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Resource selection by GPS-tagged California spotted owls in mixed-ownership forests

Fidelis A. Atuo[a,*], Kevin Roberts[b], Sheila Whitmore[a], Brian P. Dotters[b], Martin G. Raphael[c], Sarah C. Sawyer[d], John J. Keane[e], R.J. Gutiérrez[a], M. Zachariah Peery[a]

[a] Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA
[b] Sierra Pacific Industries, PO Box 496014, Redding, CA, USA
[c] USDA Forest Service, Pacific Northwest Research Station, Olympia, WA, USA
[d] USDA Forest Service, Pacific Southwest Region, Vallejo, CA, USA
[e] USDA Forest Service, Pacific Southwest Research Station, Davis, CA, USA

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ABSTRACT

The relative contribution of private and public forest to the conservation of species in mixed-ownership landscapes has often been contentious because management goals vary among owners. This tension can be exacerbated by a lack of understanding about how wildlife use habitats managed by different landowners and the relative value of habitats in having different structures, configurations, and management histories. To address this knowledge gap and enhance science-based conservation planning among different ownerships, we analyzed habitat selection by 53 GPS-tagged California spotted owls across multiple temporal scales within mixed-ownership landscapes in the Sierra Nevada. At a fine temporal scale, step-selection function analysis of hourly locations collected by GPS tags suggested that foraging spotted owls selected closed-canopy, larger-tree forest (Quadratic Mean Diameter [QMD] ≥ 33 cm, canopy cover ≥ 60%). Point selection function (PSF) analysis based on single nightly locations suggested that spotted owls selected a broader range of forest conditions including selection of forests having intermediate sized trees and intermediate canopy cover (QMD 28–33 cm, canopy cover ≥ 50%), and the strength of selection for these forest conditions increased in the less frequently used areas of home ranges. The PSF also suggested that spotted owls selected areas with relatively high cover type heterogeneity that included a mix of seral stages, except in the core of their home range where they selected relatively spatially homogenous forests characterized by large trees and closed canopy. Spotted owl home ranges increased in size with increasing elevation and cover type heterogeneity, and decreased in size with forest characterized by intermediate-sized trees. Collectively, these results indicate that landscapes having forest patches characterized by either intermediate or large-sized trees, both with high canopy cover, likely constitute the important foraging habitat for California spotted owls in Sierra Nevada mixed conifer forests. However, selection for any one particular cover type was not sufficiently strong for us to infer selection of individual landownership types, in spite of differences in forest conditions among ownerships. Collectively, our findings suggest that privately-owned lands used in our study may harbor more suitable spotted owl foraging habitat than previously recognized. Finally, given the importance of understanding the relationship between landowner management priorities and the resultant pattern of vegetation on lands with different ownerships, the development of forest management strategies relevant for broad-scale conservation of the Sierra Nevada forest will benefit from effective collaboration between forest managers, landowners, and research organizations.

1. Introduction

Balancing forest resource use and species conservation objectives has become a dominant theme in forest science and management (Chaudhary et al., 2016; Heikkala et al., 2016; Moussaoui et al., 2016). Achieving these sometimes conflicting objectives can be difficult in mixed-ownership (private and public) landscapes because forests are managed according to different priorities, silvicultural practices, and regulatory mechanisms (Thomas, 1990; Christensen et al., 1996; Bergmann and Bliss, 2004). Typically, publicly-owned forests are

* Corresponding author.
E-mail address: atuo@wisc.edu (F.A. Atuo).

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managed for a suite of objectives such as timber production, species conservation, watershed integrity, fuels management, and recreation, whereas privately-owned industrial forests are more often managed with an emphasis for commercial timber production. Spatial pattern of landownership can further challenge conservation when, for example, private lands occur in close proximity to public lands such that species use both ownership types. Despite such patterns, the relatively large global expanse of privately-owned forestlands suggests that conservation focused solely on habitat protection on public lands may be insufficient in many places to achieve species conservation objectives (Chaudhary et al., 2016). Therefore, encouraging and incentivizing private, industrial forest owners to promote species conservation during commercial timber management is considered a key component in maintaining global biodiversity (Knight, 1999).

The contribution of privately-owned forests to biodiversity conservation depends on timber management strategies that retain contributions to habitat quantity, quality, and connectivity for species of concern. Effective conservation planning in such landscapes requires an understanding of: (1) how species use different landownerships to meet their life-history requirements, and (2) what constitutes high-quality habitat in forests that are often markedly different in species composition, structure, and management histories. Addressing these questions can provide a strong scientific basis for cooperative forest management in mixed-ownership landscapes that leads to both species conservation and economic opportunities. Effective species conservation in mixed-ownership forests, however, is often hampered by a lack of research on private lands stemming from landowner concerns about regulatory actions that might result from research findings (Dale et al., 2000; Norton, 2000; Mir and Dick, 2012). Therefore, effective conservation efforts among private landowners, government agencies, and researchers will benefit from being both transparent and collaborative (Selin and Chevez, 1995; Wondolleck and Yaffee, 2000).

The California spotted owl (*Strix occidentalis occidentalis*) is one of the three subspecies of spotted owls recognized by the American Ornithologists' Union (1957). It occurs primarily in mature closed-canopy forests that are multistoried or complex in structure with abundance of large trees and large coarse woody debris (Gutiérrez et al., 1995; Verner et al., 1992a; Roberts, 2017). In the Sierra Nevada, most spotted owls are concentrated in mid-elevation mixed-conifer forests, but they also occur at lower density in lower and higher elevation forests (Gutiérrez et al., 1992, Roberts, 2017). Although the California spotted owl is not listed as a threatened/endangered species at the federal level, it is a "species of special concern" at the state level, and has experienced a steady population decline on demographic study areas within national forests over the last 20 years (Gutiérrez et al., 2017). Habitat loss and fragmentation from forest management and high-severity fire and competition with the barred owl (*Strix varius*) have been identified as threats to the owl (Eyes et al., 2017; Jones et al., 2016; Keane, 2017).

