treatments (Fig. 2A). One male (P58) accounted for 15 (42%) locations within fuels treatment; this male foraged in an area that had been treated by prescribed underburn 1–7 years prior to site occupancy, and 29% of the owl's home range was within fuels treatments (14% mechanical thin, 15% underburn). This home range was unique in the amount of underburned forest it contained, and unfortunately there was not a comparable home range within the study area to further clarify possible trends related to underburned forest. We observed spotted owls foraging in mechanical thin on 14 occasions; across all owls, a mean of $3.15 \pm 1.2\%$ ($n = 9$) of owl foraging locations occurred in mechanical thin. When calculated as a proportion of the error ellipse, the mean proportion of mechanical thin at owl locations was $5.5 \pm 1.0\%$ ($n = 446$), compared with $9.9 \pm 0.5\%$ ($n = 2{,}100$) for random locations (Fig. 3). Similarly, the mean proportion of all fuels treatments at owl locations was also lower ($\bar{x} = 11.0 \pm 1.4\%$, $n = 446$) than at random locations ($\bar{x} = 15.2 \pm 0.7\%$, $n = 2{,}100$).

The top model for owl foraging locations in a post-treatment landscape included negative correlations with mechanical thin, high (>70%) canopy cover in the ≥32-m height strata, proportion of gaps, and distance to the owl's site center, and a marginally positive correlation with slope (Table 3). Two competitive models were very similar to the top model, and differed only in their consideration of fuels treatments: a model that did not include a treatment effect (model 2, Table 3) ranked 0.47 AIC_c below, and a model with a weak positive relationship of fuels treatments (model 3, Table 3) ranked 2.40 AIC_c below the top model (Burnham and Anderson 2002). The goodness-of-fit test (area under the ROC curve) suggested that the 3 top models were all a reasonably good fit to the data (area under the ROC = 0.76, 0.75, and 0.77 for models 1, 2, and 3, respectively).

Our top model was susceptible to influential observations. When we singly removed from the dataset any of 2 individual owls containing larger proportions of mechanical thin in

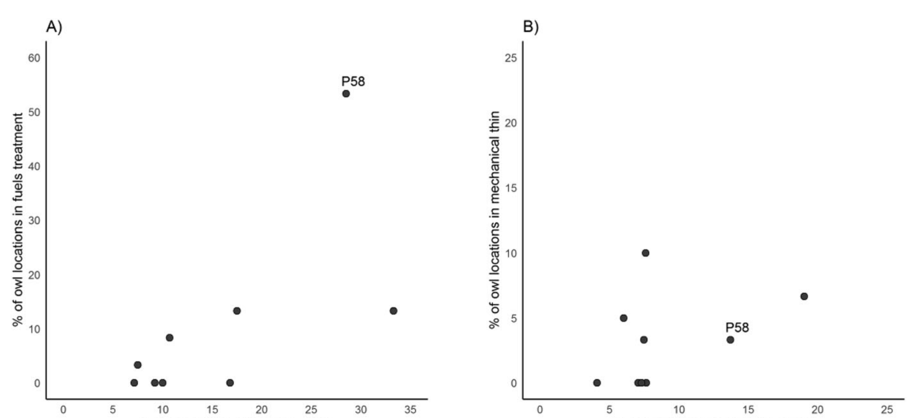

Figure 2. Percentage of spotted owl foraging locations within fuels treatments compared with availability of fuels treatments within each individual owl breeding season home range, in the Meadow Valley Project area, northern Sierra Nevada, California, USA, 2007–2008. We show this relationship for total combined fuels treatments (A), mechanical thin treatments (B), and an individual owl (P58) who accounted for 42% of all owl foraging locations within treatment.

