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RESEARCH ARTICLE

Large trees and forest heterogeneity facilitate prey capture by California Spotted Owls

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ABSTRACT

Predators are among the most threatened animal groups globally, with prey declines contributing to their endangerment. However, assessments of the habitat conditions that influence the successful capture of different prey species are rare, especially for small, cryptic predators. Accordingly, most predator conservation plans are based on the relative importance of habitats inferred from coarse-scale studies that do not consider habitat features contributing to hunting success, which can vary among prey species. To address this limitation, we integrated high-resolution global positioning system tracking and nest video monitoring to characterize habitat features at prey capture locations during the nestling provisioning stage for the Spotted Owl (*Strix occidentalis*) a small, cryptic predator that has been at the center of a decades-long forest management conflict in western North America. When all prey species were considered collectively, males provisioning nests tended to capture prey: (1) in areas with more large-tree forest, (2) in areas with more medium trees/medium canopy forest, and (3) at edges between conifer and hardwood forests. However, when we considered the owl's two key prey species separately, males captured woodrats (*Neotoma fuscipes*) and Humboldt flying squirrels (*Glaucomys oregonensis*) in areas with markedly different habitat features. Our study provides clarity for forest management in mixed-ownership landscapes because different prey species achieve high densities in different habitat types. Specifically, our results suggest that promoting large trees, increasing forest heterogeneity, and creating canopy gaps in forests with medium trees/high canopy cover could benefit Spotted Owls and their prey, which has the ancillary benefit of enhancing forest resilience. Combining high-resolution global positioning system tagging with video-based information on prey deliveries to breeding sites can strengthen conservation planning for small predators by more rigorously defining those habitat features that are associated with successful prey acquisition.

Keywords: forest heterogeneity, large trees, predator–prey interactions, prey availability, Sierra Nevada, Spotted Owl, young forest

LAY SUMMARY

- Predators capture their prey where prey are both present and available for capture. Therefore, mapping and analyzing habitat at capture locations can aid management of quality habitat for predator conservation.
- It is difficult to find the exact places where predators capture their prey. This is especially challenging for smaller, cryptic predators that do not leave behind obvious kill sites.
- We attached global positioning system (GPS) tags to Spotted Owls and placed video cameras at their nests. We assessed the GPS movements to identify places they captured prey, which we then classified into species based on the video data.
- Spotted Owls captured prey in places with big trees, with medium trees and medium canopy cover, and with a greater mixture of forest types (heterogeneity) and forest edge.
- Forest management that promotes big trees, increases forest heterogeneity, and creates canopy gaps in forests will likely result in greater foraging success by owls, as well as increase forest resilience.

Los grandes árboles y la heterogeneidad del bosque facilitan la captura de presas por parte de *Strix occidentalis* de California

RESUMEN

Los depredadores se encuentran entre los grupos de animales más amenazados a nivel mundial, y la disminución de presas contribuye a su peligro. Sin embargo, las evaluaciones de las condiciones del hábitat que influyen en la captura exitosa de diferentes especies de presas son raras, especialmente para depredadores pequeños y crípticos. En consecuencia, la mayoría de los planes de conservación de depredadores se basan en la importancia relativa de los hábitats inferidos a partir de estudios de escala gruesa que no consideran las características del hábitat que contribuyen al éxito de la caza, las cuales pueden variar entre las especies de presa. Para abordar esta limitación, integramos el seguimiento por GPS de alta resolución y el monitoreo mediante grabaciones de video de los nidos, para caracterizar las características del hábitat en las ubicaciones de captura de presas durante la etapa de aprovisionamiento de polluelos de *Strix occidentalis*, un depredador pequeño y críptico que ha estado en el centro de un conflicto de manejo forestal que lleva décadas en el oeste de América del Norte. Cuando todas las especies de presas fueron consideradas colectivamente, los machos que aprovisionaban los nidos tendieron a capturar presas: (1) en áreas de bosques con árboles grandes, (2) en áreas con más árboles medianos/bosques de dosel mediano, y (3) en los bordes entre coníferas y bosques de maderas duras. Sin embargo, cuando consideramos las dos especies de presa clave de *S. occidentalis* por separado, los machos capturaron ratas (*Neotoma fuscipes*) y ardillas (*Glaucomys oregonensis*) en áreas con características de hábitat marcadamente diferentes. Nuestro estudio proporciona claridad para el manejo forestal en sitios de propiedad mixta porque diferentes especies de presas alcanzan altas densidades en diferentes tipos de hábitat. Específicamente, nuestros resultados sugieren que la promoción de árboles grandes, el aumento de la heterogeneidad del bosque y la creación de huecos en el dosel en bosques con árboles medianos/cobertura de dosel alta podría beneficiar a *S. occidentalis* y sus presas, lo que tiene el beneficio adicional de mejorar la resiliencia del bosque. La combinación del seguimiento por GPS de alta resolución con información basada en grabaciones de video de la entrega de presas a los sitios de reproducción puede fortalecer la planificación de la conservación para los pequeños depredadores, al definir de manera más rigurosa aquellas características del hábitat que están asociadas con la adquisición exitosa de presas.

Palabras clave: árboles grandes, bosque joven, disponibilidad de presas, heterogeneidad forestal, interacciones depredador-presa, Sierra Nevada, *Strix occidentalis*

INTRODUCTION

Predators are among the most endangered animal groups (Estes et al. 2011). Many anthropogenic factors threaten predators, but prey depletion resulting from habitat degradation is an important source of endangerment (Manlick and Pauli 2020). Recent work suggests that habitat conditions can mediate trophic interactions between predators and their prey through a variety of processes (Smith et al. 2019). This recognition, coupled with the fundamental importance of prey to predators (Mitchell and Powell 2004), suggests bolstering prey populations through habitat management could contribute to the recovery of imperiled predators.

Management that seeks to enhance prey populations will benefit from understanding how habitat influences predator-prey relationships. First, prey vary in both quality (e.g., nutritional content) and habitat needs, with different species reaching different densities in different habitats. Thus, in heterogeneous landscapes, promoting high-quality habitat for populations of more energetically valuable prey might benefit predator populations (Hobart et al. 2019a). Alternatively, when populations of prey species fluctuate asynchronously, ensuring habitat for multiple or alternative prey could buffer predators from declines in any one species (Sinclair et al. 2013). Second, prey can achieve high densities in habitats that do not constitute high-quality hunting habitat for the predator because of a lack of suitable foraging structures (Dubey et al. 2019). Mismatches between predator-foraging habitats and high-density prey habitats can reduce predator access to prey but can also create prey refuges that indirectly benefit predators by producing source populations that disperse into predator-foraging habitat (Klecka and Boukal 2014). Thus, while the mechanisms by which habitat mediates predator-prey interactions are complex, understanding these processes can facilitate the development of more effective habitat-based conservation plans for endangered predators.

