


ARTICLE

Landscape heterogeneity provides co-benefits to predator and prey

Corbin C. Kuntze¹  | Jonathan N. Pauli¹ | Ceeanna J. Zulla¹ |
John J. Keane² | Kevin N. Roberts³ | Brian P. Dotters³ | Sarah C. Sawyer⁴ |
M. Zachariah Peery¹

¹Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, Wisconsin, USA

²U.S. Forest Service, Pacific Southwest Research Station, Davis, California, USA

³Sierra Pacific Industries, Anderson, California, USA

⁴U.S. Forest Service, Vallejo, California, USA

Correspondence

Corbin C. Kuntze

Email: kuntze@wisc.edu

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Abstract

Predator populations are imperiled globally, due in part to changing habitat and trophic interactions. Theoretical and laboratory studies suggest that heterogeneous landscapes containing prey refuges acting as source habitats can benefit both predator and prey populations, although the importance of heterogeneity in natural systems is uncertain. Here, we tested the hypothesis that landscape heterogeneity mediates predator–prey interactions between the California spotted owl (*Strix occidentalis occidentalis*)—a mature forest species—and one of its principal prey, the dusky-footed woodrat (*Neotoma fuscipes*)—a younger forest species—to the benefit of both. We did so by combining estimates of woodrat density and survival from live trapping and very high frequency tracking with direct observations of prey deliveries to dependent young by owls in both heterogeneous and homogeneous home ranges. Woodrat abundance was ~2.5 times higher in owl home ranges (14.12 km²) featuring greater heterogeneity in vegetation types (1805.0 ± 50.2 SE) compared to those dominated by mature forest (727.3 ± 51.9 SE), in large part because of high densities in young forests appearing to act as sources promoting woodrat densities in nearby mature forests. Woodrat mortality rates were low across vegetation types and did not differ between heterogeneous and homogeneous home ranges, yet all observed predation by owls occurred within mature forests, suggesting young forests may act as woodrat refuges. Owls exhibited a type 1 functional response, consuming ~2.5 times more woodrats in heterogeneous (31.1/month ± 5.2 SE) versus homogeneous (12.7/month ± 3.7 SE) home ranges. While consumption of smaller-bodied alternative prey partially compensated for lower woodrat consumption in homogeneous home ranges, owls nevertheless consumed 30% more biomass in heterogeneous home ranges—approximately equivalent to the energetic needs of producing one additional offspring. Thus, a mosaic of vegetation types including young forest patches increased woodrat abundance and availability that, in turn, provided energetic and potentially reproductive benefits to mature forest-associated spotted owls. More broadly, our findings provide strong empirical evidence that heterogeneous landscapes

containing prey refuges can benefit both predator and prey populations. As anthropogenic activities continue to homogenize landscapes globally, promoting heterogeneous systems with prey refuges may benefit imperiled predators.

KEYWORDS

forest management, heterogeneity, predator conservation, predator–prey, spotted owl, woodrat

INTRODUCTION

Predator populations are declining globally, often precipitated by habitat loss and changes in trophic interactions (Estes et al., 2011; Ripple et al., 2014). Many predators occur, and presumably evolved, in complex landscapes with heterogeneously distributed resources that shape many of their ecological interactions (Hunter & Price, 1992; Wiens, 1995). Among these, the composition and configuration of habitat patches can mediate predator–prey interactions, with consequences for population dynamics for both predators and their prey (Fahrig et al., 2011; Schmitz, 1998; Wilson et al., 2019). As anthropogenic land-use change increasingly homogenizes landscapes, there is a growing need for empirical studies on the effects of heterogeneity (variability of an environmental property in time and space; Li & Reynolds, 1995) in predator–prey systems (Bullock et al., 2022; Layman et al., 2007). However, to date most studies on the effects of heterogeneity on predator–prey interactions have been theoretical or conducted within controlled experimental settings subject to many simplifying assumptions (Hastings, 1977; Sih, 2005). Further, empirical studies are typically conducted at patch rather than landscape scales, do not involve mobile predators capable of accessing many patches, or fail to account for alternative prey (Ryall & Fahrig, 2006).

Landscape heterogeneity is most likely to affect predator–prey dynamics through effects on prey abundance or vulnerability. In heterogeneous systems, landscape-scale abundance of prey is an emergent property of the composition of habitat patches of varying quality, with landscapes containing a greater area of high-quality habitat patches expected to have higher prey abundance (Holt, 1985; Iles et al., 2018). However, dispersal from high-density source patches can increase densities within lower-quality patches (Holt, 1985), decoupling local abundance from habitat quality (Ehrlén & Morris, 2015; Iles et al., 2018). In some cases, landscape-scale abundance may even exceed the combined carrying capacity of all representative patches (Holt, 1985; Zhang et al., 2017). When predation rate is determined by prey density (i.e., the functional response), these patch- and landscape-scale differences in prey abundance can have

profound effects on predator populations (Coulson et al., 2006; Holling, 1959), which may be most pronounced when predators exhibit differential hunting success among patches (Hopcraft et al., 2005).