Until recently, it has been assumed that successful conservation planning for the California spotted owl hinged primarily on management within national forests, whereas private lands were believed to make a relatively modest or unknown contributions to its population viability (Verner et al., 1992a, Peery et al., 2017). However, early studies demonstrated that spotted owls selected public lands over private lands for both nesting and roosting in a mixed-ownership in the central Sierra Nevada (Bias and Gutiérrez, 1992; Gutiérrez, 1994) and owls had a 15% higher probability of using publicly- than privately-owned lands for foraging (Williams et al., 2014). By contrast, a recent study found that California spotted owl had relatively high occupancy rates and crude densities in a set of landscapes composed primarily of private lands (Roberts et al., 2017). Therefore, we studied resource selection and space use by California spotted owl during putative foraging activities in a landscape containing public and private lands to understand the contributions of mixed-ownership forests to spotted owl conservation in the Sierra Nevada. Previous studies have characterized foraging habitat and space use by California spotted owls (Call et al., 1992; Williams et al., 2011, 2014; Eyes et al., 2017; Gallagher et al., 2018), but our study represents an important advance in the understanding of spotted owl habitat selection in several respects. First, we characterized habitat selection patterns using a sample size of individuals that was considerably greater than prior studies and included individuals distributed across relatively broad environmental gradients (e.g., latitude, elevation, forest types, and landownerships). Second, individuals were marked with GPS tags capable of collecting multiple locations per night, whereas VHF radio-telemetry requires physically tracking individuals in rugged terrain and typically yields fewer locations. By collecting several locations per night, we are able to characterize fine-scale (within-night) habitat selection patterns for the first time in this species, an important advance given that the ecological factors that modulate organisms' habitat choices are often structured across ecological scales that vary in space and time (Turner, 1989; Kotliar and Wiens, 1990; McGarigal et al., 2016). Third, GPS tags typically yield more precise locations compared to VHF telemetry, which is particularly important when studying habitat selection in landscapes characterized by fine-scale heterogeneity in habitat and landownership conditions, as is the case in the Sierra Nevada. Finally, habitat selection was inferred based on a vegetation map that we developed using a combination of dense vegetation sampling and high resolution aerial imagery that provided a highly accurate depiction of habitat conditions within owl home ranges. Hence, these advances should provide novel insights into habitat selection and thus allow a stronger scientific basis for spotted owl conservation planning in mixed-ownership landscapes.

2. Materials and methods

2.1. Study area description

Our study areas occurred in the Sierra Nevada in Tehama, Eldorado, Butte, Plumas, Yuba, Sierra, Nevada, Placer, Amador, and Calaveras counties and included the Tahoe, Eldorado, Plumas, and Stanislaus National Forests Mixed conifer was the primary forest type on all study areas, which had a dominant tree canopy of Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), black oak (*Quercus kelloggii*), live oaks (*Quercus chrysolepis* and *Q. wislizeni*), Pacific madrone (*Arbutus menziesii*), and incense-cedar (*Calocedrus decurrens*) (Mayer and Laudenslayer, 1988). Elevations ranged between 400 and 2200 m. The climate was Mediterranean with an average of 1182 mm of precipitation most of which fell as snow (Tempel et al., 2015). These landscapes contained a mosaic of publicly-owned national forests managed by the US Forest Service, large privately-owned forests managed for commercial timber production, and smaller privately-owned parcels managed for other uses (Fig. 1). Sierra Pacific Industries (SPI) was our cooperating private landowner and managed 49% of the area encompassing the owl home ranges we used in this study. The US Forest Service managed 40% of these areas with the remaining 11% managed by small private landowners. Logging began in the Sierra Nevada in the late 19th century and involved the selective removal of large, commercially valuable trees. Recent logging has emphasized "diameter-limited thinning from below" on national forests while even-aged management practices such as clear-cutting and groups selection is predominant on private lands (North et al., 2017). Timber harvesting and fire suppression on national forests have resulted in spatially homogenous forest cover with high tree densities and a "large-tree deficit" (Jones et al., 2018), whereas timber harvesting on privately-owned lands typically has resulted in a mosaic of different-aged forest stands (Baker, 2014; North et al., 2017; Jones et al., 2018). Clear-cuts often result in abrupt successional differences between regenerating forest stands on private and more mature – albeit spatially homogeneous forest cover on public lands (Bias and Gutiérrez, 1992; Fedrowitz et al., 2014; Williams et al., 2014). Finally, wildfires have affected forest structure on some of these areas, particularly the 2014