Studies of the interplay between habitat and predator–prey relationships have focused primarily on large mammalian predators because prey capture locations can be characterized based on the remains of kills made by global positioning system (GPS) or very high frequency (VHF) tagged individuals (Anderson and Lindzey 2003). However, identifying prey capture sites is much more difficult for smaller-bodied, more cryptic predators because discernable remains at kill sites are typically either absent or difficult to locate. For these reasons, studies of habitat selection by small or cryptic species typically "assume" foraging behavior using locations of tagged individuals during periods when foraging activities normally occur (e.g., during nocturnal hours), when in reality few of those locations are likely to represent actual prey capture locations (Marsh et al. 2014). Thus, logistical and technological limitations associated with studying foraging ecology of small or cryptic predators have challenged a mechanistic understanding of prey habitat and conservation of predator–prey relationships.

Recent advances in GPS tagging technology such as the design of lightweight tags that record fine-scale movements with very high spatial and temporal resolution have facilitated identification of prey capture locations of small-bodied predators (Studd et al. 2021, Wood et al. 2021). For example, Marsh et al. (2014) integrated GPS dataloggers and digital video recorders to study the nocturnal foraging ecology of Burrowing Owls (*Athene cunicularia*) and identified successful captures based on (1) clusters of GPS locations followed by a straight-line movement back to a nest or den; and (2) video observation of prey delivery to the nest or den simultaneous with the arrival determined via GPS. This integrative approach can thus provide otherwise impossible insights into the successful hunting locations (and habitats) of adult individuals provisioning dependent offspring during this critical life history phase. However, to our knowledge, no previous study has characterized differences in habitat associated with the successful acquisition of different prey species in small-bodied predators.

We leveraged these new technologies to gain a more mechanistic understanding of how forest conditions influenced foraging strategies and the successful capture of prey species during the nestling-provisioning phase for the Spotted Owl (*Strix occidentalis*), a mature forest nesting species of conservation concern that is experiencing population declines across many parts of its range (e.g., Franklin et al. 2021). Concern about the Spotted Owl and its habitat has placed this species at the center of forest management planning in many forests of western North America, with substantial implications for both timber harvesting on private lands and forest management efforts intended to curb the spread of unprecedented large severe fires on public lands (Peery et al. 2017). Additionally, Spotted Owls are known to be nest site specialists, but GPS-tagging and VHF telemetry studies suggest that nocturnal activities (and therefore, inferred foraging activities) by Spotted Owls may occur in a broader range of forest types than nesting (e.g., Call et al. 1992, Atuo et al. 2019, Kramer et al. 2021). However, these nocturnal locations likely represent a range of activities besides foraging such as territory defense, pair bonding, and resting, and thus do not necessarily provide insights into the forest conditions that promote successful prey acquisition and associated fitness benefits. Given the profound effects prey availability has on Spotted Owl population dynamics (e.g., Franklin et al. 2000, Hobart et al. 2019a), an improved understanding of how forest conditions relate to the acquisition of primary prey and how habitat conditions differ among prey could substantially enhance forest management intended to benefit this species and meet other management and conservation objectives.

Two of the primary prey of Spotted Owls in California's Sierra Nevada—Humboldt flying squirrels (*Glaucomys oregonensis*) and woodrats (*Neotoma* spp.) (Gutiérrez et al. 2020)—tend to occur in different forest types. Woodrats, which are typically large in body size (mean woodrat consumed by owls = 187 g; C. Zulla personal communication) and more energetically profitable (1,205 kJ; Weathers et al. 2001), can be particularly abundant in some younger forests and brushy areas and are positively related to the presence of large oaks (Sakai and Noon 1993). Conversely, flying squirrels, which are typically smaller in body size (mean flying squirrel consumed by owls = 98 g; C. Zulla personal communication) and less energetically profitable (592 kJ; Weathers et al. 2001), tend to be more abundant in mature coniferous forests that have more arboreal lichens and tree cavities (Meyer et al. 2005). Thus, flying squirrels are more common in forest types considered to be Spotted Owl nesting habitat, while woodrats occur at high densities in areas that may be less suitable for Spotted Owl nesting (North et al. 1999). When brushy areas or some younger forest types having high woodrat density occur adjacent to mature coniferous forests, the resulting edge may provide foraging opportunities for Spotted Owls (Sakai and Noon 1993, 1997), although this hypothesis has not been tested. The consumption of woodrats, facilitated by the juxtaposition of older forest with other vegetation types (i.e. heterogeneous forest) may, in some ecological contexts, promote high territory occupancy rates, fitness, and landscape-scale density in Spotted Owls (Franklin et al. 2000, Hobart et al. 2019a).

We tested the hypothesis that forest type and structure (including edges) are related to acquisition of prey by Spotted Owls. Under this hypothesis, we predicted that Spotted Owls would tend to capture prey in mature forests overall, but that forest structure would differ between successful woodrat and flying squirrel capture sites. Specifically, we predicted that owls would capture woodrats at the edge between mature forests and areas dominated by younger forest, hardwoods, or shrubs—as well as in areas with a high diversity of vegetation types—compared to what is available within owl home ranges. Conversely, we predicted that Spotted Owls would tend to capture flying squirrels in mature forests without selecting for edges or a diversity of vegetation types. Gathering data to assess this long-standing hypothesis could substantially enhance opportunities to promote habitat for prey species that support stable owl populations.

MATERIALS AND METHODS

Study Area

Our study took place in the central and northern Sierra Nevada in 2019 and 2020 on or immediately adjacent to two long-term California Spotted Owl monitoring areas,