Landscape heterogeneity can affect prey vulnerability by creating refuges that reduce predation risk—that is, the likelihood of a predator encountering or capturing prey (Sih, 1987). When predator and prey prefer different habitats, the relative amounts and arrangements of safe (difficult for the predator to successfully capture prey) versus risky (easier for the predator to successfully capture prey) patches can decouple prey availability from abundance (Hebblewhite et al., 2005; Laundré, 2010), with ostensible tradeoffs when either habitat type predominates. Homogeneous landscapes dominated by risky habitat may increase prey accessibility but limit abundance or advance prey depletion (Coulson et al., 2006; Huffaker et al., 1963), while landscapes dominated by safe habitat may increase prey abundance but limit capture opportunities (Hopcraft et al., 2005). By reducing top-down control on prey abundance, refuge use can also promote density-driven dispersal into adjacent risky patches (Holt, 1985) and provide foraging opportunities along the edges of the two habitat types (Laundré & Hernández, 2003; Zulla et al., 2022). Therefore, compared to homogeneous landscapes where predator habitat predominates, heterogeneity may decrease the availability of hunting patches for predators but increase the encounter probability within those that remain, potentially increasing hunting success (Hopcraft et al., 2005; Zulla et al., 2022). In summary, the relationship between habitat characteristics and predation rates often depends on the landscape context, although studies need to be conducted across a gradient of heterogeneity in natural systems—that is, complex landscapes containing a mosaic of prey refuges and patches of varying density and catchability versus homogeneous ones dominated by a single habitat type and uniform catchability of prey.

We assessed how landscape heterogeneity mediates predator–prey interactions between a mature forest predator, the California spotted owl (*Strix occidentalis occidentalis*), and one of its primary prey species, the dusky-footed woodrat (*Neotoma fuscipes*). While spotted

owls consume a variety of small mammals and other taxa, woodrats represent the largest-bodied (Ward Jr et al., 1998) and, thus, most energetically profitable prey when present (Weathers, 1996). As such, woodrat consumption can drive patterns in fitness, occupancy, and space use for spotted owls (Franklin et al., 2000; Hobart, Jones, et al., 2019). Spotted owls use mature forest for nesting, roosting, and foraging (Gutierrez et al., 1992; Moen & Gutiérrez, 1997), while woodrats are predominantly associated with younger, brushier forests and large oaks (Sakai & Noon, 1993; Williams et al., 1992), which are traditionally viewed as less suitable habitat for foraging owls (Atuo et al., 2019; Kramer, Jones, Whitmore, et al., 2021). Despite this purported mismatch between predator and prey habitat, in lower-elevation forests of the Sierra Nevada, USA, woodrats can compose up to 94% of spotted owl diet by weight (Williams et al., 1992). Sakai and Noon (1997) observed intermittent, short-distance movements into mature forests by woodrats occupying dense young forests within a patchy landscape, suggesting that forays across ecotonal boundaries may increase the vulnerability of woodrats to avian predation. Indeed, recent work has linked increasing forest heterogeneity at a home range scale to woodrat consumption (Hobart, Jones, et al., 2019) and documented frequent woodrat captures by owls foraging along edges between hardwood and coniferous-dominated forests (Zulla et al., 2022). In the Sierra Nevada, differences in management practices among landownership types has created landscapes that differ dramatically in forest composition and patch configuration (North et al., 2017), providing a gradient of heterogeneity to (1) examine the mechanisms driving increased woodrat consumption by spotted owls and (2) determine whether these mechanisms also confer benefits to woodrat populations at a landscape scale.

Herein, we hypothesized that heterogeneous landscapes featuring a mixture of early and late-successional habitat would create sources or spatial refuges for prey that benefit both predator and prey populations when predators and prey are associated with different habitats. We combined live trapping and monitoring of woodrat survival with direct observations of prey deliveries by spotted owls to test several predictions related to our central hypothesis. Specifically, we predicted (1) owl home ranges with greater habitat heterogeneity, in the form of a mosaic of vegetation types including mature forest, young forest, and open areas, would contain higher densities of woodrats than homogeneous home ranges consisting primarily of mature forest. We also predicted that (2) mortality rates of woodrats would be higher in mature forest and within homogeneous home ranges because of the lack of young forest refuges, but (3) a

functional response exists where owl predation rates on woodrats would be higher in heterogeneous than homogeneous home ranges. Finally, we predicted that (4) total biomass of prey delivered to owl nests would be greater in heterogeneous home ranges because of a greater consumption of large-bodied woodrats and, accordingly, the consumption of alternative, smaller-bodied prey would not reconcile this deficit in homogeneous home ranges.

METHODS

Study system

Our study primarily occurred on the western slope of the central Sierra Nevada in California in the USA, within and adjacent to the Eldorado Demography Study Area (EDSA; Figure 1), a long-term spotted owl monitoring site encompassing roughly 355 km² of the Eldorado National Forest (Jones et al., 2021). Elevation in the EDSA ranges from 366 to 2257 m, although we concentrated our woodrat trapping efforts within ~1000 to 1500 m, a range that can contain dense woodrat

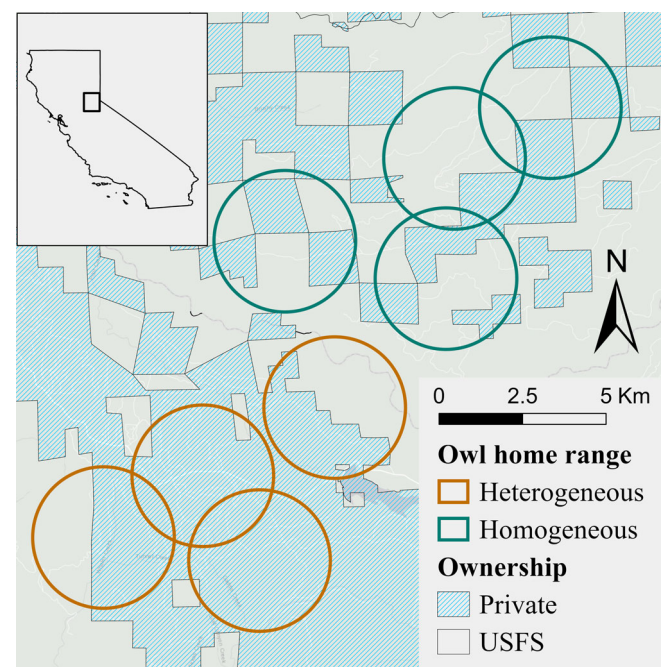


FIGURE 1 Locations of spotted owl (*Strix occidentalis*) home ranges within and adjacent to the Eldorado Demography Study Area (EDSA) in the central Sierra Nevada, California, USA, where dusky-footed woodrat (*Neotoma fuscipes*) abundance and survival (Predictions 1 and 2) were estimated in 2020 and 2021. Landscape composition is depicted by orange (heterogeneous) and teal (homogeneous) circles within private and public (USFS, United States Forest Service) land.