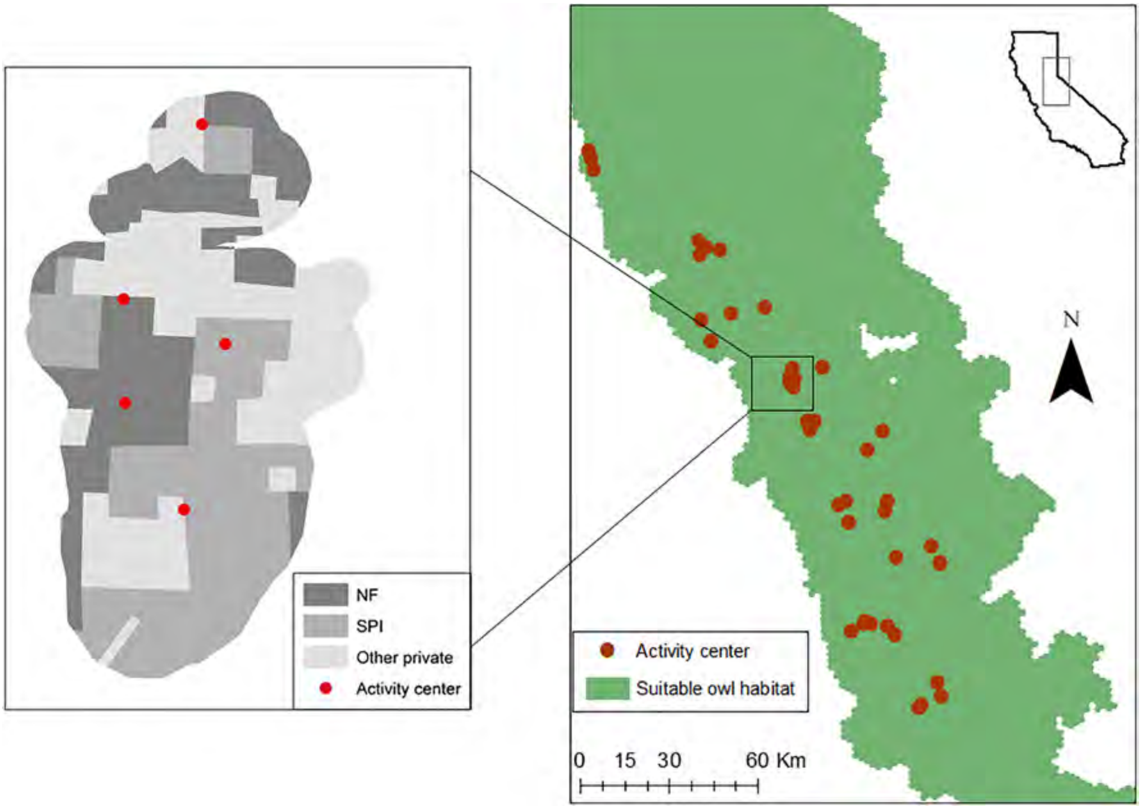

Fig. 1. California spotted owl study area showing activity centers of 53 GPS tagged owls in the Sierra Nevada, California, USA. Study area boundary was based on the 95% kernel home ranges of 53 individual owls. The suitable owl habitat (area in green) is based on the U.S Forest Service, Pacific Southwest Research Station's delineation (Keane unpublished data). The insert illustrates patterns of landownership in the study area.

King Fire that severely burned parts of several owl sites included in this study (Jones et al., 2016; see below).

2.2. Owl captures and monitoring

We captured and monitored 53 GPS-tagged California spotted owls during the breeding season (April–July) of 2017 (Fig. 1). Territories in which owls were selected for telemetry monitoring were chosen opportunistically but spanned a broad range of elevation, landownership, and vegetation conditions, which we believed represented conditions used by owls throughout the ecoregion (Fig. 2). We captured owls by hand and with snare poles as described by Franklin et al. (1996) prior to or early in the nesting season and fitted them with remotely-downloadable GPS tags (Lotek Wireless, model Pinpoint VHF 120) weighing approximately 10 g (< 2% of average California spotted owl body mass). Tags were either attached using a backpack harness or as tail mounts and were either retrieved by recapture at the end of the study or expected to be shed during molt, respectively. Tags were programmed to obtain hourly locations from 22:00 to 02:00 every night. Spotted owls are nocturnal predators that forage by moving from perch to perch (Forsman et al., 1984; Delaney et al., 1999) and we therefore assumed that most GPS fixes represented foraging locations, acknowledging that owls engage in other activities at night including resting, territory defense, and prey delivery to nests. We remotely downloaded data from GPS tags every 3–4 weeks. We removed all locations with a DOP (dilution of precision) score > 5 (resulting from poor satellite signals) prior to analysis to avoid potential erroneous inference about space use and movement. We defined activity centers for each GPS-tagged owl, in order of priority, based on the location of a (i) nest and (ii) the geometric center of all daytime (i.e., roosting) locations obtained as part of capture attempts and GPS data retrieval.

2.3. Cover type mapping

We mapped cover types within the 95% kernel home range (see home range estimation below) of each GPS-tagged owl (10,165 km^2) to determine conditions within home ranges rather than broader, landscape-scale mapping of areas outside of home ranges. Thus, our habitat analyzes corresponded to a third-order habitat selection by owls (sensu: Johnson, 1980). To take advantage of the extensive and fine-scale habitat information collected regularly by SPI for timber management purposes, we delineated and classified homogeneous patches of forest cover according to SPI's systematic forest inventory protocols (SPI's Cruise Manual available upon request from SPI), with cover types defined based on tree size (quadratic mean diameter; QMD) and canopy cover (see Table 1). We mapped seven cover types, but only retained four (HF1, HF2L, HF2H, HF4: see Table 1 for definitions and Fig. 2a–d) for resource selection and space use analysis because the other three cover types (HF0, HF3, and HF5: see Table 1 for definitions) comprised a small fraction (< 3%) of the landscape and are less frequently used by spotted owls (Jones et al., 2016; Robert, 2017). We classified areas severely burnt by the King Fire (Jones et al., 2016), early seral forest with QMD < 13 cm in replanted clear-cuts, and smaller unmapped patches of residual large trees serving as habitat retention areas within owl home ranges were included in the HF1 cover type (Table 1). HF1 comprised 13% of the landscape, with 91% of that being open areas and 9% high-severity burn areas within the King Fire perimeter. The proportion of the four cover types we used in our analyses varied among landownerships. HF4 was the dominant cover type in the landscape, respectively accounting for 58%, 45%, and 57% of national forests, SPI-owned lands, and other privately-owned lands (Fig. 2e). Other cover types also differed among landownerships with the proportion of HF1 and HF2L being greatest on SPI-owned lands (Fig. 2e).

On SPI-owned lands, a variable-radius vegetation plot was sampled

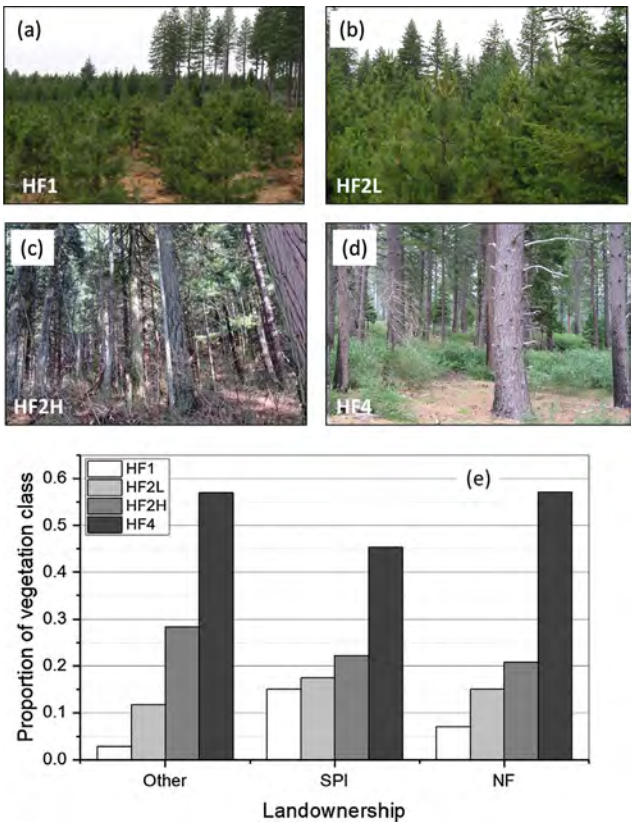

Fig. 2. (a–d) Primary cover types present in the study area, with definitions provided in Table 1. Photos were taken in spring of 2017. (e) Proportion of study areas in different cover types and landownership categories.