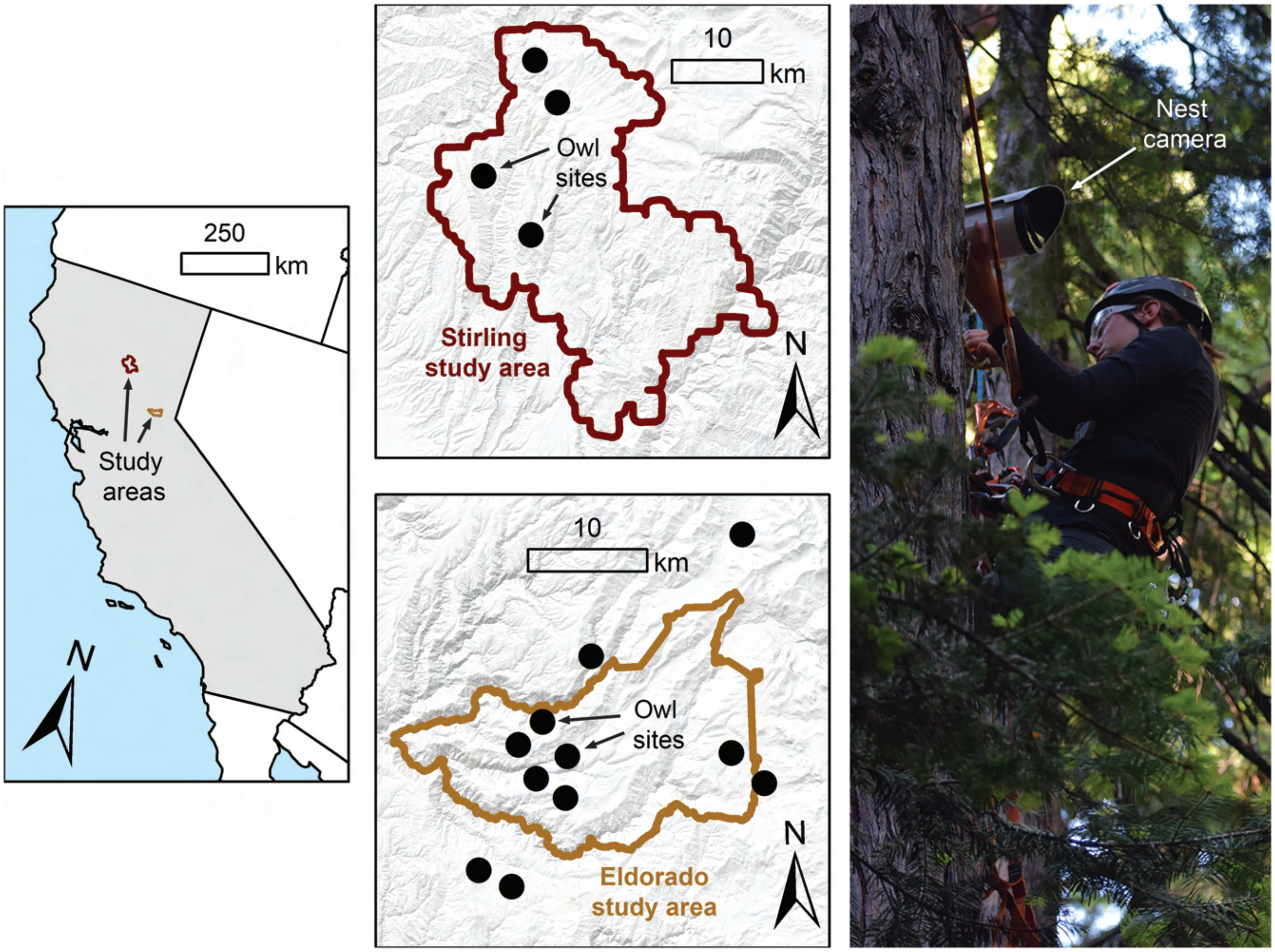

FIGURE 1. Map depicting the 15 locations where Spotted Owls were GPS tagged and video cameras were deployed in the Sierra Nevada, California, USA. Image on the right illustrates a camera installation adjacent to a California Spotted Owl nest.

the Eldorado Demography Study Area (EDSA) and Sierra Pacific Industries' Stirling Study Area (SSA) (Roberts et al. 2017, Hobart et al. 2019b; Figure 1). Elevation in the EDSA ranged from 366 to 2,257 m across 355 km^2 and elevations in the SSA ranged from 424 to 2,080 m across this 648 km^2 study area in mountainous terrain. The EDSA area was composed of ~60% public land managed by the U.S. Forest Service (USFS) and ~40% private land managed largely for commercial timber production, whereas the SSA was predominantly privately owned (81%). Forests on USFS-managed lands were typically a mix of mature forests and homogenous/dense forests dominated by small to medium-sized trees, sometimes containing residual large trees, owing to a history of fire-suppression and selective logging of large trees. Conversely, privately owned forests were a mixture of recent clear-felled areas (open and shrubby areas), tree plantations (densely stocked conifer stands), and forests similar to those on public lands. The vegetation on both study areas was typical of Sierran mixed-conifer forest dominated by the following tree species: Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense cedar (*Calocedrus deccurens*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), and California black oak (*Quercus kelloggii*). Tanoak (*Lithocarpus densiflorus*) formed a dense understory in some areas.

GPS Tagging

We located territorial breeding Spotted Owls as part of our routine monitoring surveys conducted annually on the EDSA and SSA (e.g., Roberts et al. 2017, Hobart et al. 2019b). Briefly, owls were located during call-based surveys at night and found during dawn/dusk surveys the following day to ascertain their reproductive status and locate nests (Franklin et al. 1996). Owls were fed live mice during follow-up surveys, which breeding owls then typically delivered to nest sites (Franklin et al. 1996).

We captured 15 nesting males (5 in 2019 and 10 in 2020) for GPS tagging using noose poles and "hand capture" (Wood et al. 2021). Females were not tagged because they spend most of their time incubating eggs and brooding nestlings while nesting and relatively little time foraging (Forsman et al. 1984). Males were selected opportunistically for tagging based on the accessibility of the nest for video-monitoring (see below) throughout the nesting months (May to July) and the likelihood of recapture to remove transmitters. We affixed GPS tags (Alle-300, Ecotone, Poland) weighing 10 g and with remote downloading capability as tail mounts following methods described in Kramer et al. (2021) (Figure 1). We programmed tags to collect locations at 2-min intervals to characterize Spotted Owl nocturnal movements and ultimately identify prey capture locations (described below). We recaptured 5 individuals for a second deployment to increase the number of observations of prey captures. Following the final deployment, we attempted to recapture all owls to remove GPS tags; 2 individuals that were not recaptured were expected to molt during that season or the following season, thus shedding the GPS tag.

Nest Video Monitoring

We monitored prey deliveries using infrared (IR) video cameras placed at the nest sites of the 15 GPS-tagged males concurrent with the collection of GPS locations. To do so, we climbed a nearby adjacent tree (10–50 m from the nest tree) using a single rope technique and secured a video camera across from the nest tree (Figure 1). We monitored nests using AXIS Q1786–LE 4 megapixel outdoor IR video cameras that continuously recorded high-quality video throughout the nocturnal foraging period that coincided with GPS tag data collection (2000 to 0630 Pacific Daylight Time). We reviewed each video to detect and identify the different prey species delivered to each nest.

Identifying Prey Capture Locations

We located successful foraging sites (hereafter "prey capture locations") by visually identifying tight clusters of GPS points followed immediately by a straight flight path back to the nest tree (Marsh et al. 2014, Wood et al. 2021). We defined a prey capture location as a cluster of up to 10 GPS points (within the 20 min prior to movement back to the nest), all within 250 m of one another based on that likely being the maximum hunting radius of a perched owl (S. A. Whitmore personal observation). If the two farthest points were >250 m apart, we removed the oldest point (the first point that defined the prey capture location) and continued to remove the points until they were all within 250 m of one another. Each cluster of points was transformed into a minimum convex polygon (mean: 0.38 ha, range: 0.002–2.713 ha) surrounding the cluster and assumed to represent the prey capture location. Although this approach, including the criterion of <250 m among pairs of points, was somewhat subjective in that it was based on field observations, it was repeatable and typically yielded tight, defined clusters of points (compared to the distribution of owl GPS points overall) followed by distinct straight-line movements back to the nest site (Figure 2). We then matched the time stamp of the video with the time stamp of the GPS return to the nest to link the species of prey to its putative capture location (Figure 2). The area contained by the minimum convex polygon of these GPS points that matched with a prey delivery caught on video was defined as a prey capture location. Three prey capture locations were excluded from the analysis because they likely represented the retrieval of prey from a cache site. We suspected these deliveries to be from a cache location because of their close proximity to the nest site (within 50 m) and the early timing of the delivery (all 3 instances were the first delivery of the night and occurred before sunset), which both indicated a cache delivery (S. A. Whitmore, personal observation).

