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Research Article

Activity Center Selection by Northern Spotted Owls

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ABSTRACT The federally threatened northern spotted owl (*Strix occidentalis caurina*) has been intensively studied across its range, and habitat needs for the species have influenced forest management in northwestern North America for decades. Dense forest canopies are often reported in the scientific literature and agency management plans as an important habitat attribute for spotted owls, though the means of measuring forest canopy and interpreting species requirements vary across studies and more importantly, among management plans. We used light detection and ranging (lidar) measurements of canopy cover, canopy surface heterogeneity, and upper canopy surface connectivity, and an index of the presence of a competitive invasive species, the barred owl (*S. varia*), in multinomial discrete choice models using a Bayesian framework to evaluate selection of forest cover types by spotted owls in Oregon, USA, 2008–2015. We designated yearly activity centers based on the most biologically significant observation during the nesting season (Mar–Aug), generally centered on the nest tree. Spotted owls selected activity centers with more canopy cover and higher heterogeneity of the canopy surface within 100 m than was available within their territories. The average proportion of canopy cover within 100 m of a spotted owl activity center was 0.79 ± 0.12 (SD; range = 0.34–0.99). The presence of barred owls did not explain variability in selection of spotted owl activity centers, but barred owls might not affect third-order habitat selection within territories, or our index was too spatially coarse to detect these effects on spotted owl resource selection. We demonstrate that lidar provides researchers and managers with a tool that can accurately measure forest canopies over large areas, and assist in mapping spotted owl habitat.

KEY WORDS canopy cover, habitat selection, light detection and ranging (lidar), Oregon, spotted owl *Strix occidentalis caurina*.

The northern spotted owl (*Strix occidentalis caurina* [i.e., spotted owl]) was listed as threatened in 1990 under the United States Endangered Species Act (U.S. Fish and Wildlife Service 1990) because of the relationship between spotted owls and dense, mature, conifer forests and the loss or conversion of these forest types to younger, less complex forests (Thomas et al. 1990). Forest management within the range of the spotted owl has been influenced by spotted owl-focused conservation measures since the 1970s, both on public and private forest lands (Lee 1985, Thomas et al. 1990, Marcot and Thomas 1997, Lesmeister et al. 2018).

Dense, older (usually >80 yr) forest canopies are a relatively consistent characteristic of spotted owl habitat (Forsman et al. 1984, Hershey et al. 1998, LaHaye and Gutiérrez 1999, Glenn et al. 2016). Older forest stands with closed canopies and vertical canopy layering may help regulate spotted owl exposure to weather (Barrows 1981, Forsman et al. 1984, Weathers et al. 2001), provide higher prey density (Carey et al. 1992, Ward et al. 1998), and aid in predator avoidance (Forsman et al. 1984, Johnson 1993). Older forest canopies may also favor spotted owl prey species. Carey (2000) reported such canopies allow for efficient movement of northern flying squirrels (*Glaucomys sabrinus*; a major spotted owl prey item) through the canopy, and Swingle and Forsman (2009) observed that red tree voles (*Arborimus longicaudus*; another important spotted owl prey species) generally travel through the canopy via interconnected branches.

Natural changes in dense forest canopies from fire, insects, diseases, and anthropogenic changes from thinning and timber harvest can open and alter them, potentially

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decreasing the probability of selection by spotted owls (Forsman et al. 1984, Meiman et al. 2003, Clark et al. 2013, Odion et al. 2014, Rockweit et al. 2017). Thus, for habitat managers, the ability to accurately evaluate the types of forest canopies being selected is important for determining the condition of spotted owl habitat and how various disturbances described above affect these canopies.

Light detection and ranging (lidar) technology gives biologists the ability to accurately measure forest canopy structure at very fine spatial resolutions (sub-meter) by using laser pulses to produce 3-dimensional geographical information system (GIS) data of the ground surface and the vegetation or structures covering it (Evans et al. 2009). These data have already been used to accurately classify conifer forests into successional stages (Falkowski et al. 2009, Kane et al. 2010) and to analyze forest structure and wildlife-habitat relationships (Vierling et al. 2013, Vogeler et al. 2013, Hagar et al. 2014, Johnston and Moskal 2017, Linnell et al. 2017). For California spotted owls (*S. o. occidentalis*), García-Feced et al. (2011) used lidar data to quantify residual trees in nesting areas and North et al. (2017) used lidar data to predict California spotted owl habitat based on cover of tall trees.

In spotted owl studies and in efforts to classify forest stands, canopy closure is often used interchangeably with canopy cover; however, these are 2 different measures of the forest canopy. Canopy cover is the measure of the percentage of ground covered by the vertical projection of the tree canopy, whereas canopy closure is the measure of the percentage of the sky hemisphere obscured by tree crowns when viewed from a single point on the ground (Jennings et al. 1999). This important difference makes it problematic to compare forest canopy between studies that used these 2 measures to elucidate resource selection by spotted owls. In this study we used canopy cover.

The congeneric barred owl (*S. varia*) has expanded its range over the last century and is now found across the entire range of the spotted owl (Livezey 2009). Barred owls compete for the same resources and have negative effects on spotted owl life history and demographics range-wide (Kelly et al. 2003, Wiens et al. 2014, Lesmeister et al. 2018). Thus, understanding contemporary patterns in spotted owl habitat selection are further challenged if the presence of barred owls is not considered (Olson et al. 2005, Dugger et al. 2011).

Our objective for this project was to evaluate selection of spotted owl primary activity centers based on canopy metrics derived from a common lidar data product that is readily available for use by wildlife biologists. Because the presence of barred owls likely affects habitat selection by spotted owls, we also included an index to evaluate and account for that effect. We hypothesized that spotted owls would select areas for nesting or roosting that differed from available but unused areas and predicted that used areas would have greater canopy cover, greater structural diversity as estimated by variance in tree height, more contiguous forest canopies, and greater distance from nearest known barred owl location.

STUDY AREA

We included data from 5 study areas in Oregon, USA, that were established to study the long-term (24–25 yr) trends in spotted owl demography on the west slope of the Cascade Mountains, the Coast Range, and the Klamath Mountains (Fig. 1). Each study area represented a heterogeneous forested landscape resulting from variable topography, historical disturbances, and land use. Anthony et al. (2006) and Forsman et al. (2011) provided detailed descriptions of the study areas. Although all study areas were dominated by Douglas-fir (*Pseudotsuga menziesii*), vegetative communities differed somewhat across the range of the study based on moisture and elevation gradients (~120–760 m) and distance from the coast (Anthony et al. 2006, Forsman et al. 2011). Forests in the Western Cascades and Coast Range study areas (Tyee, Coast Range, H. J. Andrews) were dominated by mesic forests with a strong western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) component. Southwestern Cascades and Klamath Mountain study areas were drier and included incense cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), western white pine (*P. monticola*), sugar pine (*P. lambertiana*), canyon live oak (*Quercus chrysolepis*), Oregon white oak (*Q. garryana*), Pacific madrone (*Arbutus menziesii*), giant chinquapin (*Castanopsis chrysophylla*), and California laurel (*Umbellularia californica*).

