



# Space use, forays, and habitat selection by California Spotted Owls (*Strix occidentalis occidentalis*) during the breeding season: New insights from high resolution GPS tracking

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## ABSTRACT

Our current understanding of the relationship between imperiled species and forest management can benefit from global positioning system (GPS) technologies. Fauna of later seral stage forests have historically been difficult to detect and track in rugged terrain, leading to challenges in movement characterization and conservation. We investigated movement of California Spotted Owls (*Strix occidentalis occidentalis*) using automated GPS loggers affixed to 15 owls in the northern Sierra Nevada, California. We used > 17,000 locations from individual owls to characterize homerange size, movement distances, and roosting and foraging habitat selection at four spatio-temporal scales (landscape, home range, foray, nightly) during the breeding season (April–August). Additionally, we assessed owl use of Protected Activity Centers (PACs), which are designated by the U.S.D.A. Forest Service to protect nesting and roosting habitat. Our results corroborated some previous findings about habitat requirements of California Spotted Owls, while also revealing new nuances in space use and habitat selection. Roosting and foraging owls selected stands with high canopy cover and large trees at multiple spatio-temporal scales, with foraging owls showing strongest selection at the largest (landscape) scale investigated. Although owls selected for PACs while foraging and roosting, PACs protected less than one quarter of foraging space use (volume of use) and fewer than half of observed roosts during the breeding season. Female owl home ranges were double the size of male home ranges, and distances travelled from the nest by females were 1.3 times greater than distances travelled by males, with non-breeding females travelling farthest and visiting up to six PACs during a single breeding season. Foraging behavior of this sort has not been documented previously in California Spotted Owls. Our findings support protection of later seral stage forest attributes for roosting and foraging California Spotted Owls. Given their selection for later seral forest attributes, strongest evidence of foraging habitat selection at the landscape scale, long distances travelled by owls and limited habitat protection afforded by PACs, habitat connectivity across the landscape is likely an important component for owl conservation, and distribution of current protected areas may be inadequate for this wide-ranging species.

## 1. Introduction

Spotted Owls (*Strix occidentalis*) are threatened by loss and fragmentation of later seral forest and invasion by congeneric Barred Owls (*Strix varia*), which displace and hybridize with Spotted Owls (Keane, 2017). Consequently, Spotted Owls have been a focus of forest

conservation efforts in the western U.S. since the 1980s (Simberloff, 1987) and a primary factor in the development of some of the country's largest and most comprehensive management plans, including the Northwest Forest Plan which addressed management of 9.9 million ha in 3 states (Tuchmann et al., 1996). While the Northern Spotted Owl (*S. o. caurina*) and Mexican Spotted Owl (*S. o. lucida*) subspecies are

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federally protected, the California Spotted Owl (*S. o. occidentalis*) is currently under review for listing (U.S. Fish and Wildlife Service, 2017). The U.S.D.A. Forest Service, which manages lands where the majority of the California subspecies occurs, is currently reviewing a draft conservation strategy for the subspecies. While the California Spotted Owl is a high-profile and well-studied species, few of the management recommendations developed and implemented to protect it have been tested empirically (Berigan et al., 2012), and numerous questions remain on the most effective strategy to prevent its extinction (Stine and Manley, 2017).

California Spotted Owls are medium-sized owls that specialize in later seral stage forests (stands with high canopy cover and large trees) in montane regions of California (Tempel et al., 2016; Moen and Gutiérrez, 1997). They are socially monogamous central place foragers that defend territories around their nests, where they hunt at night and prey upon small mammals, birds, lizards and insects (Gutiérrez et al., 2017). Previous investigations established that spotted owls preferentially roost and nest in mature forest stands with later seral or old-growth characteristics (Moen and Gutiérrez, 1997; Bond et al., 2004; Tempel et al., 2016; North et al., 2017). Within mature forests, California Spotted Owls forage within a variety of habitats including stands with moderate to high canopy cover (Call et al., 1992; Williams et al., 2011), forest edges (Eyes et al., 2017; Williams et al., 2011), unlogged burned areas (Bond et al., 2016, 2009), and riparian corridors (Bond et al., 2016; Irwin et al., 2007).

Historically, conservation of California Spotted Owls has focused on protecting nesting and roosting habitat in later seral forests with high canopy cover and prevalence of large trees (Bond et al., 2004; Moen and Gutiérrez, 1997; North et al., 2017; Tempel et al., 2016). Habitat protection on National Forest lands generally occurs at the scale of “Protected Activity Centers” (PACs), where contiguous habitats are designated to protect core breeding and roosting behaviors for known pairs or territorial but unpaired owls (Berigan et al., 2012; U.S.D.A. Forest Service, 2004). Protected Activity Centers were proposed as part of an interim conservation strategy for the California Spotted Owl in 1992 (Verner et al., 1992b) to protect areas where owl use is concentrated within the home range, including nest and roost sites (Berigan et al., 2012). In practice, PACs are delineated as  $\geq 121$  ha polygons encompassing the best quality habitat (large trees and high canopy cover) around a California Spotted Owl nest or roost site. Stand-altering activities, except for chainsaw thinning small diameter material (< 15 cm diameter at breast height) and light under-burning, are generally prohibited within the PACs (Berigan et al., 2012). However, foraging California Spotted Owls in the Sierra Nevada utilize much broader areas than those encompassed by PACs, with individual owl home range estimates during the breeding season ranging from 500 to 2800 ha and year-round home range estimates exceeding 5000 ha (Williams et al., 2011; Zabel et al., 1992).

Habitat selection is dependent on spatial and temporal scales (Mayor et al., 2009; Orians and Wittemberg, 1991). For example, Blakesley et al. (2005) found that finer scale habitat features were better predictors of breeding site occupancy of California Spotted Owls, whereas LaHaye et al. (1997) reported that landscape scale features were better predictors of nest success. For foraging owls, Bond et al. (2016) found that the strength and direction of selection of burned habitat by owls was influenced by area designated as available habitat. Past assessments of habitat selection and space use by California Spotted Owls at multiple scales, and therefore evaluations of the efficacy of management, have been limited by available survey methods. For example, current knowledge of California Spotted Owl foraging behavior is based on auditory, and very high frequency (VHF) radio telemetry surveys, both of which are inherently biased toward areas that are more accessible to observers and are limited in spatial accuracy (Tomkiewicz et al., 2010).

Recent advances in animal tracking using Global Positioning Systems (GPS) and launch of the ICARUS satellite tracking program

permit collection of increasingly precise, detailed, and extensive data on movement and locations of highly mobile and cryptic species (Tomkiewicz et al., 2010; Wikelski, 2007). These technological developments have the potential to provide insights that will greatly improve our understanding of animal-habitat relationships and inform conservation planning (Morales-Reyes et al., 2017; Shimada et al., 2017). Forest-dwelling fauna have historically been difficult to detect and track in rugged terrain (Hollenbeck et al., 2018; Phoebus et al., 2017). This limitation has constrained the scope of research questions addressed, leading to a focus on conservation of habitat components in which species can be readily detected, and a neglect of life-history phases in areas where study subjects are more difficult to detect (Koenig et al., 1996). For example, movements and activities of central place foragers during nesting are a major research and conservation focus, but relatively little is known about movements of central place foragers during forays and dispersal (Clobert et al., 2012; Kesler and Walters, 2012; Rosenberg and McKelvey, 1999). Detailed information from high resolution GPS tracking can provide more robust support for existing forest management strategies, which are rarely empirically tested, or spur development of more refined and ecologically relevant approaches.