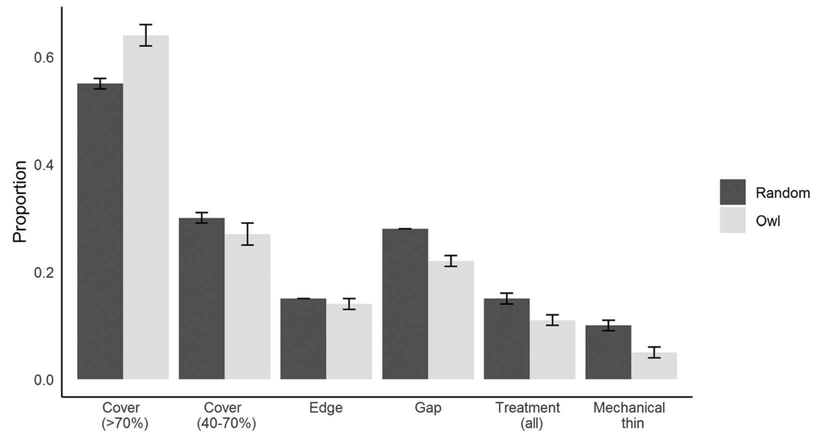

Figure 3. Means and standard errors for habitat variables at spotted owl foraging locations and random locations within owl home ranges, in the Meadow Valley Project area, northern Sierra Nevada, California, USA, 2007–2008.

their home range (Fig. 2B), the top model became model 2, which included the same covariates as the top model except it did not include a mechanical thin covariate (Table 3). Although removal of each of these owls changed the ranking of the 2 top models, model 1 remained within 1.1 AIC_c of model 2, β-parameters for model coefficients remained relatively unchanged to those for model 1 with all owls included, and the area under the ROC curve remained unchanged at 0.76, suggesting that the contribution of mechanical thin to our top model was minimal and susceptible to home range variation. The removal of each of the other owls from the dataset did not change the model ranking, β-parameters, or area under the ROC curve by any amount sufficient to alter model ranking or interpretation.

Increases in the proportion of gaps in the landscape corresponded with declining probabilities of spotted owl foraging (Table 4; Fig. 4A). The mean gap size for random locations was more than double that of owl foraging locations (Table 1), but this was not explanatory in top models (Table S1). Despite large differences in mean gap size, the proportion of edge was similar between owl and random locations (Table 1), and edge did not rank highly in model sets (Table S1).

Spotted owls foraged in a variety of canopy complexities (Table 1). The top model described declining probability of spotted owl foraging with increasing high canopy cover above 32 m (Fig. 4D), although confidence intervals overlap zero, indicating large variation among individuals (Table 4). Although high canopy cover above 32 m, restricted to areas of the landscape with large trees, was a component of top models, large tree density and proportions of large trees were not explanatory (Tables 3 and S1).

Owl foraging locations contained greater proportions of high (>70%) overall canopy cover than random locations (Table 1); however, this difference did not rank highly in candidate models as a linear or quadratic trend (Table S1). Medium cover, typically considered suitable foraging habitat, did not rank competitively in candidate models when calculated as overall cover (>2 m min. canopy height), cover of co-dominant trees (≥16 m min. canopy height), or as

Table 3. Models that best explained spotted owl foraging habitat selection in a landscape with fuels treatments, Meadow Valley Project area, northern Sierra Nevada, California, USA, 2007–2008. We present all models within 100 corrected Akaike's Information Criterion (AIC_c) points of the top model.

Model		K[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	Cum. Wt.[e]
1	Gap_{prop}[f] + $Cover_{>70\%,\ 32m}$[g] + $Distance_{core}$[h] + Slope + MechThin[i]	7	1,688.67	0.00	0.478	0.478
2	Gap_{prop} + $Cover_{>70\%,\ 32m}$ + $Distance_{core}$ + Slope	6	1,689.14	0.47	0.378	0.856
3	Gap_{prop} + $Cover_{>70\%,\ 32m}$ + $Distance_{core}$ + Slope + $Treatment_{All}$[j]	7	1,691.08	2.40	0.144	1.000
4	Gap_{prop} + $Cover_{>70\%,\ 32m}$ + MechThin	5	1,765.05	76.38	0.000	1.000
5	Gap_{prop} + $Cover_{>70\%,\ 32m}$	4	1,767.55	78.88	0.000	1.000
6	Gap_{prop} + $Cover_{>70\%,\ 32m}$ + $Treatment_{All}$	5	1,769.09	80.42	0.000	1.000

[a] Number of model parameters.
[b] Akaike's Information Criterion corrected for small sample sizes.
[c] Difference in AIC_c values between the model and the best model.
[d] Akaike weight.
[e] Cumulative model weight.
[f] Proportion of gap (≤2 m maximum canopy height).
[g] Proportion of >70% cover at >32-m height strata.
[h] Distance to site center.
[i] Proportion of mechanical thin.
[j] Proportion of fuels treatment (all).