Vegetation Classification

We visually interpreted aerial imagery from the National Agriculture Imagery Program (NAIP) collected in 2018 and 2020 to characterize vegetation conditions within prey capture locations (as well as random locations, see below) following methods developed and described by Tempel et al. (2014) that typically results in >80% classification accuracy. Specifically, we considered 10 possible vegetation classes based on species composition, canopy cover, and the size of the dominant trees that was largely based on the California Wildlife Habitat Relationships system (Mayer and Laudenslayer 1988) (Table 1). Areas classified as hardwood typically represented patches of black oaks, with tanoaks in the understory typically being obscured by overstory conifer trees and thus not measured. We digitized polygons around relatively homogenous areas of vegetation with a minimum mapping unit of 20 m^2 and then classified the area within the polygon as 1 of the 10 vegetation classes.

Prey Capture Analysis

We used mixed-effects resource-selection functions (RSFs) to test for the selection of forest structural characteristics (Table 1) and several derived covariates, described below. First, we fit a model that included data from all prey (species pooled together) to examine habitat characteristics of prey capture locations and whether and how these locations differed in forest structure compared to random locations within the home range. Second, we fit models that included only data from either of the owl's 2 primary prey items—flying squirrels and woodrats (see below)—to characterize

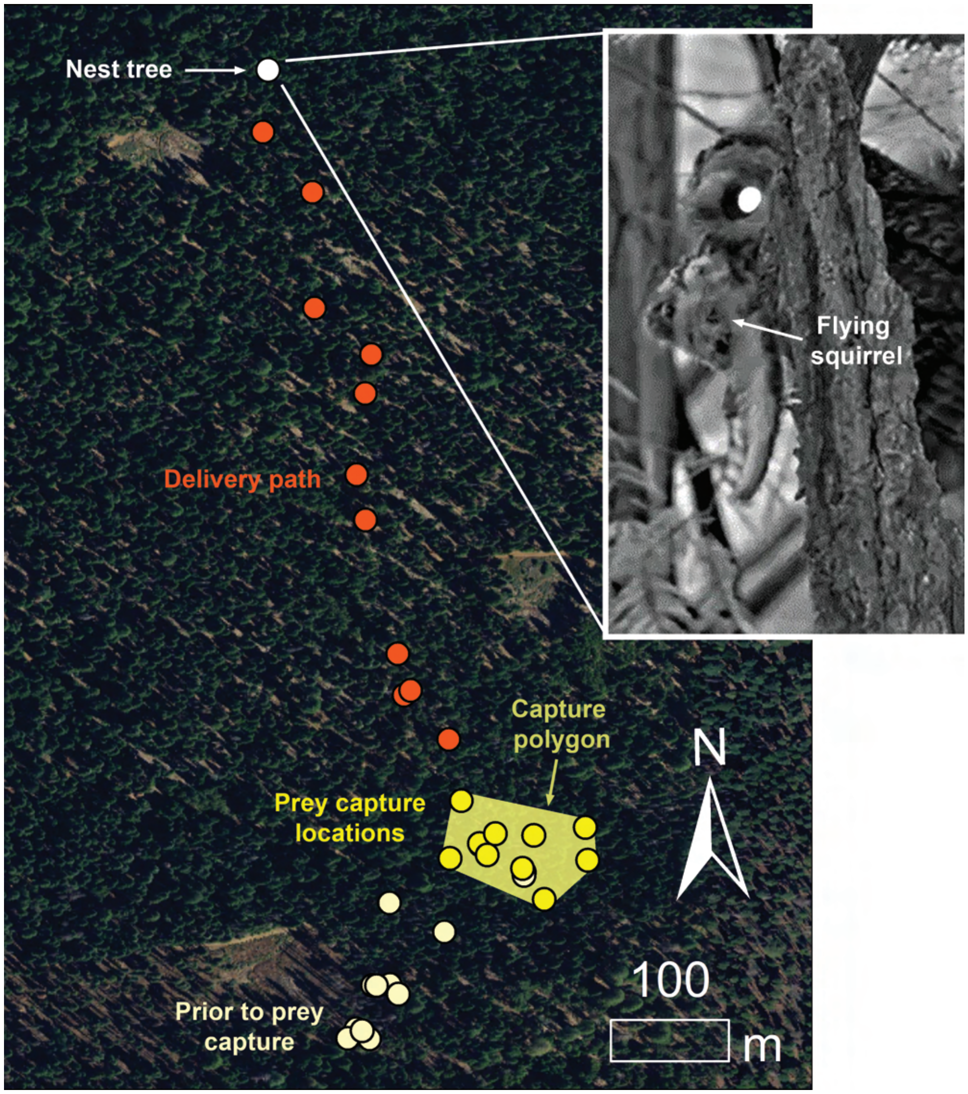

FIGURE 2. Map showing a sequence of Spotted Owl GPS locations preceding a prey delivery, and an image of the subsequent prey delivery at the nest. The prey delivery image is a single frame from an infrared camera mounted in a tree 10 m from the nest tree and shows the delivery of a flying squirrel to the nest. The approximate location of the capture can be inferred from the cluster of GPS locations before the owl's nearly direct flight back to the nest.

the forests where owls caught these 2 important prey species.

The RSFs relied on a use-availability framework to compare habitat characteristics at used locations to randomly generated available locations within a Spotted Owl's home range (Manly et al. 2002). Intercepts within the model varied by individual to account for correlation and unequal sample sizes (Muff et al. 2020). Models with random slopes (Muff et al. 2020) failed to converge; therefore, our models included only fixed covariate effects. For this analysis, a used location refers to the area within a prey capture location (explained above). We generated 5 corresponding available areas for each used area, where the size and shape of the available polygon were identical to that of the used polygon. Spotted Owl home ranges were estimated using 95% fixed-kernel density estimators (KDE; Seaman and Powell 1996). Each available polygon was centered on a random location within the given owl's home range and rotated to a random orientation. To account for GPS error and potential neighborhood effects of surrounding habitat, we buffered all used and available polygons by 50 m. Available polygons were assigned a high weight (W = 1000) to facilitate approximate convergence to the inhomogeneous Poisson process likelihood (following Muff et al. 2020). We fitted RSFs using the R package "glmmTMB," version 3.6.3 (Brooks et al. 2017).

Our model covariates (fixed effects) included the proportion of each polygon containing various vegetation

TABLE 1. Vegetation classes used to characterize forest conditions used by Spotted Owls in the Sierra Nevada, California, USA.

Vegetation class	Description	Diameter at breast height (cm)	Canopy cover (%)
1	Hardwoods	N/A	>50 hardwood
2	Shrubs	<15.2	N/A
3	Young forest	15.2–30.4	N/A
4	Medium trees/medium canopy cover	30.5–60.9	30–69
5	Medium trees/high canopy cover	30.5–60.9	≥70
6	Large trees/medium canopy cover	≥61.0	30–69
7	Large trees/high canopy cover	≥61.0	≥70
8	Water or barren rock[a]	N/A	N/A
9	Medium or large trees/low canopy cover[a]	≥30.5	<30
10	Road[a]	N/A	N/A

[a]Not included in resource selection models.

characteristics derived from NAIP imagery (Table 1) and the Shannon diversity index of the proportional contribution of those vegetation characteristics (i.e. heterogeneity). We excluded 3 vegetation classes (water or barren rock, medium/large trees with very sparse canopy cover, and road) given their rarity. We also included the total length of edges between hardwood, young forest, and shrubs with the other adjacent forest cover classes used in the analysis (Table 1) because these ecotones may provide owls with access to their most energetically profitable prey, the dusky-footed woodrat (*Neotoma fuscipes*), which are often most common in these 3 habitat types (Sakai and Noon 1993, 1997). Distributions of covariate values for both used and available prey capture locations are presented in Supplementary Material Figures S1 and S2. The size of buffered prey capture locations varied from 0.93 to 6.77 ha, so we also included a covariate for polygon area to control for potential area effects. We included an interaction term between percent public land and large trees/high canopy cover within owl home ranges to examine whether selection of this key forest type differed as a function of ownership given the different forest management approaches on public and private land.