approximately every 1.6 ha in which the diameter at breast height (dbh) of trees was measured using Basal Area Factor forestry prisms (Monserud and Sterba, 1996; Burkhart et al., 2018). We used similar approaches on national forests, but tree estimates were based on lower density of sample of plots ~1 every 8 ha ($n = 587$). Plots were randomly selected but restricted to areas having road access. Therefore, sampling plots on private lands were more evenly distributed compared to public lands. We estimated canopy cover based on tree species and diameters calculated from crown diameter measurements of trees ≥ 13 cm dbh. We then modeled the vertical projection of stand canopy cover using the inventory plot tree list and the canopy index (SPI unpublished data). Additionally, we used drone flights to gather local aerial imagery and videography of the land to estimate canopy cover on national forest lands and ensure that habitat typing from the most recent ortho-photos (2016 National Agriculture Imagery Program imagery) was accurate. we extrapolated forest stand information from the aggregate of 10 sampling points in a 16-ha vegetation polygon. When ownership fell on private lands outside SPI ownership and plot data was unavailable, we relied on ortho-photo interpretation, and visual assessments when possible, to classify cover types.

We developed topographical variables using 30-m resolution Land Management Unit (LMU) layers that were developed for the Sierra Nevada using the LMU Tool version 2 (North et al., 2012), which is a raster-based GIS tool that partitions a landscape into basic topographic categories. We identified six categories: (i) ridge; (ii) canyon/drainage bottom; (iii) NE midslope < 30%; (iv) NE midslope > 30%; (v) SW midslope < 30%; and (vi) SW midslope > 30%. We obtained data on the distribution of roads and streams from the United States Forest Service data portal (https://www.fs.usda.gov/main/r5/landmanagement/gis) and calculated their proximity to owl locations and random locations within 95% kernel-defined home ranges.

2.4. Resource selection and space use

We analyzed resource selection and space use at three different temporal scales using locations derived from GPS-tagged spotted owls. For our "fine" scale, we characterized patterns of selection for various habitat characteristics based on all locations (~5 per night collected at hourly intervals) obtained by the GPS tags. We used integrated Step Selection Analysis (iSSA; Avgar et al., 2016) to compare habitat characteristics at used and available locations when the individual animal's "choice" of habitats is conditional on where it previously occurred on the landscape. At an intermediate scale, we used a Point Selection Function (PSF) approach (Manly et al., 2007; Zeller et al., 2012) to asses selection of putatively independent foraging locations obtained on different nights given that hourly locations used in the iSSA may or may not be an appropriate time interval to capture independent foraging decisions made by spotted owls as they leave their daytime nesting and rooting sites to engage on nocturnal foraging activities (see Thurfjell et al., 2014). At the broadest scale, we related the size of home ranges during the breeding season home ranges to spatial forest conditions, with the expectation that larger home ranges are indicative of lower

Table 1
Descriptions of variables used to model resource selection by California spotted owls in the Sierra Nevada, California, USA, 2017. QMD = quadratic mean diameter and CC = percent canopy cover.

Variable	Definition
HF0	Lakes, marshlands, and wide streams
HF1	Early seral with QMD < 13 cm or severely burned forests with smaller unmapped patches of residual large trees
HF2L	Forests with small trees (QMD: 13–28 cm) and CC ≥ 40%
HF2H	Forest with intermediate trees (QMD: 28–33 cm) and CC ≥ 50%
HF3	Forest with various tree size (QMD ≥ 13) and CC < 40%
HF4	Forests with large trees and high canopy cover: QMD ≥ 33 cm, CC ≥ 60%, > 22 tree per hectare > 56 cm DBH
HF5	Bare (exposed rock, cliffs, quarries)
NF	Publicly-owned land managed by the US Forest Service
SPI	Land owned and managed by Sierra Pacific Industries
Other	Land owned and managed by other private landowners
LMU	Land Management Unit. A categorical variable with 6 levels: (i) ridge, (ii) canyon/drainage bottom, (iii) NE midslope < 30%, (iv) NE midslope > 30%, (v) SW midslope < 30%, and (vi) SW midslope > 30%.
Hindex	Shannon-Wiener index of the proportion of habitat form (HF) in a 100-m radius centered on a used or available point
Elev	Elevation gradient associated with a relocation or available point
dist.stream	Euclidian distance from a relocation or random available point to the nearest stream
dist.road	Euclidian distance from a relocation or random available point to the nearest road
dist.edge	Euclidian distance from a relocation or random available point to the nearest hard edge
Hab	A categorical variable containing HF1, HF2L, HF2H, and HF4
Own	A categorical variable with 3 landownership variables: NF, SPI, and other

habitat quality (e.g., lower prey density) than smaller home ranges (Zabel et al., 1995; Glenn et al., 2004). Collectively, this multi-scale approach was expected to yield insights into how forest conditions influence spotted owl foraging activities across several temporal scales.

2.5. Data analysis

In our iSSA analysis, we tested for patterns in resource selection with a use-versus-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. For available locations, we generated 10 random steps for each observed hourly step made by owls. We randomly generated turn angles (in radians) for available steps from a uniform distribution of $-\pi$ and π (corresponding to non-directional random walks; Prokopenko et al., 2017). We generated step lengths by randomly drawing lengths from a frequency distribution derived from observed hourly steps made by GPS-tagged owls using the package *amt 0.0.4.0* (Signer et al., 2018) in program R *version 3.4.1* (R Core Team, 2015). We estimated the probability of selection using conditional logistic regression analyses with owl location (coded as "1″) versus available location ("0") as the response using the package *survival 2.41-3* (Therneau, 2015). The conditional logistic regression approach provided maximum likelihood estimates of resource selection coefficients and their sampling errors (Fortin et al., 2005; Hooten et al., 2017). We treated each cover type and landownership category (i.e., each of the four cover types and the three landownership categories listed in Table 1) as binary variables in the iSSA model (Stockwell and Peterson, 2002). Specifically, we set the value of the cover type or landownership category to 1 when the used or random point occurred within the cover type or landownership category in question, and 0 if not. We also included the following variables in conditional logistic regression models: (i) distance to streams and roads as linear or logarithm Euclidian measurements from the owl or random location; (ii) linear or logarithmic distance to a hard edge (defined as a boundary between HF2H or HF4 and any other habitat class; and (iii) landownership (national forest, SPI, or other). We ranked a set of 12 *a priori* models based on different combinations of these variables according to their AIC values adjusted for small sample size (Burnham and Anderson, 2002) using the MuMIn package (Bartoń, 2016). We considered a model to be competitive for explaining resource selection if $\Delta AIC < 2$, providing its parameters were not simply variants of those in the best model plus one or more uninformative parameters (Arnold, 2010). Following Cade's (2015) criticisms of model averaging, we avoided averaging model parameter estimates to reduce uncertainties that may arise from correlations among independent variables. Indeed, for compositional analysis, independent variables are often correlated such that the behavior of one variable may be dependent on other variables present in a model biasing parameter interpretations (Cade, 2015; Banner and Higgs, 2017). We evaluated the influence of individual predictors within the best supported models by examining predictor effects sizes and their 95% confidence limits (Burnham and Anderson, 2002; Arnold, 2010). We considered a predictor variable as having a strong effect if its 95% confidence interval did not overlap zero.