METHODS

Spotted Owl Activity Centers

We conducted annual spotted owl territory surveys at each demographic study area by imitating spotted owl calls and then searching the response locations during the day to determine reproductive status and mark or re-sight spotted owls for mark-recapture analysis (Franklin et al. 1996). From these locations, we mapped annual activity centers from

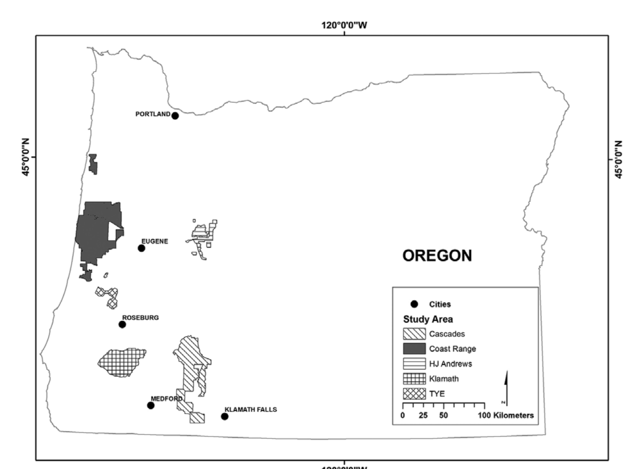

Figure 1. Spotted owl demography study areas with light detection and ranging (lidar) data available to assess selection for spotted owl activity centers, Oregon, USA, 2008–2015. Only the portions of the study areas with lidar coverage data are shown.

2008–2015 based on the most biologically significant location each year, ranking from highest to lowest: nest tree ($n = 42$), fledglings or earliest pair detection ($n = 113$), and single spotted owls ($n = 41$; Forsman et al. 2011). We created analysis circles by buffering each point to represent the immediate vicinity of the activity center (50-m buffer), an approximation of the forest stand containing the activity center (200-m buffer), and an intermediate area (100-m buffer). We found no difference in the proportion of canopy cover between nesting or paired spotted owls ($n = 155$) and single spotted owls ($n = 41$, Wilcoxen 2-sample test, 2-sided $P = 0.07$), so we pooled activity centers for single spotted owls and pairs. We selected the nest or 1 roost location per territory that was coincident with the year of lidar acquisition (Appendix A) on that study area to represent selected locations. We had only 1 instance where we had >1 activity center per territory; thus, we pooled activity center data across years assuming selection was similar among years and the single repeated measure from the same spotted owl territory would not affect results. We used global positioning system (GPS) receivers that were accurate to approximately 10 m (Wing et al. 2005) to map coordinates for nest and roost locations ($n = 159$). We estimated 37 locations based on spotted owls responding at night. Other researchers have estimated that recording locations by similar methods are accurate to ~100 m (Carey et al. 1990). We collected spotted owl data using protocols approved by the Oregon State University Institutional Animal Care and Use Committee (ACUP 4923).

Lidar Data and Forest Structure Variables

Mature forests (≥80-yr-old; Spies and Franklin 1991) positively influence spotted owl demographics (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2016). Because trees in the mature age category can be different heights among our study areas, we developed 4 height strata based on height:age relationships for each study area (Table 1) for our lidar data: strata 1 = 0–2 m (ground vegetation), strata 2 = <25-year-old trees, strata 3 = 25–80-year-old trees, and strata 4 = >80-yr-old trees. We obtained sub-meter resolution discrete-return lidar data from 2008–2015 that were collected with a variety of lidar sensors and aerial platforms (Appendix A). We used bilinear resampling in a GIS to process these lidar data into 1-m resolution ground surface and highest return rasters (Evans et al. 2009). We used the difference in height between these 2 rasters to develop a canopy height model. The canopy height model represents the height of forest vegetation above the ground surface; the vertical projection of this height conforms to the definition of canopy cover. Hereafter, our references to canopy cover (canopy) include the proportion of area covered by the canopy in the top 2 strata combined (strata 3 and 4), which is the overstory in these stands. By defining canopy cover in this way, we mimic what other methods (e.g., aerial photo interpretation) would classify as forest canopy. Non-overstory is comprised of the area covered by the 2 lowest strata (strata 1 and 2).

Within each analysis circle we calculated the area in each height strata described above. We derived descriptive canopy cover and height statistics ($\bar{x}$, median, SD, max., min.) from the Spatial Analyst extension in version 10.1 of ArcGIS (Environmental Systems Research Institute, Redlands, CA, USA). The standard deviation of canopy heights (canopy SD) served as a measure of canopy heterogeneity in our models. To assess the degree to which canopies were contiguous, we reclassified height strata rasters into a binary raster with overstory forest canopy (strata 3 and 4), and non-canopy (strata 1 and 2; Fig. 2). We used Program GUIDOS ToolBox (Vogt 2014) and the Morphological Spatial Pattern Analysis (MSPA; Soille and Vogt 2009) on our binary rasters to obtain measures of the distribution of forest canopy in our analysis circles (Davis et al. 2015). The MSPA program divided the binary raster into 7 classes based on how each pixel related to the pixels surrounding it (Fig. 2). We collapsed these 7 classes into 5 categories: the interior portion of a group of canopy pixels that are >8 m from an edge (core), canopy pixels surrounding ≥1 core pixel (edge), sum of core+edge (core-edge), strings of canopy pixels that are not wide enough to contain any core pixels but are connected to core pixels at one end (branch), and groups of pixels that are not large enough to qualify as core and do not connect with core pixels (scatter; Davis et al. 2015). We used an edge width of 8 m to mimic the crown diameter of an average old-growth Douglas-fir in Oregon (Dubrasich et al. 1997). By using this parameter in the pattern analysis, we reasoned that connected tree crowns would be classed as core. We set the connectivity variable in GUIDOS ToolBox to 4 (Vogt 2014), allowing the program to analyze only the 4 pixels in cardinal directions adjacent to each focal pixel, rather than pixels located diagonal to the focal pixel.

Individual tree crowns can account for canopy cover in >1 strata; thus, a simple stratification of canopy height does not describe the contribution of the entire tree crowns in the different age classes (Fig. 3). To map the horizontal area of each tree crown, we used a GIS to invert canopy height values, created a raster with a drainage basin for each tree crown using the Spatial Analyst extension in ArcGIS, and used the edge of the drainage basin to delineate the border of each tree crown (I. Yau, U.S. Forest Service, personal communication). This process is similar to the TREESEG routine in program FUSION (McGaughey 2016). All pixels within the crown boundary are assigned the maximum height of the tree. For each analysis circle, our young and mature

Table 1. Canopy height cutoffs for canopy height strata based on light detection and ranging at spotted owl activity centers by study area, Oregon, USA, 2008–2015. Strata 1 = ground vegetation, strata 2 = <25 year-old trees, strata 3 (young) = 25–80 year-old trees, and strata 4 (mature) = ≥80-year-old trees. Age and height relationships are for Douglas-fir from United States Forest Service Forest Inventory and Analysis plots (Bechtold and Patterson 2005).

Study area	Strata 1	Strata 2	Strata 3	Strata 4
Southwestern Cascades	<2 m	2–8 m	8–25 m	>25 m
Coast Range	<2 m	2–18 m	18–37 m	>37 m
H. J. Andrews	<2 m	2–12 m	12–28 m	>28 m
Klamath	<2 m	2–11 m	11–24 m	>24 m
Tyee	<2 m	2–8 m	8–33 m	>33 m