We tested for collinearity among model covariates using the Pearson's correlation coefficient with a threshold of $r = 0.6$. If 2 variables were correlated where $r > 0.6$, we retained the variable that we assumed was more biologically informative. We z-standardized all continuous covariates. When making inferences about statistical relationships, we evaluated the direction of the effect (positive or negative), the effect size (biological magnitude), and uncertainty (95% confidence intervals [CIs]). However, we did not interpret the "statistical significance" of effects because the use of arbitrary thresholds based on P-values is problematic (Amrhein et al. 2019). Therefore, we sometimes made inferences about statistical relationships with P-values greater than 0.05 (but not greater than 0.1) to avoid accepting a false null hypothesis and therefore ignoring variables that were potentially biologically meaningful (Fidler et al. 2006).

We used odds ratios to aid our interpretation of the effects of vegetation classes on Spotted Owl prey capture location selection. For vegetation classes (i.e. non-edge categories), we scaled the odds ratio to represent a change in odds of selection for a 10% increase in that vegetation class. For edge categories, we scaled odds ratios to represent the change in odds of selection for an increase of 10 m ha^{-1} of edge. For example, we interpreted an odds ratio of 1.2 for "medium trees/medium canopy cover" as follows: each 10% increase in medium tree/medium canopy cover forest was associated with a gain in the odds of prey capture by a factor of 1.2 (or a 20% increase in the odds).

RESULTS

We acquired 33,056 usable nocturnal GPS locations from the 15 tagged males after culling locations taken below 3.7 voltage that typically have greater positional error (S. A. Whitmore personal communication). We identified 127 prey capture locations, of which we were able to identify specific prey species using video monitoring for 91 (72%). Spotted Owls captured 43 dusky-footed woodrats, 29 Humboldt flying squirrels, 11 white-footed mice (*Peromyscus* spp.), 3 voles (*Microtus* spp.), 2 moles (*Scapanus* spp.), 2 Botta's pocket gophers (*Thomomys bottae*), and 1 bird (Order: Passeriformes). These patterns reinforced the importance of woodrats and flying squirrels as primary Spotted Owl prey and supported only conducting species-specific resource selection analyses for these 2 prey species.

All Prey Capture Analysis

All vegetation classes were present in prey capture locations, but Spotted Owls tended to capture more prey in areas with forests characterized by more medium trees/medium canopy cover forest (β = 0.41, 95% CI: 0.10 to 0.71, $P = 0.009$), more large trees/medium canopy cover forest (β = 0.41, 95% CI: 0.18 to 0.64, $P = 0.0004$), more large trees/high canopy cover forest (β = 0.61, 95% CI: 0.07 to 1.14, $P = 0.02$) and along hardwood edges

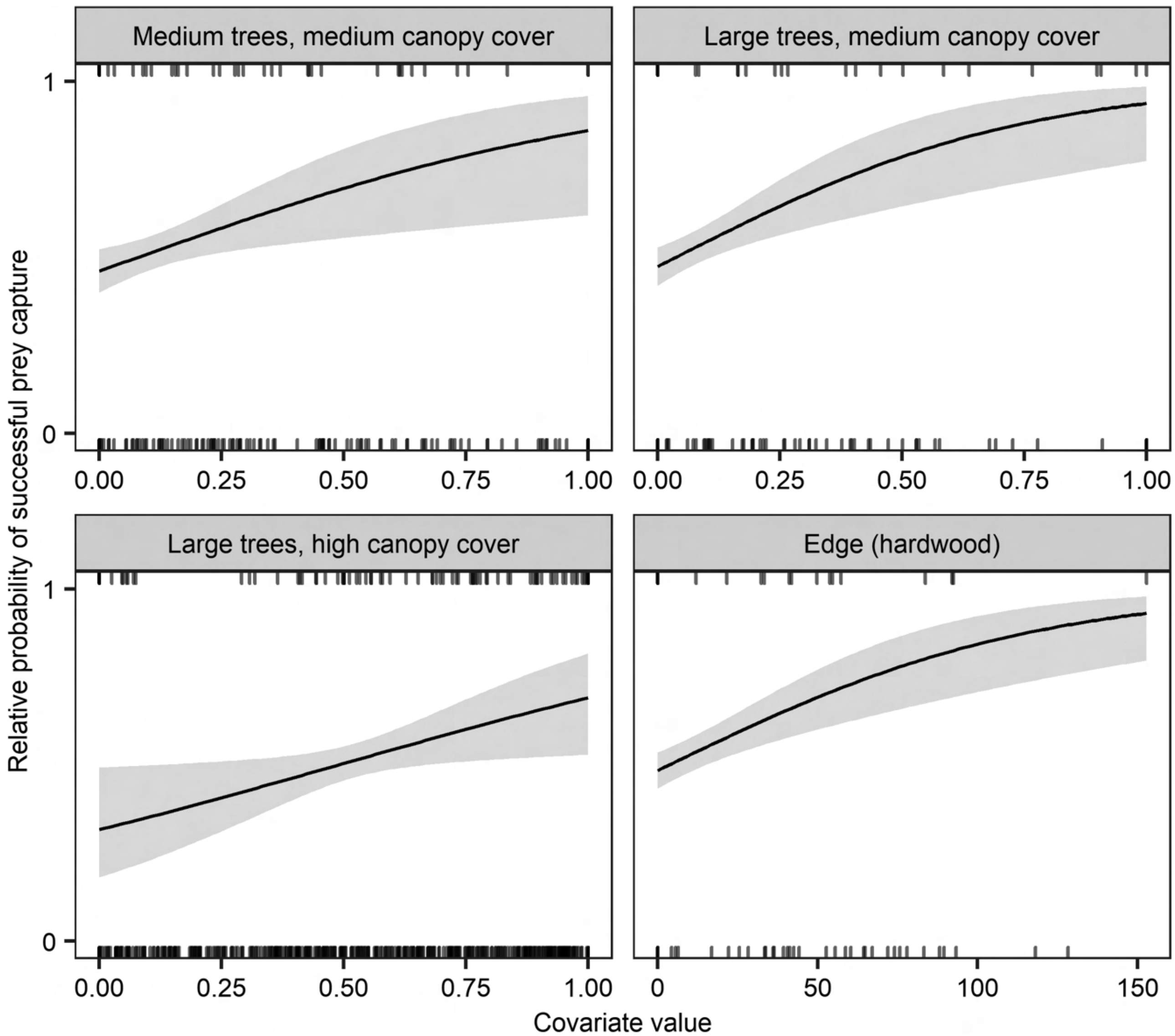

FIGURE 3. Relative probability of prey captures (with shaded areas representing 95% confidence intervals) as a function of habitat conditions for foraging Spotted Owls. Covariate values for prey capture and random polygons are visualized as rug plots at the top and bottom of each panel, respectively.