Table 4. Akaike weights (w_i), β-coefficients, standard error, lower and upper 95% confidence intervals, and *P*-values for models that best described spotted owl foraging in a treated landscape, Meadow Valley Project Area, Sierra Nevada, California, USA, 2007–2008.

Variable	Coefficient	SE	CI_{low}	CI_{high}	*P*
Model 1 ($w_i = 0.478$)					
Gaps (proportion)	−2.68	0.36	−3.39	−1.97	<0.001
Proportion of >70% cover at >32-m height strata	−2.50	4.35	−11.02	6.02	0.565
Distance from site center	−0.69	0.09	−0.86	−0.51	<0.001
Slope	0.01	0.01	0.00	0.03	0.042
Mechanical thin (proportion)	−0.43	0.28	−0.99	0.12	0.124
Model 2 ($w_i = 0.378$)					
Gaps (proportion)	−2.79	0.36	−3.49	−2.08	<0.001
Proportion of >70% cover at >32-m height strata	−2.33	4.36	−10.87	6.21	0.593
Distance from site center	−0.69	0.09	−0.86	−0.51	<0.001
Slope	0.02	0.01	0.00	0.03	0.017
Model 3 ($w_i = 0.144$)					
Gaps (proportion)	−2.81	0.37	−3.54	−2.08	<0.001
Proportion of >70% cover at >32-m height strata	−2.29	4.34	−10.81	6.22	0.597
Distance from site center	−0.69	0.09	−0.87	−0.51	<0.001
Slope	0.02	0.01	0.00	0.03	0.016
Proportion of fuels treatment (all)	0.06	0.22	−0.38	0.50	0.774

cover contribution of large trees (≥32 m min. canopy height; Table S1).

Owl foraging locations in our study were closer ($\bar{x} = 1{,}839 \pm 81$ m, $n = 446$) to the site center than expected at random ($\bar{x} = 2{,}366 \pm 34$ m, $n = 2{,}100$). Our top model similarly reflected a declining probability of owl foraging with increasing distance (Table 4; Fig. 4B). Owl foraging locations occurred in areas with slightly steeper slopes than anticipated at random (Table 1), which was also reflected in the top model as a mildly positive trend (Table 4; Fig. 4C).

DISCUSSION

The Meadow Valley Project presented a unique opportunity to investigate spotted owl foraging patterns and short-term response to full implementation of a landscape-scale fuels reduction project. At the landscape scale, spotted owl home ranges contained fuels treatments in relative proportion to their prevalence in the landscape (Table 2). Bonferroni confidence limits for the resource selection function varied from 0 to 2.65, suggesting that a larger sample size would be needed to clarify landscape trends regarding fuels treatment types (e.g., mechanical thin vs. underburn) (Fig. 5).