Our objective was to revisit current knowledge of California Spotted Owl habitat selection and space use by investigating movement of California Spotted Owls using GPS loggers that automate observations of movements at multiple temporal and spatial scales (Wilmers et al., 2015). Throughout three breeding seasons (April–August 2015–2017), we characterized California Spotted Owl homerange size, transit distances and straight-line distances from the nest, selection of roosting habitat, and selection of foraging habitat at four spatio-temporal scales. We used a model selection approach to evaluate whether owls selected for specific habitats and whether sex or breeding status influenced homerange, movement distance from the nest or habitat selection. We also assessed the proportion of each owl’s observed roost sites and foraging volume of use within designated PACs and evaluated selection for these protected areas.

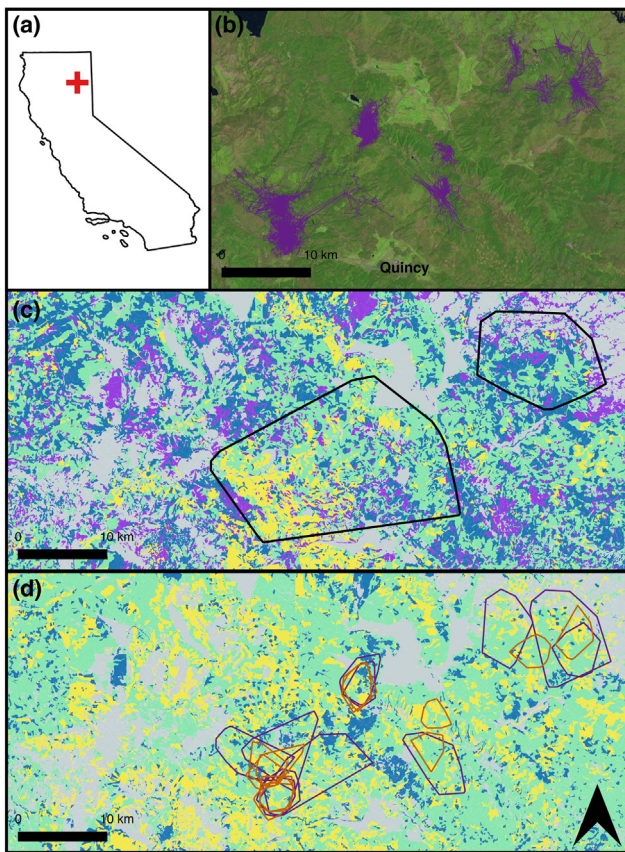
## 2. Materials and methods

### 2.1. Study area

We studied California Spotted Owls on the Mt. Hough Ranger District, Plumas National Forest (63,770 ha), within the Sierra Nevada mountain range in northern California (40°00′01″N 120°40′05″W, Fig. 1). The Forest has an elevation gradient of 311 to 2433 m and a Mediterranean and montane climate with dry, warm summers and cool, wet winters. Although conditions vary widely across the elevation gradient, mean annual precipitation within the Forest is c. 1036 mm, and mean temperature ranges from  $1.3 \pm 2.4$  °C in January to  $19.3 \pm 1.5$  °C in July (1895–2017, Western Regional Climate Center, 2017). Vegetation in Plumas National Forest is dominated by lower and upper montane forest with stands of ponderosa pine (*Pinus ponderosa*) – mixed conifer, white fir (*Abies concolor*) – mixed conifer, and red fir (*Abies magnifica*) (Fites-Kaufman et al., 2007). Common tree species include red fir, white fir, Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine, Jeffrey pine (*P. jeffreyi*), sugar pine (*P. lambertiana*), black oak (*Quercus kelloggii*) and incense cedar (*Calocedrus decurrens*) (Fites-Kaufman et al., 2007). Fire is common throughout the region and mixed-severity fire regimes dominate, with tree scar records indicating composite fire return intervals on the forest ranging from 8 to 22 years at a site between 1454 and 2001 (Moody et al., 2006).

### 2.2. Owl movement surveys

During 2015–2017 we marked and tracked 8 females and 7 males from 8 territories and collected a mean of 805 (370–1072) locations per owl\*season during 22 owl\*seasons (15 individual owls were tracked, 5



**Fig. 1.** Study area (a) in Plumas National Forest, California; (b) trajectories (purple traces) of 15 California Spotted Owls tracked during the 2015–2017 breeding seasons (April–August); (c) minimum convex polygons (MCPs) of all owl locations in east and west landscapes within the study area and overlaid on canopy cover (> 70% is yellow, 50–70% is green, 30–50% is blue, and < 30% is purple); (d) home ranges defined by MCPs for male (orange, 11 owl\*seasons) and female (purple, 11 owl\*seasons) in each season and overlaid on dominant tree size (DBH > 50 cm is yellow, 25–50 cm is green, < 25 cm is blue). Grey background in (c) and (d) show treeless areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of them during multiple breeding seasons) across > 45,000 ha of forest (Supplementary material, Appendix S1). We used Forest Service data on known nests coupled with surveys to locate owls in May and June of 2015, 2016, and 2017. We captured owls by hand and with snare and noose poles. Owls were tagged under authorization from the California Department of Fish and Wildlife (Scientific Collecting Permit #SC-8645) and the U.S.F.W.S. Bird Banding Laboratory (Permit #22423). We determined owl sex based on pitch of vocalizations or knowledge from prior banding efforts, and we classified owl age using plumage characteristics (Forsman, 1983; Franklin et al., 1996). When tracking began, one female owl was in its second year (SY, F) and 14 owls were after third year (ATY, 7F:7M). We attached an Alle-300 GPS-UHF GPS logger (Ecotone Telemetry, Sopot, Poland) and a VHF transmitter (Advanced Telemetry Systems, Isanti, U.S.A.) to each bird using a back-mounted Teflon ribbon harness (total package weight < 13 g) (n = 15, seven males and eight females). The GPS-UHF units recorded locations at defined intervals within daily duty cycles, and stored locations until a connection was established with a hand-held or stationary base station to which locations were then transmitted (EP-BS, Ecotone Telemetry). We placed base stations near nests or in areas commonly transited by owls. Additionally, owls were tracked on foot to within 50–200 m using VHF radio telemetry and data were downloaded from the GPS-UHF units using a wireless link to the base station.

These GPS-UHF units can be remotely reprogrammed, enabling use of multiple sampling regimes over time on individual owls. During the breeding season, batteries on the GPS-UHF units allowed approximately 3 months of tracking after marking (c. 10 May), with hourly locations collected daily between c. 1800 h and 600 h the following day. We also programmed GPS-UHF units to collect 3–7 nights of higher-resolution movement data for each owl, with locations collected at 1–6 min intervals. Herein, we truncated movement data to align with the California Spotted Owl breeding season from 1 April–31 August (García-Feced et al., 2011; Lee et al., 2012; Tempel and Gutiérrez, 2013). Foraging location observations were defined as position coordinates recorded between 1 h after sunset and 1 h before sunrise. We defined roost locations as locations recorded between 2 h after sunrise and 2 h before sunset. We determined the breeding status (breeding or non-breeding) of owls during each season through survey efforts or direct observation.