In our PSF analysis, we also quantified resource selection using a use-versus-availability study design (Manly et al., 2007), but randomly selected one GPS location per individual per night, such that dependence of locations was reduced. We stratified our random points such that the number of random points was equal to the number of owl locations within each quantile of the owl's fixed kernel home range (see home range estimation below) and conducted selection analyses for both the entire dataset and for individual utilization distribution categories (see below) to examine how habitat selection patterns varied among more- vs less-frequently used areas of the home range. We used the same cover types, landownership categories, and proximity variables as in the fine-scale analysis above, but we also included the categorical topographic variable LMU and an index of cover type heterogeneity. We used the Shannon-Wiener Index to estimate heterogeneity based on the proportion of each cover type within a 100-m circular buffer centered on each selected owl location and each randomly generated location (reported as Hindex in tables). Thus, our heterogeneity measure was restricted to the major vegetation cover types in our study system and did not account for possible within-stand variation in forest structure. We chose 100-m radius as being sufficiently broad to capture the diversity of vegetation cover type around a used or available location, but still sufficiently small to capture movement patterns. In this analysis, we treated cover type, landownership category, and LMU as categorical variables with multiple levels. For ease of interpretation, we avoided the conditional logistic regression approach required in the iSSA modeling approach as it does not allow for the estimation of an intercept and makes interpretation of categorical effects greater than two difficult (Agresti, 2003). Rather, we fitted PSFs using a Generalized Linear Mixed Model (GLMM) framework treating the response variable as binomially distributed and individual owl as a random effect. We then conducted model selection in the same manner as for the iSSA analysis.

For analyses of spotted owl home range size, we calculated 95% kernel home ranges for each owl based on GPS data using the package 'adehabitatHR' (Calenge, 2006) in Program R as well as the 0–10%, 11–25%, 26–50%, 51–75%, 76–95% isopleths of kernel density for use in the analyses described above. The choice of a suitable bandwidth (smoothing factor) is a key consideration when applying the kernel method (Silverman, 1986) so we used the reference bandwidth because our data distribution was bivariate normal (each owl had single centers of activity). This bandwidth minimizes discrepancy between true and estimated utilization distribution (Seaman and Powell, 1996). To examine variation in spotted owl home range size as a function of habitat conditions within the home range, we fitted GLMs with the size (ha) of the 95% kernel home range as the dependent variable and proportional landownership, cover type variables (i.e., the proportion of each cover type in home ranges), and elevation as independent variables in candidate models. We computed elevation of an individual home range as the mean elevation associated with all owl locations within the home range. We also estimated the Shannon-Weiner Index using cover type classes within the home range and included this index as a variable in our model to evaluate the potential benefits of habitat heterogeneity to owls (Table 1). At all scales, we performed Pearson correlation analyses to identify and remove highly correlated variables ($|r| \geq 0.6$) from the same model.

3. Results

We captured and tracked the movements of 53 individual California spotted owls between April–July during 2017. The activity centers of 23 individuals were located on national forests, 29 were on lands owned by SPI, and 1 was on other privately-owned lands. We collected 10,651 locations (median = 213, range 17–267) over an average 58-day individual-owl monitoring period (range: 16–85). We collected a median of 4 (range: 0–5) locations per night and a median of 87 nights with at least one location.

3.1. Fine-scale resource selection based on conditional selection (iSSA)

We obtained 4278 steps for 51 individuals (median = 85; range = 36–112) for our iSSA analysis after removing two individuals that had insufficient locations (i.e., 19 and 17) for analysis. Table S1 provides summary statistics for all covariates considered in this study. Based on the iSSA, spotted owls selected forests with larger trees and high canopy cover (i.e., HF4) and national forest lands (iSSA coefficient NF: 0.14, 95% CL: 0.01–0.26; HF4: 0.12, 95% CL: 0.05–0.19; Table 2). Lands owned by SPI were also in this top model with owls exhibiting positive selection for this landownership (Table 2), but the 95%

Table 2
Rankings of iSSA models of fine-scale habitat selection by California spotted owl in the Sierra Nevada, USA.

Model	df	logLik	ΔAIC	ω
HF4 + NF + SPI	3	−14392.80	0.00	0.41
HF4	1	−14395.18	0.76	0.28
HF4 + NF + SPI + dist.edge	5	−14391.62	1.63	0.18
HF4 + HF2L + HF1	3	−14394.59	3.57	0.07
HF4 + HF2L + HF1 + HF2H + dist.edge + dist.road + dist.stream + NF + SPI	8	−14390.85	6.09	0.02
dist.edge + NF + SPI + HF2H	4	−14395.58	7.55	0.01
dist.edge + SPI + HF2H + other	4	−14395.58	7.55	0.01
HF1	1	−14398.81	8.02	0.01
dist.edge + SPI + HF2H + other + NF + dist.road	5	−14395.19	8.78	0.01
dist.road	1	−14399.42	9.24	0.00
NF	1	−14399.66	9.72	0.00
dist.edge + NF + other + dist.road + dist.stream	5	−14396.08	10.55	0.00
Null	0	−14401.27	10.94	0.00

Starting AICc value = **28791.60**.

