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Tall, heterogeneous forests improve prey capture, delivery to nestlings, and reproductive success for Spotted Owls in southern California

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ABSTRACT

Predator–prey interactions can be profoundly influenced by vegetation conditions, particularly when predator and prey prefer different habitats. Although such interactions have proven challenging to study for small and cryptic predators, recent methodological advances substantially improve opportunities for understanding how vegetation influences prey acquisition and strengthen conservation planning for this group. The California Spotted Owl (*Strix occidentalis occidentalis*) is well known as an old-forest species of conservation concern, but whose primary prey in many regions—woodrats (*Neotoma* spp.)—occurs in a broad range of vegetation conditions. Here, we used high-resolution GPS tracking coupled with nest video monitoring to test the hypothesis that prey capture rates vary as a function of vegetation structure and heterogeneity, with emergent, reproductive consequences for Spotted Owls in Southern California. Foraging owls were more successful capturing prey, including woodrats, in taller multilayered forests, in areas with higher heterogeneity in vegetation types, and near forest-chapparal edges. Consistent with these findings, Spotted Owls delivered prey items more frequently to nests in territories with greater heterogeneity in vegetation types and delivered prey biomass at a higher rate in territories with more forest-chaparral edge. Spotted Owls had higher reproductive success in territories with higher mean canopy cover, taller trees, and more shrubby vegetation. Collectively, our results provide additional and compelling evidence that a mosaic of large tree forest with complex canopy and shrubby vegetation increases access to prey with potential reproductive benefits to Spotted Owls in landscapes where woodrats are a primary prey item. We suggest that forest management activities that enhance forest structure and vegetation heterogeneity could help curb declining Spotted Owl populations while promoting resilient ecosystems in some regions.

Keywords: chaparral, habitat selection, prey capture, reproduction, *Strix occidentalis*, southern California, woodrat

How to Cite

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LAY SUMMARY

- Identifying where prey is captured can help understand high-quality hunting habitat for predators but is very difficult to do for small cryptic predators.
- We combined high-resolution GPS and camera technology to examine how vegetation conditions influence prey capture, delivery rate, and reproductive success for a small nocturnal predator, the Spotted Owl (*Strix occidentalis occidentalis*).
- Spotted Owl prey captures increased with heterogeneous vegetation, larger trees, complex multilayered canopies, and more forest-chaparral edge. Prey delivery increased with more cover type heterogeneity and forest-chaparral edge.
- Spotted Owl reproductive success was higher in territories having taller canopies, greater canopy cover, and more shrubby vegetation.
- Forest management activities that increase the number of large trees, promote multilayered canopies, and enhance vegetative heterogeneity are likely to benefit Spotted Owls.

Los bosques altos y heterogéneos mejoran la captura de presas, la entrega a los polluelos y el éxito reproductivo de *Strix occidentalis* en el sur de California

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RESUMEN

Las interacciones depredador-presa pueden verse profundamente influenciadas por las condiciones de la vegetación, particularmente cuando el depredador y la presa prefieren diferentes hábitats. Aunque tales interacciones han demostrado ser difíciles de estudiar para depredadores pequeños y crípticos, los avances metodológicos recientes mejoran sustancialmente las oportunidades para comprender cómo la vegetación influye en la adquisición de presas y para fortalecer la planificación de la conservación de este grupo. *Strix occidentalis occidentalis* es bien conocida como una especie de bosque maduro de interés para la conservación, pero cuya presa principal en muchas regiones, la rata de bosque (*Neotoma* spp.), se presenta en una amplia gama de condiciones de vegetación. Aquí, utilizamos el seguimiento por GPS de alta resolución junto con el monitoreo por video de nidos para evaluar la hipótesis de que las tasas de captura de presas varían en función de la estructura y heterogeneidad de la vegetación, con consecuencias reproductivas emergentes para *S. o. occidentalis* en el sur de California. Los búhos que forrajearon tuvieron más éxito en la captura de presas, incluidas las ratas de bosque, en los bosques más altos con varios estratos, en áreas con mayor heterogeneidad en los tipos de vegetación y cerca de los bordes de bosque y chaparral. De acuerdo con estos hallazgos, *S. o. occidentalis* entregó presas a los nidos con mayor frecuencia en territorios con mayor heterogeneidad en los tipos de vegetación y entregó biomasa de presas a una tasa más alta en territorios con más borde de bosque y chaparral. *S. o. occidentalis* tuvo un mayor éxito reproductivo en territorios con mayor cobertura media del dosel, árboles más altos y vegetación más arbustiva. Colectivamente, nuestros resultados proporcionan evidencia adicional y convincente de que un mosaico de bosques con grandes árboles con un dosel complejo y vegetación arbustiva aumenta el acceso a las presas con beneficios reproductivos potenciales para *S. o. occidentalis* en paisajes donde las ratas de bosque son una presa principal. Sugerimos que las actividades de gestión forestal que mejoran la estructura forestal y la heterogeneidad de la vegetación podrían ayudar a frenar la disminución de las poblaciones de *S. o. occidentalis* y, al mismo tiempo, promover ecosistemas resilientes en algunas regiones.

Palabras clave: captura de presas, chaparral, rata de bosque, reproducción, selección de hábitat, *Strix occidentalis*, sur de California

INTRODUCTION

Predator–prey interactions are shaped by the ability of predator and prey to detect and respond to each other (Sih 1984, Lima and Dill 1990). Vegetation conditions can have profound effects on these interactions if they favor either predator or prey (Gorini et al. 2012). Vertical structure in vegetation can benefit either predators when it provides ambush cover (Preston 1990, Gorini et al. 2012) or prey when it provides escape cover (Boinski et al. 2003, Gorini et al. 2012). Horizonal heterogeneity in vegetation conditions (e.g., vegetation types or heights; hereafter "heterogeneity") can create spatial refuges for prey populations, such that predators preferentially hunt in areas having lower prey density without prey refuges (Hopcraft et al. 2005, Horinouchi et al. 2009). However, prey refuges constraining hunting success can benefit predators by acting as source populations for prey that disperse into habitats more favorable to hunting success (Kauffman et al. 2007, DeMars and Boutin 2018, Smith et al. 2019). Thus, understanding how vegetation influences predator–prey interactions can strengthen conservation plans, particularly for rare predators threatened by habitat change (Katzner et al. 2005, Catry et al. 2013, Hobart et al. 2019a, Smith et al. 2020).

Most studies about how vegetation conditions shape hunting success have focused on large mammalian carnivores, for which both predator and prey are easily observed (Gorini et al. 2012). Yet, the majority of predators—such as birds of prey—are small and cryptic, leaving little, if any, prey remains at a predation site, instead concentrating remains in pellets or scat (Andrews and Cook 1990). Studies of foraging habitat selection in small, cryptic predators typically rely on telemetry approaches that yield locational data agnostic to the activity of the predator and include unrelated behaviors like territory defense, general location change, courtship, and resting (Marsh et al. 2014a). Consequently, such approaches could produce misleading representations of high-quality foraging habitat, potentially compromising conservation plans (Marsh et al. 2014a). However, the pairing of small, accurate GPS telemetry units (Tomkiewicz et al. 2010) to follow predator movement and video camera technology to identify prey delivered to nests have recently—and substantially—facilitated the identification of prey capture locations for small and cryptic predators during the critical nesting or denning periods (Marsh et al. 2014a, 2014b, Sanjose et al. 2020, Wood et al. 2021).

The Spotted Owl (*Strix occidentalis*) is a small, nocturnal predator closely associated with commercially valuable older forests (i.e., large trees, high canopy cover) and has substantial influence on conservation decisions and forest management across its range (Verner et al. 1992, Marcot and Thomas 1997, Gutiérrez et al. 2017). Although it is among the most well-studied birds in the world and its diet and nocturnal habitat use are well documented (Gutiérrez et al. 1995, Löhmus 2004), vegetation conditions conferring successful hunting are generally unknown, owing to its small body size and cryptic hunting methods (but see Zulla et al. 2022). While Spotted Owls frequently use older forests during nocturnal activities, woodrats (*Neotoma* spp.) are a primary prey across the majority of their range and occur in a wide variety of environments including younger forests and shrub-dominated communities (Sakai and Noon 1993, Innes et al. 2007, Kelt et al. 2013). It has been presumed that owls do not typically forage in some environments harboring high densities of woodrats because of lack of perches, difficulty in capturing prey, or an increased risk of their own predation (Call et al. 1992, Sakai and Noon 1993, Franklin et al. 2000). However, woodrats cross ecotones along which owls are known to forage (Zabel et al. 1995, Sakai and Noon 1997, Parmenter et al. 2003, Kramer et al. 2021b). Thus, early seral stage forests, oak woodlands, and shrub communities may serve as source populations of woodrats for foraging Spotted Owls - particularly when they occur adjacent to older forest with suitable perching structures (Ward et al. 1998, Franklin et al. 2000, Hobart et al. 2019b). Abundant sources of woodrats could benefit nesting Spotted Owls as woodrat consumption by owls appears to increase reproductive success (Ward et al. 1998, Smith et al. 1999). Thus, Spotted Owl hunting success, and ultimately fitness and population status, may benefit from a mosaic of vegetation conditions including forests with vertical structure and heterogeneity in vegetation types.