At the foraging location scale, probability of use declined with increasing distance from the owl's core area, as expected for a central-place forager (Rosenberg and McKelvey 1999). Further, probability of use for owl foraging was negatively related to the proportion of gaps (canopy height <2 m) in the ellipse, and edge was not a component in competitive models. We had anticipated that gaps and edge would be features in model results, given their importance in previous findings for California spotted owl habitat use (Irwin et al. 2007, Bond et al. 2009, Williams et al. 2011, Eyes et al. 2017) and northern spotted owl habitat use (Zabel et al. 1995, Ward et al. 1998, Comfort et al. 2016). In our study, the proportion of gaps was the most important vegetation covariate, with owl foraging locations having an average gap proportion of 22%. We did not find evidence to support our hypothesis of a positive association with intermediate proportions of gap but rather found a negative relationship of owl foraging with increasing gap proportion. Prior studies have reported positive correlations of spotted owl annual survival and reproductive output with mature forest edge, hypothesizing that the intersection of late seral forest and areas of shrubs and saplings may be important for prey species associated with early seral habitat, such as woodrats (*Neotoma* spp.), pocket gophers (*Thomomys* spp.) and deer mice (*Peromyscus* spp.; Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005, Tempel 2014). Our definition of edge as the intersection of forest (≥2 m canopy height) and open gaps (<2 m maximum canopy height) at fine spatial resolution may not have been as biologically meaningful for the owl as intersections among coarsely defined vegetation classes, such as intersections of shrub patches with mature forest (Williams et al. 2011) or owl habitat with non-habitat (Franklin et al. 2000). The importance of edge to owl foraging may depend on the type of edge (hard vs. soft), land cover type, scale of patch sizes, disturbance type, and ecological context (Bond et al. 2009, Comfort et al. 2016, Eyes et al. 2017).

Fuels treatments typically incorporate a reduction of canopy cover to or near 40%, a reduction of understory density, and increased tree spacing as design features to modify fire behavior. The proportion of fuels treatment, calculated as both proportion of mechanical thin and as a combined area of all treatments, was lower at owl foraging locations versus random locations (Fig. 3), although owls exhibited considerable individual variation (Fig. 2). Although our top model included the proportion of mechanical thin as a weak negative effect, it was sensitive to influential observations; the exclusion of either of 2 owls (P58, D72) resulted in a top model that did not contain a fuels treatment covariate. A competitive model 2.40 AIC_c below the top model also contained a fuels treatment covariate, structured as all treatment types pooled together. This third-ranked model was also sensitive to influential observations; removal of owl P58 from the dataset changed the marginally positive fuels treatment effect (Table 4) to a negative, non-significant

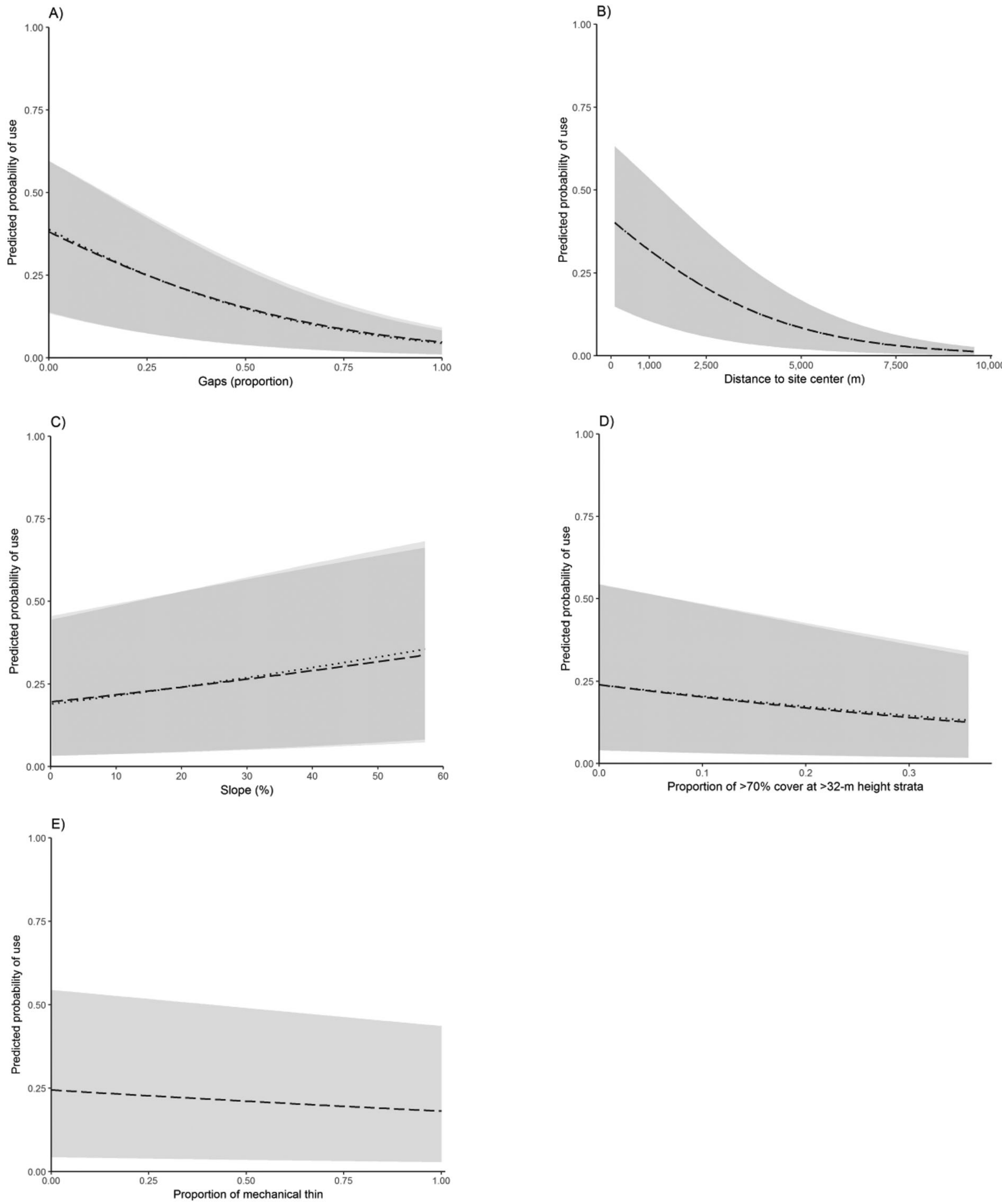

Figure 4. Predicted spotted owl foraging probabilities and 95% confidence intervals, derived from the 2 models of best fit in the Meadow Valley Project area, Sierra Nevada, California, USA, 2007–2008. We present probabilities derived from model 1 (gap + cover + distance + slope + mechanical thin) as a long-dashed line, and probabilities derived from model 2 (gap + cover + distance + slope) as a dotted line, for the following: proportion of gap (≤2-m maximum canopy height) within the ellipse (A), distance from the location to the owl's site center (B), percent slope (C), proportion of ellipse that is >70% cover at a minimum canopy height of >32 m (D), and proportion of mechanical thin within the ellipse (E).

effect, illustrating variation in owl home ranges. Of note, 53% of owl P58's locations were located within fuels treatment, predominantly in areas of underburn, a treatment type with limited or no availability to other owls in the study area. Although a single observation, this merits mention in the context of recent studies that have reported California spotted owls to forage in patches that experienced low and moderate severity wildfire (Bond et al. 2016, Jones et al. 2016, Eyes et al. 2017). Thus, we believe the instability of our top models that include fuels treatment covariates are a result

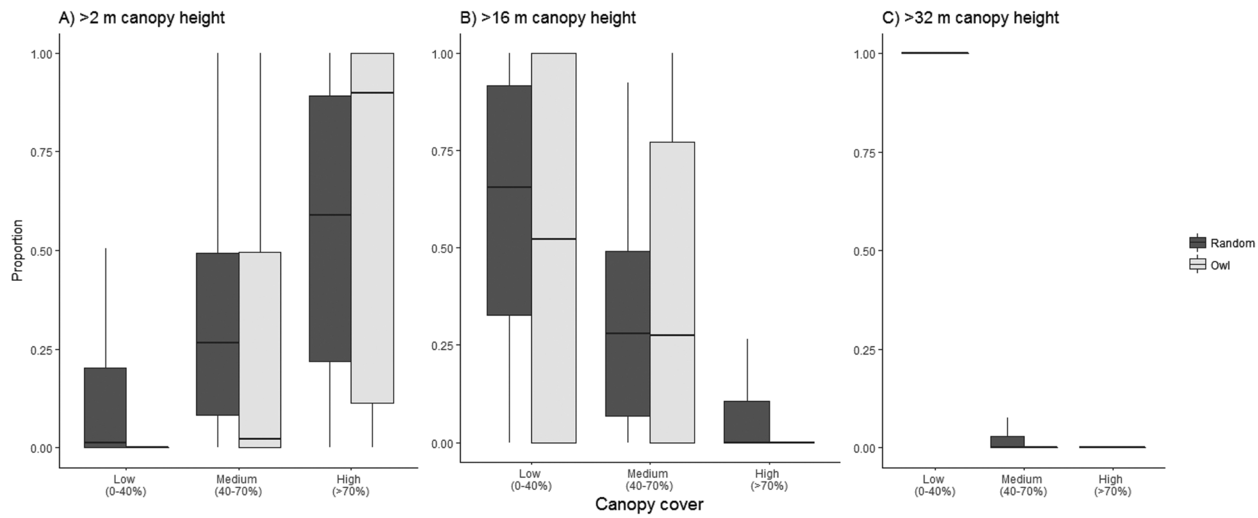

Figure 5. Comparison of canopy cover categories for spotted owl use locations and random locations within owl home ranges in a treated landscape in the Meadow Valley Project area, northern Sierra Nevada, California, USA, 2007–2008. We calculated cover as the proportion of forested 1-m pixels above a minimum canopy height of 2 m, representing overall canopy cover (A), 16 m, representing cover of co-dominant and dominant trees (B), and 32 m, describing cover of large trees (C). We show upper ($Q_{75\%}$) and lower ($Q_{25\%}$) quartiles as box extents and the median as the central horizontal line; vertical lines show the maximum and minimum values, excluding outliers which are defined as beyond $1.5 \times (Q_{75\%} - Q_{25\%})$ of the quartiles.

in part of our small sample size and the individual variation we observed across owls. Variation in foraging patterns may be characteristic for California spotted owls given differences among individuals, and prey and habitat availability across territories (Williams et al. 2011, Irwin et al. 2015).

Overall high (>70%) and medium (40–70%) canopy cover were not features of top models (Table S1), and >70% cover >32 m canopy height appeared as a non-significant negative trend in top models. These results are unexpected given a number of studies linking spotted owl site selection to areas of higher canopy cover (Franklin et al. 2000, Blakesley et al. 2005, Tempel et al. 2014), and a study in which California spotted owls selected for canopy closure more than for large tree sizes (Zabel et al. 1992). The differences in canopy cover results between our study and other studies may be in part derived from alternate mapping methods; earlier studies have used vegetation inventory plots, aerial photographs, or orthophotoquads to estimate canopy cover. Additionally, we analyzed canopy cover as a single attribute, whereas other studies have nested canopy cover within a combination metric that described canopy cover and tree stand size together as a unified covariate.

We found that the proportion of gaps and distance from the owl's site center were the strongest predictors of foraging locations for our study. The variation we observed in owl use of fuels treatments may be in part related to treatment effects on the proportion of gaps. A *post hoc* examination found that within owl home ranges, random locations in mechanically thinned forest contained greater proportions of gaps ($\bar{x} = 0.41 \pm 0.01$, $n = 205$) than found at this study's owl foraging locations ($\bar{x} = 0.22 \pm 0.01$, $n = 413$).

Mechanical thin treatments, including DFPZs and group selections, are characterized by a reduction of understory components such as large woody debris, shrub, and herbaceous cover: habitat elements important to small mammals, particularly woodrats (Lee and Tietje 2005, Innes et al. 2007) and Humboldt's flying squirrels (Lehmkuhl et al. 2006), key California spotted owl prey species (Verner et al. 1992). Zabel et al. (1995) and Ward et al. (1998) both concluded that woodrats provided an energetic benefit to spotted owls over other prey species, and that owls selected foraging sites where woodrats were abundant. In a study that spatially overlaps our study area, presence of woodrat houses was influenced by the presence of black oak, steep slopes, and logs >30 cm mean dbh (Innes et al. 2007), all features that are rare in DFPZs and group selections.

Humboldt's flying squirrels prefer forests containing numerous large live trees, snags, well-developed understories, and many large logs on the ground (Lehmkuhl et al. 2006, Manning et al. 2012); these conditions are typically not maintained in a mechanical thin. Waters and Zabel (1995) reported low densities of flying squirrels in post-treatment stands, and Meyer et al. (2007) suggested that mechanical thinning may reduce the microhabitat suitability for flying squirrels for several years post-treatment. Holloway et al. (2012) reported low flying squirrel abundance in treatments that resulted in evenly spaced trees, which is a fire management feature of DFPZs. Sollmann et al. (2016) reported reduced densities of flying squirrels within fuels treatments and a corresponding shift in flying squirrel spatial distributions, out of fuels treatments and into unharvested areas of greater canopy closure, such that pre- and post-treatment densities were similar across the larger combined treatment and surrounding area. These results suggest that treatment effects on key spotted owl prey species should be considered at scales beyond the immediate treated patches.

We were not able to assess post-treatment alterations to several habitat attributes important to small-mammal abundance, including downed woody debris, snags, shrub, and herbaceous cover, because of degradation of the 0–2-m band of the LiDAR signal in areas of complex canopy. Further, we were unable to draw definitive conclusions of understory thin and underburn treatment types because of sample size limitations. The active selection of post-understory burn selection of 1 individual on this study suggests further research may be warranted to investigate whether there may be positive benefits to owl foraging habitat from prescribed fire that are not realized from solely mechanical treatments.

Results from our study provide insight into the short-term response of spotted owls to the implementation of a landscape fuels treatment strategy. Inferences from our study should be interpreted with the understanding that we conducted an observational study susceptible to uncontrolled factors. For example, treated areas may have lacked foraging suitability before treatments were installed because of prey abundance or spatial location on the landscape. Our study was representative of the challenges of a passive adaptive management framework (Kendall 2001), in which the timing and spatial location of treatments were mandated by management objectives and thus precluded a controlled experiment. This is not an unusual circumstance on USFS lands where contracted treatments can be implemented within 5-year windows based on logistical, financial, and other operational factors. Given the broad importance of understanding how landscape forest and fuels restoration strategies affect California spotted owls and other species of concern in the Sierra Nevada, we believe that a reduction of barriers to implementing more rigorous study designs would strengthen research inferences to address these important information needs.

Our study focused on California spotted owl foraging response to fuels treatments in the immediate 2 years following implementation. Associations among owls and fuels treatments are likely to change over time as vegetation matures, and exploring patterns over longer time periods may be useful for a more comprehensive understanding of the effects of fuels treatments. In this study, the fine-resolution habitat data offered by LiDAR imagery was informative for modeling California spotted owl foraging habitat. We encourage further use and development of LiDAR vegetation data because the structural information it offers may be better suited than coarse-resolution vegetation data to address management and conservation concerns, particularly at spatial scales relevant to California spotted owls, project planning, and forest restoration.

MANAGEMENT IMPLICATIONS

As dry western forests continue to experience intensification in wildfire size and severity, a critical ecosystem management focus is forest resilience to wildfires that are outside of historical precedent. Modification of forest fuels and vegetation, implemented as fuels treatments, are likely to remain a frequently used tool to modify fire behavior and restore ecological resilience in fire-adapted forests. Current forest management guidelines emphasize structural heterogeneity, including the introduction of gaps. Our findings suggest that moderate to high proportions of gaps may reduce the probability of spotted owl foraging, which creates conflicting implications for mechanically treated areas. We suggest consideration of gap proportions within the range associated with higher owl foraging probability until additional information becomes available. Acknowledging the prevalence of fuels treatments in current forest management, we encourage further investigation of effects on California spotted owl habitat use to broaden our initial findings. Increased availability of LiDAR vegetation data coupled with recent advances in satellite geospatial-tagging technology hold promise for further understanding of the effects of fuels treatments and forest restoration approaches on California spotted owls and their habitat.

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LITERATURE CITED

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