populations (Williams et al., 1992). Dominant conifer species included incense cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), Douglas fir (*Pseudotsuga menziesii*), and white fir (*Abies concolor*), while dominant hardwoods included California black oak (*Quercus kelloggii*) and tanoak (*Lithocarpus densiflorus*), the latter of which was patchily distributed throughout the study area in dense pockets (Fites-Kaufman et al., 2007).

Landownership in the EDSA was split between ~60% public land, primarily managed by the United States Forest Service (USFS), and ~40% private land, existing mostly as commercial timberlands. Differences in land use practices among ownership types in this region have created a landscape with distinct spatial variation in forest structure, age, and configuration. On USFS-managed lands, a century of fire suppression, coupled with selective logging of large trees, has created contiguous, spatially homogeneous stands of mature trees within public forests (Stephens et al., 2015). On privately owned lands, timber harvesting occurs more frequently, often with an emphasis on even-aged management that creates a mosaic of different stand types, including open clear cuts, young plantations interspersed with brushy pockets of saplings and tanoak, and patches of mature forest similar to those occurring on public lands (North et al., 2017). Forests on private lands are on average 30–40 years younger than those on public lands and may contain fewer stand features generally found in older forests, such as large snags and logs (North et al., 2017). Thus, private lands tend to contain forests with less vertical structure but more heterogeneity in forest ages, including young stands that can harbor dense woodrat populations (Sakai & Noon, 1993). Spotted owls nest and forage on both ownership types (Atuo et al., 2019; Hobart, Roberts, et al., 2019; Roberts et al., 2017).

Overview

To test our predictions about the effects of landscape heterogeneity on predator–prey interactions between spotted owls and woodrats we (1) used live-trapping and mark-recapture methods to estimate woodrat abundance (Prediction 1); (2) deployed very high frequency (VHF) collars on woodrats to monitor individual survival and identify causes of mortality (e.g., likely owl predation; Prediction 2); and (3) quantified consumption rates by monitoring woodrat and other prey deliveries to nests with video cameras within owl home ranges (Predictions 3 and 4). All three of these field methods were used in home ranges containing varying degrees of habitat heterogeneity.

Classifying landscape composition and configuration within spotted owl home ranges

We compared occupied spotted owl home ranges that were either highly homogeneous or heterogeneous in the proportional composition and configuration of open, young, and mature forest. To identify homogeneous or heterogeneous home ranges for woodrat sampling, we visually inspected aerial imagery from the National Agriculture Imagery Program (NAIP) at all known spotted owl home ranges ($n = 28$) within and immediately adjacent to the EDSA and identified those containing predominantly mature forest in large, contiguous stands versus those that had a more even mixture of open, young, and mature forest of differing patch sizes (Figure 2A,B).

For this subset of highly homogeneous and heterogeneous home ranges, we created circular buffers with a 2.12 km radius—an area equal to the median home range of all males tagged for a minimum of 25 days (14.12 km²) from previous studies (Atuo et al., 2019; Jones et al., 2016; Zulla et al., 2022)—around the most recent known nest or roost site. Next, within each buffered home range, we used NAIP imagery collected in 2018 and 2020 to manually digitize patches of relatively uniform vegetation conditions following protocols described in Tempel et al. (2014). We defined the three predominant forest structure classes based on canopy cover and size of dominant trees as follows: mature forest (>40% canopy cover and dominant trees >12 inches diameter at breast height [dbh]), young forest (>40% canopy cover and saplings or dominant trees <12 inches dbh), and open habitat (<40% canopy cover). Heterogeneous home ranges had more even representation of habitat types, estimated by Shannon's diversity index ($\hat{H} = 0.92$, range = 0.79–1.05; mean areas = 58.8% mature, 27.9% young, and 12.2% open) than homogeneous home ranges ($\hat{H} = 0.65$, range = 0.57–0.71; mean areas = 78.6% mature, 9.9% young, and 11.5% open).

For tests of woodrat abundance and survival (Predictions 1 and 2), we excluded home ranges that were far from other home ranges we considered sampling, above elevations with high woodrat densities (>1500 m) and below elevations where owls are commonly found in our study landscape (<1000 m), or predominantly within the King Fire footprint and likely confounded substantially by severe fire (Jones et al., 2016). From the remaining subset we then selected nine home ranges (five homogeneous, four heterogeneous) by prioritizing ones that were occupied at the time of woodrat sampling based on routine spotted owl surveys conducted as part of the EDSA (Jones et al., 2021), occurred at similar

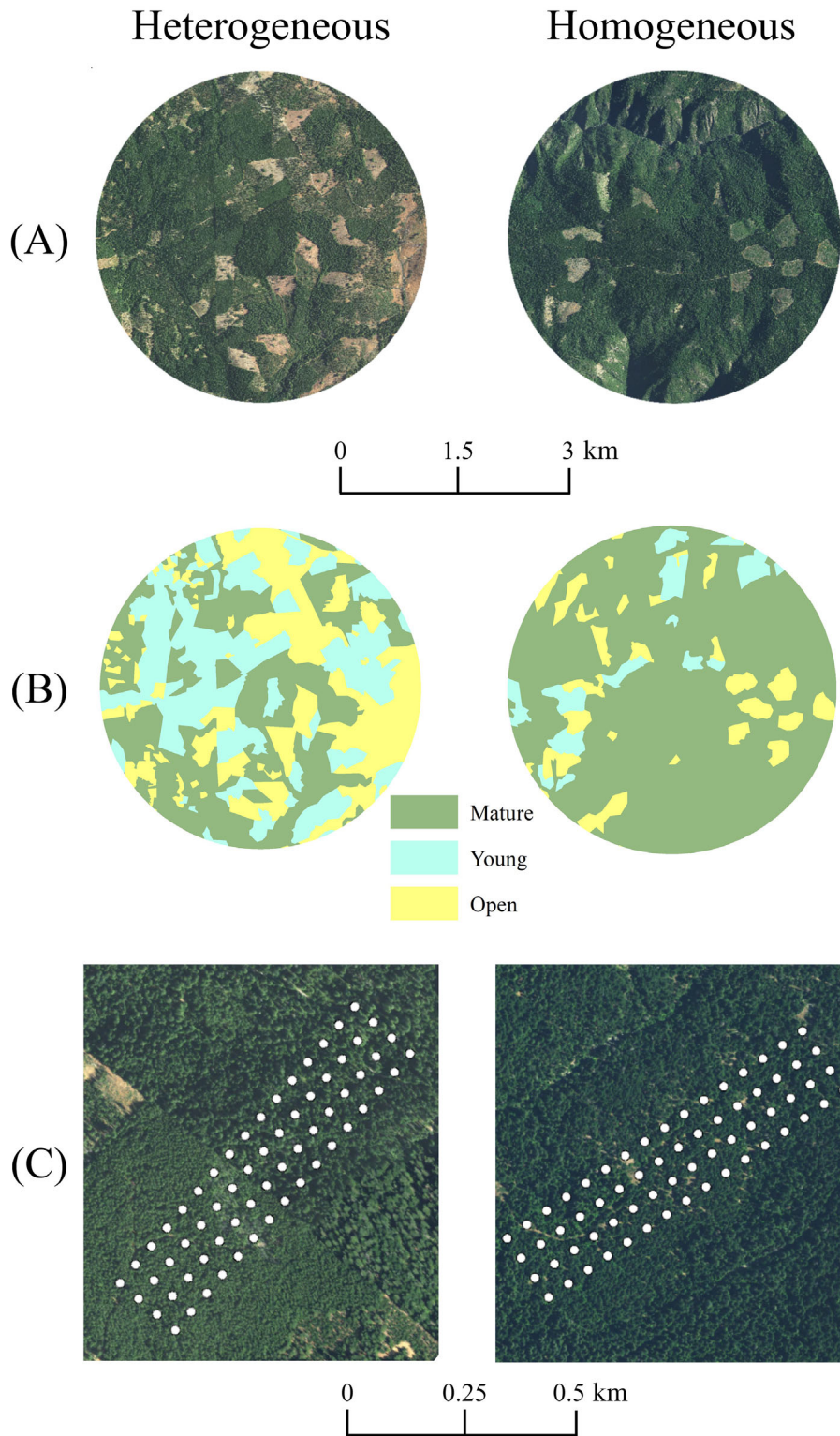


FIGURE 2 Examples of landscape composition (heterogeneous or homogeneous) within spotted owl (*Strix occidentalis*) home ranges surveyed in 2020 and 2021 in the central Sierra Nevada, California, USA. Differences are shown at the scale of a spotted owl home range with both (A) National Agriculture Imagery Program (NAIP) imagery and (B) habitat type (mature, young, and open), and (C) at the scale of a trapping grid visualized with NAIP imagery.

elevations (mean elevation range 1290–1372 m), and occurred in close proximity. For tests of prey delivery rates by owls (Predictions 3 and 4), we selected four of

these home ranges along with an additional 11 from the EDSA and Sierra Pacific Industries’ Stirling Study Area (SSA) in the northern Sierra Nevada (Zulla et al., 2022).

Among these, home ranges had similar representation of habitat types compared to those from Predictions 1 and 2, with greater evenness in heterogeneous ($H = 0.99$, range = 0.82–1.05; mean areas = 54.3% mature, 27.9% young, and 17.8% open) than homogeneous home ranges ($H = 0.71$, range = 0.62–0.74; mean areas = 76.4% mature, 10.9% young, and 12.7% open).

Field methods and analysis

Prediction 1: Estimating woodrat abundance

To compare woodrat abundance within homogeneous and heterogeneous home ranges, in 2020 and 2021 we deployed grids of 64 traps (in 8×8 or 4×16 configuration) spaced at 50-m intervals among eight of the nine occupied spotted owl home ranges classified as homogeneous ($n = 4$) or heterogeneous ($n = 4$; Figure 1). Within homogeneous home ranges, we randomly placed grids within large stands of contiguous mature forest (Figure 2C). Within heterogeneous home ranges, we deployed trapping grids stratified by habitat—using ArcMap and NAIP imagery where, specifically, we created an algorithm to identify edge areas between young-mature and open-mature patches of a minimum size to center our trapping grids. We centered our trapping grids along habitat edges to ensure adequate representation of core and edge for each habitat type; variable patch size and distribution in heterogeneous home ranges posed challenges to sampling (e.g., uneven representation of habitat types) if we followed a truly random grid placement strategy (Figure 2B). As part of this process, we constrained grid locations such that they contained at least 30% each of mature forest and either young forest or open area (Figure 2C).

We deployed traps for six consecutive days following a paired approach in which two grids were sampled concurrently—one each within a heterogeneous and homogeneous home range. Within each home range, we deployed one ($n = 2$), two ($n = 2$), or four ($n = 4$) trapping grids. Trapping occurred from late spring through summer in 2020 and 2021. We captured woodrats in steel mesh traps (Model 105; Tomahawk Live Trap Company, Hazelhurst, Wisconsin, USA) baited with a mix of birdseed, dried fruit, and peanuts. All captured animals were ear punched and marked with a unique ear tag (Model 1005-1; National Band & Tag Company, Newport, KY, USA) or passive integrated transponder (PIT) tag (Avid Identification Systems, Norco, CA, USA). All captures were done with approval by the Institutional Animal Care and Use Committee of the University of Wisconsin, Madison (IACUC No. A006173-A01) and followed

guidelines from the American Society of Mammalogists (Sikes et al., 2019).

We estimated abundance using Huggins closed-capture models in the program MARK (White & Burnham, 1999). We modeled initial capture probability (p) and recapture probability (c) accounting for time (i.e., sampling occasion), sampling year, habitat type (open, young, mature), and home range configuration (heterogeneous or homogeneous). For model selection, we used Akaike's information criterion corrected for small sample size (AIC_c) and AIC_c weights (w) to select the best-supported model and assessed significance using 95% CIs. If a competitive model contained one or more uninformative parameters (i.e., parameter CIs overlapped zero), we dropped this model from consideration (Arnold, 2010). We then used our top model to derive woodrat abundance for each habitat type.

To estimate relative densities by habitat type, we applied these abundance estimates to the effective trapping area (ETA) surveyed (Gerber & Parmenter, 2015). We estimated ETA (in square kilometers) following Parmenter et al. (2003); in this, we buffered all grids by 50 m, equal to half of the estimated mean for maximum nightly distance moved by woodrats, then summed the total area of each habitat type captured across all buffered grids. Then we calculated density estimates for each habitat type by dividing the model-derived abundance estimates by their respective ETA (Schwemm et al., 2018). Given that dispersal from patches of adjacent young forest may facilitate increased woodrat densities (Sakai & Noon, 1993, 1997), we considered mature forest in heterogeneous and homogeneous home ranges as two separate habitat classes. We obtained estimates for woodrat abundance within homogeneous (\hat{N}_H) and heterogeneous (\hat{N}_E) home ranges by scaling up our density estimates relative to the area of open (A_O), young (A_Y), and mature (A_M) forest within each home range (Appendix S1: Section S1). We calculated SE values for density and abundance using the Delta method (Powell, 2007), which allowed us to estimate the variance of a parameter derived from multiple variables, each with its own variances. We also performed statistical comparisons of abundance between homogeneous and heterogeneous home ranges using a two-sample Welch's t -test.

Prediction 2: Estimating woodrat survival

To test Prediction 2, we monitored survival with radio transmitters and assessed cause-specific mortality. We selected a subsample of the woodrats caught within seven of the eight occupied spotted owl home ranges (three homogeneous, four heterogeneous) during our

mark-recapture surveys from Prediction 1, along with other individuals trapped opportunistically among these and one additional homogeneous home range, for survival monitoring. In 2020 and 2021, we fit woodrats weighing above 120 g with VHF collars (Lotek Model TW-5, 10 g; Lotek Wireless Inc., Newmarket, Ontario, Canada or Telenax Model TXE-116C, 6 g; Titley Scientific, Columbia, Missouri, USA) equipped with onboard activity sensors, which allowed us to detect mortality events shortly after they occurred. Within 2 days of collar deployment, we tracked individual woodrats to their nests (hereafter “middens”) and recorded relevant information about each area. We assigned habitat designations (open, young, mature) for all collared individuals based on where the midden was located, not where they were trapped—although these were typically the same habitat type.

We initiated VHF monitoring in 2020 in the week of 14 June and in 2021 in the week of 11 May. We located collared woodrats one to two times per week and recorded status (alive, dead, missing/collar failure) on each occasion from the first capture until death, disappearance, or the end of the study (17 October 2020 or 11 September 2021). We also performed monthly midden checks—repeating triangulation of collared woodrats to middens—to ensure that an individual had not permanently dispersed during our monitoring period. If a signal for a woodrat collar disappeared, we set traps outside of its midden for several days. In all but one incident, the source of the lost signal was a dead collar battery—in these cases, the individual was recaptured alive, the collar removed, and monitoring ended.

Once an inactive signal was detected, we immediately recovered the collar. We recorded images and took detailed notes for each mortality event, including location, habitat type, distance to midden, and state of collar, to assess cause of mortality. Avian predation was considered the cause of death if the collar was recovered with minor damage under a spotted owl nest tree or perch site with whitewash and/or viscera in the vicinity; while other raptor species were present in our study area, we attributed avian predation to spotted owls given that all sites were owl-occupied, mortalities occurred at night, and all recovered collars were found in close proximity to active spotted owl nest sites. Additionally, woodrats are the most common spotted owl prey and are rarely consumed by other predators of a similar size class (e.g., red-tailed hawk, *Buteo jamaicensis*). Mammalian predation was considered the cause of death if the collar was recovered in more open, brushy habitat absent any roosting or perching trees, with considerable damage and teeth marks to the collar. Finally, if the collar was tracked to a midden with a mortality signal active, we set traps for

several days to ensure that the collar was not malfunctioning and the individual was not alive—after which it was determined to be a mortality of unknown or of natural cause (e.g., age, nutritional deficiency, disease) and not a predation event.

We estimated weekly woodrat survival rates by constructing known-fate models in the program MARK (White & Burnham, 1999), with a staggered entry design to allow introduction of individuals throughout the study (Pollock et al., 1989). We analyzed two sets of known-fate models, one considering all mortality events and one only including mortalities that were attributed to avian (likely spotted owl) predation. In 2020, we constructed encounter histories from 14 June until 17 October; in 2021, we constructed encounter histories from 9 May until 11 September. We set Sunday as the start of each sampling week and introduced covariates relative to habitat type, home range composition, month, year, and distance to owl nest tree or territory center and considered a categorical effect relative to each unique home range.

Prediction 3: Estimating woodrat consumption rates by owls

We directly observed prey deliveries to dependent young by nesting spotted owls within home ranges classified as either homogeneous or heterogeneous. We used Global Positioning System (GPS) tagging and nest-video monitoring data collected and described previously by Zulla et al. (2022). Briefly, in 2019 and 2020, breeding spotted owls were located as part of ongoing work within the EDSA and SSA (Hobart, Roberts, et al., 2019; Roberts et al., 2017; Zulla et al., 2022), and 15 nesting males were captured and GPS tagged (five in 2019, 10 in 2020). Infrared video cameras (AXIS Q1786-LE 4; Axis Communications AB, Lund, Sweden) were placed at the nest sites of these individuals, secured to an adjacent tree with a clear view of the nest. These cameras continuously recorded high-quality video throughout the nocturnal foraging period (20:00–06:30 pacific daylight time). All video footage was reviewed, and prey deliveries to the nest were identified to species whenever possible. We detected 26 larger-bodied prey deliveries over the course of monitoring that could not be identified to species; these were split relatively evenly among homogeneous and heterogeneous sites, and we do not believe that excluding these from our count of woodrat deliveries compromised any results. We estimated woodrat delivery rates (in number delivered per hour) and scaled these to monthly estimates with bootstrapped CIs. We conducted a two-sample Welch’s *t*-test to determine differences in mean monthly woodrat delivery rates between homogeneous and heterogeneous home ranges.

We corroborated the previously described estimates of monthly woodrat consumption rates in homogeneous and heterogeneous home ranges by multiplying per-capita mortality rates scaled to monthly values (Prediction 2) with woodrat abundance estimates for each home range within our landscape composition categories (Prediction 1). We calculated SE and 95% CI for these values using the Delta method (Powell, 2007). We then conducted a two-sample Welch's *t*-test to test for differences in monthly woodrat consumption rates between homogeneous and heterogeneous home ranges. We corroborated these estimated mortality rates with those derived from nest camera data by conducting a one-way ANOVA with two factors: estimation method (nest camera or known-fate estimates) and landscape composition (heterogeneous or homogeneous). This allowed us to determine whether the number of monthly woodrat mortalities differed between our methods of estimation.

Prediction 4: Estimating biomass delivery rates by owls

To estimate total biomass delivery rates (in grams per unit time), we used nest video data described in Prediction 3 and considered all prey deliveries. To convert number of prey items into biomass rates, we used mean values for body mass of each prey item collected and described in Zulla et al. (2022). Briefly, mean values for mass of woodrats and Humboldt flying squirrels (*Glaucomys oregonensis*) were estimated using regurgitated pellets collected from previous studies in the EDSA. Skull and mandible measurements of skeletons from these pellets were compared to those of museum specimens for which masses were available, and predictive relationships between mass and skull measurements were quantified to determine estimates of body mass for each skeleton collected from pellets. The estimated mean body mass of woodrats was 187.4 g (range 110.9–271.2 g), while that of flying squirrels was 98.8 g (range 80.2–117.2 g). Other prey species were assigned a mass based on the midpoint of mass ranges in the literature (e.g., mouse 20 g; Reid, 2006). Finally, if the species of a prey delivery could not be determined, then it was assigned to a size class (extra small: 5.3 g, small: 47.5 g, medium: 175 g, large: 205 g), with the corresponding mass derived from the average mass of species within this size class.

We summed deliveries of all species or size classes and converted these into biomass values, then standardized them to biomass delivery rates (in grams delivered per hour) and scaled these to monthly estimates. We also

conducted two-sample Welch's *t*-tests to determine whether there were differences in delivery rates of each prey group and total biomass delivery between homogeneous and heterogeneous home ranges.

Results

Prediction 1: Higher woodrat abundance within heterogeneous home ranges

Over the two field seasons, we deployed 22 grids of 64 traps each among eight spotted owl home ranges (four heterogeneous, four homogeneous) for a total of 8448 trap nights and captured 236 unique individuals a total of 460 times. Our most supported mark-recapture model for woodrat abundance suggested a behavioral response to capture, as $p = 0.12$ (95% CI: 0.07, 0.20) and $c = 0.33$ (95% CI: 0.30, 0.37), with neither parameter varying as a function of sampling year, habitat type, or landscape composition. Several other models occurred within 2 AIC_c, yet all included uninformative parameters (Arnold, 2010) so were deemed noncompetitive (Table 1).

Woodrat density was greatest in young forest (215.3 woodrats/km²; 95% CI: 156.0, 359.0) and mature forest in heterogeneous home ranges (134.2 woodrats/km²; 95% CI: 97.9, 220.0), followed by mature forest in homogeneous home ranges (57.8 woodrats/km²; 95% CI: 42.0, 95.7), with the lowest densities in open area (9.5 woodrats/km²; 95% CI: 5.8, 31.2; Figure 3). Extrapolating woodrat density estimates relative to the area of each habitat type within owl home ranges, woodrat abundance was ~2.5 times higher ($t_6 = 14.92$, $p < 0.001$) in heterogeneous home ranges ($\hat{N}_H = 1805.0$ woodrats; range: 1662.3–1897.8) than homogeneous home ranges ($\hat{N}_O = 727.3$ woodrats; range: 648.9–817.9).

TABLE 1 Top Huggins closed-capture models for estimating dusky-footed woodrat (*Neotoma fuscipes*) abundance in 2020 and 2021 in the central Sierra Nevada, California, USA.

Covariate(s)	AIC _c	ΔAIC _c	w	k
$p(\cdot), c(\cdot)$	1535.607	0.000	0.260	2
$p(\text{year}), c(\cdot)$	1536.610	1.003	0.158	3
$p(\cdot), c(t)$	1536.775	1.168	0.145	6
$p(\cdot), c(\text{year})$	1537.439	1.831	0.104	3
$p(t) = c(t)$	1537.517	1.909	0.100	6

Note: Information includes model covariates for initial capture probability (p) and recapture probability (c), ranked by AIC_c (Akaike's information criterion adjusted for small sample size) and compared by ΔAIC_c (difference in AIC_c between a model and the top-ranked model), w (model weight), and k (number of parameters).

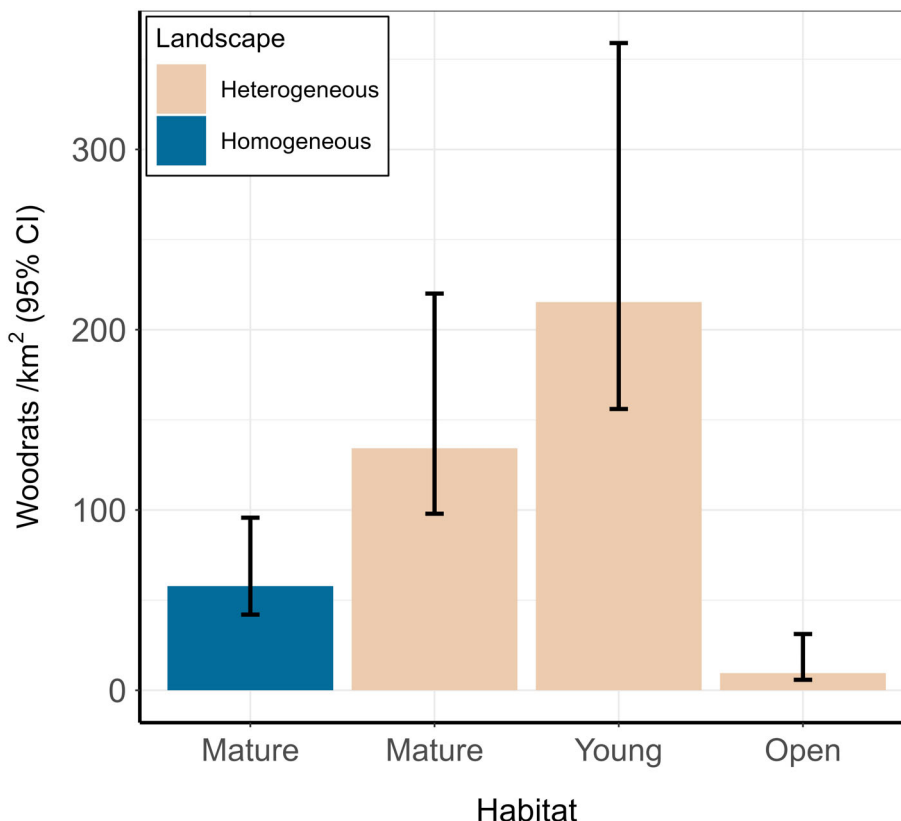


FIGURE 3 Estimated density ($\pm 95\%$ CI) of dusky-footed woodrats (*Neotoma fuscipes*) in 2020 and 2021 within habitat types in the central Sierra Nevada, California, USA. Density is shown as number of woodrats per square kilometer in open habitat, young forest, and mature forest within home ranges classified as heterogeneous and homogeneous.

Prediction 2: Higher woodrat mortality within mature forests and homogeneous home ranges

We radio-collared and monitored 108 woodrats (35 in 2020, 73 in 2021) within eight owl home ranges (four heterogeneous, four homogeneous) and compiled a total of 1030 weekly monitoring records. Collars were deployed evenly among three of the four habitat classes (37 mature-homogeneous, 36 mature-heterogeneous, 35 young). Woodrats were not collared in open areas given the low densities that occurred in this vegetation type. We observed minimal dispersal over the survey period. During monthly checks, only two individuals moved to a different midden with an average dispersal distance of 90 m, and neither of these individuals dispersed to a different habitat type. We confirmed 12 mortalities over the course of our study: three from avian (and presumably spotted owl) predation, three from mammalian predation, and six from nonpredation events.

The top model for woodrat survival contained only an intercept, indicating that woodrat survival rates did not vary by landscape composition, among habitat types, or year. Models including covariates for sampling year and habitat type were within 2 AIC_c yet involved

TABLE 2 Top known-fate survival models for estimating dusky-footed woodrat (*Neotoma fuscipes*) survival in 2020 and 2021 in the central Sierra Nevada, California, USA.

Covariate(s)	AIC_c	ΔAIC_c	w	k
Null	132.721	0	0.319	1
Year	133.942	1.221	0.173	2
Habitat	134.241	1.520	0.149	2
Landscape	134.725	2.004	0.117	2
Year + Habitat	135.419	2.697	0.082	3

Note: Information includes model covariates, ranked by AIC_c (Akaike’s information criterion adjusted for small sample size) and compared by ΔAIC_c (difference in AIC_c between a model and the top-ranked model), w (model weight), and k (number of parameters).

uninformative parameters (Arnold, 2010), so they were deemed noncompetitive (Table 2). Weekly woodrat survival relative to all mortality sources was low ($\hat{s} = 0.988$; 95% CI: 0.980, 0.993), while weekly survival relative to avian (likely spotted owl) predation alone was even lower ($\hat{s} = 0.997$; 95% CI: 0.991, 0.999). While we did not detect an effect of habitat on survival rates, all three mortalities from avian predation occurred within mature forest (two mature-heterogeneous, one mature-homogeneous).

Prediction 3: Greater woodrat consumption by owls in heterogeneous home ranges

We monitored 15 nesting owl pairs over 115 days for 1173.3 total monitoring hours. One camera was removed from analysis due to limited deployment duration (10.5 h). We confirmed 306 prey delivery events and identified 243 deliveries to species. Of these, we identified 93 individual deliveries of woodrats (i.e., 30.4% of all deliveries of known species) to owl nestlings. From the video-based nest delivery data we estimated a consumption rate of 22.8 woodrats per month (95% CI: 13.5, 34.5) across all home ranges, with greater monthly consumption in heterogeneous ($\bar{x} = 32.4$ woodrats/month; 95% CI: 19.2, 48.8) versus homogeneous ($\bar{x} = 13.3$ woodrats/month; 95% CI: 5.2, 25.4) home ranges ($t_{12} = 1.85$, $p = 0.09$; Figure 4), significant at the $\alpha = 0.1$ but not 0.05 level. Based on our combined data from Predictions 1 and 2, we estimated an average mortality rate relative to avian (likely spotted owl) predation of 20.2 woodrats per month (95% CI: 14.1, 26.4) across all home ranges, with a greater number of monthly mortalities in

heterogeneous ($\bar{x} = 28.8$ woodrats/month; 95% CI: 27.2, 30.0) versus homogeneous ($\bar{x} = 11.6$ woodrats/month; 95% CI: 10.2, 13.0) home ranges ($t_6 = 14.92$, $p < 0.001$; Figure 4). This corroborated estimates from nest camera data, as there were no significant differences in woodrat consumption rates in homogeneous or heterogeneous home ranges between estimation methods (ANOVA: $p = 0.71$).

Prediction 4: Greater biomass delivery by owls within heterogeneous home ranges

In addition to woodrats, we confirmed deliveries of 90 flying squirrels, 30 *Peromyscus* spp., four voles, two pocket gophers, two moles, one bird, and one bat among the 306 confirmed deliveries. Another 63 deliveries were not identified to species but were grouped into size class to allow for biomass estimates; of these, nine were extra small, 19 were small, nine were medium, and 26 were large. The remaining 20 prey deliveries were not categorized into size classes. While woodrat consumption was much greater among spotted owls occupying

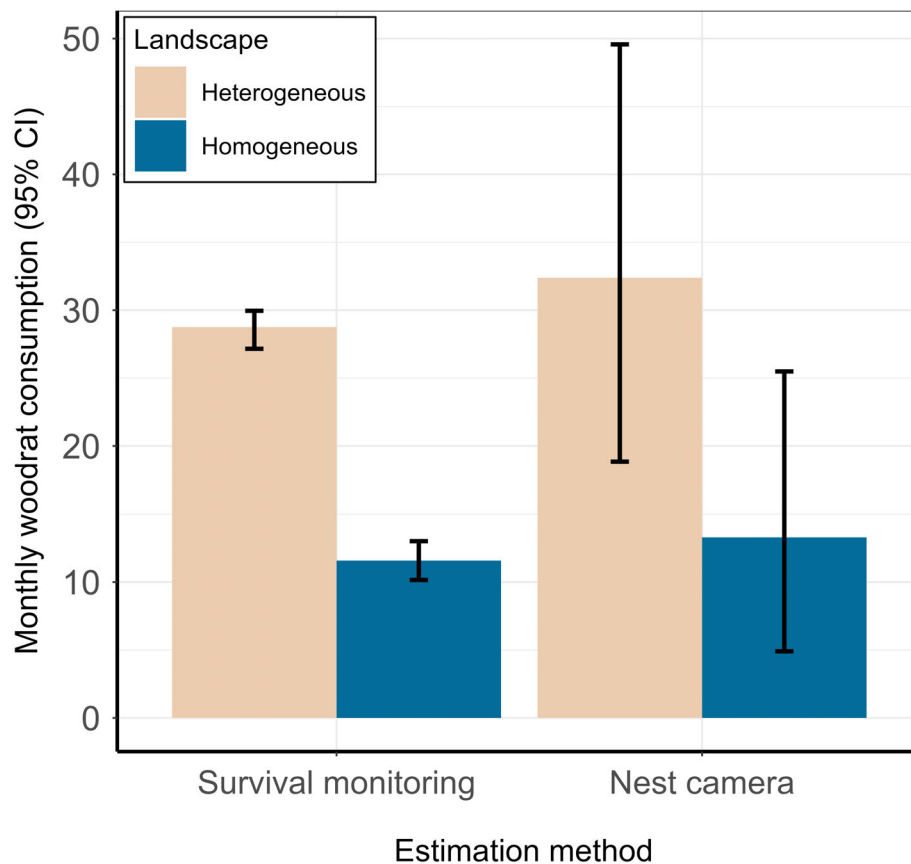


FIGURE 4 Estimated monthly consumption rate ($\pm 95\%$ CI) of dusky-footed woodrats (*Neotoma fuscipes*) by spotted owls (*Strix occidentalis*) within the central and northern Sierra Nevada, California, USA, derived from monitoring and mark-recapture data (survival monitoring) or nest camera data (nest camera) within home ranges classified as heterogeneous or homogeneous.

heterogeneous home ranges (see preceding discussion), we found no effect of landscape composition on the delivery frequency of flying squirrels ($t_{12} = 0.14, p = 0.89$) or all other alternative prey combined ($t_{12} = 0.80, p = 0.44$; