



Elevational gradients strongly mediate habitat selection patterns in a nocturnal predator

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Abstract. Mountain ecosystems contain strong elevational gradients in climate and vegetation that shape species distributions and the structure of animal communities. Nevertheless, studies of habitat selection for individual species rarely account for such gradients that often result in species being managed uniformly across their range, which may not improve conservation as intended. Therefore, we characterized variation in nocturnal habitat selection by 18 GPS-tagged California spotted owls (*Strix occidentalis occidentalis*) along a 1400-m elevational gradient in the Sierra Nevada, California. We characterized three-dimensional forest structure with light detection and ranging data that we used in mixed-effects resource- and step-selection analyses of owl habitat selection. At lower elevations, owls selected stands with shorter trees, sites closer to hard edges between tall forests and open areas, sites with less diversity in forest seral types and sites with more ridge and southwest aspects. In contrast, owls at higher elevations selected the opposite. Within public forests that had taller trees and within their home range core (45% kernel density estimate of GPS points) areas, owls selected forests with less and more canopy cover at low and high elevations, respectively. Outside of their core areas, owls selected areas with fewer and more tall trees at low and high elevations, respectively. These findings may be explained by elevational gradients in prey distribution and variation in owl diet because owls consume more woodrats (*Neotoma* spp; earlier seral species) at lower elevations and more flying squirrels (*Glaucomys sabrinus*; older forest species) at higher elevations. Thus, at low elevations and in areas unlikely to support nesting, spotted owls could benefit from management that promotes woodrat habitat by encouraging oak regeneration and creating small brushy openings within forests with shorter (younger) trees. Conversely, at higher elevations, (1) enhancing flying squirrel habitat by promoting large trees and denser canopy on mesic sites and (2) managing for greater cover type diversity on southwest-facing slopes and ridgetops is more likely to improve foraging habitat quality for spotted owls. The patterns of owl selection over elevational gradients has not been explicitly considered in most habitat management plans but clearly would improve management throughout mountain ecosystems.

Key words: California; elevational gradient; forest management; habitat selection; light detection and ranging; predator; spotted owl; *Strix occidentalis*.

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INTRODUCTION

Elevation has a major influence on local and regional climatic and vegetation variation (Woodward 1987, Körner 2003), which, in turn, shapes the diversity and distribution of predator, competitor, and prey communities (Rahbek 1997, Callaway 1998). Although some species inhabiting mountain ecosystems may be restricted to narrow elevational ranges (Santhakumar et al. 2018, Khatiwada et al. 2019), other species, particularly larger and more mobile ones, occur over wider elevational gradients that span a range of environmental conditions, climate regimes, and ecological communities (Loiselle and Blake 1991, Rice 2008). For wide-ranging species, the life history strategies, behaviors, and choices made by individuals that confer fitness benefits at lower elevations may not confer fitness benefits at higher elevations and vice versa (Loiselle and Blake 1991). For example, the presence of a competitor, predator, or prey species at low elevations and its absence at high elevations could promote elevational niche partitioning and habitat selection patterns that vary as a function of elevation. Moreover, elevational gradients in local climate may interact with habitat or topographical features to create refugia for species from regional climate warming, providing opportunities for elevational-based conservation under climate change (Sears et al. 2011, Jones et al. 2016). Exploring how ecological relationships vary across elevations has important implications for understanding species' ecology and improving conservation outcomes in mountain ecosystems.

The conservation of wildlife species in mountain ecosystems has an important influence on forest management (US Forest Service 2004, Spies et al. 2018, Phalan et al. 2019). Habitat selection studies of focal species of conservation concern often provide information that forms the basis for decisions about how forest structure and composition will be managed, with substantial implications for other species and forest health (Bias and Gutiérrez 1992, Greenwald et al. 2005, Purcell

et al. 2009, Ackers et al. 2015). For example, evidence for the selection of a particular habitat element (i.e., greater use of large trees than expected based on their availability) by a species of conservation concern is often used to guide forest management activities that promote those conditions across the species' geographical range (Gutiérrez et al. 2017). However, when habitat selection by species is variable across elevations or latitudes, it complicates management strategies. Therefore, creating flexible forest management strategies to accommodate species' habitat selection patterns that vary along these gradients is likely to be a more effective conservation approach, which requires a better understanding of species' habitat selection over elevation and latitudinal gradients.

The spotted owl (*Strix occidentalis*) is distributed across broad elevational gradients in many montane forest ecosystems of western North America (Bias and Gutiérrez 1992, Gutiérrez et al. 2017). This species also has long resided at the epicenter of regional-scale forest management planning owing to its use of older forests (Simberloff 1987). Despite many studies of spotted owl habitat selection in forest ecosystems, individual habitat selection across elevational gradients has not been studied—information that is critical to managing this wide-ranging species. Thus, we hypothesize that elevation in the Sierra Nevada will have a strong influence on the selection of features such as forest height, tree species assemblages, canopy cover, and understory conditions by California spotted owls (*Strix occidentalis occidentalis*, hereafter referred to as spotted owls) because of its influence on climate, moisture, edaphic conditions, and fire regimes, which in turn influences the distribution and habitat associations of key spotted owl prey species such as woodrats (*Neotoma* spp.) and flying squirrels (*Glaucomys oregonensis*; Arbogast et al. 2017). Recent stable isotope-based work revealed that variation in the relative composition of these prey species in the spotted owl diet may partly explain differences in regional population dynamics (Hobart et al.

2019a). Woodrats, which prefer shrubby areas with masting oaks, may be particularly vulnerable to predation by owls near edges between relatively open area and closed-canopy forest (Sakai and Noon 1997, Innes et al. 2007), and were found to be a greater component of the spotted owl diet on private land and at lower elevations (Munton et al. 2002, Hobart et al. 2019a). Flying squirrels, which prefer areas of dense canopy and older, taller trees with abundant hypogeous fungi (Waters and Zabel 1995, Meyer et al. 2007, Holloway et al. 2012), were a greater component of owl diets at higher elevations, and also on US Forest Service land (Hobart et al. 2019a). Note that while Hobart et al. (2019a) was not able to discriminate woodrats from pocket gophers (*Thomomys* spp.) isotopically, woodrats constitute a considerably greater portion of spotted owl diets by biomass, and gradients in isotopically derived diets were thus assumed to be predominantly the result of a shift from woodrats at low elevation to flying squirrels at high elevations (Hobart et al. 2019a). Nevertheless, it is uncertain whether elevational gradients in spotted owl prey consumption lead to different forest habitat selection patterns.

In our study, we characterized habitat selection by GPS-tagged spotted owls along an elevational gradient in the Sierra Nevada, California, using high-resolution measurements of forest structure derived from aerial-based light detection and ranging (LiDAR) technology. We assessed how spotted owl nocturnal selection for different forest stand types, configurations, and forest structures varied as a function of elevation. Given our hypothesis that habitat selection varied by elevation, we predicted that owl foraging would reflect habitat features of their primary prey at lower (woodrats) and higher (flying squirrels) elevations. We further predicted that these patterns of stand selection would be consistent across ownerships, as well as when limited to public forests with taller trees (henceforth taller public forests).

METHODS

Study area

Our study area covered 270 km² that encompassed the home ranges of 18 spotted owls located primarily on the Tahoe National Forest in

the central Sierra Nevada of California, USA, but also had private land interspersed within and bordering the National Forest (Fig. 1). Lands within the study area were managed by the US Forest Service (61%) and private owners (39%), and thus, forests were a mix of plantations and recent clear cuts as well as unlogged and selectively logged forest that was more mature with a closed canopy. The climate was Mediterranean with warm, dry summers and cool, wet winters. Elevations ranged from 400 to 1800 m. The dominant tree species of these Sierran mixed conifer forests included ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), California black oak (*Quercus kelloggii*), and white fir (*Abies concolor*) (Mayer and Laudenslayer 1988). These were intermixed with Jeffrey pine (*Pinus jeffreyi*) and red fir (*Abies magnifica*) at high elevations and live oak (*Quercus chrysolepis* and *Quercus wislizeni*), tanoak (*Notholithocarpus densiflorus*), and Pacific madrone (*Arbutus menziesii*) at lower elevations (Mayer and Laudenslayer 1988).

GPS-tagged owl data

We captured and GPS-tagged 18 adult (four females and 14 males) spotted owls between March and May, 2017 and 2018, which we then monitored during the breeding season (May–August) of the year they were captured. Two of the four paired females were nesting. One male was single, while the remaining 13 paired males were split between six nesting and seven non-nesting. We captured owls opportunistically, but all were well within the geographic area of LiDAR coverage taken 5 yr before the owls were tagged and included a range of elevations, forest conditions, and land ownerships that we believed was representative of the broader landscape (Fig. 1). We captured owls by hand or with snare poles using modifications of the methods used by Franklin et al. (1996) before or early in the breeding season and fitted birds with backpack- or tail-mounted dual GPS/VHF tags that allowed remote downloading of data (Pinpoint VHF 120; Lotek, Newmarket, Ontario, Canada; hereafter “GPS tags”). Tags and harnesses weighed 7–10 g (under 2% of average spotted owl body weight). We recaptured most owls to remove the GPS tags, but owls that we did not recapture all had tail-mounted transmitters,

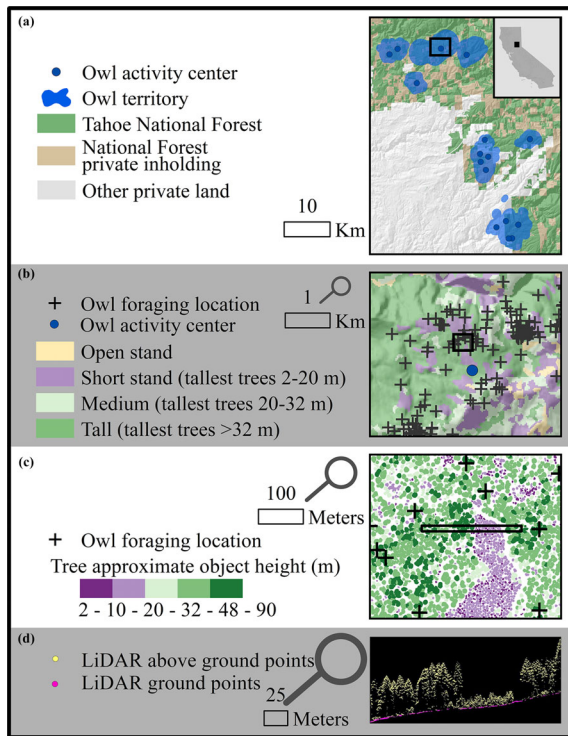


Fig. 1. The study area, showing (a) the location in the state of California, owl 400-m buffered 95% kernel density estimate polygons, the Tahoe National Forest, and private inholdings on the National Forest, (b) landscape classifications into open, short, medium, and tall stands generated by the LiDAR (light detection and ranging), as well as used owl GPS points, (c) tree-approximate objects generated by the LiDAR, and (d) a cross-sectional view of the LiDAR point cloud itself as it crosses from tall to short to tall stands. Note that the scale bars listed to the left of each map show the scale for that map, whereas the black box on each map shows the boundaries of the subsequent map, for instance, the wide rectangle shown in map (c) corresponds to the boundaries of the data presented in map (d).

which we expected to be shed during the subsequent molt. All habitat selection analyses were conducted using GPS locations derived from the transmitters, whereas VHF was used to relocate tagged owls for recapture and GPS data retrieval. GPS tags were programmed to collect five hourly GPS locations per night (22:00–02:00 or 23:00–03:00) and one diurnal location. We removed all diurnal GPS point locations from

analyses, and because owls are nocturnal predators, we assumed that nighttime GPS locations primarily represented locations of foraging activities, but we acknowledge that they could represent other activities such as territory defense and social interactions (Forsman et al. 1984, Delaney et al. 1999). For the two nesting females, we removed all GPS points within 50 m of the nest from our analyses to reduce the potential biases associated with nesting rather than foraging activities. This eliminated 20% and 23% of GPS points, respectively, for each nesting female, but left sufficient foraging locations (over 250 GPS points, mostly from later in the summer) to conduct our analyses.

Habitat selection analyses

To test our prediction that spotted owls would select putative nocturnal foraging sites characteristic of woodrat habitat at lower elevations and flying squirrel habitat at higher elevations, we conducted two parallel analyses that examined these relationships under different spatial filters and management strategies, taking advantage of different GPS accuracy thresholds to filter owl locations. The first analysis (hereafter “mixed ownership stand selection”) was an examination of habitat selection across multiple land ownerships (US Forest Service and private) at the stand scale that focused on the spatial distribution of relatively coarse vegetation height classes that approximated forest seral stage (described below and in Table 1) in relation to where owls moved from one hour to the next. In the mixed-ownership stand selection analysis, we used a greater proportion of owl movement data with a more inclusive GPS accuracy threshold (see section *Mixed-ownership stand selection* below) with the goal of assessing movement patterns and habitat selection across the broader landscape that included both public and private lands. The second analysis (hereafter “selection of structure within taller public forests”) was an examination of the nocturnal habitat selection of forest structure by owls on US Forest Service land only and relied on high spatial accuracy of both the owl GPS points and the LiDAR-derived environmental variables. We focused these analyses on National Forest lands and stands with medium and tall trees in light of current efforts to integrate spotted owl habitat management with

forest restoration activities intended to reduce large severe fires and drought-related tree mortality on this landownership (North 2012, USDA Forest Service 2019). The invasive barred owl (*Strix varia*) has been documented in our study area and may have affected habitat selection of spotted owls, but only one barred owl was detected in our study area in 2019. Therefore, we suggest that there was minimal influence by barred owls on spotted owl habitat selection.

LiDAR data

Discrete-return LiDAR was flown by the National Center for Airborne Laser Mapping (NCALM) for the study area during 2013 (October 24–November 24) and 2014 (June 10–30), with an average pulse density of 8.56 pulses/m². Although the 2013 LiDAR flight occurred late in the season, we confirmed that deciduous hardwood canopies (such as California black oak) had likely not yet dropped their leaves and were recognized as tree canopies in the LiDAR point cloud. However, because hardwood and conifer canopies were mixed together in the LiDAR point cloud, we were not able to differentiate hardwood from conifer foliage. We used different LiDAR-derived metrics to characterize stand size and forest structure for the mixed-ownership stand selection analysis and the analysis examining the selection of structure within taller public forests, respectively. For the mixed-ownership stand selection analysis, we processed the raw point clouds using FUSION software (McGaughey 2012) to produce 30-m rasters of average canopy height and the 95th percentile LiDAR height (representing the height of the dominant trees in each pixel). These rasters were used to classify the landscape into four height-based forest stand types: (1) open, canopy height under 2 m, (2) short, tallest trees ≥ 2 and < 20 m, (3) medium, tallest trees ≥ 20 and < 32 m, and (4) tall, tallest trees ≥ 32 m tall (Table 1; Fig. 2).

We estimated forest structure using a combination of LiDAR-derived metrics from the area within 30 m of each point and a suite of metrics utilizing tree-approximate objects (TAOs). The watershed transform algorithm, like almost all LiDAR tree identification algorithms, identifies overstory trees directly visible to the LiDAR instrument. Subordinate trees, which often are the most numerous on a site, are not detected.

We adopted the TAO paradigm where each TAO represents an identified tree that may have none to several subordinate trees beneath its outer crown surface (North et al. 2017, Jeronimo et al. 2018, 2019). Treating tree detection results as TAOs is a way to make use of tree-scale measurements while explicitly recognizing that subordinate trees are not identified. We estimated (1) vertical complexity, the coefficient of variation in all LiDAR points over 2 m, (2) average, (3) maximum tree height, estimated using TAOs, (4) tall tree density, the density of TAOs over 32 m, (5) shrub/understory density, the relative density of LiDAR points 0.5–2.0 m (Wing et al. 2012, Kramer et al. 2016), and (6) percent canopy cover: the percent area of TAO coverage (North et al. 2017, Jeronimo et al. 2018, Kane et al. 2019, Table 1). TAOs were used to calculate canopy cover defined as the total horizontal area covered by tree canopy (Table 1).

We assumed that vegetative growth between the 2013–2014 LiDAR acquisition and the 2017–2018 collection of owl GPS data would not affect our results, but we accounted for disturbance that significantly altered vegetative structure. To identify areas that had changed as a result of timber harvest, fire, or drought mortality between 2013 and 2014 and 2017 and 2018, we used a combination of (1) 5-m RapidEye imagery from 2017 and 2018 (to match the year that the owl had been tagged; downloaded from PlanetLabs (<https://www.planet.com/>)) and (2) the eDaRT forest change product (USFS Pacific Southwest Region Remote Sensing Lab and UC Davis CSTARs; Slaton et al. 2016, Koltunov et al. 2018, 2020), which highlighted areas that had changed between the baseline year of 2007 and 2018. Using these two products, we hand-digitized all areas that had visibly changed, which comprised 2% of the 1 km buffered 95% kernel density estimates (KDE) for each owl.

KDEs were generated using the reference bandwidth and the adehabitatHR package in R (Calenge 2011, Silverman 1986). We excluded areas that had been altered, but where trees were still present (due to partial harvesting or drought mortality), from further analyses, since these changes could not be accurately updated in the LiDAR. In areas where all trees were removed, we reclassified the cover to open for the mixed-ownership stand selection analysis (open areas

Table 1. Habitat variables and a description of how each variable was calculated in the analyses of (a) mixed-ownership stand selection and (b) selection of structure within taller public forests.

Habitat variable	Description
(a) Mixed-ownership stand selection	
% Short stand area	Proportional area within 100 m of owl location where 95% LiDAR height <20 m and mean canopy height >2 m
% Medium stand area	Proportional area within 100 m of owl location where 95% LiDAR height between 20 and 32 m and mean canopy height >2 m
% Tall stand area	Proportional area within 100 m of owl location where 95% LiDAR height \geq 32 m and mean canopy height >2 m
Distance to soft edge (m)	Euclidian distance from point to nearest soft edge between smoothed† cover classes (open, short, medium, and tall)
Distance to hard edge (m)	Euclidian distance from point to nearest hard edge between smoothed† open and tall stand types
Seral stage diversity	Shannon-Weiner diversity index of all four cover types within 100 m of the point on unsmoothed, classed data
Distance to stream (m)	Euclidian distance to perennial stream from the USGS National Hydrography Dataset (https://www.usgs.gov/core-science-systems/ngp/national-hydrography)
% Ridge	The proportion of ridge topographic position class within 100 m (North et al. 2012)
% SW aspect	The proportion of southwest topographic position class within 100 m (North et al. 2012)
Elevation (m)	Elevation above sea level in meters
(b) Selection of structure within taller public forests	
Elevation (m)	Elevation above sea level in meters
Vertical complexity	Coefficient of variation for all LiDAR points over 2 m and within 30 m of the owl point
Max tree height (m)	Maximum height of LiDAR-derived TAOs within 30 m
Tall tree density (per ha)	The density of tall (over 32 m) LiDAR-derived tree-approximate object centroids within 30 m
Shrub/understory density	Relative LiDAR point density for Stratum (0.5, 2), where R_x = the number of returns at or below height x and $\text{Stratum}_{a,b} = \frac{R_b - R_a}{R_b}$
% Canopy cover	Proportional area of LiDAR-derived TAOs within 30 m
Distance to activity center (m)	Euclidian distance to owl activity center (m)
Squared distance to activity center (m ²)	The squared distance to owl activity center (m ²)—included to account for an exponential relationship between distance and behavior

Notes: LiDAR, light detection and ranging; TAOs, tree-approximate objects.

† We smoothed polygons by simplifying edges when converting from raster to polygon and eliminating slivers with area <1 ha to address uncertainty with owl location and to better identify continuous areas of cover.

were not considered in the analysis that focused on the selection of structure within taller public forests).

Mixed ownership stand selection

The mixed-ownership stand selection analysis was intended to elucidate patterns of foraging habitat selection at a coarse scale of forest stands, testing whether elevation influenced selection for different spatial configurations of cover types across the range of forest conditions present within spotted owl home ranges. We considered all area present within owl home ranges, classifying 30-m pixels by maximum canopy height, as described above (i.e., open, short, medium, and

tall; Table 1), grouping same-height pixels into putative stands, and merging single-pixel stands with the most common neighboring stand type to create relatively homogeneous stands (in terms of the height of the tallest trees) that ranged in size between 0.18 and 18.06 ha (Fig. 2). We excluded areas that had undergone significant forest changes between the LiDAR acquisition and the owl monitoring (described above).

We characterized patterns of selection for habitat characteristics of stands based on all locations (~5 per night collected at hourly intervals) obtained by the GPS tags. Because this analysis focused on attributes of stands and was thus a coarse characterization of the landscape, we



Fig. 2. Representative photographs of areas with nearby owl use categorized into different forest and edge types: (a) hard edge between open and tall stands, (b) open, (c, d) short forest, (e) medium forest, and (f) tall forest. Due to our method of classifying the forest by the tallest tree per 30-m pixel, short forest included areas that were fairly dense (c), as well as much more open, with widely spaced trees (d). Note that (a) was taken on the edge between private and public land, (b) and (c) were taken on private land, and (d–f) were taken on public land.

expected it would be relatively insensitive (compared with our second analysis of forest structure) to positional error of GPS locations. As such, we used relatively relaxed criteria for including GPS locations (dilution of precision (DOP) between 0 and 5 and at least four satellites), which resulted in the retention of a mean of 4.02 near-hourly locations per night, and an estimated median accuracy of 20 m overall and 29 m in forested areas (Appendix S1). Removing GPS points that did not meet the threshold may have resulted in GPS bias, but we assumed this would be minimal because of the low reduction in locations per night (from 5 to 4.02) and the assumption that this bias would remain fairly constant across the elevational gradient (but see Frair et al. 2004). We removed two owls that had

less than 100 locations because of insufficient data, which left 16 owls for this analysis.

Step-selection analysis.—A step selection function (SSF; Fortin et al. 2005) takes advantage of non-independent GPS points collected as an animal moves from one location to the next over time, allowing us to make use of the multiple nightly GPS locations we had collected for each owl. We used SSF (Fortin et al. 2005, Duchesne et al. 2010, Muff et al. 2020) to test for patterns in habitat selection with a use-vs.-available study design where available habitat associated with a given owl location was conditional on where the individual occurred at the time of the previous GPS location in the same night. Hereafter, we refer to “used” points as the owl GPS locations retained for the analysis and “available” points as potential locations that the owl could have chosen according to an empirical distribution of step length and turn angles. The mean covariate values for used and available points are provided in Appendix S2: Table S1. Used and available points were compared in the modeling framework to determine foraging habitat selection patterns. We generated 10 available points for each observed hourly step made by owls by first generating thousands of randomly placed points within the 400 m buffered 95% KDE of each owl. We used a 400-m buffer to allow the random steps the opportunity to go in any direction. From these random points, we chose those where the step length to a given used point matched the frequency distribution of step lengths for that owl (to account for differences in individual behavior), based on the length of time since the last GPS reading. For example, if 10% of 1-h step lengths for a given owl were between 400 and 500 m, then 10% of available points for that owl were 400–500 m from the owl’s GPS point an hour earlier. Because there was variability in the times between steps by owls (owl GPS points that did not meet the DOP and satellite thresholds were excluded, so some steps were 2 or 3 h apart), we used distributions of hourly, bi-hourly, and tri-hourly step lengths. Turn angles were random and represented a uniform distribution (corresponding to non-directional random walks [Prokopenko et al. 2017]).

In order to include differences in habitat selection preferences among individuals in the SSF framework, we estimated the relative probability

of use using mixed conditional Poisson regression models with stratum-specific intercepts, which are likelihood-equivalent to mixed conditional logistic regression models (Duchesne et al. 2010, Muff et al. 2020) and yielded equivalent parameter estimates and standard errors (Muff et al. 2020). The model was formulated as:

$$E(y_{ijk}) = \mu_{ijk} = \exp(\alpha_{ik} + \beta^T x_{ijk} + u_i^T z_{ijk})$$

with $y_{ijk} \sim \text{Po}(\mu_{ijk})$,

where $i = 1, \dots, I$ individuals, $j = 1, \dots, J$ indexed used or available locations at a given time, and $k = 1, \dots, K$ strata, α_{ik} was the stratum-specific intercept with $\alpha_{ik} \sim N(0, \sigma_\alpha^2)$ and σ_α^2 fixed to a very large value (i.e., 10^4), β^T was the transposed of the vector of coefficients being estimated, x_{ijk} was the covariate vector, u_i^T was the vector of individual-specific random slopes, and z_{ijk} was the design vector. The Poisson formulation allows the SSF to be fitted in a single step using standard statistical software where variance for the stratum-specific random intercept effect can be fixed to a large value (Muff et al. 2020). Conditional Poisson (logistic) regression approaches allow for the testing of habitat selection when observed and available locations represent matched pairs (strata) because of the underlying temporally correlated data generating process, as was the case with our data.

We treated owl location (coded as 1) vs. available location (0) as the response using the package `glmmTMB` version 0.2.0 (Magnusson et al. 2017). We tested covariate correlation and found none with a correlation coefficient >0.7 (Appendix S2: Fig. S1). However, preliminary analysis suggested high multicollinearity (variance inflation factor) for the three tree height classes (short, medium, and tall stand area), which was remedied by excluding one of the three tree height classes from the model. We included the following continuous variables as fixed effects: (1) proportion of medium and tall stand area; (2) distance to soft edge; (3) distance to hard edge; (4) seral stage diversity; (5) distance to stream; (6) proportion of ridge and southwest aspect (representing topographic position (sensu North et al. 2012); and (7) elevation of each GPS location. We also obtained a coefficient for short stand area by fitting an additional model, substituting the short term for the medium and tall

model terms. The abundance and distribution of hardwoods are key habitat factors that may vary by elevation, but data were not available to include in this analysis. Soft edge was defined as the boundary between two stand types after smoothing, while hard edge was the boundary between open and tall stands only (after smoothing). We smoothed stands to ensure that we were measuring edges between large patches by removing all stands <1 ha in area and merging them with the most common nearby stand. We estimated seral stage diversity using the Shannon-Wiener diversity index among the proportional area of all four vegetation height types within 100 m of each used and available point, assuming that diversity of stand heights would also indicate a diversity in seral stage. We considered interactions between elevation and other predictors, which provided a means to test whether habitat selection was mediated by elevation. For example, spotted owls might be more likely to use open and shorter stands, hard edges, and a greater seral stage diversity at lower elevations, where woodrats are more prevalent, than high elevations where flying squirrels are more common (Jones et al. 2016, Gutiérrez et al. 2017).

In addition to fixed effects, we estimated random slope effects for each additive main effect (excluding interactions) that varied by individual owl. We included random slopes not to assess individual variation, but to account for it so as to avoid bias in the fixed effects. Therefore, this approach provided unbiased estimates of population-level selection in the presence of individual heterogeneity (Duchesne et al. 2010). Then, following Muff et al. (2020), we treated the strata-specific intercepts as a random effect with a very large ($\sim 10,000$) fixed variance to facilitate model fitting and prevent shrinkage toward an overall mean. We evaluated the support of each fixed effect by examining whether 95% confidence intervals for coefficients overlapped zero, but did not use this as a strict threshold for assessing potential variable importance to avoid possible Type II error (Amrhein et al. 2019); thus, we also considered effects with 90% confidence intervals that did not overlap zero to be potentially meaningful. We evaluated model goodness of fit by calculating the conditional coefficient of determination for generalized linear mixed-effects models (R_{GLMM}^2 ; Nakagawa and Schielzeth

2013, Johnson 2014, Nakagawa et al. 2017) using the MuMIn package in program R (Barton 2020). We used odds ratios, which can facilitate linear interpretation of covariate effects in logistic models containing interactions (Jones and Peery 2019), to understand the potential management effects of altering forest characteristics by small amounts (e.g., 10% increase in tall trees) at lower (1000 m; 16th percentile) and higher (1500 m; 87th percentile) elevations for covariates that interacted significantly with elevation. We expressed odds ratios as proportional changes in effects, so odds ratios between 0 and 1 represent a decrease in the odds of selection, and odds ratios >1 represent an increase in the odds of selection. For example, an odds ratio of 1.33 indicates that the odds of selection increase by a factor of 1.33, or in other words, owls are 1.33 times as likely to select that given habitat, whereas an odds ratio of 0.75 indicates that the odds of selection decrease by a factor of 1.33 (the inverse of 0.75 or 1 divided by 0.75).

Selection of structure within taller public forests

In our analysis of selection of structure within taller public forests, we tested whether elevation affected spotted owl nocturnal habitat selection of forest structural characteristics, limiting our area of interest to public forests with taller trees (the medium and tall forest stand classes used in the mixed-ownership stand selection analysis where the tallest trees measured at least 20 m in height; Table 1). A better understanding of very fine-scale selection for forest structure is needed to guide forest restoration efforts on national forests, given that retaining owl habitat and managing for wildfire resilience are often at odds. Following historical logging of large trees and over a century of fire suppression, forests are now primarily composed (80%) of homogenized medium and tall stands in our study area. Because this analysis required substantial locational precision to match the finer-scale LiDAR metrics used to estimate forest structure, we used a stricter criterion for including GPS locations ($0 < \text{DOP} < 3$ and at least five satellites), which resulted in a median error of 17.5 m under forest canopy (Appendix S1).

Resource selection analysis.—This stricter criteria yielded fewer GPS locations and fewer points in a given night for each owl (2.8 points per owl,

per night, on average), making SSF a less appropriate analytical framework (Appendix S1). As a result, we instead used a resource selection function (RSF) approach in which the locations of used and available points were not treated as conditional on the location of the previous used location. While the stricter DOP and satellite threshold may have resulted in some GPS bias in our data (eliminating more points under denser canopy because they reached relatively fewer satellites), we assumed that this bias was constant across the elevational gradient and thus would not have a large effect on our findings (but see Frair et al. 2004). For our analysis of selection of structure within taller public forests, we generated five available points for every used point within the area of interest. The mean covariate values for used and available points for this analysis are provided in Appendix S2: Table S2.

We ran two models to test for selection of structure within taller public forests that differed in the portion of the home range considered in the model. We split the 400 m buffered 95% KDE for each owl into inner and outer portions because (1) as central place foragers (Carey and Peeler 1995), owls tend to concentrate activities in areas closer to nests and roost sites; and (2) these often have different habitat characteristics than areas further from nest and roost sites that can lead to different patterns of nocturnal habitat selection (Atuo et al. 2019). The inner portion was defined as the 0–45% (KDE), hereafter referred to as “home range core,” and the outer portion was defined as the 45–95% KDE and hereafter referred to as “outer home range.” We assumed that when multiple GPS points were recorded in either the outer home range or home range core in a single night that they were spatially independent because fixes were typically separated by several hours. We excluded owls with fewer than 10 used points for each RSF analysis (reducing our sample size from 18 to 14 owls for the analysis of the home range core and 11 owls for the analysis of the outer home range). The high proportion of private land within either the owl home range core, outer home range, or both was the key reason that owls were removed by these analyses with the exception of one owl (this one owl had few GPS points overall, likely because of a failing GPS transmitter). While this

was not a large sample of owls, it was within the range of other such spotted owl GPS studies and we expected that the many used locations for each owl, combined with our multi-faceted analyses, would reveal any strong underlying selection patterns relative to what had previously been reported for spotted owls.

We used mixed-effects logistic regression models (1 = used, 0 = available) to test for patterns of selection of structure within taller public forests. As in the SSF above, we allowed intercepts as well as slopes (regression coefficients) to vary by individual owl. The probability π_{ij} that used/available point $y_{ij} \sim \text{Bern}(\pi_{ij})$ was used by individual $i = 1, \dots, I$ at location $j = 1, \dots, J_i$ was modeled as:

$$\text{logit}(\pi_{ij}) = \mu + \alpha_i + \beta^T x_{ij} + b_i^T z_{ij},$$

where μ was the overall mean (intercept), α_i was the individual-specific random deviation from the intercept, β^T and x_{ij} were the vectors of fixed-effects coefficients and covariate values, respectively, b_i^T was the vector of individual-specific random slope coefficients, and z_{ij} was a design vector (Muff et al. 2020). For each used and available point, we analyzed the LiDAR point cloud within 30 m of the point to calculate the (1) elevation, (2) vertical complexity, (3) max tree height, (4) tall tree density, (5) shrub/understory density, (6) % canopy cover, (7) distance to activity center, and (8) squared distance to the activity center, as well as the interaction between each of the above terms and elevation (Table 1). We chose not to examine horizontal diversity in this analysis because the plot area was small and vertical diversity has been shown to be strong predictor of California spotted owl site selection (e.g., Bias and Gutiérrez 1992, Gutiérrez et al. 1992). As with the SSF, we tested covariates for high correlation (correlation coefficient >0.7 ; Appendix S2: Fig. S2). We also considered interactions between elevation and habitat variables to test whether selection varied as a function of elevation and reported odds ratios for covariates that interacted significantly with elevation. As in the SSF analysis, we evaluated the support for each fixed effect by examining whether the 90% or 95% confidence intervals for coefficients overlapped zero, and evaluated goodness of fit for both the home range core and outer home range using the R_{GLMM}^2 (Nakagawa and Schielzeth

2013, Johnson 2014, Nakagawa et al. 2017) using the MuMIn package in program R (Barton 2020).

RESULTS

Mixed ownership stand selection

We tracked owls included in the mixed-ownership stand selection analysis for a mean of 50 nights (range 15–88 nights, $n = 16$ owls) and recorded a mean of 3.5 steps per owl-night, which resulted in a mean of 173 steps (range 130–237 steps) per owl and a total of 2765 used locations (Appendix S2: Table S3). The mean 95% KDE with a buffer of 400 m for owls included in this analysis was 2134 ha (range 832–5985 ha, $n = 16$; Appendix S2: Table S3). See Appendix S2 for additional tables and figures describing mean values for each input variable used in each analysis (Appendix S2: Tables S1, S2), correlations between these variables (Appendix S2: Fig. S1; Appendix S2: Fig. S2), distribution of each variable across elevations (Appendix S2: Figs. S3, S4), description of the owl sample sizes and areas (Appendix S2: Table S3), and the parameter estimates, confidence intervals, and standard errors for each model (Appendix S2: Tables S4–S6).

The mixed conditional SSF revealed that mixed-ownership stand selection was generally dependent on elevation, with multiple significant interactions between elevation and other variables (Fig. 3, Appendix S2: Table S4). The interaction between elevation and short stand area ($\beta_{e^*sh} = -0.68$, 95% CI = -1.24 to -0.12) indicated that owls tended to select areas with proportionally less short stand area at higher elevations but with proportionally more short stand area at lower elevations (Fig. 3a). Odds ratios (hereafter “OR”) indicated that owls were more likely (selection increased by a factor of 1.41; OR = 1.41) to select areas with 10% more short stand area (e.g., increasing from 5% to 15%) at lower elevations, but less likely (selection decreased by a factor of 0.70; OR = 0.70) to select areas with 10% more short stand area at higher elevations (Table 2). Conversely, the interaction between elevation and medium stand area ($\beta_{e^*med} = 0.79$, 95% CI = 0.02 – 1.56), as well as tall stand area ($\beta_{e^*tall} = 0.88$, 95% CI = 0.14 – 1.63) indicated that at higher elevations owls tended to select areas with proportionally more medium

and tall stand area (OR = 1.33 and 1.35, respectively, for every 10% increase in medium and tall stand area) with an opposite trend at lower elevations (Fig. 3b,c; Table 2).

There were also interactions between elevation and each of the following variables: distance to hard edge ($\beta_{e*hed} = 1.49$, 95% CI = 0.62–2.36), seral stage diversity ($\beta_{e*ssd} = 0.67$, 95% CI = 0.09–1.24), ridge area ($\beta_{e*ridg} = -0.83$, 95% CI = -1.49 to -0.17), and SW slope area ($\beta_{e*sw} = -1.37$, 95% CI = -1.98 to -0.75; Fig. 3). Odds ratios indicated that owls at higher elevations selected areas further from hard edges (OR = 1.11 for each 100 m increase in distance from a hard edge), with proportionally more seral stage diversity (OR = 1.14 for every 10% increase in seral stage diversity), and proportionally less ridge and SW aspect area (OR = 0.84 and 0.83, respectively, for every 10% increase in ridge and SW aspect area; Table 2). At low elevations, owls selected the opposite. The goodness-of-fit test statistic suggested the SSF model explained a moderate amount of the total variation ($R_{GLMM}^2 = 0.47$).

Selection of structure within taller public forests

Within taller public forests, we analyzed 580 used points in the home range core of 14 birds over a mean area of 166 ha (Appendix S2: Table S3). Mean values for used and available points for independent variables are in Appendix S2: Table S2. The models for selection of structure within taller public forests for the home range core showed a positive interaction between elevation and canopy cover ($\beta_{e*cc} = 1.18$, 95% CI = 0.14–2.22; Fig. 4a; Appendix S2: Table S5). This interaction suggested that within taller public forests in the home range core, owls tended to select areas with proportionally more canopy cover at higher elevations (OR = 1.59 for every 10% increase in canopy cover), but with less canopy cover at lower elevations (OR = 0.14 for every 10% increase in canopy cover; Table 2). Note that areas available to owls all had relatively high levels of canopy cover (mean = 93% in the home range core; Appendix S2: Table S2). The goodness-of-fit test statistic suggested the model describing the home range core explained approximately 68% of the total variation ($R_{GLMM}^2 = 0.68$).

We also analyzed 276 used points in taller public forests in the outer home range of 11 birds over a mean area of 487 ha (Appendix S2: Table S3). There was a positive interaction between elevation and the tall tree density ($\beta_{e*tall} = 0.89$, 95% CI = -0.07 to 1.86; Fig. 4b; Appendix S2: Table S6), although the 95% CI slightly overlapped zero. These results, combined with odds ratios, suggested that within taller public forests in the outer home range, owls tended to select areas with more tall trees at higher elevations (OR = 1.49 for each additional 20 tall trees/ha) but with fewer tall trees at lower elevations (OR = 0.04 for each additional 20 tall trees/ha; Fig. 4b; Table 2). Also note that areas available to owls all had relatively high tall tree densities (mean = 51 tall trees/ha [over 32 m tall] in the outer home range; Appendix S2: Table S2). The goodness-of-fit test statistic suggested the outer home range model explained approximately 46% of the total variation ($R_{GLMM}^2 = 0.46$).