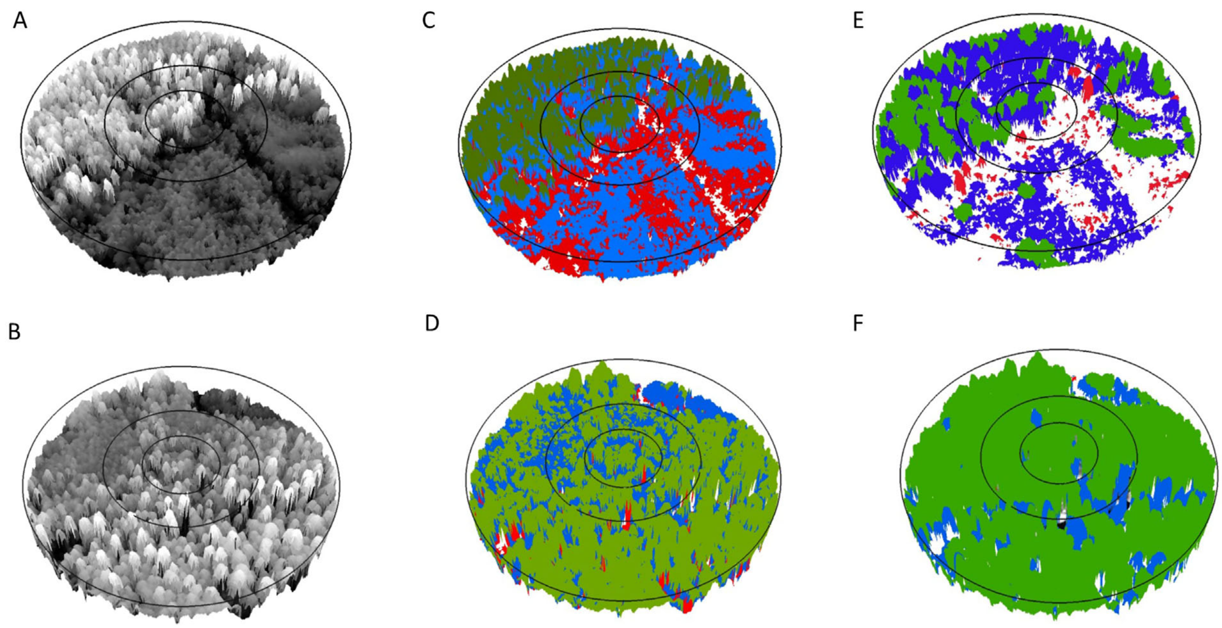

Figure 2. Examples of 3-dimensional canopy surfaces derived from light detection and ranging (lidar) canopy height models in spotted owl territories in Oregon, USA, 2008–2015. Three buffers (50 m, 100 m, and 200 m) at a random location within an owl territory (A; for 50-m buffer, canopy cover = 0.45 ± 15.40 m [SD]); an owl activity center (B; for 50-m buffer, canopy cover = 0.99 ± 12.63 m); binned canopy strata (C and D, same sites as A and B): white = ground vegetation, red = <25 year-old trees, blue = young trees (25–80 yr), and green = mature trees (>80 yr); Morphological Spatial Pattern Analysis (E and F) for the same activity centers as A and B (green = core + edge, blue = branches, red = scatter). Actual heights are 0–94 m; graphics are scaled by 0.2 for easier viewing.

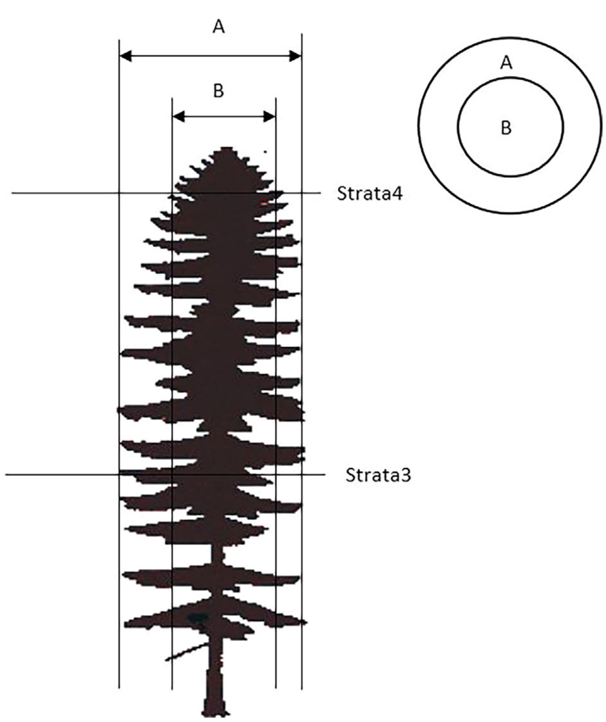

Figure 3. An example of how splitting the tree height profile into strata potentially underestimates the crown cover of a tree that spans >1 strata. A = the total area of the crown, B = the area of the crown in strata 4. The area of A–B is assigned to strata 3 in a simple division of the canopy height profile, even though the maximum height and age class of the tree is in strata 4. Tree graphic from http://www.nwplants.com. Accessed 20 August 2018.

covariates were the proportion of crown area of trees with maximum height in strata 3 and strata 4, respectively. We mapped only tree crowns higher than the bottom of strata 3 for the canopy covariates.

Barred Owl Effect

We had no direct monitoring data for barred owls in these study areas; however, during 1985–2015 we recorded over 16,000 barred owl responses during spotted owl surveys. These data are not comprehensive, as the surveys were not designed to estimate barred owl occupancy or abundance. Over the course of a survey season, however, if ≥3 nighttime surveys for spotted owls were conducted, the negative bias in detecting the presence of ≥1 barred owl on a given spotted owl territory each year was only about 14% (Wiens et al. 2011). Thus, these data could serve as an effective metric to quantify the effect of barred owls on spotted owl behavior, space use, and population performance (Bailey et al. 2009, Yackulic et al. 2014, Dugger et al. 2016). We generated a binary covariate of barred owl presence for barred owl responses occurring before or during the sampled year for each point; barred owl = 0 if there were no barred owl detections within 800 m, and barred owl = 1 if ≥1 barred owl was detected. We chose 800 m as our initial distance threshold because the proportion of inhabited spotted owl territories in a study in Oregon declined after barred owls were detected within 800 m (Kelly et al. 2003).

Resource Selection Analysis

We used multinomial logit discrete choice models in a Bayesian framework to evaluate the selection of activity centers within spotted owl territories. Discrete choice models link resource availability to specific animal locations via choice sets, supporting comparisons of environmental variables that change over time or space (Cooper and Millspaugh 1999). Discrete choice models are also more intuitive than traditional measures of habitat selection because results show the relative probability that a resource unit will be selected during 1 choice rather than across many choices (Cooper and Millspaugh 1999). Discrete choice models estimate the utility of each location in the choice-set as a linear function of regression coefficients and characteristics hypothesized to affect selection. The relative probability of selection for any one location within a choice set is solved as a function of utilities within choice sets (Thomas et al. 2006). We used Thiessen polygons from Dugger et al. (2016) that encompassed the interannual activity centers to represent spotted owl territories. To develop a choice set, we selected 2 random locations within each territory $\geq$400 m from the selected location. Random locations were constrained to forested cover in strata 3 and strata 4 (Table 1). We restricted these locations from recent clear cuts or other open areas because spotted owls nest only in forested areas (Thomas et al. 1990).

We fit discrete choice models using Markov chain Monte Carlo (MCMC) methods implemented in JAGS using the jagsUI package within Program R version 3.3.2 (Plummer 2015, R Core Team 2015, Kellner 2016). We assigned diffuse prior distributions for all parameters to reflect our lack of knowledge of parameter values. We assumed normal prior distributions, N ($\bar{x} = 0$, variance $= 100$) on all regression coefficients. For ease of reading, hereafter we refer to each regression coefficient distribution by the name of the associated covariate (i.e., canopy SD refers to the canopy SD coefficient). We examined 3 Markov chains for each model, using trace plots to confirm that no burn-in phase or thinning was necessary. All models converged after 1,000 iterations, yielding 3,000 samples from the joint posterior. We assessed convergence using the Brooks-Gelman-Rubin convergence diagnostic ($\widehat{R} \leq 1.1$) for all monitored parameters.

Model Selection and Fit

We used an information-theoretic approach in 2 stages to evaluate relative support for models containing habitat covariates and barred owl presence on the selection of activity centers within territories. In stage 1, we evaluated 25 *a priori* habitat models, representing plausible selection hypotheses for spotted owls, including a null model of uniform selection probability for each scale (50 m, 100 m, 200 m; Appendix B). We did not allow highly correlated variables (Spearman correlation >0.6) to occur in the same model and normalized all continuous variables prior to analysis to simplify covariate coefficient comparisons and aid model convergence. We assessed single factor and biologically plausible additive and interactive models related to canopy structure and distribution. We ranked all models using the Watanabe-Akaike Information Criterion (WAIC), a fully Bayesian alternative to Akaike's Information Criterion (AIC) estimating expected predictive error (Hooten and Hobbs 2015). We considered models within 2 WAIC as equally competitive. For each covariate in top models (in terms of WAIC), we present the mean of the posterior distribution (β), the 95% credible interval (CRI), and the proportion of the posterior with the same sign as the mean (f). Higher values of f (approaching 1) represent increasing confidence of the direction of a covariate effect. We calculated Estrella's R^2 as an indication of model fit for our top-ranked discrete choice models. Values of Estrella's R^2 range from 0 (i.e., predicts at random) to 1 (i.e., perfect prediction) with intermediate values of 0.25 and 0.50 generally considered to indicate modest and strong predictive accuracy, respectively (Estrella 1998, Rota et al. 2014). We predicted that the proportion of cover of ground level vegetation and very young age trees (strata 1 and strata 2) would be negatively related to activity center selection, whereas mature and canopy cover would be positively related because spotted owls select forested areas over non-forested (Lesmeister et al. 2018). We hypothesized that larger patches of overstory tree cover (core + edge), canopy, and canopy SD would also show positive relationships with activity center selection, whereas scattered overstory trees (scatter) would negatively influence selection, and strings of connected canopies (branch) would be scale-dependent. We carried the WAIC-selected best model from each scale-specific set of models forward to stage 2. In stage 2, we evaluated the effect of including barred owl as an additive or interactive effect on top models from stage 1. The candidate set also included a univariate barred owl model, and the null model for comparison. Because of the differences in forest structure among the study areas mentioned above, we examined an *a posteriori* model with a random effect for study area added to each covariate in the top model from the resource selection analysis following Thomas et al. (2006). We modeled study-wide resource selection by assuming area-level parameter coefficients arise from normal study-level distributions.

RESULTS

The mean canopy cover for spotted owl activity centers based on the 50-m analysis circles was 0.81 ± 0.12 (SD; range $= 0.14$–1.0; Table 2). There were differences in canopy cover among study areas, with Tyee showing the highest mean canopy cover (0.91, range = 0.62–1.0), and Southwestern Cascades showing the lowest (0.76, range = 0.51–0.95). The mean proportion of canopy cover for randomly available 50-m analysis circles was 0.68 ± 0.23 (range 0.04–1.0). As expected, canopy cover was slightly lower for selected locations at the larger analytical scales (100-m circle = 0.79, 200-m radius circle = 0.77). There were 254 locations (90 selected and 164 random) within choice sets where a barred owl was observed within 800 m; however, among most choice sets (116 of 196), both selected and random locations had the same barred owl status.

Our discrete choice modeling included 196 spotted owl choice sets (196 activity centers and 392 random available points). All habitat models performed better than the null model of random selection (Table 3; Appendix B). The model including covariates for canopy cover and canopy height heterogeneity (canopy SD) had the highest predictive accuracy and highest ranking at each of the 3 scales investigated (Table 3; Fig. 4). Top model coefficient distributions for canopy and canopy SD were both strongly positive ($f = 1$) and similar across all spatial scales, with canopy contributing slightly more to selection (Table 4). Estrella's R^2 was 0.59 for the top model (canopy + canopy SD, 100-m scale), indicating strong predictive accuracy (Rota et al. 2014; Fig. 5).

The presence or absence of barred owls as an additive or interactive effect did not improve performance (via WAIC ranking or Estrella's R^2) for any of the top habitat models. Although there were models containing barred owl presence that scored above other habitat-only models, all barred owl coefficient distributions were centered around zero ($f < 0.6$), indicating low confidence for contribution to selection (Table 5). For example, the addition of barred owl presence to the top model in the 100-m scale resulted in a ΔWAIC of 2.26 (Table 5), but the 95% CRI for the barred owl covariate was −0.55–0.62 ($\beta = 0.038$, $f = 0.55$). The addition of the random effect for study area improved the fit of the top model by 0.01 ($R^2 = 0.60$) but did not result in a competing model (ΔWAIC = 2.79) and area-specific coefficients overlapped and did not affect the interpretation of coefficients (Fig. 6).

DISCUSSION

We demonstrated the use of lidar-based metrics and discrete choice analysis in a Bayesian framework to quantify activity center selection by spotted owls. Many methods have been previously used to evaluate spotted owl habitat, nest, and roost site selection, including ground-based (Hershey et al. 1998), photo-interpreted (Forsman et al. 2015), or LandSat-based (Davis et al. 2016) delineation of habitat components. Ackers et al. (2015) reported fair to moderate agreement between lidar-based metrics and aerial photo interpretation of spotted owl nesting habitat, and other studies have reported correlations between lidar measurements and ground-based measurements of forest attributes in conifer forests (Hyde et al. 2005). The advantage of using lidar to measure canopy cover is that it can provide an accurate direct measurement of entire stands and larger areas, whereas ground plots need to be extrapolated or correlated with other remote-sensed data such as aerial photos or satellite data.

Table 2. Summary statistics ($\bar{x}$, SD, range = min. and max.) for canopy metrics for used spotted owl activity centers (selected) and random locations (available) within spotted owl territories. Values represent the proportion of each specific metric in the corresponding analysis circles (50-, 100-, and 200-m radii) in 5 study areas in Oregon, USA, 2008–2015.

	Selected				Available			
Covariate[a]	$\bar{x}$	**SD**	**min.**	**max.**	$\bar{x}$	**SD**	**min.**	**max.**
Core-edge.050	0.44	0.27	0.00	0.98	0.34	0.30	0.00	0.99
Core-edge.100	0.42	0.24	0.00	0.99	0.31	0.27	0.00	0.95
Core-edge.200	0.39	0.22	0.00	0.95	0.30	0.24	0.00	0.94
Canopy.050	0.81	0.12	0.14	1.00	0.68	0.22	0.04	1.00
Canopy.100	0.79	0.12	0.34	0.99	0.65	0.22	0.02	0.99
Canopy.200	0.77	0.11	0.39	0.98	0.64	0.20	0.01	0.98
Branch.050	0.36	0.19	0.01	0.76	0.29	0.20	0.00	0.83
Branch.100	0.35	0.16	0.01	0.70	0.27	0.17	0.00	0.78
Branch.200	0.34	0.14	0.03	0.64	0.27	0.15	0.00	0.69
Scatter.050	0.02	0.04	0.00	0.33	0.06	0.11	0.00	0.56
Scatter.100	0.02	0.05	0.00	0.38	0.07	0.10	0.00	0.54
Scatter.200	0.03	0.06	0.00	0.39	0.07	0.09	0.00	0.55
Canopy SD.050	13.44	3.45	2.82	23.67	11.54	4.04	2.91	25.19
Canopy SD.100	13.98	3.12	5.57	23.98	11.85	3.83	4.79	24.00
Canopy SD.200	14.33	2.80	8.27	24.52	12.26	3.67	4.44	22.43
Strata 1.100	0.07	0.08	0.00	0.45	0.14	0.16	0.00	0.78
Strata 1.200	0.08	0.08	0.00	0.43	0.15	0.15	0.00	0.83
Strata 1.050	0.06	0.08	0.00	0.38	0.13	0.16	0.00	0.85
Strata 2.050	0.13	0.10	0.01	0.86	0.19	0.15	0.00	0.78
Strata 2.100	0.14	0.09	0.01	0.61	0.21	0.14	0.01	0.81
Strata 2.200	0.16	0.08	0.01	0.50	0.22	0.14	0.02	0.83
Young.050	0.10	0.14	0.00	0.96	0.17	0.16	0.00	0.91
Young.100	0.11	0.12	0.00	0.87	0.19	0.15	0.00	0.77
Young.200	0.13	0.11	0.01	0.66	0.19	0.15	0.00	0.70
Mature.050	0.71	0.19	0.00	0.98	0.52	0.26	0.02	1.00
Mature.100	0.68	0.17	0.09	0.99	0.47	0.25	0.01	0.97
Mature.200	0.64	0.15	0.10	0.97	0.45	0.23	0.00	0.95

[a] Covariates are: canopy = the proportion canopy cover of young and mature tree crowns (young + mature); canopy SD = standard deviation of canopy height (m); strata 1 = ground vegetation 0–2 m; strata 2 = < 25-year-old trees; young = 25–80-year-old trees; mature = >80-year-old trees; core-edge = core (interior portion of a group of canopy pixels that are >8 m from an edge) + edge (pixels along the edge of core pixels that are large enough to contain at least 1 core pixel; branch = strings of canopy pixels that are not wide enough to contain any core pixels; scatter = groups of canopy pixels that are not large enough to qualify as core and do not connect with core pixels. The number after the covariate indicates the scale at which we measured the covariate: 50 m, 100 m, and 200 m.