### 2.3. Home range size

We calculated home range size using the **minimum convex polygon (MCP)** method (Worton, 1987), so that our calculations would be comparable to the majority of literature on California Spotted Owl home range (see Roberts, 2017 and references therein). MCPs were derived for each owl\*season using all available locations. For robustness, we also calculated home ranges using the 95% isopleth of the kernel density utilization distribution (Worton, 1989). We compared home range size between sexes and breeding status classes using a model selection process to test specific hypotheses about home range size (Table 1). We used an information-theoretic approach to model selection (Burnham and Anderson, 2003) and evaluated support for 4 hypotheses related to home range size (Table 1). For each dataset, we compared candidate models using the Akaike information criterion, adjusted for sample size ( $AIC_c$ ), and retained the best approximating model with the lowest  $AIC_c$  value, or the best set of models, if top models were within  $2 \Delta AIC_c$  (Burnham and Anderson, 2003). As a final step, we assessed the effect of survey year (2015, 2016, 2017) by adding it to the best approximating model as a categorical fixed variable and evaluating whether it significantly improved model fit (reduced  $AIC_c > 2$ ). We interpreted variables using parameter estimates from the best approximating model, or model-averaged estimates from the best model set. Models were fit using log-transformed home range size (ha) as the response variable, to satisfy the assumption of normality. We included *territory* as a random effect only (not individual) because a parametric bootstrap test showed that when *individual* was added to the final model it was not significantly different from the model containing only *territory* (LRT = 74.22,  $P = 0.500$ ). We conducted all analysis within the R environment for statistical computing (R Development Core Team, 2016). We used the *adehabitatHR* v3.3.0 (Calenge, 2006) package to fit MCPs and kernel density utilization distributions, packages *lme4* v1.1-12 (Bates et al., 2013) and *lmerTest* v 2.0-33 (Kuznetsova et al., 2017) to fit linear mixed effects models and *MuMIn* v 1.40.4 was used for model averaging and to calculate  $R^2$  of all models using methods described in Nakagawa and Schielzeth (2013). We considered differences significant at  $\alpha < 0.05$ , and we report test statistics (TS) and 95% confidence intervals (95% CI) where appropriate; test statistics were t values for single models and z values for model-averaged sets.

### 2.4. Distance travelled

We calculated nightly distance transited (sum of all nightly movements) using only high resolution data (1–6 min position interval) for full nights (> 6 h data collection). We also calculated maximum distance travelled from the nest (straight-line distance) for each owl\*season and each night. We defined nest locations as active nests for breeding birds and nest site from prior year for non-breeding birds, due



**Table 1**

Hypotheses and corresponding models developed to explain variation in California Spotted Owl homerange size and distance travelled from nest during breeding seasons of 2015–2017. Homerange size (ha) was defined by MCP for each owl\*season and models were linear mixed effects models with territory included as a random effect. Distance travelled from nest was the maximum straight-line distance from the nest for each night and models were Gaussian mixed effects models with a log-link and with individual owl included as a random effect. Nest locations represented active nests for breeding birds and nest sites during prior years for non-breeding birds.

Hypothesis	Model equation
<i>Homerange size</i>	
1. Owl homerange size was not influenced by sex or breeding status	Homerange size $\sim \beta_0 + (1 territory)$
2. Home range size differed between males and females	Homerange size $\sim \beta_0 + \beta_1 * sex + (1 territory)$
3. Home range size differed between non-breeding and breeding birds	Homerange size $\sim \beta_0 + \beta_1 * breeding\_status + (1 territory)$
4. Sex and breeding status influenced homerange size	Homerange size $\sim \beta_0 + \beta_1 * sex + \beta_2 * breeding\_status + (1 territory)$
<i>Distance travelled from nest</i>	
1. Nightly maximum distance from the nest was not influenced by sex or breeding status.	Distance from nest $\sim \beta_0 + (1 individual)$
2. Distance travelled from nest differed between sexes	Distance from nest $\sim \beta_0 + \beta_1 * sex + (1 individual)$
3. Distances travelled from nest differed between breeding and nonbreeding birds	Distance from nest $\sim \beta_0 + \beta_1 * breeding\_status + (1 individual)$
4. Sex and breeding status influenced distances travelled from the nest	Distance from nest $\sim \beta_0 + \beta_1 * sex + \beta_2 * breeding\_status + (1 individual)$
5. Sex and breeding status interacted to influence distance travelled from the nest	Distance from nest $\sim \beta_0 + \beta_1 * sex + \beta_2 * breeding\_status + \beta_3 * (sex:breeding\_status) + (1 individual)$

to high nest site fidelity (Berigan et al., 2012). We compared distance travelled from the nest between sexes and between breeding and non-breeding birds, using the same methods and hypotheses used for the homerange size analysis described above, except that distance traveled was the response variable and individual owl was included as a random effect (Table 1). Models were fit using distance from nest as the response variable and the Gaussian family with a log-link.

## 2.5. Foraging habitat selection

To evaluate foraging habitat selection, we tested whether owls used habitats disproportionately to the amount available (Johnson, 1980) by comparing intensity of habitat use to availability of habitat (Thomas and Taylor, 2006). We restricted our analysis to two measures of forest structure (canopy cover and dominant tree size) that are known to be highly important for California Spotted Owls (Call et al., 1992; Williams et al., 2011), however we acknowledge that habitat selection for this species comprises a much wider range of factors including other components of habitat structure (North et al., 2017), fire history (Bond et al., 2016, 2009), prey availability, habitat configuration (Eyes et al., 2017), and presence or water or riparian areas (Bond et al., 2016), as well as conspecific and interspecific interactions. We assessed habitat selection by foraging owls at four spatio-temporal scales: landscape (2nd order), home range (3rd order), foray, and nightly (Johnson, 1980). We analyzed all owl movements using the R packages *BBMM* v3.0 (Nielson et al., 2015), *adehabitatLT* v3.3.0 (Calenge, 2006) and *adehabitatHR* v3.3.0 (Calenge, 2006).

### 2.5.1. Landscape scale

To evaluate foraging habitat selection at the landscape scale, we tested whether owls used habitats disproportionately to the amount available by comparing habitat use at the home range scale to availability of habitat within the eastern or western (Fig. 1c) study areas. We characterized habitat using vegetation mapping data (U.S.D.A. Forest Service, 2015) based on the CALVEG (“Classification and Assessment with Landsat of Visible Ecological Groupings”) classification (Nelson et al., 2015). From these spatial data we selected two habitat variables that have been associated with California Spotted Owl habitat use, are widely quantified, and are often targeted for manipulation by forest managers: percent canopy cover and dominant tree size (Blakesley et al., 2005; North et al., 2017). Areas of non-forested land, roads, water, and cleared or naturally open areas were categorized as “open treeless areas”.

We treated four categories of canopy cover, three categories of

dominant tree size, and open treeless areas as eight separate datasets. Canopy cover categories included high (> 70%), medium (50–70%), low (30–50%) and very low (< 30%). Dominant tree size was based on the mean size of the dominant trees in the stand, measured as diameter at breast height (DBH), categorized as large (> 50 cm), medium (25–50 cm), or small (< 25 cm). We delineated the landscape available to owls as the MCP of every foraging location obtained for all the owls in our study, separated into eastern and western landscapes to account for a substantial gap in used habitat near the center of our study area (Fig. 1c).