(β = 0.27, 95% CI: 0.13 to 0.40; $P < 0.0001$) (Figure 3). Odds ratios indicated that with each 10% increase in medium trees/medium canopy cover forest, the odds of prey capture increased by a factor of 1.20 (i.e. a 20% increase in odds). The odds of prey capture increased by a factor of 1.30 and 1.16 with each 10% increase in large trees/medium canopy cover forest and large trees/high canopy cover forest, respectively. Lastly, odds of prey capture increased by a factor of 1.12 with every additional 10 m ha^{-1} of hardwood edge.

Woodrat Capture Analysis

Spotted Owls tended to capture woodrats in areas with more young forest (β = 0.55, 95% CI: −0.01 to 1.12, $P = 0.056$), more medium trees/medium canopy cover forest (β = 0.62, 95% CI: −0.02 to 1.27, $P = 0.06$), more large trees/medium canopy cover forest (β = 0.71, 95% CI: 0.24 to 1.19, $P = 0.003$), more large trees/high canopy cover forest (β = 1.96, 95% CI: 0.83 to 3.09, $P = 0.0007$), in areas with a higher density of hardwood edges (β = 1.29, 95% CI: 0.53 to 2.04, $p = 0.0008$), and areas with higher forest heterogeneity (β = 0.48, 95% CI: −0.02 to 1.00, $P = 0.06$; Figure 4). Odds ratios indicated that the odds of prey capture increased by a factor of 1.39 with every 10% increase in young forest and by a factor of 1.33 with every 10% increase in medium trees/medium canopy cover forest. The odds of prey capture increased by a factor of 1.60 with every 10% increase in large trees/medium canopy cover forest and 1.61 with

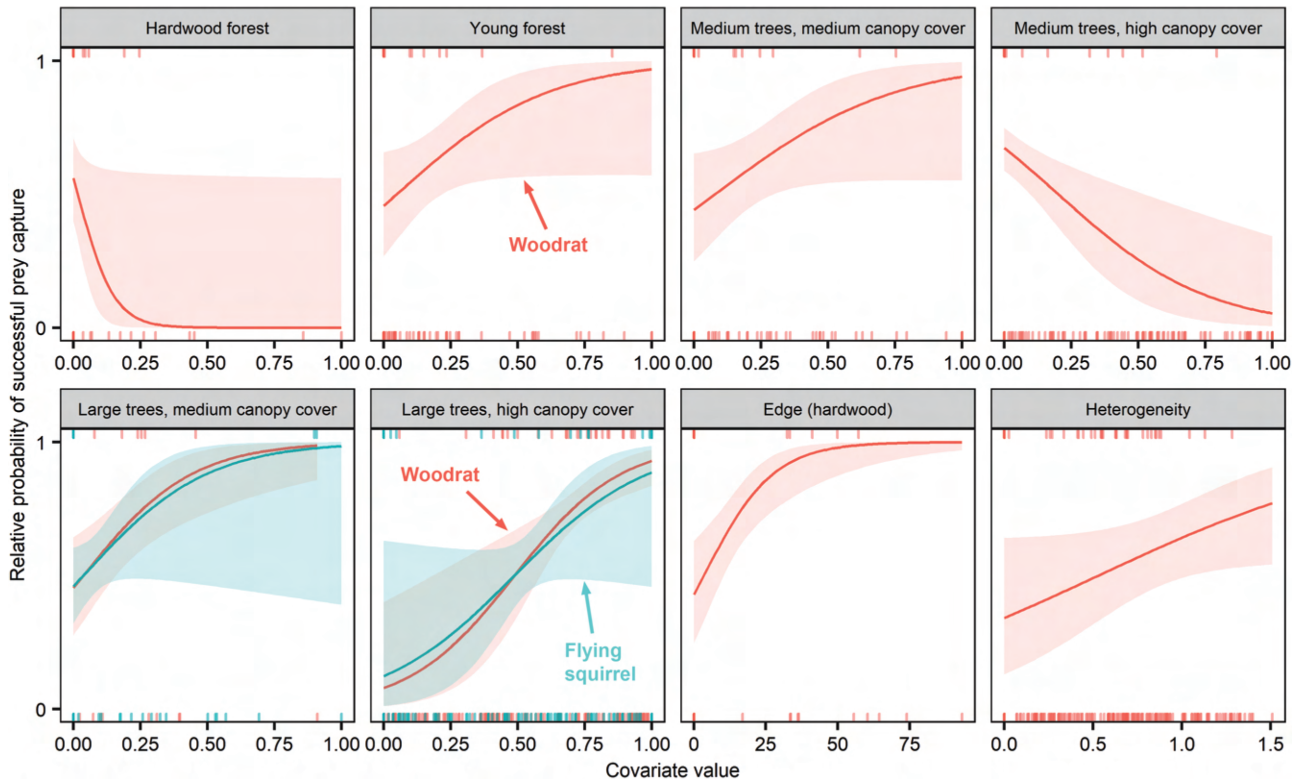

FIGURE 4. Relative probability of woodrat and flying squirrel captures (with shared areas representing 95% confidence intervals) as a function of habitat conditions for foraging Spotted Owls. Covariate values for prey capture and random polygons are visualized as rug plots at the top and bottom of each panel, respectively.

every 10% increase in large trees/high canopy cover forest. Each 10 m ha^{-1} increase in hardwood edge increased the odds of prey capture by a factor of 1.73, and each 10% increase in cover type heterogeneity increased the odds of prey capture by a factor of 1.22.

Spotted Owls were less likely to capture woodrats in areas with more hardwoods ($\beta = -1.27$, 95% CI: −2.47 to −0.06, $P = 0.049$; Figure 4). The odds of prey capture decreased by a factor of 0.24 (or a 4.2-fold decrease) with each 10% increase in hardwood forest. Spotted Owls also tended to avoid areas characterized by medium trees/high canopy cover forest when capturing woodrats ($\beta = -1.13$, 95% CI: −1.85 to −0.41, $P = 0.002$; Figure 4). The odds of prey capture decreased by a factor of 0.71 (or a 1.4-fold decrease) with each 10% increase in medium trees/high canopy cover forest.

Flying Squirrel Habitat Selection Analysis

Spotted Owls tended to capture flying squirrels in areas with more, large tree/medium canopy cover forest ($\beta = 0.63$, 95% CI: −0.09 to 1.36, $P = 0.09$) and more large tree/high canopy cover forest ($\beta = 1.56$, 95% CI: −0.23 to 3.36, $P = 0.09$; Figure 4). The odds of prey capture increased by a factor of 1.51 with every 10% increase in large trees/medium canopy cover forest and increased by a factor of 1.65 times for each 10% increase in larger trees/high canopy cover forest. Unlike the "all prey" and "woodrat" analyses, we found evidence of a negative interaction between ownership and large trees/high canopy cover forest for flying squirrels ($\beta = -0.42$, 95% CI: −0.91 to 0.06, $P = 0.09$). The odds of flying squirrel prey capture increased by a factor of 1.65 with each 10% increase in large trees/high canopy cover forest when no public land was present, but weakened by a factor of 1.25 when all land in an owl's home range was public. Example capture locations illustrating areas with high values for selected covariates are provided in Figure 5.