Table 3. Summary of model selection results from the best-ranked models of resource selection when criteria are summarized at the 50-, 100-, and 200-m scales for spotted owl activity centers in Oregon, USA, 2008–2015. The top 2 models from each candidate set along with the null model of random selection are listed. Models are ranked according to the Wantanabe-Akaike Information Criterion (WAIC).

Model[a]	WAIC	loglik[b]	ΔWAIC	K[c]	Estrella's R^{2}[d]
50-m candidate set					
Canopy+canopy SD	308.82	−152.34	0.00	2	0.53
Mature+canopy SD	322.74	−159.40	13.92	2	0.48
Null	430.66	−215.33	121.84	0	0.00
100-m candidate set					
Canopy+canopy SD	290.93	−143.79	0.00	2	0.59
Mature+canopy SD	297.65	−146.92	6.72	2	0.57
Null	430.66	−215.33	139.73	0	0.00
200-m candidate set					
Canopy+canopy SD	293.93	−145.13	0.00	2	0.58
Mature+canopy SD	299.24	−147.47	5.31	2	0.56
Null	430.66	−215.33	136.72	0	0.00

[a] Covariates are canopy = the proportion canopy cover of young (25–80-yr-old) and mature tree crowns (young + mature); canopy SD = standard deviation of canopy height (m); mature = canopy cover of = >80-year-old trees.
[b] Log-likelihood.
[c] Number of parameters.
[d] Estrella's R^2 is an estimate of model fit, with 1 representing perfect prediction and 0 representing random selection.

We found that spotted owl activity center selection was most strongly related to greater canopy cover and greater structural complexity at the 100-m scale. Our results agree with other studies that showed spotted owls concentrate their activity in areas with the greatest canopy cover (Forsman et al. 1984, Ripple et al. 1997, Hershey et al. 1998, Swindle et al. 1999). As stated earlier, spotted owls may choose forests with greater canopy cover because these forests offer greater prey densities (Carey et al. 1992, Ward et al. 1998), a more temperate microclimate (Barrows 1981, Forsman et al. 1984, Jennings et al. 1999, Weathers et al. 2001), possibly a decreased probability of high-severity fire (Frey et al. 2016), and protection from predators (Forsman et al. 1984, Johnson 1993).

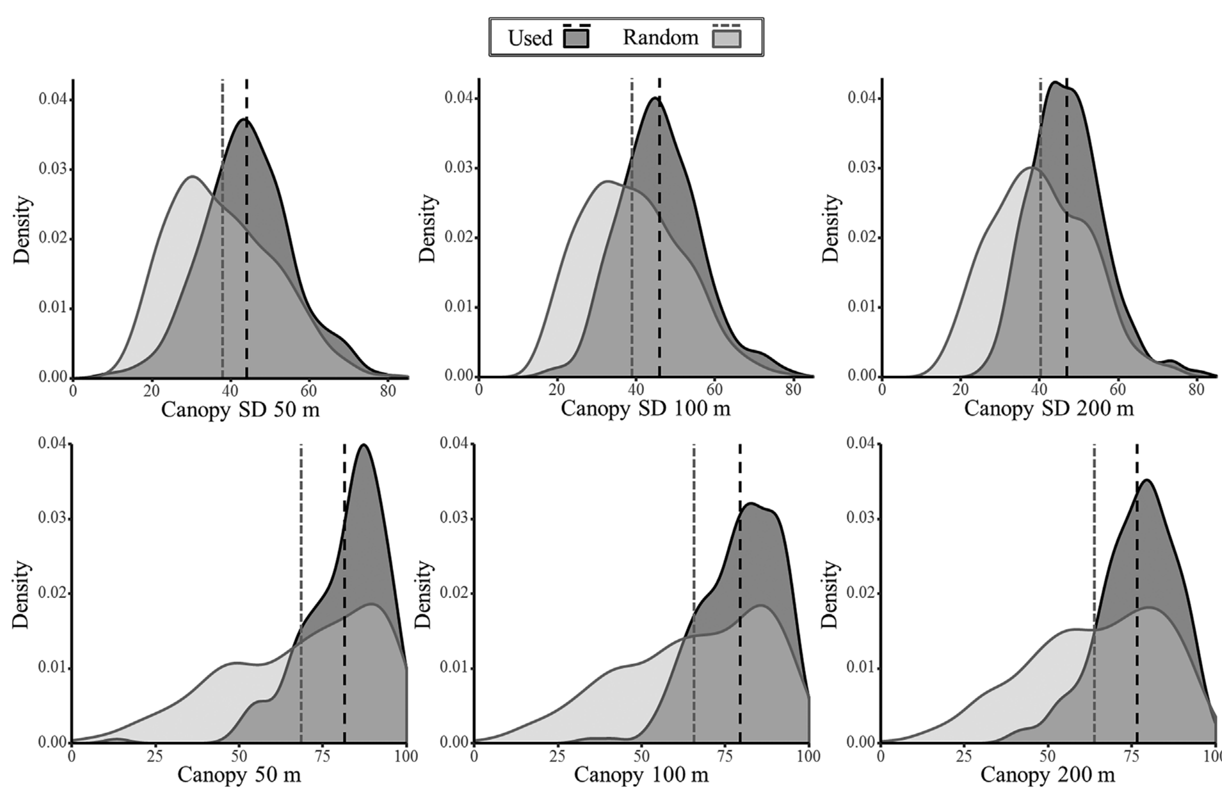

Figure 4. Density plots (summed area under each curve = 1) for the top covariates in terms of Watanabe-Akaike Information Criterion from discrete choice models of spotted owl activity centers, Oregon, USA, 2008–2015. Black and gray dashed lines represent the mean for each covariate for used and random locations, respectively. Canopy = the proportion canopy cover of young and mature tree crowns (young + mature); canopy SD = standard deviation of canopy height (m).

Table 4. Selection ratios (ratio), coefficient mean values (β), coefficient 95% credible intervals (CRI), and proportion of posterior with the same sign as the mean (*f*) for the top model at each scale for spotted owl activity centers in Oregon, USA, 2008–2015.

Covariate[a]	Ratio[b]	*β*	95% CRI	*f*
50-m scale				
Canopy	4.22	1.44	1.04, 1.84	1
Canopy SD	2.47	0.90	0.63, 1.18	1
100-m scale				
Canopy	4.14	1.42	1.04, 1.83	1
Canopy SD	2.77	1.02	0.72, 1.33	1
200-m scale				
Canopy	3.67	1.30	0.93, 1.71	1
Canopy SD	3.06	1.12	0.77, 1.50	1

[a] Covariates are: canopy = the proportion canopy cover of young (25–80-yr-old) and mature (>80-yr-old) tree crowns; canopy SD = standard deviation of canopy height (m).

[b] The selection ratio from model coefficients (exp[β]) measures the multiplicative change in relative probability of use when a covariate changes by one unit, assuming all others remain constant.