To quantify habitat use, we calculated volume of the Brownian bridge utilization distribution (UD) for each owl\*season (Horne et al., 2007; e.g. Cox and Kesler, 2012a). The Brownian bridge method extends traditional methods of quantifying animal space use (e.g. kernel density, MCPs) by accounting for temporal autocorrelation among locations to estimate the probability density function (PDF) and utilization distribution (Calenge, 2006). When calculating UD, we excluded time lags longer than 62 min (our longest nightly sampling interval), reduced our data to one location per hour (higher resolution data addressed below) and used a spatial accuracy of 30 m (corresponding to accuracy of our GPS units) and a grid cell size of 50 m. Within each UD, we calculated the volume of use within eight habitat categories (Fig. 1c, d) for each owl\*season, and within available landscape (i.e., east or west). We produced a landscape-scale dataset for each of the 8 habitat categories, each with 22 owl\*seasons of proportional used habitat, and 22 measurements of proportional owl\*season available area (representing either the east or west landscape). We developed seven generalized linear mixed effects models to test hypotheses on foraging habitat selection (Appendix S2, models 1–7) and used model selection to determine the most parsimonious model. Territory was included as a random effect in all models. We retained the model with the lowest AIC<sub>c</sub> as the best approximating, or the best set of models, if top models were within 2 ΔAIC<sub>c</sub> (Burnham and Anderson, 2003). We evaluated the effect of survey year (2015, 2016, 2017) by adding it to the best approximating model as a categorical fixed variable and assessed whether it significantly improved model fit (reduced AIC<sub>c</sub> > 2). We interpreted variables using parameter estimates from the best approximating model, or model-averaged estimates from the best model set. Test statistics were t values for single models and z values for model-averaged sets. Models were fit using proportion as the response variable, with the Gaussian family and the log link.

### 2.5.2. Home range scale

We used methods similar to those described above to compare

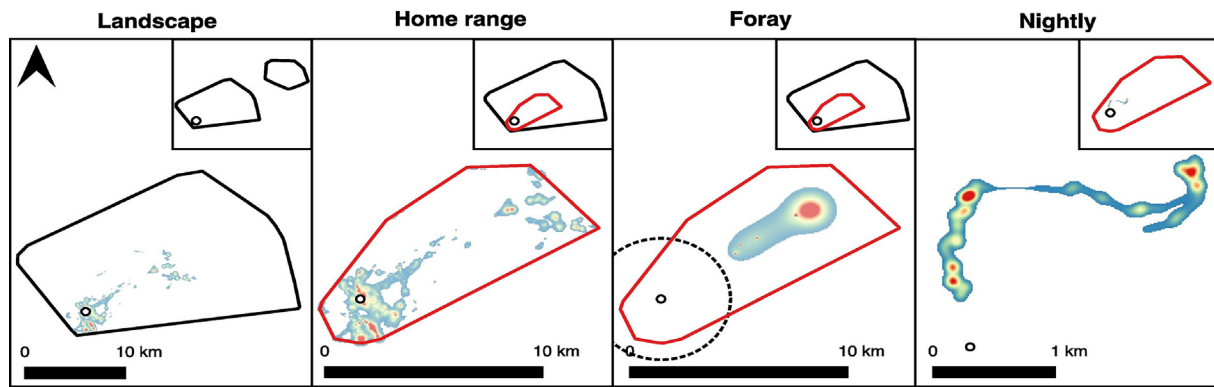


Fig. 2. Example of foraging habitat selection analysis at four spatio-temporal scales (landscape, home range, foray and nightly) for a nonbreeding female California Spotted Owl (1177–40374, Appendix S1) tracked during the 2016 breeding season (April 1–August 31) in the Sierra Nevada, California. At the landscape scale, the volume of use by owls in each habitat category, based on a utilization distribution (UD) for each owl\*season (high use red to low use blue), was compared to the proportion of area for each habitat category (see text) within the western landscape of the study area (black polygon – see inset for both landscapes). Habitat use (volume of UD in each habitat category) was also compared to available habitat within the home range minimum convex polygon (MCP) for the owl\*season; (red polygon). The foray scale compared volume of use by owls in each habitat category based on the UD of owls during forays to the proportion of habitat categories within the home range (red polygon). We defined forays as movements outside a 3.2-km buffer around the nest (dotted circle), the mean distance to nearest neighboring nest of study subjects. Foray and nightly scale insets show location of the home range within the western landscape. The nightly scale compared habitat use within the UD, for each night of high resolution data, to habitat availability within the home range (red polygon, see inset). Nest location is denoted by a black circle on all panels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

proportional habitat use within the UD and available habitats within the MCP home range (Fig. 2). We produced a home range dataset for each of the eight habitat categories in the MCPs (available area) and 22 owl\*seasons of proportional habitat use. We used the same habitat variables described above, and the same alternative models (Appendix S2, models 1–7) and model selection process. Mixed effect models were fit using proportion as the response variable, with the Gaussian family and the log link.

### 2.5.3. Foray scale

We examined habitat selection during forays, which occurred in six non-breeding females in our study. The mean distance to nearest neighboring nest of study subjects was 3.2 km, so we defined forays as movements farther than 3.2 km from the nest and temporally extending for  $\geq 10$  locations and 10 h. We estimated the proportional used area for each habitat with UD for each foray\*night ( $n = 18$  in 6 owl\*seasons), and compared those to the proportional area of each habitat within the MCP home range for the owl\*season using a generalized linear mixed effects model that included individual as a random effect, using the Gaussian family and the log link. We used the same habitat categories described above with a similar model fitting and selection process, but examined only the effect of the habitat category (Appendix S2, models 1–2). Most birds were sampled hourly during forays, however we also included four foray nights with high resolution sampling (every 5 min). As a final step, we tested our models with and without the high resolution data and as we found no difference in the direction or significance of results, we retained the high resolution data.

### 2.5.4. Nightly scale

For 21 of the 22 owl\*seasons, high resolution location data (locations recorded every 1–6 min) were available, enabling analysis of habitat use at the nightly scale. Nightly records ranged from 2.4 to 7.4 h periods over 103 nights (mean 6.4 h, 1.5 SD) and 88% of nights had  $> 6$  h sampling. We obtained a mean of 87 (SD 12.6, range 72–126) locations within each sampling period. We derived a UD for each owl night and estimated the proportional used area by habitat. We used the same available area as for home range analysis, the MCP, and included individual owl as a random effect. We used the same habitat categories described above, the same model fitting and selection process, and similar alternative models (Appendix S2, all models).

### 2.6. Roost habitat selection

We evaluated owl selection of roost habitat by comparing used and available habitat with package *adehabitatHS v0.3.13* (Calenge, 2006). Roost locations were defined by the location temporally closest to 1200 h for each owl from the set of locations recorded between 2 h after sunrise and 2 h before sunset. We summed the number of roost locations within each habitat category for each owl\*season to define use. Available roost habitats were defined as the proportion of each habitat category within the corresponding MCP home range. We then calculated Manly selectivity measures for each habitat category and tested overall habitat selection using a log-likelihood test statistic (Khi2L) (Manly et al., 2007). We treated canopy cover and dominant tree size as separate categorical variables, both of which included open treeless areas as a variable level. Manly selection ratios were interpreted as indicating selection for a habitat if the ratio and its confidence interval was  $> 1$  and selection against a habitat if the ratio and its confidence interval were  $< 1$ . We used a type III test because the use and availability were measured for each owl\*season (Thomas and Taylor, 1990).

### 2.7. Protected activity center analysis

We analyzed overlap between PACs and owl home ranges, and selection for or against PACs, using foraging space use (volume of use) and roost locations. PACs (designated to comprise the best available 121 ha of owl habitat surrounding known and suspected nest stands) were delineated in previous years by Forest Service biologists. For each owl\*season we identified the “nest PAC” as the PAC that contained the nest, or the previous year’s nest for non-breeding birds, and “all PACs”, or sections of PACs, intersected by the MCP home range.

We compared PAC use (UD volume within PAC/s) with the percent area of PACs within each owl’s MCP home range (available) for all owls, regardless of reproductive status (22 owl\*seasons). We used a method similar to the foraging habitat selection analysis to test for selection for or against PACs. To assess the overlap of PACs with roost locations, we used a similar approach, but rather than intersecting PACs with volume of foraging space use, we intersected PACs with roost locations for 15 out of the 22 owl\*seasons for which there were  $> 20$  roost locations. We used Manly selectivity measures to compare proportional use of PAC and non-PAC areas, using number of roost sites within and outside PACs (used) and percent area of PACs within each owl’s MCP home

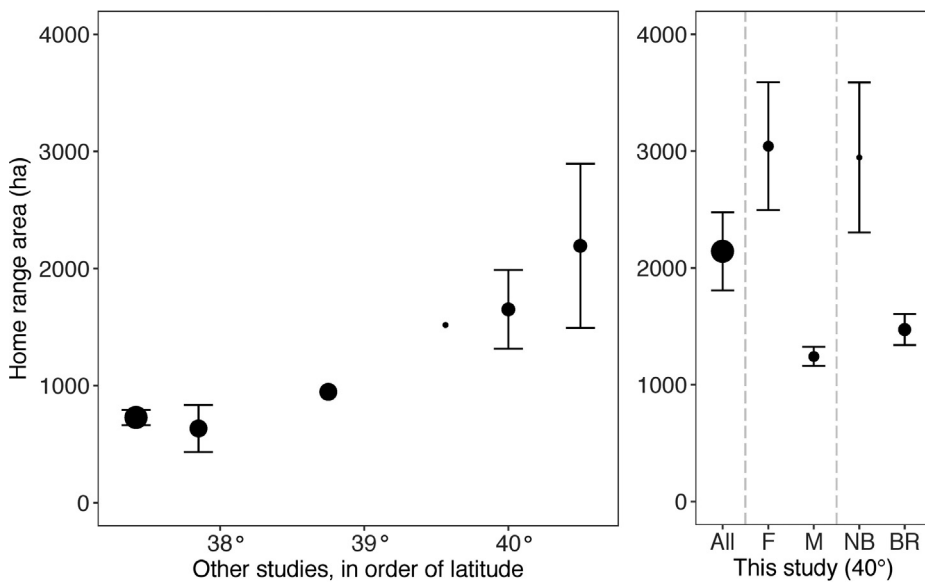


Fig. 3. California Spotted Owl breeding season (1 April–31 August) home range (MCP) estimates and SE (whiskers) reported elsewhere in the Sierra Nevada (left) (from Roberts, 2017, references listed below), and reported herein [this study] for the Plumas National Forest during 2015–2017 (right). Other studies, ordered by latitude, were conducted in Sierra National Forest (Zabel et al., 1992); Yosemite National Park (Eyes, 2014); Eldorado and Tahoe National Forests (Williams et al., 2011); Tahoe National Forest (Call et al., 1992); Plumas National Forest (Gallagher, 2010); and, Lassen National Forest (Zabel et al., 1992). Dot-size represents sample size, which ranged from  $n = 5$  (Tahoe National Forest) to  $n = 22$  (this study). We report estimated homerange sizes by sex and breeding status for birds evaluated herein as arithmetic means and SE of observed data for comparison to other studies, though this differs from least squared means reported in the text. Only studies using the 100% minimum convex polygon method to calculate home range were included to facilitate comparisons.

range (available), using the same test statistic as for roost selection analysis (Khi2L).

### 3. Results

#### 3.1. Homerange size

Mean California Spotted Owl homerange size (2143 ha, 334 SE) was similar to estimates from previous studies within the Plumas National Forest (1653 ha, 336 SE) and the adjacent Lassen National Forest (2195, 701 SE; Fig. 3). Mean kernel density estimates of home range (2319 ha, 442 SE) were 8% higher than minimum convex polygon estimates. Homerange sizes differed significantly by sex ( $TS = 3.74, p < 0.001$ ) and breeding status ( $TS = 1.97, p = 0.049$ ) (Appendix S3). For the sex-only model, least squared mean home range of female owls (2611 ha, 95% CI 1961–3476) was more than double mean male home range (1216 ha, 95% CI 914–1619). Survey year did not influence home range size as the best models outranked the models including year.

#### 3.2. Distance travelled

Breeding owl maximum nightly transit distances (sum of all nightly movements) ranged from 12.3 ( $7.0 \pm 1.9$ ) km for males to 17.9 ( $8.3 \pm 3.0$ ) km for females. Nightly maximum transit distances for non-breeding owls ranged from 7.9 km for males ( $6.2 \pm 1.1$ ) to 32.1 km for females ( $8.6 \pm 4.8$ ). All non-breeding females travelled outside the home range of their mate (Fig. 4) and visited (location points were recorded within) a mean of 4.5 (range 3–6) PACs (Appendix S1), while their home ranges overlapped with 4.7 (3–8) PACs. One non-breeding female (1177–40,374; Fig. 4b, green) left her territory and forayed to locations  $> 10$  km from the previous year's nest on her home territory on four occasions between 17 May and 31 August for periods of 2, 8, 21 and 2 days. During the forays she visited six PACs in total and passed through the adjacent home ranges of another marked owl pair (Fig. 4b).

Distances travelled from the nest (straight-line distance, not transit distance) by non-breeding owls differed between sexes, with sex and breeding status interacting significantly (Appendix S3). Female owls travelled 1.3 times farther from the nest ( $TS = 4.70, p < 0.001$ ) than male owls (respective mean distances of 2.3 km, 95% CI 1.84–2.91; and 1.76 km, CI 1.38–2.25). Breeding status alone was not a reliable predictor of maximum distance travelled from nest ( $TS = 1.25, p = 0.221$ ); however, the interaction between sex and breeding status