DISCUSSION

We leveraged recently developed GPS tagging technologies to identify capture sites of different prey species for Spotted Owls, which led to novel inferences and implications for species conservation and forest management. Importantly, several of the habitats that promoted the capture of one prey species (woodrats), such as forest heterogeneity and young forests, were not identified as informative covariates in RSFs when all prey species were considered jointly. Thus, our work builds on the findings of Marsh et al. (2014) who found that RSFs for predators including all GPS points do

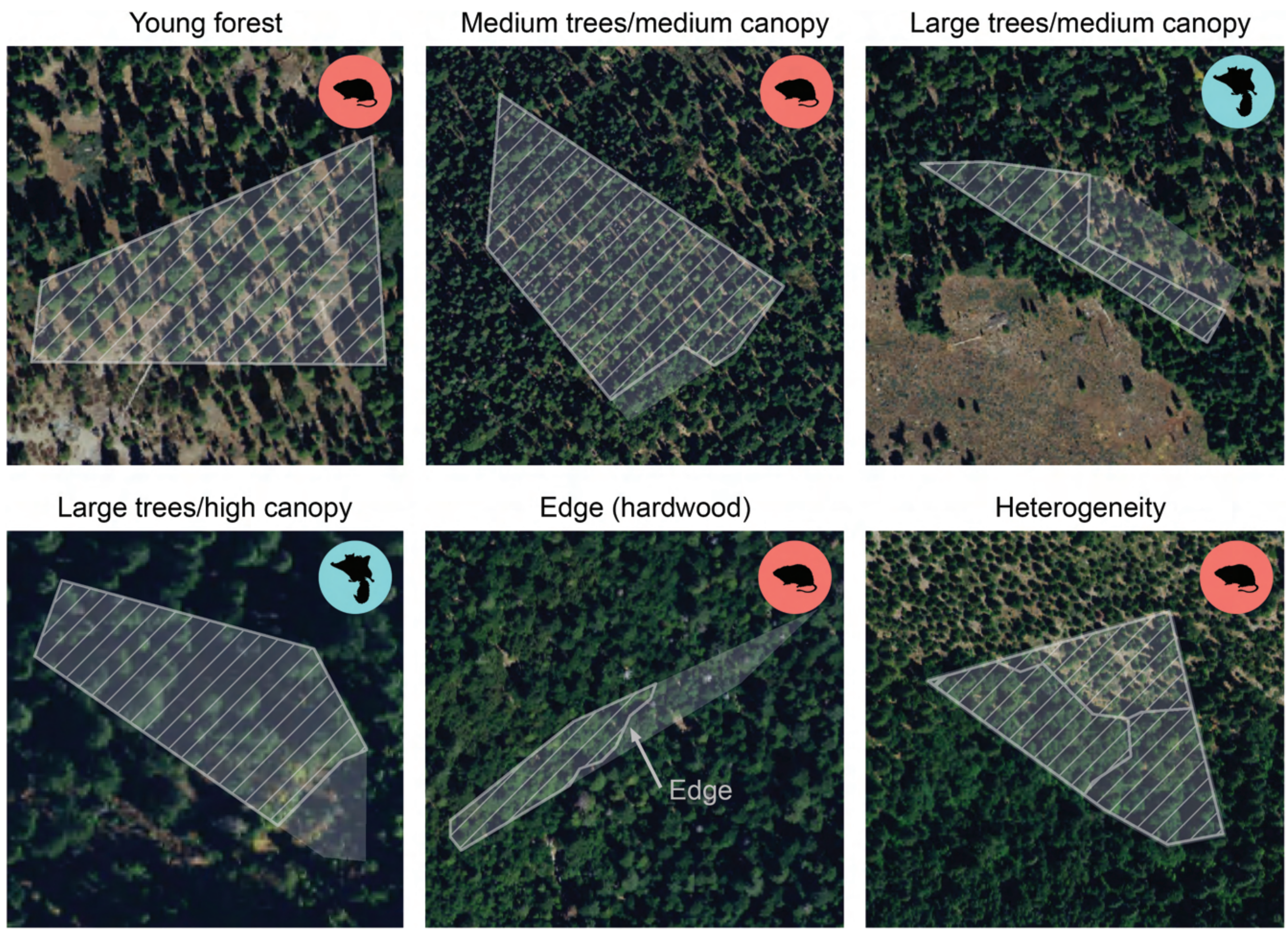

FIGURE 5. Example polygons where Spotted Owls captured either a woodrat or flying squirrel. The capture polygon is the entire shaded area, while the areas in each capture polygon containing the focal covariate (noted above each panel) are illustrated with cross-hatching. The relevant covariate value for the "edge (hardwood)" panel is the length of the internal line between the cross-hatched area (representing hardwood forest) and the shaded area (other cover types). The "heterogeneity" panel shows a mixture of three cover types (separated by thick lines) within a single capture polygon.

not necessarily reveal habitat types that confer successful prey capture. Had we not ascertained the species identity of individual prey items using nest video monitoring, we would not have identified young forests as an important habitat type, nor forest heterogeneity as important for the capture of woodrats by Spotted Owls. Such a limitation could lead to sub-optimal habitat management, given that the consumption of woodrats—a large and energetically profitable prey species—has been closely and positively linked to population-level density, reproductive rates, and territory occupancy rates of Spotted Owls (Smith et al. 1999, Hobart et al. 2019a). Indeed, the fact that previous GPS and VHF telemetry studies of Spotted Owls have been conducted without specifically accounting for prey capture locations, or linking the capture locations to the species of those prey, could account for the fact that these features are often not found to be selected by owls (Call et al. 1992). Accordingly, when practical, we encourage future studies of predator habitat selection to not only distinguish successful prey capture from other locations (e.g., resting, commuting, territorial defense) but also to discriminate among the capture of different prey species so key ecological relationships are not obscured. Studies of prey delivery rates and/or biomass of different prey types are critical to building a more complete picture of the foraging needs and tradeoffs of nesting Spotted Owls.

Whereas we have known for many decades that Spotted Owls preferentially use mature forest for nesting, roosting, and foraging (Gutiérrez et al. 2020), more recent work has indicated the importance of other habitat types (e.g., Call et al. 1992, Atuo et al. 2019, Kramer et al. 2021). These different habitat preferences can perhaps be explained by our results, which demonstrate that successful hunting—particularly for woodrats—tends to occur in a broad range of conditions, including in areas with more young forest and higher heterogeneity. Thus, our results may partially explain observations of high owl densities on some private lands (which include young forest and higher heterogeneity; Roberts et al. 2017), as well as the potential for life-history tradeoffs hypothesized to occur owing to forest heterogeneity (Franklin et al. 2000). In addition, the finding that Spotted Owls tended to not capture woodrats in areas with medium trees and high canopy cover supports previous stable isotope analyses demonstrating that owls with relatively high proportions of this forest type in their territories consume fewer woodrats, which can lead to lower territory occupancy rates and landscape-scale density (Hobart et al. 2019a). Similarly, the higher likelihood of woodrat capture in areas of high heterogeneity and young forests supports stable isotope analyses suggesting that these conditions promote woodrats that are then more available to owls (Hobart et al. 2019a)—and that young forests with a hardwood component can increase Spotted Owl reproductive success presumably because they promote populations of this energetically valuable prey species (Hobart et al. 2019b). Thus, our resource selection analysis appears to provide a mechanistic explanation for previously observed population-level phenomena in Spotted Owls.

Habitats that conferred successful prey captures by Spotted Owls likely did so by promoting hunting efficiency, high prey densities, access to areas with high prey densities, or some combination of these processes. Spotted Owls, as ambush predators, may have increased hunting efficiency due to a prevalence of suitable perching structures characteristic of mature forests with substantial vertical heterogeneity in tree height that conferred relatively high hunting success for multiple prey species (North et al. 1999). Further, forests with larger trees, and thus taller canopies, can harbor higher densities of flying squirrels due to accessibility to denning options and suitable microclimate conditions for lichen and hypogeous fungi—key food resources of flying squirrels (Waters and Zabel 1995). Spotted Owls may have rarely captured woodrats in medium tree forests with high canopy cover because of sparse shrub cover (due to reduced sunlight reaching the understory), which represents a key feature of woodrat habitat; conversely, owls may have selected for medium tree forests with medium canopy cover because of a more robust shrub component and denser woodrat populations. Furthermore, higher landscape heterogeneity in cover types may increase flying squirrel densities in remnant mature forests (Sollmann et al. 2016) and therefore might increase hunting success by owls in those areas. This could partly explain our result (Figure 6) of a stronger selection of large tree forests with high canopy cover in areas with more private lands, where mature forests occur in more discrete units and are surrounded by a greater variety of cover types. High woodrat capture success in young forests was likely the result of what can be very high woodrat densities in this forest type (Sakai and Noon 1993, Hamm and Diller 2009). While we originally predicted that edges between young forests and

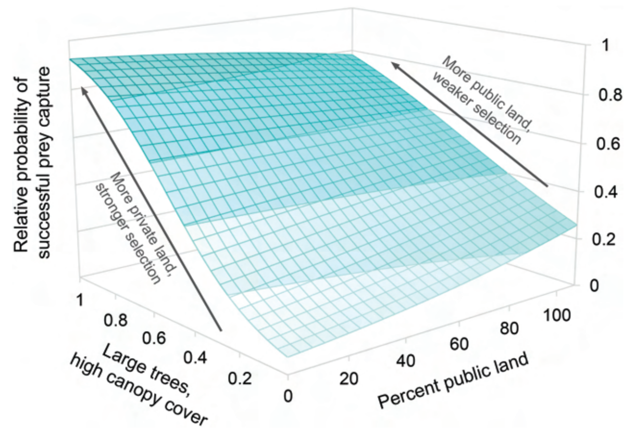

FIGURE 6. Relative probability of flying squirrel capture as a function of an interaction between large trees/high canopy cover forest and percentage of public land in a home range. The interaction term shows that positive selection for large tree forests with high canopy cover tends to weaken (though remains positive) for owls that have more public land in their 95% kernel density estimated (KDE) home range.

forests with medium and large trees would confer higher woodrat capture success by providing owls access to high-density woodrat areas (Sakai and Noon 1993), some young forests perhaps contained sufficient perching structures in the form of residual old trees or other structures (Atuo et al. 2019). Conversely, woodrats were captured less frequently in hardwood forests, which can also contain high densities of woodrats (Sakai and Noon 1993), whereas edges between hardwood and coniferous-dominated forests promoted woodrat captures by owls – consistent with our predictions. This finding suggests that hardwood forests may not provide suitable foraging structures but do appear to provide a source of woodrats for Spotted Owls foraging along the edge of hardwood and conifer forests as was hypothesized several decades ago (Sakai and Noon 1993). In this study, areas of forest classified as hardwood were generally patches of black oaks, with tanoaks in the understory typically being obscured by overstory conifer trees and thus not measured—yet are also likely potential sources of woodrats for Spotted Owls (Sakai and Noon 1993).

Our study demonstrates the opportunity to promote the conservation of Spotted Owls through habitat management. By understanding the specific habitat types and configurations that confer hunting success during a critical life-history period (the provisioning of young in nests and dens), management actions can promote higher prey densities in areas where capture is likely. Numerous predators have become endangered because of direct exploitation (Carter et al. 2017), yet declines in prey resources that reduce reproduction (Becker and Beissinger 2006), as well as indirect effects associated with anthropogenic habitat change (Hanski 2011), can also cause species declines. Hence, enhancing the habitat of key prey species, especially large-bodied or nutritionally important ones that promote individual fitness components and population density, hold promise for recovering endangered predators. Recent advances in very small GPS packages with high accuracy, combined with video-based breeding site monitoring, now make fine-scale studies practical for a broader suite of predators, including small-bodied and cryptic ones (Studd et al. 2021, Wood et al. 2021). Such investigations will certainly be fruitful in forested systems such as the one studied here, but similar opportunities also exist in other terrestrial and aquatic ecosystems.

Several findings in this study point to co-benefits between Spotted Owl conservation and forest management activities intended to reduce forest fuels, two objectives often seen as diametrically opposed in a region experiencing megafires without modern precedent that can lead to Spotted Owl population losses (Jones et al. 2016, 2021). First, the selection of forests with large trees for the capture of both key prey species underscores that these structures are both "ecological backbones" of dry forests and a key component of foraging habitat for mature forest species such as Spotted Owls (Hessburg et al. 2015). Second, Spotted Owls tended not to capture woodrats in forests characterized by medium trees and high canopy cover, a forest type that is often synonymous with the historical legacy of fire exclusion and selective large tree removal in the dry forest ecosystems in western North America, which are now at great risk of large severe fires (Peery et al. 2017). Thus, promoting large tree recruitment and creating canopy openings in such forests as part of management activities could enhance the ability of Spotted Owls to capture and consume woodrats and lead to population-level benefits. Such forests could benefit Spotted Owls even prior to large tree recruitment given that medium tree forests with medium canopy cover tended to promote successful woodrat hunting. Further, promoting heterogeneous forests characterized by a mosaic of mature and younger forests, as well as a mixture of conifer and hardwood species, could both reduce severe fire risk and benefit Spotted Owls and other taxa.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement: Data collectors were trained in the responsible handling of birds following our IACUC (Institutional Animal Care and Use Committee) protocol # A005367-R02 and were authorized from California Department of Fish and Wildlife's scientific collection permit (S-193180001-19324-001) and under USGS Bird Banding Lab permit # 23685 before undertaking the work. We also adhered to the University of Wisconsin–Madison Responsible Conduct of Research policy in carrying out this work.

Conflict of interest statement: The authors declare no conflict of interest.

Author contributions: J.J.K., K.N.R., B.P.D., S.C.S., and M.Z.P. conceived the idea, design, experiment (supervised research, formulated question or hypothesis). C.J.Z. performed the experiments (collected data, conducted the research). C.J.Z., H.A.K., G.M.J., and M.Z.P. developed or designed statistical methods. C.J.Z., H.A.K., G.M.J., A.K.W., and MZP analyzed the data. All authors contributed to writing the or substantially editing the paper.

Data availability: Analyses reported in this article can be reproduced using the data provided by Zulla et al. (2022).

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