The cover of mature trees accounted for a larger proportion of canopy cover than did young trees across all scales at our spotted owl activity centers. This result is consistent with a recent study that reported the canopy cover of tall (>48 m) trees predicted California spotted owl activity centers (North et al. 2017). Neither of our models containing individual covariates for young or mature forest were competitive for predicting spotted owl activity center selection. We constrained our random points to be in young or mature forest stages (i.e., ≥25 yr old), which may have weakened our ability to detect the effect of these covariates on spotted owl nest and roost site selection.

We demonstrated a repeatable method for assessing canopy cover that should be applicable throughout the range of spotted owls for mapping potential nesting and roosting forest cover. Lidar-based metrics, however, have ≥3 limitations for determining exact tree height. First, determining the actual ground surface is difficult in high canopy cover conditions because the number of laser pulses reaching the ground is less than in more open canopy conditions (Lefsky et al. 2002). This is potentially further confounded in areas of substantial ground cover (i.e., 0–2 m) vegetation. Errors in estimating the ground surface would result in errors estimating canopy height because the canopy height is the difference between the height of the first lidar returns and the ground surface, but these errors are generally minimal (Reutebuch et al. 2003). Second, the actual top of the tree may be missed by laser pulses so the exact height may be underestimated (Lefsky et al. 2002). Third, in highly dissected and steep terrains, the lean of trees can also incur error in tree height based on the difference between highest hit and bare earth. These problems would not likely have affected our estimates of canopy cover because canopy height was binned into strata that are coarse enough to render small errors in height estimates unimportant. Our measure of

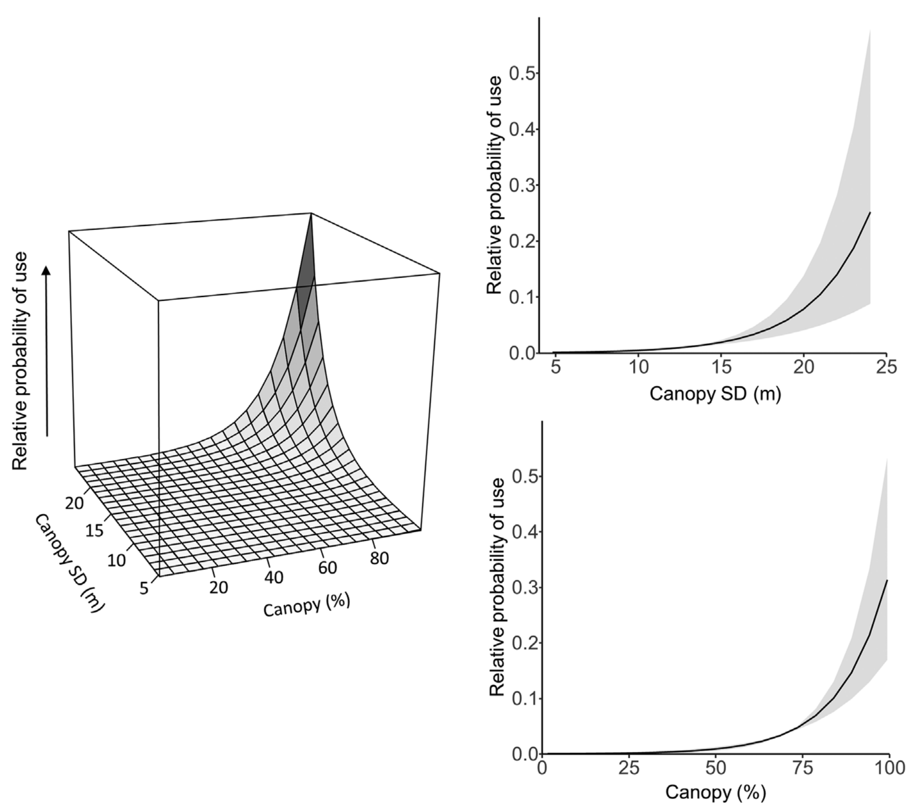

Figure 5. Probability of selection versus the proportion of canopy cover of young (25–80-yr-old) and mature (>80-yr-old) tree crowns (canopy), and standard deviation of canopy height (canopy SD; m) for spotted owl activity centers in Oregon, USA, 2008–2015, based on the top model in terms of Wantanabe-Akaike Information Criterion (WAIC): canopy + SD. Shading indicates 95% credible interval.

Table 5. Model selection results from additive and interactive resource selection models for spotted owl activity centers combining the top habitat model at each scale with barred owl presence (barred owl) for 5 study areas in Oregon, USA, 2008–2015. Models are ranked according to the Wantanabe-Akaike Information Criterion (WAIC). Numeric values coupled with covariate acronyms signify the radius (m) of the analysis circle.

Model[a]	WAIC	loglik[b]	ΔWAIC	K[c]	R^2[d]
Canopy100+canopy SD100	290.98	−143.79	0.00	2	0.59
Canopy100+canopy SD100+barred owl	293.24	−143.73	2.26	3	0.59
Canopy200+canopy SD200	293.97	−145.13	3.00	2	0.58
Canopy100+canopy SD100+barred owl+(canopy SD100×barred owl)	294.93	−143.73	3.96	4	0.59
Canopy100+canopy SD100+barred owl+(canopy100 × barred owl)	295.05	−143.80	4.08	4	0.59
Canopy200+canopy SD200+barred owl	296.26	−145.07	5.28	3	0.58
Canopy100+canopy SD100+barred owl+(canopy100×barred owl)+(canopy SD100×barred owl)	296.67	−143.78	5.69	5	0.59
Canopy200+canopy SD200+barred owl+(canopy SD200×barred owl)	298.02	−145.12	7.05	4	0.58
Canopy200+canopy SD200+barred owl+(canopy200×barred owl)	298.08	−145.03	7.10	4	0.58
Canopy200+canopy SD200+barred owl+(canopy200×barred owl)+(canopy SD200×barred owl)	300.35	−145.08	9.37	5	0.58
Canopy50+canopy SD50	308.83	−152.34	17.86	2	0.53
Canopy50+canopy SD50+barred owl	310.78	−152.37	19.80	3	0.53
Canopy50+canopy SD50+barred owl+(canopy50×barred owl)	312.51	−152.21	21.53	4	0.53
Canopy50+canopy SD50+barred owl+(canopy SD50×barred owl)	312.86	−152.32	21.88	4	0.53
Canopy50+canopy SD50+barred owl+(canopy50×barred owl)+(canopy SD50×barred owl)	314.80	−152.13	23.83	5	0.53
Null	430.66	−215.33	139.68	0	0.00
Barred owl	430.96	−214.56	139.98	1	0.01

[a] Covariates are canopy = the proportion canopy cover of young (25–80-yr-old) and mature (>80-yr-old) tree crowns; canopy SD = standard deviation of canopy height (m); barred owl = barred owl detected within 800 m.
[b] Log likelihood.
[c] Number of parameters.
[d] Estrella's R^2 is an estimate of model fit, with 1 representing perfect prediction and 0 representing random selection.