DISCUSSION

Spotted owl nocturnal habitat selection patterns at higher elevations in this study were generally consistent with the results presented in previous studies (Gutiérrez et al. 1992, 2017, Irwin et al. 2007, Atuo et al. 2019, Blakey et al. 2019, Gallagher et al. 2019). However, habitat selection at lower elevations exhibited a different pattern and was consistent with our hypothesis of elevation-dependent habitat selection. Despite our modest sample of owls, these elevational trends were apparent across our analyses. We also observed trends consistent with our prediction that the differences in selection would correspond with habitat features associated with owl primary prey—flying squirrels at high elevations and woodrats at low elevations. Our analyses showed that spotted owls at higher elevations selected interior areas of forest stands with medium and tall trees and with higher seral stage diversity overall and less ridge and southwest aspects. When limited to taller forests on publicly owned land, spotted owls at higher elevations selected sites with higher canopy cover inside their home range core and more large trees outside their home range core. By contrast, spotted owls at low elevations selected more homogeneous stands with shorter trees that were closer

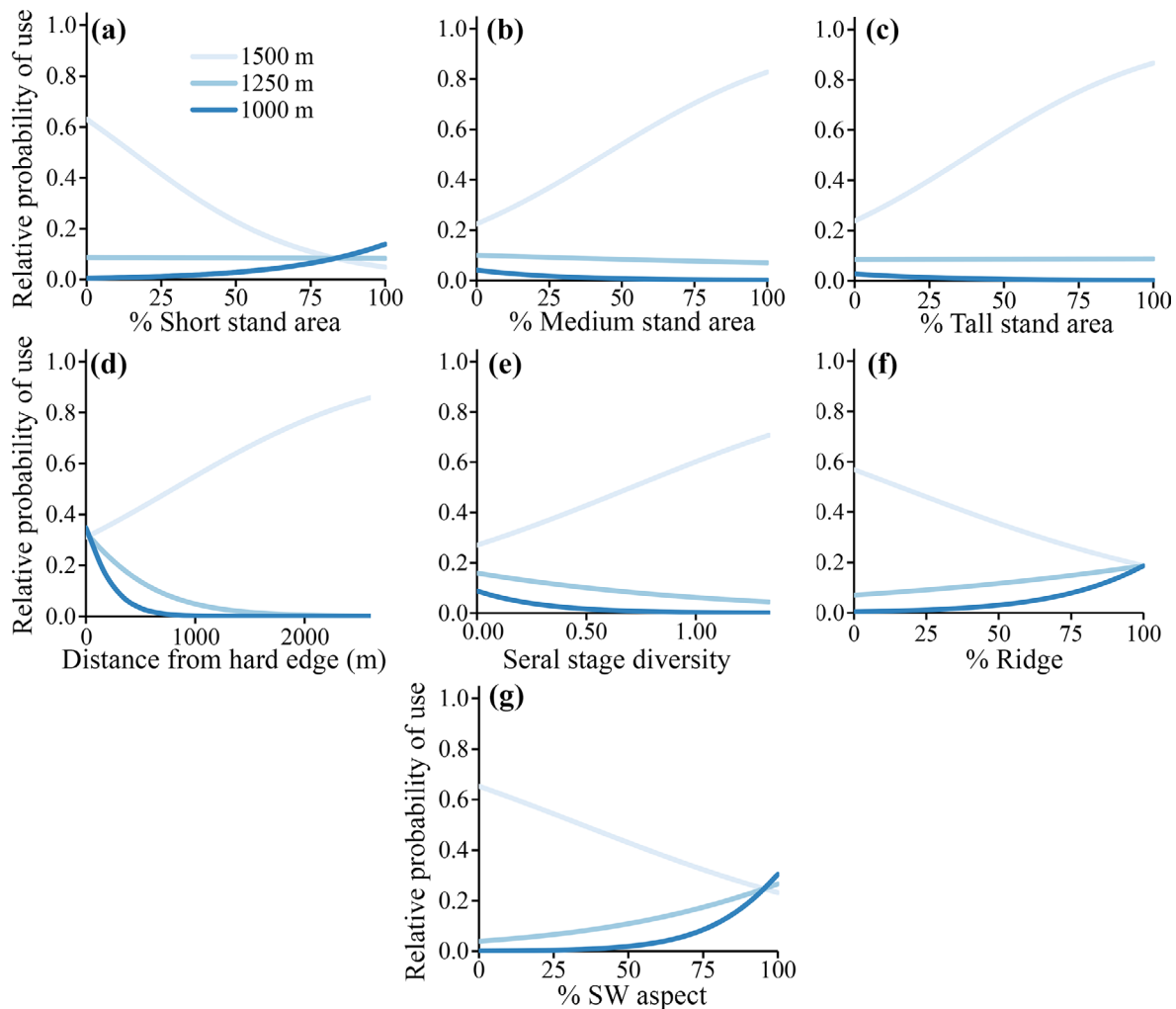


Fig. 3. Graphical depiction of results from the mixed-ownership stand selection analysis derived from a SSF. Covariates displayed are those that revealed significant interaction with elevation in the model. Panels (a–g) show the SSF fixed-effect interaction between the focal x -axis variable and elevation. Note that the model-based interaction term included elevation as a continuous term but here we have displayed elevation as discrete values for easier visualization and interpretation. The legend in panel (a) applies to all panels. For all panels, the intercept term used for graphical display of fixed effects was the median of all stratum-specific intercepts. Note that the apparent slopes of the lines are influenced by the intercept, and while the slope of the low-elevation line in panel (c) is close to 0, this does not equate to a weak effect. Odds ratios should be used to determine the difference in owl selection at low vs. high elevations for each variable. For example, panel (a) shows a higher relative probability of use of short-tree stands for birds at low elevations compared with high, but odds ratios provide the specific change in use probability at a given elevation as the proportional area of nearby short-tree forest changes by a given amount (Table 2).

to edges and that included more ridge and southwest aspect. Within taller public forests, owls at lower elevations selected areas with more open canopies inside their home range core and

fewer large trees outside their home range core. While our results do not preclude elevationally consistent and potentially stronger (Blakey et al. 2019) selection for older and more closed canopy

conditions at landscape scales (i.e., second-order selection; *sensu* Johnson 1980), they provided strong evidence that spotted owls selected for putative foraging habitat differently at low vs. high elevations within their home ranges, which was predicted by Gutiérrez et al. (1992).

Elevational gradients in habitat selection

We predicted that variation in spotted owl habitat selection by elevation would reflect the habitat preferences of their woodrat and flying squirrel prey that are relatively abundant at high and low elevations, respectively (Gutiérrez et al. 1992, Munton et al. 2002, Hobart et al. 2019b). Woodrats are often associated with younger, shorter forests containing hardwoods and brushy understories (Sakai and Noon 1993, Innes et al. 2007, Hamm and Diller 2009), such that selection for shorter forests by GPS-tagged owls at lower elevations may have reflected a woodrat-focused foraging strategy. Although there were generally few areas with short trees, their availability was reasonably consistent across elevations, suggesting that observed patterns in selection were simply not the result of the differences in availability of cover types (Appendix S2: Fig. S3). Moreover, selection for hard edges (between open and tall stand types) may be indicative of use as a movement corridor while avoiding open areas or using taller forests for perch sites adjacent to shorter forests containing relatively dense woodrat populations (see Fig. 2a for a photograph of a hard edge visited repeatedly by one individual owl), consistent with previous research (Sakai and Noon 1993, Zabel et al. 1995, Franklin et al. 2000). Similarly, spotted owls may have selected southwest-facing slopes and ridgetops, which tend to have more open, shrubby vegetation cover, as a strategy to prey on woodrats. However, we acknowledge that selection for some covariates in our analysis might also reflect non-foraging behaviors, as some short forest areas used by owls had widely spaced trees and occurred on ridgetops that could potentially be serving as territorial calling locations (see Fig. 2d). Finally, and somewhat surprisingly, we did not detect selection or avoidance for the shrub/understory covariate at any elevation. Dense shrub cover could make successful foraging by spotted owls difficult, which could moderate its impact on foraging habitat

selection, despite potentially higher densities of woodrats, as suggested by Sakai and Noon (1993). Our finding of neutral selection for shrub density could also be explained by differences in the composition of those shrubs, with potentially positive selection for hardwood shrubs that provide food for woodrats canceled out by potentially negative selection for areas with dense coniferous understory that might be avoided by woodrats (Sakai and Noon 1993). However, LiDAR and other current remote sensing products are not able to discriminate among the various tree or shrub species in the understory, so we were unable to investigate this question further (Su and Bork 2007, Martinuzzi et al. 2009).