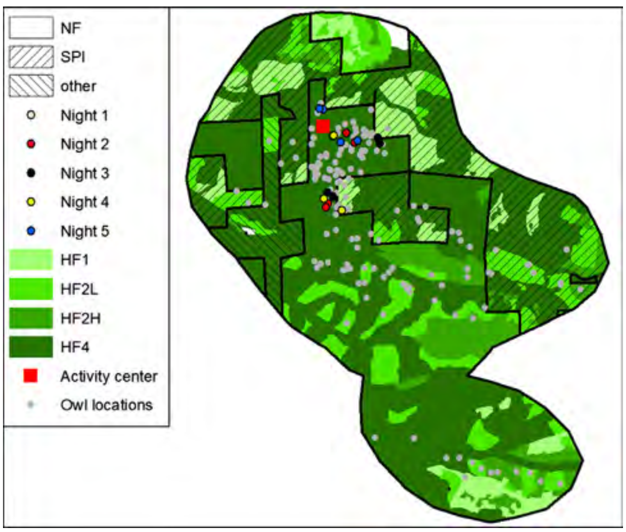

Fig. 3. Distribution of GPS locations within 95% kernel home range across different cover types and landownership categories. Circular symbols of the same color indicate locations collected on a single night for five different nights and grey symbols represent locations from all other nights.

confidence intervals associated with this parameter estimate overlapped zero (0.10, 95% CL = −0.03 to 0.23). Fig. 3 shows GPS locations of an adult male California spotted owl within 95% kernel home range across difference cover types and landownership categories.

3.2. Intermediate-scale resource selection based on point selection function (PSF)

We used 2938 putatively independent nightly locations among 53 individuals for our PSF analysis. Spotted owls selected forests with large trees and intermediate-sized trees (HF2H and HF4), lands owned by SPI, and locations that had high spatial heterogeneity in cover type composition (Table 3). This model had an AIC weight of 0.57 and there were no competing models. Based on this model, odds ratios indicated that cover types HF4 and HF2H were 1.94 and 1.67 times more likely to be selected than HF1, respectively. Moreover, selection coefficients for both of these classes were greater than the coefficients associated with HF1 and HF2L (Fig. 4a). We conducted a *post-hoc* analysis where we treated each cover type as a binary variable (i.e., we set the value of the cover type to 1 when the used or random point occurred within the cover type in question, and 0 if not) in a separate model. This model indicated selection for HF4 and HF2H (HF4: 0.60, 95% CL: 0.40–0.80; HF2H: 0.47, 95% CL: 0.27–0.67); HF2L was selected in proportion to availability (0.05, 95% CL: −0.19 to 0.29), and HF1 was selected

Table 3
Rankings of PSF models of intermediate-scale habitat selection by California spotted owl in the Sierra Nevada, USA. Variable abbreviations are explained in Table 1.

Model	df	logLik	ΔAICc	ω
hab + Hindex + own	8	−5598.29	0.00	0.57
dist.stream + hab + Hindex + own	10	−5597.47	2.37	0.18
dist.edge + hab + Hindex + LMU	12	−5595.57	2.58	0.16
dist.edge + dist.stream + Hindex	8	−5601.19	5.80	0.03
dist.edge + hab + LMU	11	−5598.36	6.16	0.03
hab + LMU	10	−5599.90	7.23	0.02
hab	5	−5605.27	7.96	0.01
dist.edge + dist.stream + hab + LMU	12	−5598.36	8.16	0.01
dist.edge + dist.stream + dist.road	5	−5641.24	79.88	0.00
Null	2	−5645.30	82.00	0.00

Starting AIC value = **11212.60**.

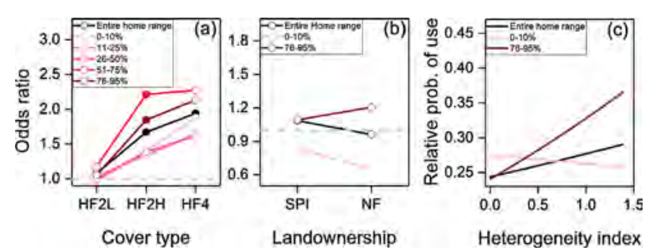

Fig 4. Odd ratios from California spotted owl resource selection function models (a) for three cover types relative to HF1, (b) two landownership categories relative to "other", and (c) relative probability of use as a function of habitat heterogeneity. Plotted are odds ratios for selection patterns across the entire home range and for individual utilization distributions when effects were supported in PSF models. The dashed lines at a value of 1 indicate equal odds of selecting a cover type or landownership category relative to the reference level. A closed circular symbol for a given cover type or landownership category indicates that the associated coefficient is significantly greater than the coefficient for the preceding coefficient (e.g., a closed circular symbol for HF4 indicates that the coefficient for this level is significantly greater than the coefficient for HF2H).

against relative to availability (−0.50, 95% CL: −0.68 to −0.32). Although the top model indicated selection for SPI-owned land, selection coefficients did not differ significantly between SPI-owned lands and national forests (Fig. 4b). Finally, spotted owls appeared to select areas with greater cover type heterogeneity as the relative probability of use increased with the heterogeneity index (0.17, 95% CL: 0.04–0.30; Fig. 4c).

Resource selection patterns among the five utilization distribution categories reinforced the importance of cover type as this variable was present in the top model for each category (Table S2. As was the case when the entire home range was considered, odds ratios for HF4 and HF2H – relative to HF1 – exceeded 1 for all home range distribution categories (Fig. 4a). Notably, odds ratios were greatest for these two cover types in the 51–75% and 76–95% utilization distribution categories and reached as high as 2.21 and 2.27 for HF2H and HF4, respectively. Thus, in these categories, spotted owls were almost two and half times more likely to select these two cover types than HF1. Odds ratios for HF2L – relative to HF1 – were low and always ≤ 1.18. Landownership was present in the top model for both the 0–10% and 76–95% utilization distribution categories (Table S2), although odds ratios indicated that patterns of selection for the three landownerships were inconsistent and selection coefficients were not significantly different (Fig. 4b). The heterogeneity index was present in the top model for both the 0–10% and 76–95% utilization distribution categories (Table S2). The relative probability of use tended to decrease with increasing cover type heterogeneity in the 0–10% category, although confidence intervals overlapped zero (−0.06, 95% CL: −0.36 to 0.22), and increased with increasing cover type heterogeneity in the 76–95% category (0.43, 95% CL: 0.10–0.76; Fig. 4c).

3.3. Correlates of home range size

Median home range size was 931.6 ha (range = 195.1–4280.7; n = 53) with males (1206.8 ha; range = 273.7–4280.7; n = 33) having larger home ranges than females (median 659.1 ha; range = 195.1–1828.5; n = 20; $F_{(1,\ 51)} = 7.7$, $p = 0.007$). Home range size increased with spatial heterogeneity and elevation, and decreased with the amount forest with intermediate-sized trees (HF2H; AIC model weight = 0.51; Table 4, Fig. 5). The only competing model contained all these variables plus one uninformative variable – national forest lands (Table 4). Parameter estimates associated with all three variables in the top model had 95% confidence intervals that did not overlap zero (HF2H: −0.24, 95% CL: −0.41 to −0.06; elevation: 0.17, 95% CL: 0.01–0.33; heterogeneity index: 0.35, 95% CL: 0.18–0.52), and were thus considered important in explaining variation in spotted owl home range size.

4. Discussion

We did not observe strong patterns of selection for different landownerships by spotted owls in this study. While the landownership covariate was present in the top intermediate-scale PSF model (for the entire home range), odds ratios indicated there were no substantive difference in owl use among landownerships. In the fine-scale iSSA analysis, selection coefficients for national forest and SPI-owned lands were similar in magnitude (0.14 and 0.10, respectively), suggesting

Table 4
Rankings of models of home range size for California spotted owls in the Sierra Nevada forests, USA. Variable abbreviations are explained in Table 1.

Model	df	logLik	ΔAICc	ω
Hindex + Elev + HF2H	5	−41.93	0.00	0.51
Hindex + Elev + HF2H + NF	6	−41.35	1.40	0.25
Hindex + Elev + HF2H + SPI	6	−41.91	2.51	0.14
Hindex + HF2H + SPI	5	−44.06	4.27	0.06
Hindex + Elev + NF	5	−45.11	6.36	0.02
Hindex + Elev + HF1 + HF2L	6	−45.38	9.45	0.00
Hindex + Elev + HF1 + SPI	6	−45.56	9.81	0.00
Hindex + NF	4	−48.29	10.28	0.00
Elev + HF2H + HF4	5	−47.46	11.06	0.00
Elev + HF2H + HF4 + HF1 + HF2L	7	−45.22	11.79	0.00
Elev + HF2H + HF4 + HF1	6	−47.38	13.46	0.00
Elev + HF2H + HF4 + HF1 + HF2L + NF	8	−44.90	13.93	0.00
HF1 + SPI	4	−51.65	17.00	0.00
Null	2	−54.41	17.93	0.00

Starting AICc values: **95**.

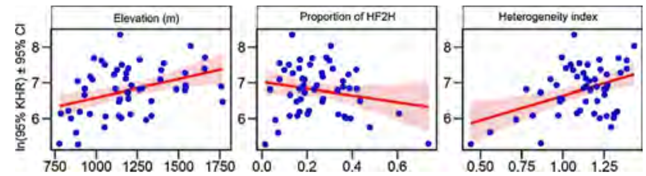

Fig. 5. Relationships between 95% kernel home range (KHR) size (km^2) and elevation, proportion of HF2H in the home range, and habitat heterogeneity for California spotted owls in the Sierra Nevada, USA. Data are plotted on a log scale and the shaded areas around fitted regression lines represent 95% confidence intervals (CI).

little difference in selection for these two landownerships. Moreover, we suspect that spotted owls tended to exhibit selection for national forests and SPI-owned lands over other privately-owned lands in the fine-scale iSSA analysis because only one owl had an activity center occurring on other private lands. As such, used steps may have been more likely to occur on national forests and SPI-owned lands when owls returned to their activity centers (e.g., to deliver prey to nest sites), whereas random (available) steps were generated without this tendency. Thus, we infer that national forests, SPI-owned, and other privately-owned lands provided foraging habitat to spotted owls in an approximately equal manner. Differences in selection patterns observed in our study and those reported in previous studies such as Williams et al. (2014) could be the result of either differences in sample sizes (53 owls in our study vs 13 owls in their study), differences in transmitters (GPS vs VHF), or differences in management strategies between private lands in the two studies. Thus, despite differences in cover types, forest structure, and management priorities among landownerships, privately-owned forests can provide more foraging habitat for California spotted owls than previously believed – although it is important to note that previously reported differences in selection between landownerships was modest (Williams et al., 2014).

We also found that spotted owls selected forests with intermediate- and large-sized trees and canopy cover > 50%, and areas with high heterogeneity in cover type composition. Thus, both vegetation and cover type composition appeared to influence foraging decisions by California spotted owls. However, the strength of selection we observed for the cover types considered in this study was modest given that odds ratios for forests with large- and intermediate-sized trees and high canopy cover relative to early seral stages were < 2 at the home-range scale (Fig. 4a) and differences in the proportion of used versus available points among cover types were also not large (Fig. 6). Indeed, the modest level of selection we observed among cover types may be the

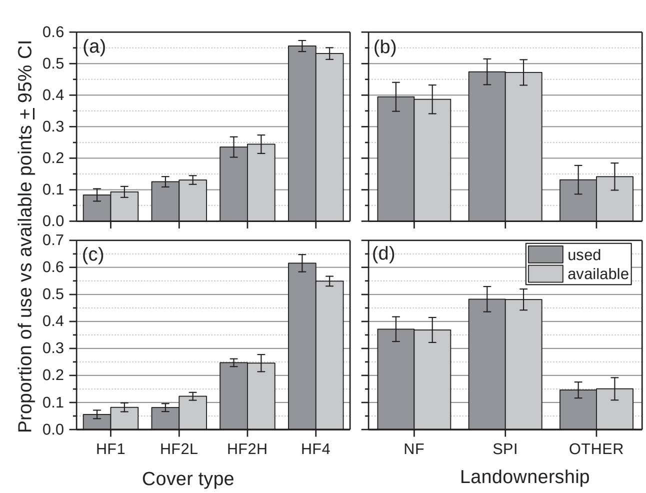

Fig. 6. Proportion of used and available points for (a) cover types and (b) landownership categories in the iSSA analysis, and points for (c) cover types and (d) landownership categories in the intermediate-scale PSF analysis.

reason differences in forest conditions between public and private lands (e.g., greater prevalence of large-tree high canopy-cover forest on public lands) may not have resulted in strong foraging preferences for any single landownership.

4.1. Hourly vs. nightly foraging patterns

Consistent with previous studies, California spotted owls in our area selected resources non-randomly and exhibited differential selection patterns depending on behavior and the scale of observation (Gutiérrez et al., 1992; Call et al., 1992; Williams et al., 2014). However, our conditional analysis (hourly movement data) was novel and corroborated selection analyses done by a more recent study of California spotted owl habitat selection (Blakey et al., 2019) as well as earlier studies of other spotted owl subspecies (e.g., Carey et al., 1990; Ganey and Balda, 1994). However, our PSF analysis based on putatively independent nightly locations suggested that spotted owls used cover types characterized by both intermediate- and large-sized trees and higher canopy cover (i.e., trees > 28 cm QMD and ≥50% canopy cover). Therefore, the use of the intermediate-sized tree cover types supported what has long been known about spotted owls (i.e. they expand their cover type use when foraging; Call et al., 1992; Irwin et al., 2007; Williams et al., 2011), while the analysis based on conditional use suggests that spotted owls might spend more time in forests having larger trees. The contrast in selection between the iSSA and PSF analyses (mainly the lack of selection for intermediate-sized trees in the iSSA analysis) might be attributed to the fact that some movements in the iSSA relates to central place foraging by owls where owls return frequently to centers of activity centers such as nest sites (Carey and Peeler, 1995), which typically are in areas with larger trees and higher canopy cover, whereas random steps implied no central place foraging tendency. On the other hand, our analysis based on independent (once per night) observations was based on single nightly locations and may have been better positioned to capture independent foraging decisions made by spotted owls, such as the selection of intermediate-sized trees. The *post-hoc* PSF analysis, where cover types were examined independently rather than as a categorical effect, provided further insight into cover type selection. In this analysis owls selected for intermediate- and large-sized trees with high canopy cover, whereas they used forests with small trees in proportion to availability and selected against early seral cover type, which also supports the hypothesis that owls expand cover type selection when foraging. When owls occurred in open areas such as recent clear-cuts, they often used individual or groups of legacy ("leave") trees retained as part of silvicultural prescriptions or residual survivors of fire (Fig. S1).

Overall, spotted owls selected for areas containing high heterogeneity in cover types, a relationship that was also detected at the periphery of home ranges (i.e., 76–95% utilization distribution category). Franklin et al. (2000) and Roberts (2017) suggested that different cover types and different seral stages may promote higher prey density and owl reproductive output. Spotted owls in our study likely exploited different forest conditions if they harbor a diverse prey base, suitable perch sites, and open flying space as noted by others (Gutiérrez et al., 1995, Franklin et al., 2000). However, spotted owls selected relatively homogenous forest conditions consisting mainly of large trees and closed-canopy cover in the core of their home ranges (0–10% utilization distribution category; Table S3). Although owls exploited variable forest conditions for foraging they exhibited increasing selection of cover types having intermediate- and large-sized trees with higher canopy at greater distances from core areas. This pattern in combination with patches of mature closed-canopy forests have been shown to be important characteristics of spotted owl nesting and roosting habitat in the Sierra Nevada (Bias and Gutiérrez, 1992; Williams et al., 2011).

4.2. Home range size and habitat use

Spotted owl home ranges in our study were similar to those reported previously for the northern and central Sierra Nevada (Call et al., 1992; Williams et al., 2011), but were larger than those reported for the southern Sierra Nevada (Zabel et al., 1992; Eyes et al., 2017). Home range size generally increased with cover type heterogeneity and elevation and tended to decrease when home ranges contained higher proportions of cover types with intermediate-sized trees and higher canopy cover. Fretwell and Lucas (1969) predicted that individual home range size would decline as the quality and amount of resources increased because individuals would not have to travel as far to meet their life-history requirements. Thus, the reduction in home range size associated with intermediate-sized trees and higher canopy cover suggested that this cover type may provide quality foraging for spotted owls in the area of the study. Conversely, the increase in home range size with cover type heterogeneity suggested that high heterogeneity of cover types may reduce foraging opportunities for owls by increasing travel time and distance to foraging areas. We hypothesized that these contrasting results reflected a tradeoff between the benefits that heterogeneity can provide for prey and the increased energetic costs of traveling to forage in preferred cover types more widely across home ranges when heterogeneity is high. Zabel et al. (1995), Glenn et al. (2004) suggested that smaller home ranges for spotted owls represented higher quality habitat conditions, but it is possible that elevation also plays a role in home range size because owl home ranges are smaller at lower elevations that may reflect higher woodrats (*Neotoma* sp.) abundance versus higher flying squirrel (*Glaucomys sabrinus*) abundance at higher elevations (Munton et al., 2002; Innes et al., 2007; Wilson et al., 2008). Woodrats are larger and occur in higher density than flying squirrels, which could lead to higher quality foraging habitat at lower elevations and explain smaller home range sizes in these areas (Zabel et al., 1995). Home ranges at lower elevations may also be constrained by topography because many low elevation sites are in riparian zones that are disjunct from other suitable habitats (Verner et al., 1992b). Therefore, we infer that the determination of home range size in the Sierra Nevada spotted owls is complex and likely dependent on relative distribution and abundance of prey among cover types and elevations.

4.3. Conclusions: owls in mixed-ownership landscapes

The mosaic of cover types created by the interspersion of privately-owned forests with publicly-owned forest allows foraging by spotted owls on both landownerships. However, our measure of heterogeneity in this study was compositional and measured only the diversity of some seral stages in the landscape. These types of mosaics may not be consistent with restoration goals for public lands in the Sierra Nevada landscapes intended to help reestablish low- to moderate-severity fire regimes in the mixed-conifer zone, reduce the risk of high-severity fires, and promote a heterogeneous mix of vegetation conditions more representative of the natural range of variation. Nevertheless, selection of spatially heterogeneous environments that includes documents that privately owned lands can contribute to owl conservation by, at minimum, providing owl foraging habitat. Within this context of mixed landownership patterns on large landscapes of the Sierra Nevada, it is important to develop collaborative research focused on designing economically feasible ways that private landownerships can also provide patches of suitable mature forest capable of supporting nesting to augment their existing spotted owl foraging habitat.

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Research ethics statement

Owl capture, marking, and tracking activities were performed in compliance with institutional animal care and use protocols and state wildlife research permits.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.11.011.

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