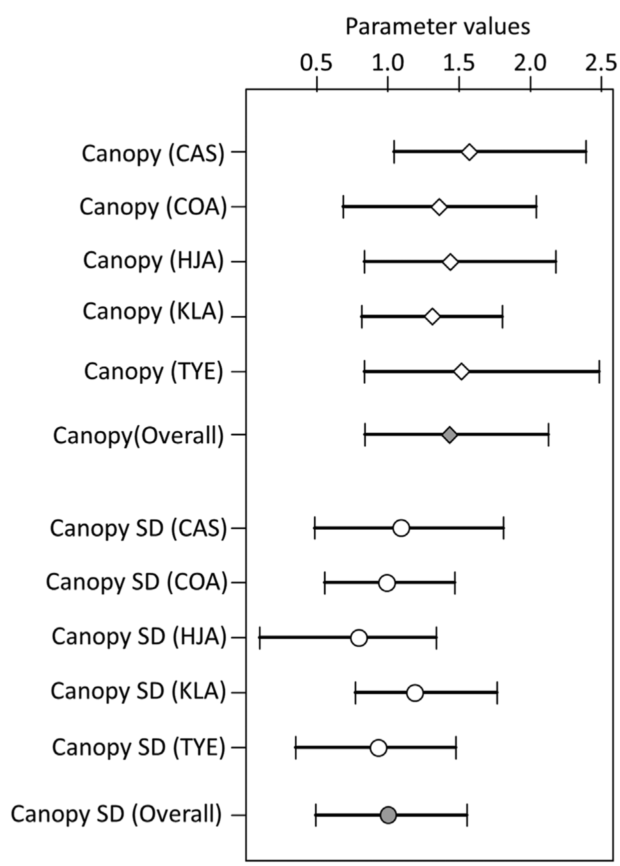

Figure 6. Area-specific (open) and study-wide (filled) parameter coefficients for the top model with random effects of area for activity center selection by spotted owls in Oregon, USA, 2008–2015. Error bars represent 95% credible intervals. Canopy = the proportion canopy cover of young (25–80-yr-old) and mature (>80-yr-old) tree crowns; SD = standard deviation of canopy height. Study areas include Southwestern Cascades (CAS), Coast Range (COA), H. J. Andrews (HJI), Klamath (KLA), and Tyee (TYE).

vertical heterogeneity (SD of canopy surface), however, may be slightly biased low if the canopy height measurements are biased low. Despite these minor limitations, lidar remains one of the most efficient and repeatable tools available to measure forest canopy structure at large scales. The accuracy and precision of measurements obtained by lidar would be nearly impossible and more expensive to obtain with field-based methods.

We expected to observe stronger selection for stands with a more contiguous canopy, but there was little support for models that contained these metrics. This finding is probably because as stands mature, trees senesce, break, and fall over creating small openings in the canopy (Franklin et al. 2002), which could contribute to a less contiguous canopy in the analysis circle as stands progress through successional stages.

Nearly all existing literature describing spotted owl nest areas shows these stands have dense, structurally diverse canopies (Table 6), and spotted owls inhabit forests with substantial mature cover and heterogeneous canopy structure (Forsman et al. 1984, Hershey et al. 1998, LaHaye and Gutiérrez 1999). The values given for canopy cover and canopy closure, however, can vary to the extent these metrics are measuring different attributes of the forest canopy, as described earlier. The repeatability and fine-scale resolution offered by lidar supports its adoption for consistent assessment of canopy cover and habitat for spotted owls.

Our barred owl covariate did little to explain selection of spotted owl activity centers, which could be the result of our barred owl data being too coarse, spatially, or temporally. Nest sites and primary roost sites likely reflect key habitat within a territory (third-order selection; Johnson 1980) that spotted owls must defend against barred owls throughout the year if they are going to remain in a territory and attempt to

Table 6. Comparison of canopy cover and closure values from selected studies of spotted owls.

Metric	How measured	$\bar{x}$ (%)	Range (%)	Activity center type	Region	Source
Closure	Occular	68	35–91	Nest stands	Oregon	Forsman et al. (1984:30)
Closure	Spherical densiometer	77	73–79	Nest stands	Oregon	Hershey et al. (1998:1403)
Closure	Spherical densiometer	75		Nest stands	N. California	Lahay and Guiterrez (1999:327)
Cover	Aerial photo, ground based	na	71–100	Nest stands	E. Washington Cascades	Loehle et al. (2011:92)
Closure	Fisheye lens	75	57–95	Nest stands	E. Washington Cascades	Buchanan et al. (1995:305)
Closure	Concave densiometer	>80		Nesting, foraging	W. Oregon	Irwin et al. (2000:180)
Closure	Hemisperical densiometer	93	50–100	Foraging, roosting	E. Washington Cascades	King et al. (1993:A1)
Cover	Lidar[a]	81	13–100	Activity centers	Oregon	This study
Closure	Moosehorn densiometer	66		Dispersal	E. Washington Cascades	Sovern et al. (2015:257)
Closure	Moosehorn densiometer	84		Roost sites	Central Washington	Herter et al. (2002:440)
Cover	Lidar[a]	82		Activity centers	California[b]	North et al. (2017:172)

[a] Light detection and ranging.
[b] California spotted owl.

reproduce. A large body of literature suggests a negative effect of barred owls on many aspects of spotted owl life history (Lesmeister et al. 2018), but the strongest effects have been observed on territory occupancy dynamics (second-order selection; Johnson 1980; Olson et al. 2005; Kroll et al. 2010; Dugger et al. 2011, 2016) and with the exception of Wiens et al. (2014), the effect on reproductive success is more difficult to document. When spotted owls can maintain pair status and defend a territory, they can at least attempt to breed (Forsman et al. 2011, Dugger et al. 2016). A relatively long history of competition with barred owls may have already affected where spotted owl territories in our study were placed, but that effect is acting at a different scale than this analysis.

MANAGEMENT IMPLICATIONS

A large proportion of the overstory canopy cover in spotted owl activity centers comes from taller (older) trees. A combination of old and young trees may be more important than just tall, old trees. In light of efforts to thin forested stands to reduce susceptibility to fire or to promote faster tree growth and structural complexity, tree mapping GIS tools and high-resolution canopy height data from techniques such as lidar can assist planners in mapping pre- and post-thinning canopy heights, providing valuable information as to the potential effects of thinning treatments. A consistent method for determining canopy cover is needed to compare management prescriptions with relevant habitat studies; this project demonstrates an important step in accomplishing that goal.

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APPENDIX A. LIDAR DATA

Table A1. Description of the light detection and ranging (lidar) acquisition parameters for lidar missions across 5 spotted owl study areas sampled in Oregon, USA, 2008–2015. All projects had 100% swath overlap. Asterisks denote missing data.

Project	Year	Sensor(s)[a]	Aircraft(s)[b]	Altitude (m)	Field of view (degrees)	Side-lap (%)	Pulse rate	Pulse density ($\bar{x}$)	Absolute vertical accuracy
Big Windy	2013	1	1	900	30	*	96–105	10.7	0.03
Blue River	2011	2	1	900	28	*	105	10.4	0.05
Central Coast	2012	1,3,5	1,2	900–1,400	30	60	105	11.5	0.05
Crater Lake	2010	2,3	1,2	900–1,300	28–30	50	83	8.4	0.05
H.J. Andrews[c]	2008	2	1	900	28	50	105	9.1	0.02
Keno	2012	1,3	1,2	900	30	60	96–105	8.02	0.04
Klamath	2011	1,4	1	900–1,500	24–30	50	105–150	8.6	0.03
Lane County	2014	1,5	1,3	900–1,400	30	65	190–198	10.4–10.6	0.03
North Coast	2009	2	1,2	900	30	60	99	8.6	0.03
Rogue River	2012	1,3,5	1,2	900–1,300	28–30	60	47–52	10.4	0.05
South Coast	2009	2	1	*	*	75	*	8.1	0.05
Umpqua River	2009	2	1	900	28	50	105	8.8	0.04
Willamette Valley	2009	2	1,2	900	30	60	99	8.1	0.04
Yambo	2010	2,3	1	900–13,00	28	50	105	9.2	0.04

[a] Sensor key: 1) Leica ALS50; 2) Leica ALS50 phase II; 3) Leica ALS60; 4) Leica ALS60 phase II; 5) Leica ALS70.
[b] Aircraft key: 1) Cessna Caravan 208B; 2) Parnavia P68; 3) Piper PA-31.
[c] Values from Blue River project.

APPENDIX B. COMPLETE MODEL SELECTION RESULTS

Table B1. Model selection results for 50-m radius analysis circle candidate set for spotted owl activity centers in 5 study areas in Oregon, USA, 2008–2015. Interaction models (e.g., strata 1 × branch) also included additive component covariates but are omitted below for brevity.