The selection of putative foraging sites that had tall trees and closed canopies at higher elevations was consistent with a foraging strategy targeting flying squirrels (Waters and Zabel 1995, Munton et al. 2002, Meyer et al. 2007). Studies have shown that flying squirrels are typically associated with older coniferous forests, where they consume fungi and lichen found in these forests (McKeever 1960, Waters and Zabel 1995, Meyer et al. 2007, Sollmann et al. 2016). But selection for closed canopy forests in the home range cores and large trees in the outer home ranges at higher elevations may also have reflected a trade-off between forest conditions providing concealment from predators (canopy cover) near activity centers and key prey habitat elements (large trees) in foraging areas. Consequently, the selection of sites with greater seral stage diversity at higher elevations and lower seral stage diversity at lower elevations was opposite of what we expected, given our hypothesis that owls preyed on species that reach their highest abundance under conditions opposite of this (Sakai and Noon 1993, Hobart et al. 2019a). Still, it is possible that the higher seral stage diversity within owl home ranges at higher elevations may be linked to diet diversification beyond smaller-bodied flying squirrels (Munton et al. 2002) or may be a strategy to mitigate prey depletion in primary foraging patches (Carey et al. 1992, Ward Jr et al. 1998).

The gradients we observed in habitat selection by spotted owls, which we posit were proximately mediated by changes in prey communities, could ultimately have been driven by elevational gradients in both environmental

Table 2. Expected odds ratios associated with a 10% increase in a given habitat variable at lower (1000 m) vs. higher (1500 m) elevations in the analyses of (a) mixed-ownership stand selection and (b) selection of structure within taller public forests.

Variable	Variable change	Low elevation	High elevation
(a) Mixed-ownership stand selection			
% Short stand area	10% increase	1.41	0.70
% Medium stand area	10% increase	0.70	1.33
% Tall stand area	10% increase	0.74	1.35
Distance to hard edge (m)	100 m further	0.57	1.11
Seral stage diversity	10% increase	0.71	1.14
% Ridge	10% increase	1.49	0.84
% SW aspect	10% increase	1.86	0.83
(b) Selection of structure within taller public forests			
% Canopy cover [†]	10% increase	0.14	1.59
Tall tree density (per ha) [‡]	20 trees/ha increase	0.04	1.49

Notes: All covariates showed significant interaction with elevation in the underlying step or resource selection model (see Appendix S2 for parameter estimates and associated measures of uncertainty). For example, owls were more likely (selection increased by a factor of 1.41; odds ratio = 1.41) to select areas having 10% more short-tree stand area (e.g., increasing from 5 to 15% short stand area) at lower elevations, but less likely (selection decreased by a factor of 0.70; odds ratio = 0.70) to select areas with 10% more short stand area at higher elevations.

[†] Home range core.

[‡] Outer home range where tall trees are over 32 m in height.

conditions and management practices. Certainly, natural gradients in woodrats and flying squirrels occur in Sierra Nevada mixed coniferous forests, and this pattern likely shaped the change in the importance of large trees when analyses were limited to taller public forests. However, low-elevation landscapes contain a higher fraction of privately owned forests (primarily industrial) managed in ways that could benefit woodrats at the expense of flying squirrels (Hobart et al. 2019b). Thus, we suspect that stronger selection for, for example, shorter forests and lower elevations was the result of some combination of private lands management (e.g., that creates brushy open or young areas) and ecological conditions (e.g., the presence of hardwoods) that promote woodrat populations in shorter forests at low but not high elevations. Distinguishing between the relative importance of management vs. environmental conditions in shaping elevational gradients in habitat selection is challenging and beyond the scope of this study, but would enhance the ability to manage prey populations for the benefit of spotted owls across the elevations at which they occur.

Barred owls have the potential to affect habitat selection by spotted owls (Gutierrez et al. 2007, Wiens et al. 2014). Although one barred owl was detected close to the home range boundaries of

two owls in this study, it was not detected until the following year (N. Kryshak and D. Hofstatter, *unpublished data*). Thus, the low density of barred owls (possibly not even present during our study) combined with our inclusion of random effects to account for variation among individual owls should have minimized any differences in behavior of these two owls.

Population implications of elevational gradients in selection and future research

In conjunction with previous studies (Zabel et al. 1995, Munton et al. 2002, Hobart et al. 2019b), our results suggest that the elevational gradients in habitat selection, which are likely a response to the distribution of primary prey, have consequences for spotted owl populations. At lower elevations, spotted owl territory occupancy and breeding probabilities tend to be higher, home ranges smaller, and woodrats more prevalent in the diet (Zabel et al. 1995, Hobart et al. 2019a, b). Moreover, spotted owl breeding probabilities can be positively associated with the prevalence of younger forests at low elevations where there is a significant hardwood component (a forest type that likely harbors relatively abundant woodrat populations) in owl territories (Thome et al. 1999, Hobart et al. 2019b). But territory occupancy can be

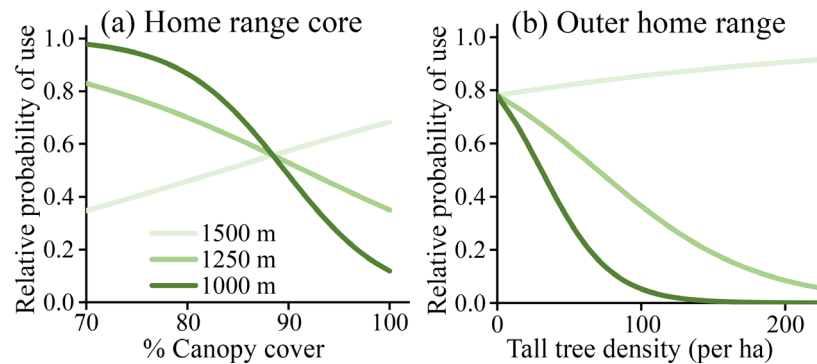


Fig. 4. Graphical depiction of results from the analysis of selection of structure within taller public forests derived from a resource selection function (RSF) analysis. Covariates displayed are those that significantly interacted with elevation in the model. Fixed-effect interactions between the focal x -axis variable and elevation input are shown at two spatial extents: (a) home range core, defined as the 0–45% kernel density estimate, and (b) outside the core area, defined as the 46–95% kernel density estimate. Note that the model-based interaction term included elevation as a continuous term but here we have displayed elevation as discrete values for easier visualization and interpretation. Also note that while the minimum canopy cover in used locations was 48%, we set a lower bound of 70%, which represents nearly a 99% confidence interval of canopy cover at available locations. As in Fig. 3, the apparent slopes of the lines are influenced by the intercept, and odds ratios should be used to determine the difference in owl selection at low vs. high elevations for both variables.

more sensitive to variation in the amount of closed canopy forest within territories at higher elevations, potentially because of spotted owls' greater reliance on flying squirrels at higher elevations (Jones et al. 2016). Certainly, several studies have shown that older and closed canopy forests benefit spotted owl territory occupancy and demographic rates (Seamans and Gutiérrez 2007, Blakesley et al. 2010, Tempel et al. 2014, 2016, Jones et al. 2018), but—unlike Jones et al. (2016)—these studies did not consider the potential mediating effects of elevation or latitude on relationships between habitat and populations.

Thus, our finding that habitat selection varies across elevation supports a growing body of research that links elevational-dependent distributions of small mammal communities with emergent effects on individual fitness and population metrics such as population density and trend (Jones et al. 2016, Hobart et al. 2019a, b). Collectively, these results suggest that lower elevations within the range of the spotted owl in the Sierra Nevada are particularly important for maintaining viable populations of this species—acknowledging that, in the future, the potential adverse effects of anthropogenic climate change

on spotted owls might be greatest at lower elevations (Peery et al. 2012).

Management implications

Our results provide further indication that managing forests for conditions that promote access to abundant woodrat—and perhaps pocket gopher—populations could benefit spotted owl populations within the lower elevations of the species' range if sufficient nest and roost habitat are available (Hobart et al. 2019b). In particular, managing for heterogeneous forests within spotted owl home ranges, such as a juxtaposition of owl nesting habitat (older forests) and woodrat habitat that includes smaller patches of younger forests with a significant shrub and hardwood component could benefit both spotted owl reproduction and territory occupancy (Sakai and Noon 1997). In northwestern California, Franklin et al. (2000) found that the juxtaposition of nesting with non-nesting habitat for spotted owls increased fitness presumably by facilitating access to woodrats as prey. Moreover, promoting woodrat food resources such as masting California black oak and nesting resources such as cavities in snags and large diameter logs (Innes et al. 2007) would not only boost woodrat abundance,

but would also increase habitat suitability for other species such as pacific fisher (*Pekania pennanti*) and owls (Long et al. 2016).

Nevertheless, promoting woodrat habitat at lower elevation without adverse effects to spotted owl populations is challenged by several considerations. First, spotted owls at lower elevations in our study area consume flying squirrels as well as woodrats based on pellet analyses (R. J. Gutiérrez, *unpublished data*), such that promoting sufficient habitat for both species—including older, closed canopy forests for flying squirrels—could buffer spotted owls from variability in the populations of either prey species. Second, spotted owls use forests characterized by tall, old trees, and more complex canopies for nesting and roosting in the Sierra Nevada regardless of elevation (Verner et al. 1992, Gutiérrez et al. 2017, North et al. 2017). Creating gaps in older, more complex-canopied forests that are being used by the owls for nesting and roosting could compromise the nesting habitat quality by increasing predation risk as well as the thermal exposure (Barrows 1981). Therefore, potentially suitable areas for such gap creation (thus increasing seral stage diversity) could include dense canopy forests without a large-tree component and drier sites unlikely to support tall trees and dense cover (sites less suitable for nesting by spotted owls; Fricker et al. 2019). Third, canopy cover was high at used sites within the owl home range cores across elevations, averaging 93% (as measured using TAO area derived from LiDAR; Appendix S2: Table S2). For instance, 99% of available points had 69–100% canopy cover, but reducing forest cover below this level over significant portions of a home range core could have unknown effects on foraging habitat, even at lower elevations. Fourth, the tendency for individuals to avoid high seral stage diversity at lower elevations (Fig. 3) suggests limits to the extent to which owls will benefit from heterogeneity—at least as we defined and measured it. Fifth, few researchers have studied spotted owl diet and foraging habitat selection during the winter, when starvation is likely a higher risk than during our study period and prey dynamics may shift to species that are more prevalent or easier to locate and capture when snow is present. Greater knowledge of winter behaviors would contribute to a

more complete understanding of spotted owl conservation. Finally, while spotted owls tended to select hard edges in this study, and non-juvenile survival rates appear to benefit from edge between similar edge types (Tempel et al. 2014), relatively high levels of edge have also been associated with reduced territory occupancy in the Sierra Nevada and tendency to avoid nesting close to edges (Phillips et al. 2010, Tempel et al. 2016). Certainly, some of this ambiguity could have resulted from previous studies not considering how the effects of edge may vary across elevations, or alternatively because studies examined properties that occur at different spatiotemporal scales (i.e., population responses vs. individual movement processes). Caution is merited when considering the creation of edge as a management tool owing to potential negative impacts of predation, increased thermal profile, and forest fragmentation on owls.

By contrast, selection of forest conditions typically associated with abundant flying squirrel populations, coupled with the dietary shift from woodrats to flying squirrels at higher elevations (Munton et al. 2002), suggests that maintaining older, closed canopy forests is more likely to provide high-quality foraging habitat at those high elevations (see Jones et al. 2016), as long as sufficient habitat diversity is promoted. Flying squirrels are typically more abundant in forests with a greater basal area of larger trees and higher canopy cover, and can decline following forest thinning activities (Meyer et al. 2007, Holloway et al. 2012, Sollmann et al. 2016), although declines are not universal (Rosenberg and Anthony 1992, Ransome et al. 2004, Gomez et al. 2005) and responses can be scale-dependent (Sollmann et al. 2016). Thus, at higher elevations, managing for forest conditions such as tall (older) trees that promote flying squirrel populations could benefit spotted owls, whereas opening forests or removing tall trees at higher elevations is more likely to have an adverse effect, especially given the population decline at higher elevations, on spotted owl foraging habitat than at lower elevations. Areas of high cover provided by tall trees may currently be a limiting factor for spotted owl and their prey at higher elevations (North et al. 2017) and due to the legacy of fire suppression and historic logging practices, restoration of this cover type likely requires tree density

reductions (of smaller trees) to reduce competition for limited resources (and promote growth in taller trees; see also Eyes et al. [2017] and Kramer et al. [2021] for owl response to fire use). Thus, managing higher elevation forests to increase seral diversity could benefit spotted owls through both the diversification of their prey base and the promotion of tall tree growth and resilience through reduced resource competition. Given that owls at higher elevation tend to select against southwest-facing slopes and ridges, these may be appropriate locations to reduce tree cover densities and increase seral stage diversity when forest cover is homogenous—objectives consistent with forest restoration objectives (North 2012)—while minimizing potential effects to spotted owls.

Our results, combined with other studies (Hobart et al. 2019a), suggest that increasing woodrat populations at higher elevations via forest management could have potential benefits to spotted owls, though more research is needed on prey populations and spotted owl dietary and movement patterns (e.g., are woodrat populations limited by high elevation climatic and biotic factors; e.g., diet and predation; even if suitable habitat is created; does owl diet shift seasonally in areas with heavy snowfall to rely on flying squirrels more heavily in the winter, or do owls migrate downslope, as indicated by Laymon 1989). But such management efforts are most likely to be successful in higher elevation areas that currently contain woodrats at low densities while less likely to be successful in the highest areas of owl distributions where woodrats are often absent potentially because of unsuitable climate rather than vegetation conditions. In addition, several species of woodrats occur in the Sierra Nevada, each with different elevational distributions and habitat associations, which complicates their management (Carey et al. 1999, Innes et al. 2007, Hobart et al. 2019a). Thus, more research is needed on range, abundance, and limiting factors of these prey species across elevation and latitudinal gradients to assess the potential effectiveness of such an approach for woodrats at higher elevations—especially in light of future climate change. We also caution against developing management prescriptions directly from the elevational values presented in this study (e.g., Figs. 3, 4) given that latitudinal gradients interact

with elevation to shape vegetation and thus prey communities. The transition between a mixed woodrat-flying squirrel diet to a primarily flying squirrel diet likely occurs at higher elevations in the southern Sierra Nevada and lower elevations in the northern portion of the range as a result of latitudinal change in climate and forest conditions (Gutiérrez et al. 2017).

Beyond spotted owls, we recommend future research focused on habitat selection patterns by species in montane ecosystems consider how selection varies along elevational gradients. Such assessments can be conducted in a straightforward manner—as we did here—by evaluating support for resource selection models containing interactions between elevation and covariates representing habitat features of interest such as canopy cover, tree size, and vertical structure. Linking such assessments with detailed studies of prey ecology would help untangle what are inevitably complex relationships between forest structure and composition, prey abundance and availability, and foraging strategies and population outcomes. Regardless, these previously underappreciated elevational gradients revealed here merit additional study in additional systems and could provide key insights leading to more effective habitat management for montane species of conservation concern.

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LITERATURE CITED

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SUPPORTING INFORMATION

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