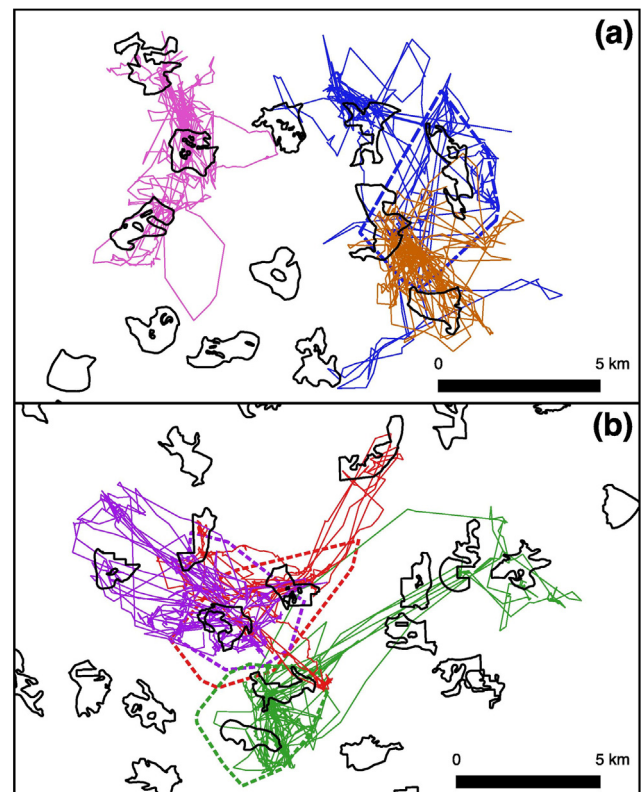
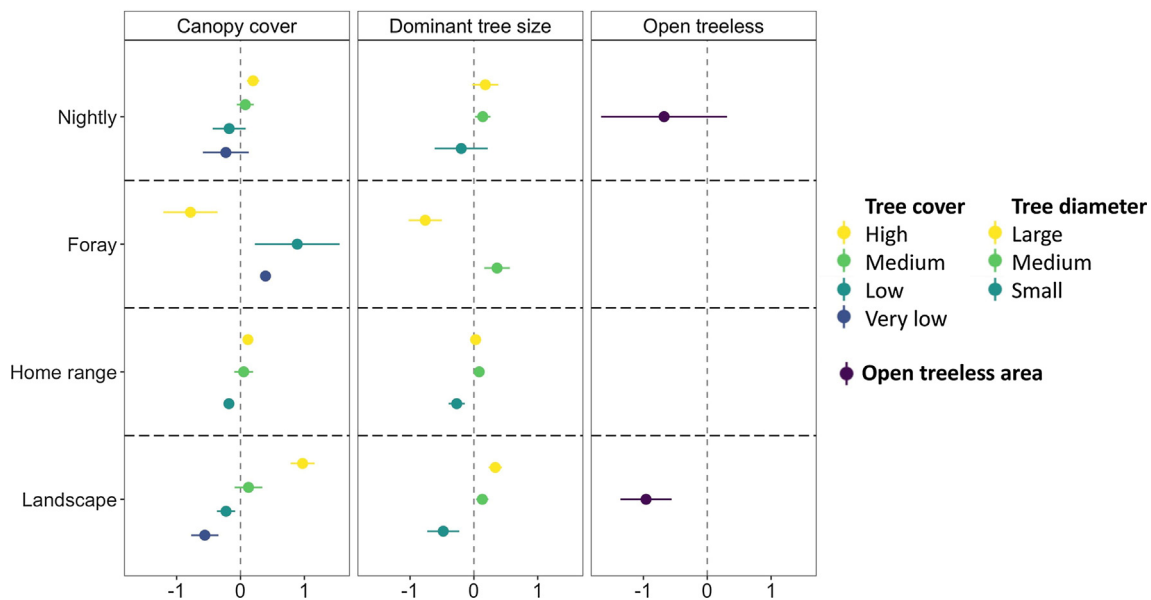


Fig. 4. Movement paths of six non-breeding female California Spotted Owls (traces), home ranges of mates in the same year (if tracked, dashed polygons) and Protected Activity Centers (black polygons). All owls presented in this figure were either non-breeding or had their nest fail in the season tracked and were tracked during breeding seasons (1 April–31 August) of 2016 and 2017. Panel (a) shows three non-breeding females in the eastern landscape (pink traces depict a female whose mate was not tracked, while blue and brown depict two females that paired with the same male, but in a different year). Panel (b) illustrates three non-breeding female\*seasons from two territories in the western landscape (red and purple traces are from two separate female owls that paired with the same male in different years). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 5.** Summary of best models describing habitat selection by California Spotted Owls during breeding seasons of 2015–2017 at four spatio-temporal scales, including landscape, home range, foray and nightly. Coefficients and 95% CI (whiskers) from top ranked models (or model-averaged model sets) that included the used/available categorical variable are shown. Positive coefficients indicate selection for a habitat category and negative coefficients indicate selection against. Three habitat categories are shown: canopy cover [high (> 70%), medium (50–70%), low (30–50%), very low (< 30%)], dominant tree size [large (> 50 cm), medium (25–50 cm), small (< 25 cm)] and open treeless areas (one category).

was significant ( $TS = -7.74$ ,  $p < 0.001$ ) due to greater distances travelled by female non-breeding owls (Appendix S4). Male owls travelled similar distances from the nest irrespective of breeding status (Appendix S4). Survey year did not influence distance travelled from the nest as the best model outranked the model including year.

### 3.3. Foraging habitat selection

After accounting for differences between sexes and breeding status, California Spotted Owls used habitats selectively at landscape, home range, foray and nightly scales. Survey year did not appear to influence foraging habitat selection, as only 3 models were improved by adding year (home range: open treeless area, nightly: very low cover, small dominant tree size), none of which demonstrated significant habitat selection (Fig. 5, Appendix S6). Landscape scale best approximating models indicated that owls selected for high canopy cover ( $TS = 10.1$ ,  $p < 0.001$ ), selected against low ( $TS = 3.1$ ,  $p = 0.002$ ) and very low canopy cover ( $TS = -5.1$ ,  $p < 0.001$ ) and used medium canopy cover in proportion to availability (Fig. 5, Appendices S5 and S6). Owls selected habitat at the landscape scale that was dominated by large ( $TS = 6.2$ ,  $p < 0.001$ ) and medium ( $TS = 2.7$ ,  $p = 0.007$ ) diameter trees, and selected against stands dominated by small trees ( $TS = -3.7$ ,  $p < 0.001$ ) or open treeless areas ( $TS = 4.7$ ,  $p < 0.001$ ). The best approximating landscape models for large trees included breeding status, however no landscape scale models included sex (Appendices S5 and S6). Models at the landscape scale had the greatest explanatory power among the three scales that included all owls (Landscape, home range, nightly; Appendix S5).

At the home range scale, after accounting for differences between sexes and breeding status, we found that owls selected for high canopy cover ( $TS = 3.7$ ,  $p < 0.001$ ), selected against low canopy cover ( $TS = 4.8$ ,  $p < 0.001$ ) and used medium and very low canopy cover in proportion to availability (Fig. 5, Appendix S6). Owls also selected habitat within the home range that was dominated by medium-sized trees ( $TS = 2.3$ ,  $p = 0.022$ ) and against stands dominated by small trees ( $TS = 4.1$ ,  $p < 0.001$ ), whereas stands dominated by large trees and open treeless areas were used in proportion to their availability (Appendices S5 and S6). The best fitting home range models for seven

variables included breeding status and sex (Appendices S5 and S6).

In contrast to habitat selection at other spatio-temporal scales, six non-breeding females in our study selected against high canopy cover ( $TS = -3.6$ ,  $p < 0.001$ ) and large dominant tree size ( $TS = -5.7$ ,  $p = 0.003$ ) during forays, while selecting for areas with low ( $TS = 2.6$ ,  $p = 0.009$ ) and very low ( $TS = 12.3$ ,  $p < 0.001$ ) canopy cover dominated by medium sized trees ( $TS = 3.5$ ,  $p < 0.001$ ) (Appendices S5 and S6).

At the nightly scale, accounting for differences between sexes and breeding status, owls selected for high canopy cover ( $TS = 4.0$ ,  $p < 0.001$ ) and stands dominated by medium-sized ( $TS = 2.2$ ,  $p = 0.025$ ) but not large ( $TS = 1.7$ ,  $p = 0.087$ ) trees. All of the best approximating models or model sets for the nightly scale contained interaction terms with sex and/or breeding status, indicating differential selection between sexes and breeding/non-breeding owls (Appendices S5 and S6).

### 3.4. Roost habitat selection

Owls selected roost sites based on canopy cover ( $TS = 319$ ,  $df = 28$ ,  $p < 0.001$ ) and dominant tree size ( $TS = 264$ ,  $df = 23$ ,  $p < 0.001$ ). Owls selected for high canopy cover (Manly selection ratio = 1.61 [1.39–1.82]) and against areas with canopy cover < 50% (Fig. 6; Manly selection ratio for low = 0.10 [0.02–0.19], Manly selection ratio for very low = 0.06 [–0.02 to 0.13]). Owls also selected against stands dominated by small trees and open treeless areas for roosting (Fig. 6, Manly selection ratio for trees < 25 cm = 0.20 [0.12–0.28] and Manly selection ratio for open treeless areas = 0.09 [–0.08 to 0.27]). Habitat with medium canopy cover (50–70%) or dominated by either medium or large dominant tree sizes (> 25 cm), was used by roosting owls in proportion to availability in the home range (MCP), indicated by Manly selection ratios with intervals overlapping 1.0 (Fig. 6).

### 3.5. Protected activity center analysis

The PACs that contained the nest (or previous year's nest) encompassed a mean of 14.6% (range 3.7–31.6%, 1.5 SE) of owl\*season UD. When all PACs were considered, they accounted for a mean of



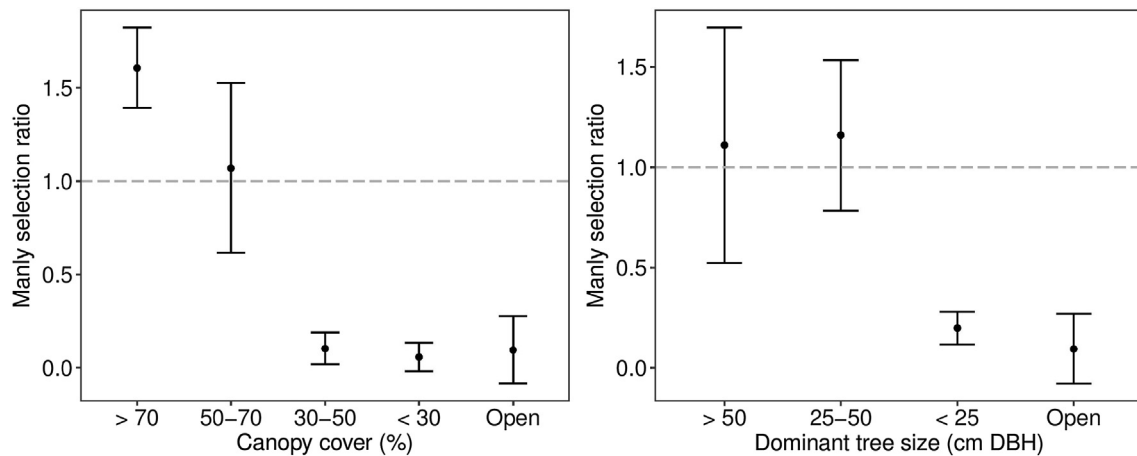


Fig. 6. Manly selection ratios showing positive ( $> 1$ ) and negative ( $< 1$ ) selection of canopy cover and tree size categories by roosting California Spotted Owls across 22 owl\*seasons, during breeding seasons of 2015–2017.

22.1% (range 4.3–39.2, 1.6 SE) of owl\*season UD. Owls used multiple PACs throughout the breeding season with Owl\*season UD overlapping a mean of 2.7 PACs (range = 1–6), regardless of breeding status or sex [mean (range) number of PACs within owl UD: breeding females = 2.2 (2–3), breeding males = 2.1 (2–3), non-breeding females = 4.5 (3–6), non-breeding males = 1.8 (1–2); Appendix S1]. The PACs containing nests (or containing nests during previous year) contained an average of 48% of roost sites used per owl (range 2.3–90.4, 8.0 SE), and the average proportion of roost sites contained within PACs did not increase significantly when all PACs were considered (mean of 49.8%, range 4.7–92.0, 8.0 SE). Owls selected for PACs while foraging, whether considering only the PACs containing their nest ( $TS = 3.8$ ,  $p < 0.001$ ) or all PACs ( $TS = 4.0$ ,  $p < 0.001$ ). Owls also selected for PACs while roosting, considering PACs containing their nest ( $TS = 638$ ,  $df = 15$ ,  $p < 0.001$ ; Manly selection ratio = 6.35 [4.67–8.03]) or all PACs ( $TS = 372$ ,  $df = 15$ ,  $p < 0.001$ ; Manly selection ratio = 3.13 [2.27–3.99]).

#### 4. Discussion

High resolution GPS observations of the movements of California Spotted Owls confirmed the importance of late seral stage habitat (high canopy cover and large trees) for roosting and foraging at multiple scales and revealed previously undocumented foraging behaviors by non-breeding females during the breeding season. Our findings also highlight potential limitations of existing PACs in protecting owl habitat, as individual PACs overlapped with only 48% of roosts and 14.6% of foraging space use for owls that nested within them and individual owls visited up to 6 different PACs during one season.

The tendency of owls to select roost sites with greater canopy cover and larger diameter trees than foraging sites corroborates previous findings (Gutiérrez et al., 1992; Irwin et al., 2007; Kramer et al., 2016; North et al., 2017; Tempel et al., 2016). We found strongest evidence of foraging habitat selection at the landscape scale, where owls selected for substantial canopy cover ( $> 70\%$ ) and stands with medium to large trees ( $> 25$  cm DBH), while selecting against low to very low canopy cover ( $< 50\%$ ), stands dominated by small ( $< 25$  cm) trees, or open treeless areas (Fig. 5). Habitat selection at home range and nightly scales exhibited similar but weaker patterns, due to a stronger influence of sex and breeding status on habitat availability and selection, as well as variability among individual owls (Fig. 5, Appendices S5 and S6). Selection at finer scales (home range and nightly) may be limited by selection occurring at larger scales (Johnson, 1980), and others have reported strongest habitat selection at broader scales (Boyce et al., 2003; Stolen et al., 2007). We hypothesize that owls select high quality habitats at the landscape scale, potentially masking the importance of

finer-scale habitat selection. However, weaker habitat selection relationships at finer scales also may be due to preferences for habitat features outside the focus of this study, such as forest edges (Eyes et al., 2017; Williams et al., 2011), burned areas (Bond et al., 2016, 2009), or riparian corridors (Bond et al., 2016; Irwin et al., 2007) or other factors including conspecific and interspecific interactions. In contrast to other spatio-temporal scales, our results indicated that California Spotted Owls selected for less dense vegetation ( $< 50\%$  canopy cover) during forays. Foraging birds could have been attempting to minimize transit to known distant locations, or attempting to avoid encounters with other territorial birds during forays. Mobile species, such as Spotted Owls, rely on multiple patches of suitable habitat within their home range and often traverse environments that are unsuitable for some activities (Holloway and Miller, 2017). California Spotted Owl movement patterns indicated birds are likely able to acquire environmental information (e.g., food and nest site availability, mortality risk) on alternative habitat choices across the landscape, when the costs of gathering such information does not outweigh the benefits.

Our estimates of California Spotted Owl breeding homerange sizes were comparable with those observed for this subspecies in nearby Lassen National Forest (Zabel et al., 1992; Fig. 3). Our estimates were larger than breeding home range estimates of Mexican Spotted Owls (regional means of 228–562 ha; U.S. Fish and Wildlife Service, 2012) and of Northern Spotted Owls (regional means of 388–1150 ha; Carey et al., 1992; Forsman et al., 2015), with which they hybridize in the Northern part of their range (Miller et al., 2017). We found differences attributable to sex and breeding status (Fig. 3, Appendix S3), which have not previously been reported for California Spotted Owls (Roberts, 2017). Non-breeding females had the largest home ranges, the greatest of which was a 6496 ha breeding-season MCP, 5 times the mean reported in the literature (Roberts, 2017). Larger female home range is partially attributable to foraging behavior, wherein females left home territories and visited multiple (up to 6) surrounding PACs. One female transited  $> 30$  km in a night, and undertook multiple forays of  $> 10$  km while repeatedly visiting areas where she nested in previous years (Fig. 4b, green traces). Males may incur relatively greater costs (e.g. reduced territory defense) compared to females when using areas at great distances from the nest site, which could explain why we did not observe male forays. Foraging females are not likely seeking current year or future extra-pair copulations, as California Spotted Owls exhibit synchronous biennial cycles in reproductive output (Blakesley et al., 2010) and extra pair fertilizations are not commonly reported among owl species (Arsenault et al., 2002; Koopman et al., 2007; Lawless et al., 1997; Marks et al., 1999; Saladin et al., 2007). Rather, foraging may represent prospecting for future opportunities, an exploratory behavior pattern not previously documented in this species.



Prospecting, or gathering advanced information about potential breeding habitat within an area before settling there, has been described in > 100 bird species (Reed et al., 1999 and references therein). Accurate assessment of quantity, quality and configuration of available habitat is important to individual fitness, population dynamics and distribution (Howard, 1920; Lack, 1971; Reed et al., 1999; Wiens, 1976). Individuals must be able to acquire reliable environmental information (e.g., food and nest site availability, mortality risk) on alternative habitat choices across a landscape without costs of information gathering outweighing the benefits (Cox and Kesler, 2012b; Kesler et al., 2010; Johnson, 1989; Reed and Oring, 1992). Our documented foraging behavior may be a precursor to dispersal, given 7% of breeding California Spotted Owls in a nearby study dispersed into new territories between breeding seasons and 42% of breeding dispersals were into adjacent territories (Blakesley et al., 2006). A recent study noted observations of California Spotted Owls in multiple PACs during a breeding season, but did not examine the behavior in detail nor report sex or breeding status of birds (Berigan et al., in press). To our knowledge, foray behavior has not been recorded for the Mexican Spotted Owls and has been noted but not studied for the Northern Spotted Owl (Forsman et al., 2002). Investigations using VHF telemetry typically have not reported the frequency or duration of periods when birds went undetected, but inability to locate birds during VHF studies could indicate foraging behavior. Recent declines in Northern Spotted Owl natal dispersal distances of 1 km per year, alongside habitat fragmentation and increases in Barred Owl populations, indicate a more detailed understanding of multi-scale movements of all Spotted Owl subspecies afforded by GPS-tracking is likely an important component for their conservation (Hollenbeck et al., 2018).

Protection of owl core use areas (nesting and roosting sites) through exclusion of stand-altering activities within designated PACs is currently the management focus for California Spotted Owls. In addition to establishing PACs, the U.S.D.A. Forest Service designates up to 971 ha of the best available California Spotted Owl habitat in the closest proximity to a PAC as a “Home Range Core Area” (HRCA) (U.S.D.A. Forest Service, 2004), where owl habitat needs are to be considered in management decisions, but stand-altering vegetation management practices are allowable and routinely undertaken. Berigan et al. (2012) reported high overlap between PACs and core use areas based on long-term roosting and nesting data. Although our results indicated positive selection for PACs by foraging and roosting California Spotted Owls on the Plumas National Forest, we found relatively low overlap between PACs and both roost locations (< 50%) and foraging space use (< 25%). Indeed, for some owls < 5% of their foraging or roost locations were contained within the PAC in which they nested (or nested in the previous year). Furthermore, our estimates of owl home range size and distance travelled were restricted to the breeding season. Owls are likely to range over much wider distances annually, with PACs and even HRCAs consequently protecting only a small fraction of habitat used for complete annual life-history needs.

PACs were developed specifically to protect nesting and roosting sites, rather than the much broader foraging areas used by Spotted Owls. Nevertheless, California Spotted Owl populations continue to decline, particularly within study areas on National Forest lands (Blakesley et al., 2010; Conner et al., 2016; Tempel et al., 2016) for reasons that are not well understood but may include past and ongoing forest management activities (Jones et al., 2018; Tempel et al., 2017). Based on the relatively low overlap between PAC areas and roosting and foraging habitat use by the owls we studied, we hypothesize that insufficient habitat protection from stand-altering activities outside PAC areas could partially explain ongoing population declines. Most of the habitat used by owls for roosting and foraging in our study was outside of PACs and therefore available for stand-altering forestry activities. Even where PACs protect nesting stand conditions conducive to successful reproduction, stand-altering activities elsewhere in owl home ranges may reduce occupancy or reproductive success. For example, a

simulation study by Tempel et al. (2015) found that stand-wide fuel-reduction treatments that reduced canopy cover had a negative effect on owl nesting habitat and demographic rates 30 years into the future in the absence of fire. The same study predicted positive effects of fuel reduction treatments on owl nesting habitat and demographic rates if fire occurred in the study area (Tempel et al., 2015). While limited research to date has not indicated negative effects of timber harvest on California Spotted Owl foraging (Irwin et al., 2015), harvesting can reduce populations of key California Spotted Owl prey (Lehmkuhl et al., 2006; Williams et al., 1992). Relationships between prey dynamics and owl fitness are still poorly understood (Roberts, 2017).

Cumulatively, past results combined with our findings suggest that habitat conditions throughout individual California Spotted Owl home ranges – but beyond the boundaries of PACs – may be critical for fulfilling life history needs, and if inadequate, could be contributing to ongoing declines. Additionally, even habitat outside usual home ranges may be more important than has been previously considered. Non-breeding female owls traveled great distances (forays), sometimes roosting and spending over a week > 10 km from their territory centers before returning. Although it would seem obvious that connectivity of later seral forest across the landscape is important for this species, our finding that foraging owls selected habitat attributes (< 50% cover) in contrast to those selected during non-foray movements requires further study. Understanding the role of long distance foray movements in facilitating breeding dispersal, as well as genetic and demographic connectivity, and more generally, the importance of habitat well outside what has historically been considered the activity center of California Spotted Owls, is likely important for addressing ongoing population declines.

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## Data accessibility

Data will be available by request from Plumas National Forest at the conclusion of this ongoing study.

## Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.10.017>.

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