Model[a]	WAIC[b]	loglik[c]	ΔWAIC	K[d]	Estrella's R^{2}[e]
Canopy+canopy SD	308.82	−152.34	0.00	2	0.53
Mature+canopy SD	322.74	−159.40	13.92	2	0.48
Mature+branch	325.34	−160.77	16.53	2	0.47
Strata 1×mature	329.04	−161.18	20.22	3	0.47
Mature	334.92	−166.52	26.10	1	0.43
Scatter+canopy SD	344.44	−170.01	35.62	2	0.41
Scatter×canopy SD	345.13	−169.42	36.32	3	0.41
Branch×core-edge	345.88	−170.16	37.06	3	0.40
Branch+core-edge	347.49	−171.67	38.67	2	0.39
Branch×canopy	351.50	−172.81	42.69	3	0.38
Core-edge+canopy SD	356.80	−176.46	47.98	2	0.35
Canopy	357.98	−178.14	49.16	1	0.34
Strata 1+strata 2	358.03	−177.22	49.21	2	0.35
Branch+scatter	373.47	−184.49	64.65	2	0.29
Scatter	374.12	−186.01	65.30	1	0.28
Strata 1	375.07	−186.65	66.25	1	0.27
Canopy SD	391.06	−194.48	82.24	1	0.20
Strata 2	392.38	−195.00	83.56	1	0.20
Young	402.38	−199.79	93.57	1	0.15
Branch	409.32	−203.79	100.50	1	0.11
Core-edge	409.50	−203.68	100.69	1	0.12
Null	430.66	−215.33	121.84	0	0.00

[a] Covariates are canopy = the proportion canopy cover of young and mature tree crowns (young + mature); canopy SD = standard deviation of canopy height (m); strata 1 = ground vegetation 0–3 m; strata 2 = < 25-year-old trees; young = 25–80-year-old trees; mature = >80-year-old trees; core-edge = core (interior portion of a group of canopy pixels that are >8 m from an edge) + edge (pixels along the edge of core pixels that are large enough to contain at least 1 core pixel; branch = strings of canopy pixels that are not wide enough to contain any core pixels; scatter = groups of canopy pixels that are not large enough to qualify as core and do not connect with core pixels.
[b] Watanabe-Akaike Information Criterion.
[c] Log-likelihood.
[d] Number of parameters.
[e] Estrella's R^2 is an estimate of model fit, with 1 representing perfect prediction and 0 representing random selection.

Table B2. Model selection results for 100-m radius analysis circle candidate set for spotted owl activity centers in 5 study areas in Oregon, USA, 2008–2015. Interaction models (e.g., strata 1 × branch) also included additive component covariates but are omitted below for brevity.

Model[a]	WAIC[b]	Loglik[c]	ΔWAIC	K[d]	Estrella's R^{2}[e]
Canopy+canopy SD	290.93	−143.79	0.00	2	0.59
Mature+canopy SD	297.65	−146.92	6.72	2	0.57
Mature+branch	305.87	−151.04	14.94	2	0.54
Strata 1×mature	310.10	−150.32	19.17	3	0.55
Mature	313.01	−155.53	22.08	1	0.51
Scatter+canopy SD	330.98	−163.68	40.05	2	0.45
Core-edge+canopy SD	332.04	−164.22	41.11	2	0.45
Scatter×canopy SD	333.07	−163.86	42.14	3	0.45
Branch+core-edge	339.41	−167.90	48.48	2	0.42
Branch×core-edge	340.68	−167.52	49.75	3	0.42
Branch×mature	341.52	−168.10	50.59	3	0.42
Canopy	344.56	−171.58	53.63	1	0.39
Strata 1+strata 2	345.17	−171.13	54.24	2	0.40
Strata 1	366.75	−182.60	75.82	1	0.30
Canopy SD	369.99	−184.04	79.06	1	0.29
Branch+scatter	371.67	−183.83	80.74	2	0.29
Scatter	375.79	−186.91	84.86	1	0.27
Strata 2	381.82	−189.93	90.89	1	0.24
Young	387.85	−192.72	96.92	1	0.22
Core-edge	396.75	−197.43	105.82	1	0.17
Branch	401.65	−200.02	110.72	1	0.15
Null	430.66	−215.33	139.73	0	0.00

[a] Covariates are canopy = the proportion canopy cover of young and mature tree crowns (young + mature); canopy SD = standard deviation of canopy height (m); strata 1 = ground vegetation 0–3 m; strata 2 = < 25-year-old trees; young = 25–80-year-old trees; mature = >80-year-old trees; core-edge = core (interior portion of a group of canopy pixels that are >8 m from an edge) + edge (pixels along the edge of core pixels that are large enough to contain at least 1 core pixel; branch = strings of canopy pixels that are not wide enough to contain any core pixels; scatter = groups of canopy pixels that are not large enough to qualify as core and do not connect with core pixels.

[b] Watanabe-Akaike Information Criterion.

[c] Log-likelihood.

[d] Number of parameters.

[e] Estrella's R^2 is an estimate of model fit, with 1 representing perfect prediction and 0 representing random selection.

Table B3. Model selection results for 200-m radius analysis circle candidate set for spotted owl activity centers in 5 study areas in Oregon, USA, 2008–2015. Interaction models (e.g., strata 1 × branch) also included additive component covariates but are omitted below for brevity.

Model[a]	WAIC[b]	loglik[c]	ΔWAIC	K[d]	Estrella's R^{2}[e]
Canopy+canopy SD	293.93	−145.13	0.00	2	0.58
Mature+canopy SD	299.24	−147.47	5.31	2	0.56
Mature+branch	306.68	−151.32	12.75	2	0.54
Strata 1×mature	312.56	−152.34	18.63	3	0.53
Mature	314.42	−156.27	20.49	1	0.51
Core-edge+canopy SD	329.14	−162.48	35.21	2	0.46
Scatter+canopy SD	329.92	−162.30	35.99	2	0.46
Scatter×canopy SD	330.74	−162.18	36.81	3	0.46
Branch+core-edge	340.20	−168.11	46.27	2	0.42
Branch×core-edge	341.32	−167.63	47.39	3	0.42
Branch×mature	341.46	−168.13	47.53	3	0.42
Strata 1+strata 2	345.47	−171.23	51.53	2	0.40
Canopy	345.72	−172.08	51.79	1	0.39
Canopy SD	356.95	−177.46	63.02	1	0.35
Strata 1	364.91	−181.54	70.98	1	0.31
Branch+scatter	370.04	−182.35	76.10	2	0.31
Scatter	379.55	−188.21	85.62	1	0.26
Strata 2	387.36	−192.72	93.42	1	0.22
Branch	391.17	−194.58	97.23	1	0.20
Young	392.62	−195.21	98.69	1	0.19
Core-edge	393.69	−195.85	99.76	1	0.19
Null	430.66	−215.33	136.72	0	0.00

[a] Covariates are canopy = the proportion canopy cover of young and mature tree crowns (young + mature); canopy SD = standard deviation of canopy height (m); strata 1 = ground vegetation 0–3 m; strata 2 = < 25-year-old trees; young = 25–80-year-old trees; mature = >80-year-old trees; core-edge = core (interior portion of a group of canopy pixels that are >8 m from an edge) + edge (pixels along the edge of core pixels that are large enough to contain at least 1 core pixel; branch = strings of canopy pixels that are not wide enough to contain any core pixels; scatter = groups of canopy pixels that are not large enough to qualify as core and do not connect with core pixels.

[b] Watanabe-Akaike Information Criterion.

[c] Log-likelihood.

[d] Number of parameters.

[e] Estrella's R^2 is an estimate of model fit, with 1 representing perfect prediction and 0 representing random selection.