Here, we paired recent advances in GPS telemetry with nest video monitoring to understand how vegetation structure and heterogeneity influenced Spotted Owl hunting success and nest provisioning. Spotted Owls in southern California provide a unique opportunity to understand how vegetation structure and heterogeneity shape prey capture

success given: (1) that woodrats constitute the dominant prey species (composing 74% of diet by biomass; Smith et al. 1999), and (2) the broad range of vegetation conditions that occur in this region (see study area below). We hypothesized that both vertical structure and heterogeneity in vegetation conditions influence the ability of Spotted Owls to acquire prey, with emergent effects on reproductive success. Under this hypothesis, we predicted that Spotted Owls would capture woodrats and potentially other prey species in areas having greater vertical structure, more spatial heterogeneity in vegetation composition, and more edge between forest and shrubby areas. We also predicted that Spotted Owls would deliver more prey to nest sites when their territories contained greater amounts of the vegetation conditions that facilitated prey captures (identified in the first analysis). Finally, we predicted that Spotted Owls would have higher reproductive success when their territories contained more of the vegetation conditions that facilitated prey captures and deliveries to nests (identified in the first and second analyses). Our study population occurs near the southern range boundary of California Spotted Owls and has experienced substantial declines, in part due to interactions among vegetation change (e.g., loss of large trees), climate change, and severe wildfire (Tempel et al. 2022). Thus, an improved understanding of the vegetation conditions that promote successful prey acquisition, nest provisioning, and reproductive success could strengthen conservation planning for owls in this region.

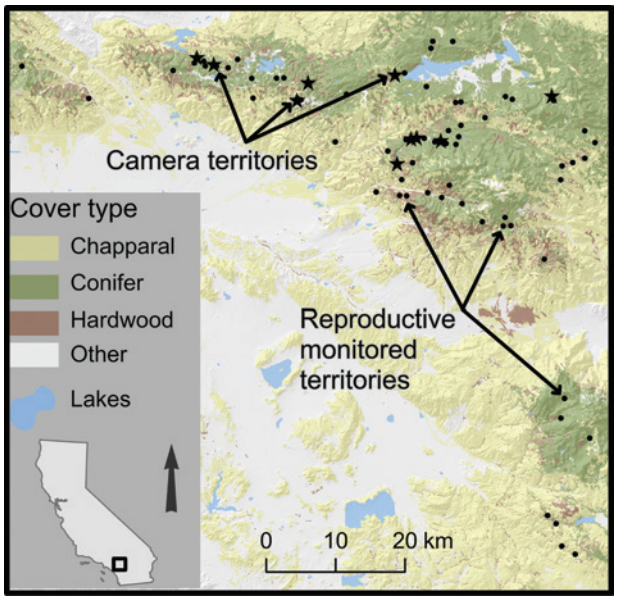

FIGURE 1. Map depicting 10 nest video camera locations for California Spotted Owl (*Strix occidentalis occidentalis*) hunting success and delivery rate analyses (black stars) as well as the 71 territories used in the reproductive success analysis (black circles) overlayed over dominant vegetation types. Elevations in the study area ranged from ~800 to 2,600 m with camera territories sampled between ~1,200 and 2,300 m. Inset map shows broader location in southern California, USA.

METHODS

Study Area

We studied Spotted Owls in the San Bernardino and San Jacinto Mountains of southern California (Figure 1), which have been almost continuously monitored for over 3 decades. Elevations ranged from ~800 to 2,600 m. Vegetation community types included mixed conifer, bigcone Douglas fir/live oak woodlands, hardwood forests/riparian areas, and chaparral. Mixed-conifer forests primarily occur at higher elevations and consisted of a mixture of pines and other conifer species as well as scattered hardwoods. Woodlands occurring at intermediate elevations, were dominated by bigcone Douglas fir (*Pseudotsuga macrocarpa*) and canyon live oak (*Quercus chrysolepis*). Chaparral vegetation was often found interspersed with bigcone Douglas fir/canyon live oak woodlands. Hardwood forests/riparian areas dominated the canyon bottoms and were primarily comprised of canyon live oak, California sycamore (*Platanus racemose*), cottonwood (*Populus spp.*), and white alder (*Alnus rhombifolia*). For our analyses, we reduced these community types to the dominant vegetation types of conifer, hardwood, or chaparral (Figure 1).

GPS Tagging and Video Monitoring

We used standard call-based survey methods to locate breeding pairs of Spotted Owls in 2021 (Franklin et al. 1996), from which we selected 10 owl pairs for GPS tagging and video camera monitoring of prey deliveries to nest sites between late April and early June. Sites with nesting owls were selected to include a wide range of elevations (~1,200–2,300 m), contain the 3 dominant vegetation cover types (conifer, hardwood, and chaparral), and not have been exposed to widespread (>10% of the territory) high severity wildfire. Additionally, while first ensuring a range of elevations and cover type abundances, we prioritized sites closer to roads and trails, with males that could be captured, and accessible nests. At each site, we captured male Spotted Owls using noose poles and "hand capture" techniques (Wood et al. 2021) and attached GPS tags (Alle-300, Ecotone, Poland) via tail mounts (Kramer et al. 2021b). Males are responsible for the vast majority of foraging by Spotted Owls during incubation and brooding, such that focusing on males should provide reasonable insights into foraging patterns during nesting for this species (Delaney et al. 1999). We programmed GPS tags to record a location every 2 min, for 10 hr each night (2000–0600 PDT) over the life of the tag ($\bar{x} = 6$ nights). Median positional error was 45 m (individual tag median range: 15–74 m; S.A. Whitmore and H.A. Kramer, personal communication) and GPS filtering to improve accuracy was not possible with the details associated with each GPS location (i.e., dilution of precision or other similar metrics were not reported by the tags).

We installed infrared cameras (AXIS Q1786 – LE, 4 megapixel) in a tree adjacent to each nest tree to monitor nests during the same 10-hr period that the GPS tags were collecting locations, plus an additional 30 min each morning (2000–0630 PDT). Owing to the effort required to install and remove cameras, we frequently acquired extra nights of video data ($\bar{x} = 8.9$ nights, $\bar{x} = 93.5$ hr). Cameras were placed at least 10 m from the nest tree to minimize disturbance to nesting activities. To install video cameras, we climbed trees using single rope technique, which avoids climbing spurs and thus does much less damage to trees and increases the safety and efficiency of climbers (Anderson et al. 2015).

Identifying Successful Hunting Locations

To identify successful hunting locations, we first reviewed all video data and identified the time of prey delivery and the species delivered (when possible). We then examined GPS data for clusters of GPS points recorded just before a relatively straight movement path back to the nest (Marsh et al. 2014a, Wood et al. 2021). Following Zulla et al. (2022) we defined clusters as containing up to 10 GPS locations before the male's return to the nest, where all points in the cluster occurred over a span of 20 min or less and with no more than 250 m between the farthest points (Figure 2). After we linked prey deliveries observed in video recordings to a GPS point cluster, we calculated a minimum convex polygon around those points, then enlarged the perimeter of ("buffered") that polygon by 50 m (hereafter "capture polygon") to better account for GPS positional error, the potential effects of surrounding habitat on prey acquisition, and to maintain consistency with a similar study completed in the Sierra Nevada (Zulla et al. 2022). To compare vegetation conditions in these polygons to the overall composition of the owl's territory (see statistical analysis for more details), we generated 10 available polygons that matched the shape and size of each capture polygon within Spotted Owl home ranges. We placed each of these available polygons at a random location within the owl's home range and rotated each to a random orientation. We defined approximate home ranges using a 95% kernel density estimate (KDE) of each tagged owl, estimated using fixed kernel width using the *adehabitat* package in R ($\bar{x}$ = 142.57 ha, range: 86.50–238.55 ha; Seaman and Powell 1996, Calenge 2006).

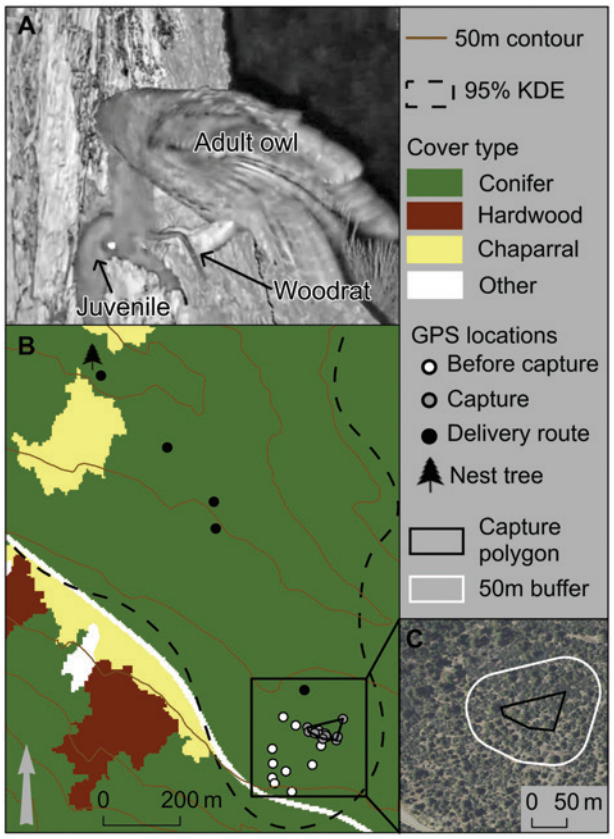

FIGURE 2. (**A**) Male delivering a woodrat to a juvenile on video camera. (**B**) Map of GPS points before (white), during (grey), and after (black) a successful hunt by a Spotted Owl as it returns to the nest with the prey, within the owl's 95% kernel density estimate (KDE). Note that the grey points in (**B**) are used to create the capture polygon shown in a map (**C**) over NAIP imagery, including both the capture polygon (black) and buffered capture polygon (white).

Estimating Prey Delivery Rates

To estimate prey delivery rate, we recorded the number of prey deliveries captured on video per hour. To further investigate the relationship between vegetative conditions and prey delivery rate to nest, we analyzed how prey biomass (i.e., estimated mass in grams of prey items delivered to nests) was related to vegetative conditions in a home range. For prey identified to the species level, we assigned body mass (g). For woodrats and flying squirrels (*Glaucomys sabrinus*), we estimated an average body mass of individuals captured by owls by relating measurements of bones collected from regurgitated pellets to bones of museum specimens of known body mass following Zulla (2021). Briefly, this approach involved developing allometric relationships between body mass and skeletal measurements using museum specimens and then using these relationships to predict the average body mass of woodrats and flying squirrels in owl pellets based on skeletal measurements in those pellets (Zulla 2021). We then assumed that the average body mass of these two prey species was equivalent between pellets and the prey we observed delivered to nests in this study. For other identified species, we obtained an average mass for delivered individuals of each prey species by averaging masses of museum specimens from the southern California region (latitude: 32.3 to 34.6°N, longitude: –117.9 to –115.9°W) using the ARCTOS collections database (https://arctos.database.museum/search.cfm; specimens from collections MVZ, UWBM, MSB, and DMNS). In cases that we could not identify to the species level ("unknown"), we assigned prey to 1–4 size classes (tiny, small, medium, and large) based on the prey's size relative to the owl delivering it and other, known prey items delivered to the nest. To calibrate the size ranges in each category, we assigned identified prey species into size classes (e.g., deer mice [*Peromyscus* spp.] were small, whereas woodrats were large). We then used the average mass of all identified species within each size class to assign a mass to that size class, and thus assigned that mass to each unknown prey in that size class.

Characterizing Vegetation Conditions

We characterized vegetation conditions within both used and available polygons to test for selection of vegetation that was associated with capture sites (Table 1). We also characterized vegetation conditions within home ranges to understand how vegetation conditions are related to prey delivery rates and reproductive success (Table 1). We estimated vegetation structure using remotely sensed data from the California Forest Observatory (CFO) which uses deep learning models to link available airborne LiDAR with satellite imagery using pattern recognition to predict vegetation structure across the state of California at a spatial scale of 100 m^2 on an annual basis (CFO 2020). We used CFO data from 2020 to estimate average canopy cover (%), canopy height (m), canopy layer count (0–3), and ladder fuel density (%). For clarity we renamed ladder fuel density "shrubby

vegetation density," henceforth, since the term "ladder fuel" is often associated with vegetation under overstory vegetation, yet this metric is simply an estimate of the density of vegetation between 1 and 4 m, agnostic to overstory. We used vegetation type data from the Classification and Assessment with Landsat of Visible Ecological Groupings (CALVEG) vegetation classification system, specifically the Anderson land use/land cover level two classification system (Anderson et al. 1976), a mid-level vegetation mapping product that classifies existing dominant vegetation with a rough minimum polygon size of 2 ha (Brewer et al. 2015). We used the CALVEG dataset, last updated in 2018, to estimate percentage of conifer, hardwood, and chaparral dominated vegetation types within polygons. To minimize the temporal mismatch between the timing of vegetation metric and foraging data collection, we avoided collecting GPS and camera data in areas with large impacts from recent fires or other vegetation altering events.

We then used a combination of the CFO and CALVEG data to estimate 2 measures of relative edge and two measures of vegetation heterogeneity within capture polygons, available polygons, and home ranges (Table 1, Supplementary Material Figure 1). We defined "primary edge" as any boundary between chaparral and a forest type (conifer or hardwood). We defined "secondary edge" as any boundary between vegetation types and between short (<10 m canopy height) or tall (>10 m canopy height) vegetation of the same or different type. We normalized primary and secondary edge measures in polygons and home ranges by dividing the sum of edge length by the area of each polygon so that they represented a measure of the "density" of edge. We estimated coarse heterogeneity within capture polygons using the Shannon Diversity Index of the proportions of each of the 3 main vegetation classes (conifer, hardwood, chaparral) and a class representing any other ("other") vegetation. We estimated "fine heterogeneity" similarly to coarse heterogeneity, but we split conifer and hardwood forest classes into 3 classes each, short forests (canopy height <10 m), tall forests sparse canopy (canopy height >10 m, canopy cover <70%), and tall forests dense canopy (canopy height >10 m, canopy cover >70%).

Assessing Reproductive Success

To examine the relationship between vegetation conditions and reproductive success, we used a broader set of reproductive outcomes for Spotted Owl territories in both the San Bernardino and San Jacinto Mountains collected between 2006 and 2020 (Tempel et al. 2022). These historical reproductive outcomes were estimated by assuming that a pair of owls was not nesting if (1) when offered mice by researchers, one member ate or cached four or more mice; or (2) a female was observed roosting for more than 45 min before 15 May (Tempel et al. 2022). For nesting owls, the number of young fledged was counted during follow-up visits following fledging young. Reproductive data collected before 2006 was not considered because southern California experienced widespread drought related tree mortality between 2002 and 2005 (Preisler et al. 2017) and the remotely sensed vegetation data we used (see characterizing vegetation conditions above) were collected after this period. Hence, the vegetation conditions during the study were different before 2006.

TABLE 1. Vegetation covariates used to investigate Spotted Owl hunting success, prey delivery rate, and reproductive success. California forest observatory ("CFO") and Classification and Assessment with Landsat of Visible Ecological Groupings ("CALVEG").

Variable	Description	Data source
Canopy cover	Mean percent canopy cover	CFO
Canopy height	Mean canopy height	CFO
Shrubby vegetation density	Mean "ladder fuels density" (estimated vegetation density 1–4 m above ground divided by estimated vegetation 0–4 m)	CFO
Canopy layers	Mean count of canopy layers	CFO
Percent hardwood	Percent of vegetation considered hardwood within a polygon	CALVEG
Percent chaparral	Percent vegetation considered chaparral within a polygon	CALVEG
Percent conifer	Percent vegetation considered conifer/mixed conifer within a polygon	CALVEG
Primary edge density	Boundaries between Chaparral and any conifer or hardwood	Smoothed CALVEG layer
Secondary edge density[a]	Boundaries between Chaparral, small conifer, small hardwood, large conifer and large hardwood stands	Merged smooth CALVEG layer and smoothed canopy height layer >10
Coarse heterogeneity	Shannon diversity index of chaparral, conifer, hardwood, and other vegetation	CALVEG
Fine heterogeneity[a,b]	Shannon diversity index of 8 classes 3 Conifer (small trees, large trees sparse canopy, large trees dense canopy) 3 Hardwood (small trees, large trees sparse canopy, large trees dense canopy) Chaparral and other vegetation	Merged CALVEG with CFO canopy height and canopy cover layers

[a] Small: canopy height <10 m; large: canopy height >10 m.
[b] Sparse canopy: canopy cover <70%; dense canopy: canopy cover >70%.

Statistical Analyses

To test for vegetation conditions correlated with hunting success, we compared used and available polygons in a resource selection framework. We conducted 2 separate analyses, one where we considered all prey and one for only woodrats, given the importance of this species for Spotted Owls in the region (e.g. Smith et al. 1999). We used binomial generalized linear mixed models (GLMMs), with capture polygons coded as 1 and available polygons coded as 0, while treating all vegetation covariates as fixed effects. Following Duchesne et al. (2010), we allowed for individual random intercepts to relax the assumption of homogenous selection among individuals. We weighted available polygons (W = 1,000) to enable convergence to an inhomogeneous Poisson process, where "W" refers to the weight given to available polygons in the GLMMs (Muff et al. 2020). We included the fixed effects of polygon area and distance to nest to account for different polygon sizes between prey types and to control for Spotted Owls central place foraging tendency, respectively (Rosenberg and McKelvey 1999).

To determine how vegetation affected prey deliveries to nests, we used 2 sets of linear regression analyses: the first treating prey delivery rate (prey items prey hour) as the response variable, and the second treating prey biomass delivery (grams per hour) as the response variable. We treated vegetation metrics within Spotted Owl 95% KDE approximate home ranges as explanatory variables but limited potential covariates to those deemed informative from our first analysis because of smaller sample sizes (n = 10).

To determine if vegetation features that influence foraging also influence reproductive success, we evaluated how the same eleven vegetation covariates from our first analysis (Table 1) related to historical reproductive success (0–3 young fledged) using GLMMs. To account for lack of independence for reproductive success within sites and between years and to account for Spotted Owl reproductive cycling unrelated to vegetation conditions, we included both site and year as random effects. We delineated hypothetical home ranges as circles centered on the geometric mean of nest trees found within a territory with a radius of 1,000 m. Thus, each "home range" area was 314 ha, which approximates owl home range areas in the San Bernardino Mountains, which range between about 220 and 650 ha (Zimmerman et al. 2001). We excluded samples for sites which were either not occupied by pairs or occupied by pairs that did not attempt to nest because our first two analyses were fundamentally limited to nesting pairs. Further, events besides foraging success can influence an owl pair's decision to nest each year (e.g., winter/spring weather; North et al. 2000). We also removed any home ranges where over 10% of their area burned in high severity wildfire since 2006 to avoid mismatch between the measured vegetation (based on CALVEG [2018] and CFO [2020] data) and vegetation when owls attempted reproduction. Previous research showed owl territories that did not experience major events like wildfire or timber harvest showed minimal changes in vegetation over an 18-yr period (Tempel et al. 2016). As our study area has no substantive timber harvests, we assumed that any other differences in vegetation type or structure were minimal over the period for which nesting data was analyzed (2006–2020). After removing sites and samples because of fire impacts or lack of nesting pairs, we retained 71 sites and 268 samples for an average of 3.7 years of reproductive data per site.

Our objective in these analyses was to identify the suite of vegetation conditions potentially, but meaningfully, influencing the location of prey captures, prey delivery rates, and reproductive success rather than identifying a "top model" per se. Therefore, we performed an all-subsets model selection procedure for each of the 3 analyses using Akaike's Information Criterion with a correction for small sample sizes (AIC_c) and considered all models within 2 AIC_c of the most supported model to be competitive (Burnham and Anderson 2002). We did not allow highly correlated ($r \geq 0.7$) variables to be included in the same model. We z-standardized all covariates (mean = 0, SD = 1) to aid in interpreting the relative importance of covariates with different units (Schielzeth 2010). Owing to considerable model selection uncertainty with multiple competitive models in the hunting success and reproductive success analyses, we averaged model predictions of covariate relationships to make inferences. For the hunting success and reproductive success analyses we report model averaged coefficients to aid in contextualizing the results (using the structure β, [confidence interval]), and adopted 85% confidence intervals as recommended by Arnold (2010). We avoided using model averaged coefficients to make inferences directly, because multicollinearity among covariates increases uncertainty and can cloud the interpretation of model-averaged coefficients (Cade 2015). Thus, note that some confidence intervals for model-averaged coefficients may overlap zero due to uncertainty introduced from the model averaging procedure. We also did not make inferences about uninformative parameters (Arnold 2010) or parameters that appeared in only one competitive model, which we assumed could be spurious effects. We did not perform corrections for multiple comparisons because such corrections decrease the probability of detecting relationships as more statistical tests are performed (Moran 2003). We conducted all analyses in program R 4.0.2 (R core team 2021). We fit GLMMs using package *glmmTMB* (Bolker 2021) and performed model selection using package *MuMIn* (Barton 2020).

RESULTS

Characteristics of Successful Hunting Locations

We identified 120 putatively successful hunting locations and the prey caught in those locations by combining the GPS clusters we defined as capture polygons with the subsequent prey delivery to the nest recorded by the cameras at the 10 nest sites. These capture polygons were an average of 0.80 ha in size (range: 0.47–2.76 ha), while capture polygons with a 50-m buffer averaged 3.94 ha in size (range: 1.46–6.91). Woodrats were the most common prey item captured within the 120 capture polygons, accounting for 42 (35%) of all prey items. The next most common prey were deer mice (24%), followed by pocket gophers (*Thomomys bottae*; 12%), and flying squirrels (3%); 22% of captured prey could not be identified.

Spotted Owls generally captured prey ("all-prey" analysis) in areas with higher canopy height (model-averaged coefficient 0.33, model-averaged 85% CI [0.17, 0.49]), more canopy layers (0.34, [0.16, 0.53]), greater fine heterogeneity (0.14, [–0.03, 0.31]), and increased primary edge (0.15, [–0.02, 0.32]) and secondary edge densities (0.22, [0.06, 0.38]) than expected based on available polygons. Model averaged predictions of these relationships are provided in

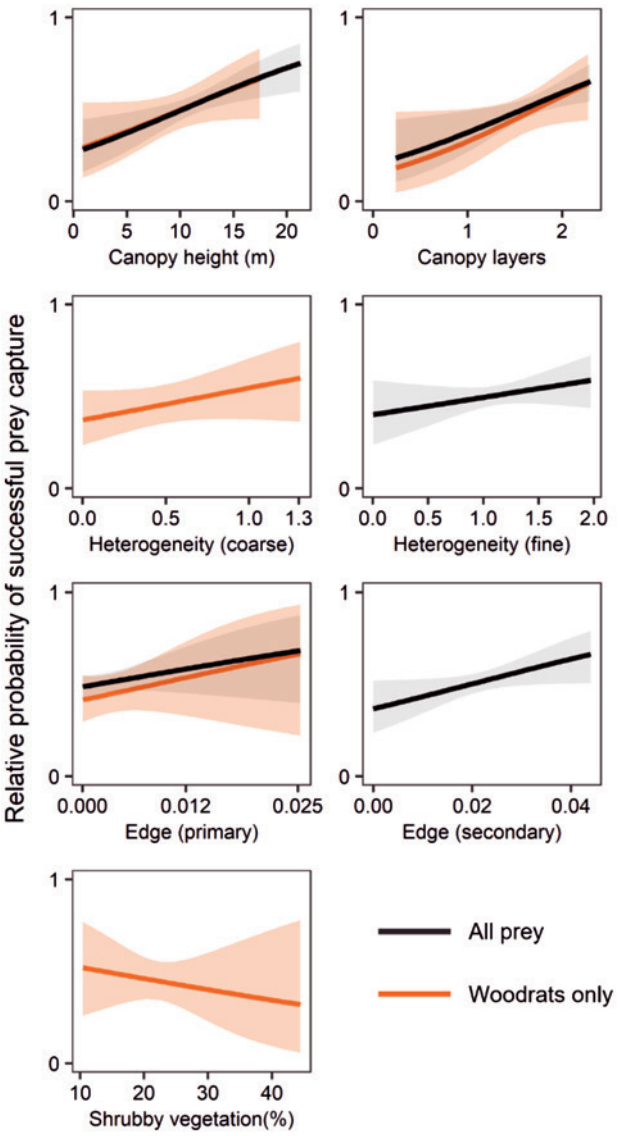

FIGURE 3. Averaged model predictions for relative probability of hunting success for all prey and woodrats only plotted against vegetation conditions for foraging Spotted Owls, with 95% confidence intervals shown as shaded areas. Heterogeneity metrics calculated as Shannon diversity of vegetation types within polygons and edge is calculated as the edge density within polygons (see Characterizing vegetation conditions).

Figure 3. Spotted Owls were more likely to capture woodrats ("woodrat only" analysis) in areas with higher canopy height (0.31, [0.06, 0.57]), more canopy layers (0.4, [0.11, 0.70]), greater coarse heterogeneity (0.24, [–0.02, 0.50]) and more primary edge density (0.19, [–0.11, 0.48]) and were less likely to capture woodrats in areas of higher shrubby vegetation density (–0.12, [–0.45, 0.20]) compared to available polygons (Figure 3). A considerable degree of model selection uncertainty occurred in both the "all-prey" and "woodrat only" analyses because there were 13 and 12 competitive models, respectively (<2 ΔAIC; Supplementary Material Tables 1 and 2). Nevertheless, canopy height and secondary edge density occurred in 8 and 10 of the 13 top models, respectively, in the all-prey analysis. In contrast, canopy layers occurred in 11 of the 12 top woodrat models. The null model in the all-prey analysis had a ΔAIC of 9.30 (w_i < 0.001) whereas ΔAIC for the null model was 2.94 (w_i = 0.01) in the woodrat-only analysis.

Prey Delivery Rates

We observed 289 prey deliveries at the 10 nests, with individual males delivering between 15 and 46 prey items ($\bar{x}$ = 28.9). Among these deliveries were 91 woodrats (31% count, 62% biomass), 72 deer mice (24% count, 4% biomass), 28 pocket gophers (10% count, 9% biomass), 10 flying squirrels (3.0% count, 4% biomass), 2 grey squirrels (*Sciurus griseus*), 2 passerine birds, 2 chipmunks (*Tamias* spp.), 1 Townsend's mole (*Scapanus townsendii*), 1 vole (*Microtus* spp.), and 80 unknown prey items (28% count, 18% biomass). Unknown prey items included 11 large, 25 medium, 32 small, and 12 tiny deliveries. Delivery rates ranged from 0.22 to 0.45 prey items per hour ($\bar{x}$ = 0.30 items hr^{-1}) while biomass delivery rates ranged from 17.74 to 51.05 grams per hour ($\bar{x}$ = 29.22 g hr^{-1}).

Spotted Owls delivered prey at a higher rate in home ranges with higher coarse heterogeneity (0.06, [0.04, 0.09]; Figure 4A), and the null model was not competitive (ΔAIC = 5.74, w_i = 0.04; Supplementary Material Table 3). Spotted Owls delivered biomass to nests at higher rates in home ranges with more primary edge density (7.20, [4.49, 9.90]; Figure 4B), and the null model was not competitive (ΔAIC = 6.15, w_i = 0.03; Supplementary Material Table 4). The positive association between prey biomass delivered and primary edge density was sensitive to a single influential male which occurred in a territory with a high value for primary edge, without which the association was not supported (i.e., the null model was more supported). However, the association between coarse heterogeneity and prey delivery rates remained important even when this "outlier" territory with the highest heterogeneity value was removed (i.e., the top model based on AIC remained the same and no other models became competitive).

Reproductive Success

Spotted Owl reproductive success was most strongly related to canopy cover, canopy height, and shrubby vegetation (Figure 5). Of the 5 top models 2 contained uninformative parameters, which we did not report (see Arnold 2010). Thus, we retained 3 top models: (1) canopy cover only, (2) canopy height and shrubby vegetation density, and (3) canopy height only (Supplementary Material Table 5). Spotted Owl reproductive success increased with greater canopy cover (model averaged coefficient 0.12, model averaged 85% CI [0.04, 0.20]) and taller canopy height in a home range (0.10, [0.02, 0.18]). Spotted Owls reproduced more successfully in areas with on average more shrubby vegetation, (0.08, [0.003, 0.13]). The null model was not competitive (ΔAIC = 2.60, w_i = 0.04; Supplementary Material Table 5).

DISCUSSION

Consistent with our predictions, Spotted Owls more frequently captured prey in areas with greater vertical structure in vegetation (canopy layers and height), spatial heterogeneity in vegetation types or structures (coarse and fine heterogeneity), and along edges of different vegetation types or structures

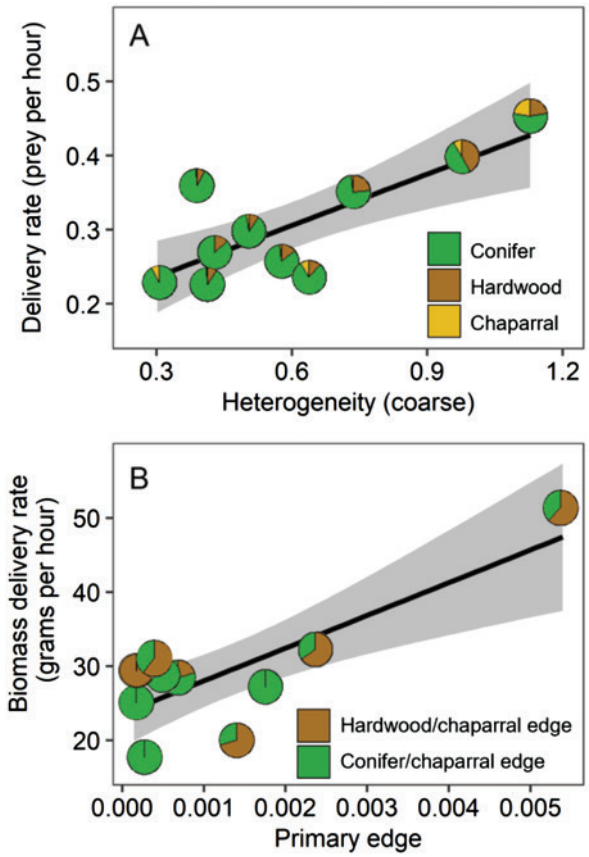

FIGURE 4. Prey delivery rate per hour (**A**) and prey biomass delivery rate (**B**) as functions of coarse vegetative heterogeneity (Shannon diversity of vegetation types) and primary edge (edge density of chaparral-forest edge), respectively. Each point represents an owl territory, with points in (**A**) displayed as pie charts of the proportion of the three main vegetation types (conifer forest in green, hardwood forest in brown, and chaparral in yellow) in the territory and points in (**B**) displayed as the proportion of the two primary edge types in the territory: conifer-chaparral edge (green) or hardwood-chaparral edge (brown).

(primary and secondary edge density). Our results support results from a similar study in the Sierra Nevada (Zulla et al. 2022), which also found Spotted Owls tended to capture prey, and particularly woodrats, in areas with more large trees, heterogeneity in vegetation conditions, and edge. Relationships between prey acquisition and canopy layers and height supported numerous previous studies demonstrating that VHF- and GPS-marked individuals preferentially use forests with larger trees and vertically complex structure during nocturnal activities, but indicates that owls do so, in part, because they promote successful foraging (Atuo et al. 2019, Blakey et al. 2019, Kramer et al. 2021b, Zulla et al. 2022). However, our findings also indicate that foraging owls likely benefits from a mosaic of large tree forest with complex canopy and other vegetation types given that woodrats, the primary Spotted Owl prey species in the southern California region, were more likely to be captured in areas with (1) high heterogeneity in vegetation types (conifer forest, hardwood forest, chapparal) and (2) along forest-chapparal edges. Indeed, associations between woodrat capture locations and both heterogeneity and edge density provide compelling support for previous suggestions that areas with low-lying vegetation serve as sources of woodrat prey for owls foraging in adjacent older forests (Zabel et al. 1995, Sakai and Noon 1997, Kramer et al. 2021b, Zulla et al. 2022). While shrubby vegetation appeared to provide habitat for woodrats and provide foraging opportunities for Spotted Owls along forest-chapparal edges, owls were less likely to capture woodrats in areas with more shrubby vegetation, which included both pure chapparal vegetation and shrubby understories of forested areas. Without adjacent forests, larger areas of chaparral may not offer suitable perching for owls to hunt for and capture woodrats, whereas dense shrubby areas within forests may provide woodrats with sufficient cover to avoid predation. Associations between all prey captured and both secondary edge density and fine heterogeneity suggest that fine-scale variation in heterogeneity and vertical structure also improve overall hunting success. These features could provide foraging owls, as ambush predators,

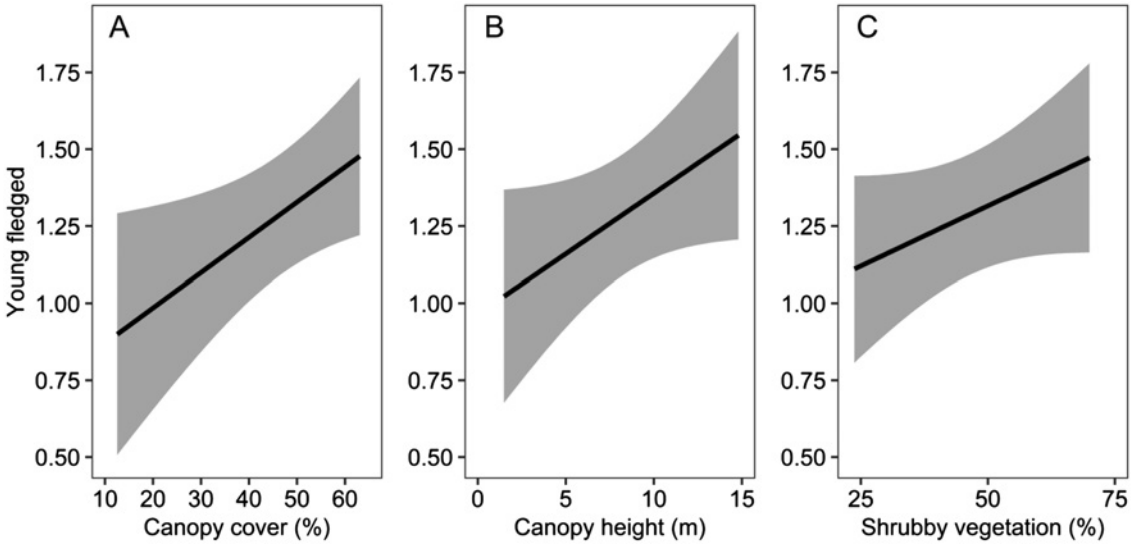

FIGURE 5. Averaged model predictions of number of young fledged plotted against (**A**) mean percent canopy cover, (**B**) mean canopy height, and (**C**) mean shrubby vegetation density within the territory, with shaded 95% confidence intervals.

with more perches to locate and approach prey. Higher variation in vegetation types and forest structure could also provide a greater diversity of niches for prey, such that owls encounter more species of prey in forests with these features.

Prey delivery rates by Spotted Owls to nests were greater when territories contained more of some of the vegetation conditions (coarse heterogeneity and primary edge density) that promoted successful prey acquisition. Higher prey delivery rates in territories with more coarse heterogeneity suggest that a diversity of vegetation types increase either prey abundance or accessibility to prey by Spotted Owls or both. In comparison, the delivery of prey biomass to nests was greatest in owl territories containing more forest chaparral edge (i.e., "primary edge density"), with woodrats likely driving this relationship as the most frequent and one of the largest species of prey delivered to nests. The biomass delivery-edge density relationship was sensitive to a single influential data point with high forest chapparal edge density. While additional studies involving larger sample sizes are merited, a clear ecological basis exists for believing the relationship is real. Indeed, in conjunction with the prey capture analysis, these two results provide further evidence that although Spotted Owls' primary prey species (woodrats) may be more abundant in vegetation cover types like chaparral, they become increasingly vulnerable to predation by owls when they occur near ecotones with older forests, where owls tend to forage (Zabel et al. 1995, Sakai and Noon 1997, Ward et al. 1998). Hence, there appears to be a direct link between vegetation conditions that promote successful foraging and the energy, in the form of prey biomass, provided by adult owls to nestlings.

Spotted Owl reproductive success was greater when owls occurred in territories that contained some of the vegetation conditions (e.g., taller forest) that apparently benefited prey captures, yet reproductive success was also higher under conditions: (1) unrelated to prey captures (denser canopy cover); (2) associated with fewer captures (more shrubby cover); and (3) unrelated to higher prey delivery rates to nests (denser canopy cover). Canopy height and cover had a positive influence on reproductive success, likely because older forest also serves as nesting habitat that provides a suitably cool microclimate and concealment from nest predators (LaHaye et al. 1997, North et al. 2000, Weathers et al. 2001). However, taller forests (with larger trees) may also provide Spotted Owls with better hunting perches or ambush cover, given the positive association we observed between the probability of prey capture and taller forests (see Figure 2A; Atuo et al. 2019, Blakey et al. 2019, Kramer et al. 2021a), which could have contributed to higher reproductive success. The apparent contradiction between higher reproductive success, yet lower prey capture, in areas with more shrubby cover is likely a matter of scale. At the fine scale at which we assessed foraging habitat (mean polygon size = 3.6 ha), owls may encounter fewer prey—or be less successful capturing prey—in dense shrubby areas because of the concealment or refuge it provides. But at a larger, territory scale (314 ha), areas of dense shrubby vegetation such as chapparal or shrubby areas within forested patches may serve as sources for small mammal prey (particularly woodrats) for Spotted Owls (Zabel et al. 1995, Sakai and Noon 1997, Parmenter et al. 2003). Thus, even though heterogeneity or edge density, strictly speaking, were not associated with higher reproductive success, we suggest that the juxtaposition of the taller, closed canopy forest and shrubby conditions (both in forest understories and as chapparal vegetation) constitutes forms of vertical structure and spatial heterogeneity that were indeed positively associated with Spotted Owl reproductive success—presumably because they improved prey acquisition. Broadly, these results supported our predictions that some of the vegetation conditions that facilitated prey captures by Spotted Owls would also increase reproductive success, but also suggested that other processes affect successful reproduction.

Environmental features such as vegetation conditions can strongly influence encounter and kill rates of prey by predators, and thus likely predator fitness and population status. The vast majority of predator–prey studies in the wild have focused on large carnivores, which typically leave noticeable kill sites (Gorini et al. 2012). We capitalized on new GPS tagging and nest video monitoring techniques (Marsh et al. 2014a, Wood et al. 2021) to better understand how vegetation conditions, including forest structure and heterogeneity, affect these processes in a small-bodied, nocturnal predator at the center of forest management in western North America. In doing so, we provide a more mechanistic understanding of previous observations suggesting that a mosaic of large-treed forests with complex canopies and shrubby vegetation increases prey availability and provides fitness-level benefits to Spotted Owls in landscapes where woodrats are a primary prey (Ward et al. 1998, Hobart et al. 2019a, Kramer et al. 2021b). Future studies involving concurrent woodrat trapping to estimate densities in owl foraging areas and habitats could provide additional mechanistic insights into predator–prey interactions between the two species. Additionally, this study was limited to actively nesting owls—albeit a critical stage for population dynamics—and further research would be required to determine if observed patterns change when breeding owls are no longer constrained to feeding juveniles. However, our work in conjunction with similar research in the Sierra Nevada (Zulla et al. 2022), suggests that continued development and implementation of forest management practices intended to promote vegetation heterogeneity (North and Manley 2012) could also benefit declining Spotted Owl populations (Peery et al. 2017).

Conservation Implications

Characterizing vegetation conditions constituting high-quality foraging habitat and how those conditions translate to fitness components such as reproductive success can strengthen conservation planning for threatened predators (Katzner et al. 2005, Catry et al. 2013, Hobart et al. 2019a, Smith et al. 2020). Spotted Owl populations in southern California have declined upwards of 40% in occupancy over the past 30 years and appear vulnerable to extirpation, likely due to complex interactions between vegetation conditions, climate change, and large severe wildfires (Tempel et al. 2022). The exclusion of historically frequent wildfires from southern California forests over the past century has promoted denser, more homogenous stands of trees and denser stands of chapparal (Minnich et al. 1995), driving a transition from frequent low- and moderate-severity wildfires to large high-severity wildfires that (1) can eliminate extensive areas of habitat (Jones et al. 2016), and (2) reduce foraging opportunities (this study) for Spotted Owls. Our study indicates that increasing forest heterogeneity, and particularly taller, vertically complex forests with higher canopy that are interspersed with chapparal

could benefit owl foraging and reproduction. Specifically, restoration of more frequent low- to moderate- severity fire regimes to these forests could both increase forest heterogeneity and resilience to severe wildfire and other disturbances (Stephens et al. 2008, Collins et al. 2009), and ultimately improve Spotted Owl viability in the region. Integral to such efforts is consideration of temporal scales and the importance of conserving and restoring large trees which can take decades to centuries to grow, with the dynamics of chapparal and shrub types adapted to disturbance and replacement over much shorter time scales.

Importantly, fire management with purely fuels-reduction objectives may not increase vegetation heterogeneity in a way that will improve foraging success, because such practices typically remove understory vegetation and can simplify vertical forest structure (Tempel et al. 2015). Rather, fire and vegetation management that creates a mosaic of fuel and vegetation condition, including juxtaposed areas of higher resistance (e.g., taller forests with minimal ladder fuels) and potential lower resistance (e.g., areas of shrub cover both independent of and under overstory trees) is more likely to improve owl fitness. While such juxtaposition may also put forest edges at higher risk of severe fire, a diverse vegetation mosaic should result in self-limiting fire behavior at the landscape scale (Lydersen et al. 2013), perpetuating heterogeneous conditions—potentially helping recover declining owl populations. A future study investigating thresholds in the beneficial effects of chapparal or shrubby vegetation, as well as the influence of patch size, could provide insights into the potential costs of too much heterogeneity. Nevertheless, we suspect that many smaller patches may benefit owls by providing more edge habitat with a lower risk of large severe fire that is associated with large, dense stands of chapparal. Similarly, the judicious application of mechanical vegetation management practices or variable retention harvesting that increases tree sizes and fine-scale variation in vegetative conditions (Kuehne et al. 2015), by creating canopy openings that promote shrub cover and edges in foraging areas, could also benefit Spotted Owls in this region. Forest management in nest stands, however, should avoid simplifying forest structure or creating gaps that reduce survival by increasing predation risk or thermoregulatory costs (Franklin et al. 2000, Weathers et al. 2001, Ma et al. 2010). In conclusion, this study adds to the growing body of literature indicating that forest management activities intended to promote forest heterogeneity could benefit the conservation of Spotted Owls (e.g., Tempel et al. 2015, Jones et al. 2021, Kramer et al. 2021a, Zulla et al. 2022).

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

Data collection was performed under USGS Bird banding lab permit #23685 and California department of fish and wildlife scientific collection permit S-193180001-19324-001). Handling of all animals was performed in accordance with the University of Wisconsin -Madison IACUC (Institutional animal care and use committee) protocol #A005367-R02.

Author contributions

MZP, SCS, JJK, RJG Conceived the idea, design, or experiment (supervised research, formulated questions or hypotheses). ZAW Performed the experiments (collected data, conducted the research) with support from CJZ, KM, JMB, RT, RJG. ZAW, HAK, GMJ, RJG, MZP wrote the paper (or substantially edited the paper). ZAW, HAK, GMJ, MZP, CJZ developed or designed methods. ZAW, HAK, GMJ, MZP analyzed the data and RT contributed substantial materials, resources, or funding.

Data deposits

Analyses reported in this article can be reproduced using the data provided by Wilkinson et al. (2022).

LITERATURE CITED

Anderson, J. R., E. E. Hardy, J. T. Roach, and R. E. Witmer (1976). A land use and land cover classification system for use with remote sensor data. Geological Survey Professional Paper 964. U.S. Department of the Interior, U.S. Government Printing Office, Washington, D.C., USA.

Anderson, D. L., W. Koomjian, B. French, S. R. Altenhoff, and J. Luce (2015). Review of rope-based access methods for the forest canopy: Safe and unsafe practices in published information sources and a summary of current methods. *Methods in Ecology and Evolution* 6:865–872.

Andrews, P., and J. Cook (1990). *Owls, Caves and Fossils: Predation, Preservation and Accumulation of Small Mammal Bones in Caves, With an Analysis of the Pleistocene Cave Faunas From Westbury-Sub-Mendip, Somerset, UK*. University of Chicago Press, Chicago, IL, USA.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *The Journal of Wildlife Management* 74:1175–1178.

Atuo, F. A., K. Roberts, S. Whitmore, B. P. Dotters, M. G. Raphael, S. C. Sawyer, J. J. Keane, R. J. Gutiérrez, and M. Z. Peery (2019). Resource selection by GPS-tagged California Spotted Owls in mixed-ownership forests. *Forest Ecology and Management* 433:295–304.

Barton, K. (2020). MuMIn: Multi-Model Inference. R package version 1.43.17. https://cran.r-project.org/package=MuMIn

Blakey, R. V., R. B. Siegel, E. B. Webb, C. P. Dillingham, R. L. Bauer, M. Johnson, and D. C. Kesler (2019). Space use, forays, and habitat selection by California Spotted Owls (*Strix occidentalis occidentalis*) during the breeding season: New insights from high resolution GPS tracking. *Forest Ecology and Management* 432:912–922.

Boinski, S., L. Kauffman, A. Westoll, C. M. Stickler, S. Cropp, and E. Ehmke (2003). Are vigilance, risk from avian predators and group size consequences of habitat structure? A comparison of three species of squirrel monkey (*Saimiri oerstedii, S. boliviensis, and S. sciureus*). *Behaviour* 140:1421–1467.

Bolker, B. (2021). Getting Started With the glmmTMB Package. Cran.R-Project Vignette. https://cran.r-project.org/web/packages/glmmTMB/vignettes/glmmTMB.pdf

Brewer, C. K., W. Goetz, A. J. Lister, K. Megown, M. Riley, and P. Maus (2015). Section 3: Existing vegetation mapping. In *Existing Vegetation Classification, Mapping, and Inventory Technical Guide, Version 2* (M. L. Nelson, C. K. Brewer, and S. J. Solem, Editors). General Technical Report WO–90, U.S. Department of Agriculture, Forest Service, Ecosystem Management Coordination Staff, Washington, D.C., USA.

Burnham, K. P., and D. R. Anderson (2002). *Model Selection and Inference: A Practical Information-Theoretic Approach*, Second Edition. Springer-Verlag, New York, NY, USA.

Cade, B. S. (2015). Model averaging and muddled multimodel inferences. *Ecology* 96:2370–2382.

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.

Call, D. R., R. J. Gutiérrez, and J. Verner (1992). Foraging habitat and home-range characteristics of California Spotted Owls in the Sierra Nevada. *The Condor* 94:880–888.

Catry, I., A. M. A. Franco, P. Rocha, R. Alcazar, S. Reis, A. Cordeiro, R. Ventim, J. Teodósio, and F. Moreira (2013). Foraging habitat quality constrains effectiveness of artificial nest-site provisioning in reversing population declines in a colonial cavity nester. *PLoS One* 8:e583201–e583210.

CFO (California Forest Observatory) (2020). *A Statewide Tree-Level Forest Monitoring System*. Salo Sciences, Inc. San Francisco, CA, USA. https://forestobservatory.com

Collins, B. M., J. D. Miller, A. E. Thode, M. Kelly, J. W. Van Wagtendonk, and S. L. Stephens (2009). Interactions among wildland fires in a long-established Sierra Nevada natural fire area. *Ecosystems* 12:114–128.

Delaney, D. K., T. G. Grubb, and P. Beier (1999). Activity patterns of nesting Mexican Spotted Owls. *The Condor* 101:42–49.

DeMars, C. A., and S. Boutin (2018). Nowhere to hide: Effects of linear features on predator–prey dynamics in a large mammal system. *Journal of Animal Ecology* 87:274–284.

Duchesne, T., D. Fortin, and N. Courbin (2010). Mixed conditional logistic regression for habitat selection studies. *Journal of Animal Ecology* 79:548–555.

Franklin, A. B., D. R. Anderson, E. D. Forsman, K. P. Burnham, and F. W. Wagner (1996). Methods for collecting and analyzing demographic data on the northern Spotted Owl. In *Demography of the Northern Spotted Owl* (E. D. Forsman, M. G. Raphael, R. J. Gutierrez, and S. DeStefano, Editors). *Studies in Avian Biology* 17:12–20.

Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham (2000). Climate, habitat quality, and fitness in northern Spotted Owl populations in northwestern California. *Ecological Monographs* 70:539–590.

Gorini, L., J. D. C. Linnell, R. May, M. Panzacchi, L. Boitani, M. Odden, and E. B. Nilsen (2012). Habitat heterogeneity and mammalian predator–prey interactions. *Mammal Review* 42:55–77.

Gutiérrez, R. J., A. B. Franklin, and W. S. LaHaye (1995). Spotted Owl (Strix occidentalis). In The Birds of North America No. 179: Life histories for the Twenty-first Century (A. Poole and F. Gill, Editors). The Philadelphia Academy of Sciences and The American Ornithologists' Union, Washington, D.C., USA.

Gutiérrez, R. J., P. N. Manley, and P. A. Stine (2017). The California Spotted Owl: Current state of knowledge. General Technical Report PSW-GTR-254. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, USA.

Hobart, B. K., G. M. Jones, K. N. Roberts, B. P. Dotters, S. A. Whitmore, W. J. Berigan, M. G. Raphael, J. J. Keane, R. J. Gutiérrez, and M. Z. Peery (2019a). Trophic interactions mediate the response of predator populations to habitat change. *Biological Conservation* 238:108217.

Hobart, B. K., K. N. Roberts, B. P. Dotters, W. J. Berigan, S. A. Whitmore, M. G. Raphael, J. J. Keane, R. J. Gutiérrez, and M. Z. Peery (2019b). Site occupancy and reproductive dynamics of California Spotted Owls in a mixed-ownership landscape. *Forest Ecology and Management* 437:188–200.

Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology* 74:559–566.

Horinouchi, M., N. Mizuno, Y. Jo, M. Fujita, M. Sano, and Y. Suzuki (2009). Seagrass habitat complexity does not always decrease foraging efficiencies of piscivorous fishes. *Marine Ecology Progress Series* 377:43–49.

Innes, R. J., D. H. Van Vuren, D. A. Kelt, M. L. Johnson, J. A. Wilson, and P. A. Stine (2007). Habitat associations of Dusky-footed Woodrats (*Neotoma fuscipes*) in mixed-conifer forest of the northern Sierra Nevada. *Journal of Mammalogy* 88:1523–1531.

Jones, G. M., R. J. Gutiérrez, D. J. Tempel, S. A. Whitmore, J. William, and M. Z. Peery (2016). Megafires: An emerging threat to old-forest species. *Frontiers in Ecology and the Environment* 14:300–306.

Jones, G. M., A. R. Keyser, A. L. Westerling, W. J. Baldwin, J. J. Keane, S. C. Sawyer, J. D. J. Clare, R. J. Gutiérrez, and M. Z. Peery (2021). Forest restoration limits megafires and supports species conservation under climate change. *Frontiers in Ecology and the Environment* 20:210–216.

Katzner, T. E., E. A. Bragin, S. T. Knick, and A. T. Smith (2005). Relationship between demographics and diet specificity of Imperial Eagles (*Aquila heliaca*) in Kazakhstan. *Ibis* 147:576–586.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce (2007). Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecology Letters* 10:690–700.

Kelt, D. A., D. H. Van Vuren, M. L. Johnson, J. A. Wilson, R. J. Innes, B. R. Jesmer, K. P. Ingram, J. R. Smith, S. W. Bigelow, R. D. Burnett, et al. (2013). Small mammals exhibit limited spatiotemporal structure in Sierra Nevada forests. *Journal of Mammalogy* 94:1197–1213.

Kramer, A., G. M. Jones, S. A. Whitmore, J. J. Keane, F. A. Atuo, B. P. Dotters, S. C. Sawyer, S. L. Stock, R. J. Gutiérrez, and M. Z. Peery (2021a). California Spotted Owl habitat selection in a fire-managed landscape suggests conservation benefit of restoring historical fire regimes. *Forest Ecology and Management* 479:118576.

Kramer, H. A., G. M. Jones, V. R. Kane, B. Bartl-Geller, J. T. Kane, S. A. Whitmore, W. J. Berigan, B. P. Dotters, K. N. Roberts, S. C. Sawyer, et al. (2021b). Elevational gradients strongly mediate habitat selection patterns in a nocturnal predator. *Ecosphere* 12:e03500.

Kuehne, C., A. R. Weiskittel, S. Fraver, and K. J. Puettmann (2015). Effects of thinning-induced changes in structural heterogeneity on growth, ingrowth, and mortality in secondary coastal Douglas-fir forests. *Canadian Journal of Forest Research* 45:1448–1461.

LaHaye, W. S., R. J. Gutiérrez, and D. R. Call (1997). Nest-site selection and reproductive success of California Spotted Owls. *The Wilson Bulletin* 109:42–51.

Lima, S. L., and L. M. Dill (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68:619–640.

Löhmus, A. (2004). Raptor habitat studies—The state of the art. In *Raptors Worldwide: Proceedings of the 6th World Conference on Birds of Prey and Owls May 2003, Budapest, Hungary* (R. D. Chancellor and B.-U. Meyburg, Editors). World Working Group on Birds of Prey and Owls, Wangenheimstrasse 32, Berlin, Germany:279–296.

Lydersen, J. M., M. P. North, E. E. Knapp, and B. M. Collins (2013). Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: Reference conditions and long-term changes following fire suppression and logging. *Forest Ecology and Management* 304:370–382.

Ma, S., A. Concilio, B. Oakley, M. North, and J. Chen (2010). Spatial variability in microclimate in a mixed-conifer forest before and after thinning and burning treatments. *Forest Ecology and Management* 259:904–915.

Marcot, B. G., and J. W. Thomas (1997). Of Spotted Owls, old growth, and new policies: a history since the Interagency Scientific Committee report. General Technical Report PNW-GTR-408. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, USA.

Marsh, A., E. M. Bayne, and T. I. Wellicome (2014a). Using vertebrate prey capture locations to identify cover type selection patterns of nocturnally foraging Burrowing Owls. *Ecological Applications* 24:950–959.

Marsh, A., T. I. Wellicome, and E. Bayne (2014b). Influence of vegetation on the nocturnal foraging behaviors and vertebrate prey capture by endangered Burrowing Owls. *Avian Conservation and Ecology* 9:2.

Minnich, R. A., M. G. Barbour, J. H. Burk, and R. F. Fernau (1995). Sixty years of change in Californian conifer forests of the San Bernardino Mountains. *Conservation Biology* 9:902–914.

Moran, M. D. (2003). Arguments for rejecting the sequential bonferroni in ecological studies. *Oikos* 100:403–405.

Muff, S., J. Signer, and J. Fieberg (2020). Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. *Journal of Animal Ecology* 89:80–92.

North, M., and P. Manley (2012). Managing forests for wildlife communities. In *Managing Sierra Nevada Forests* (M. North, Editor). General Technical Report PSW-GTR-237, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, USA. pp. 73–80.

North, M., G. Steger, R. Denton, G. Eberlein, T. Munton, and K. Johnson (2000). Association of weather and nest-site structure with reproductive success in California Spotted Owls. *The Journal of Wildlife Management* 64:797–807.

Parmenter, R. R., T. L. Yates, D. R. Anderson, K. P. Burnham, J. L. Dunnum, A. B. Franklin, M. T. Friggens, B. C. Lubow, M. Miller, G. S. Olson, et al. (2003). Small-mammal density estimation: A field comparison of grid-based vs. web-based density estimators. *Ecological Monographs* 73:1–26.

Peery, M. Z., R. J. Gutiérrez, P. N. Manley, and P. A. Stine (2017). Synthesis and interpretation of California Spotted Owl research within the context of public forest management. In *The California Spotted Owl: Current State of Knowledge* (R. J. Gutiérrez, P. N. Manley, and P. A. Stine, Editors). General Technical Report PSW-GTR-254. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, USA. pp. 263–291.

Preisler, H. K., N. E. Grulke, Z. Heath, and S. L. Smith (2017). Analysis and out-year forecast of beetle, borer, and drought-induced tree mortality in California. *Forest Ecology and Management* 399:166–178.

Preston, C. R. (1990). Distribution of raptor foraging in relation to prey biomass and habitat structure. *The Condor* 92:107–112.

R Core Team (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Rosenberg, D. K., and K. S. McKelvey (1999). Estimation of habitat selection for central-place foraging animals. *The Journal of Wildlife Management* 63:1028–1038.

Sakai, H. F., and B. R. Noon (1993). Dusky-footed Woodrat abundance in different-aged forests in northwestern California. *The Journal of Wildlife Management* 57:373–382.

Sakai, H. F., and B. R. Noon (1997). Between-habitat movement of Dusky-footed Woodrats and vulnerability to predation. *The Journal of Wildlife Management* 61:343–350.

San-jose, L. M., R. Séchaud, K. Schalcher, C. Judes, A. Oliveira-xavier, C. Gémard, B. Almasi, P. Béziers, A. Kelber, A. Amar, et al. (2020). Differential fitness effects of moonlight on plumage colour morphs in Barn Owls. *Nature Ecology and Evolution* 2019:1331–1340.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* 1:103–113.

Seaman, E. D., and R. A. Powell (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085.

Sih, A. (1984). The behavioral response race between predator and prey. *The American Naturalist* 123:143–150.

Smith, R. B., M. Z. Peery, R. J. Gutiérrez, and W. S. Lahaye (1999). The relationship between Spotted Owl diet and reproductive success in the San Bernardino Mountains, California. *The Wilson Bulletin* 111:22–29.

Smith, J. A., E. Donadio, J. N. Pauli, M. J. Sheriff, O. R. Bidder, and A. D. Middleton (2019). Habitat complexity mediates the predator–prey space race. *Ecology* 100:1–9.

Smith, J. A., E. Donadio, O. R. Bidder, J. N. Pauli, M. J. Sheriff, P. L. Perrig, and A. D. Middleton (2020). Where and when to hunt? Decomposing predation success of an ambush carnivore. *Ecology* 101:1–12.

Stephens, S. L., D. L. Fry, and E. Franco-Vizcaíno (2008). Wildfire and spatial patterns in forests in Northwestern Mexico: United States wishes it had similar fire problems. *Ecology and Society* 13:10.

Tempel, D. J., R. J. Gutiérrez, J. J. Battles, D. L. Fry, Y. Su, Q. Guo, M. J. Reetz, S. A. Whitmore, G. M. Jones, B. M. Collins, et al. (2015). Evaluating short- and long-term impacts of fuels treatments and simulated wildfire on an old-forest species. *Ecosphere* 6:art2611–art2619.

Tempel, D. J., J. J. Keane, R. J. Gutiérrez, J. D. Wolfe, G. M. Jones, A. Koltunov, C. M. Ramirez, W. J. Berigan, C. V. Gallagher, T. E. Munton, et al. (2016). Meta-analysis of California Spotted Owl (*Strix occidentalis occidentalis*) territory occupancy in the Sierra Nevada: Habitat associations and their implications for forest management. *The Condor: Ornithological Applications* 118:747–765.

Tempel, D. J., H. A. Kramer, G. M. Jones, R. J. Gutiérrez, S. C. Sawyer, A. Koltunov, M. Slaton, R. Tanner, B. K. Hobart, and M. Z. Peery (2022). Population decline in California Spotted Owls near their southern range boundary. *The Journal of Wildlife Management* 86:e22168.

Tomkiewicz, S. M., M. R. Fuller, J. G. Kie, and K. K. Bates (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society: Biological Sciences* 365:2163–2176.

Verner, J., K. Mckelvey, B. Noon, R. J. Gutierrez, G. I. Gould, and T. W. Beck (1992). The California Spotted Owl: A Technical Assessment. USDA Forest Service General Technical Report PSW-GTR-133, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA, USA.

Ward, J. P., R. J. Gutiérrez, and B. R. Noon (1998). Habitat selection by Northern Spotted Owls: The consequences of prey selection and distribution. *The Condor* 100:79–92.

Weathers, W. W., P. J. Hodum, and J. A. Blakesley (2001). Thermal ecology and ecological energetics of California Spotted Owls. *The Condor* 103:678–690.

Wilkinson, Z. A., H. A. Kramer, G. M. Jones, C. J. Zulla, K. McGinn, J. M. Barry, S. C. Sawyer, R. Tanner, R. J. Gutiérrez, J. J. Keane, et al. (2022). Data from: Tall, heterogenous forests improve prey capture, delivery to nestlings, and reproductive success for Spotted Owls in southern California. *Ornithological Applications* 125:duac048. doi:10.5061/dryad.h70rxwdnq

Wood, C. M., C. Zulla, S. A. Whitmore, D. Reid, H. A. Kramer, J. J. Keane, S. C. Sawyer, K. Roberts, B. Dotters, H. Klinck, et al. (2021). Illuminating the nocturnal habits of owls with emerging tagging technologies. *Wildlife Society Bulletin* 45:138–143.

Zabel, C. J., K. McKelvey, and J. P. Ward (1995). Influence of primary prey on home-range size and habitat-use patterns of northern Spotted Owls (*Strix occidentalis caurina*). *Canadian Journal of Zoology* 73:433–439.

Zimmerman, G. S., W. S. Lahaye, and R. J. G. Rrez (2001). Breeding-season home ranges of Spotted Owls in the San Bernardino Mountains, California. *Western Birds* 32:83–87.

Zulla, C. (2021). Foraging ecology of Spotted Owls in heterogenous forests. Masters thesis. University of Wisconsin, Madison, WI, USA.

Zulla, C. J., H. A. Kramer, G. M. Jones, J. J. Keane, K. N. Roberts, B. P. Dotters, S. C. Sawyer, S. A. Whitmore, W. J. Berigan, K. G. Kelly, et al. (2022). Large trees and forest heterogeneity facilitate prey capture by California Spotted Owls. *Ornithological Applications* 124:duac024.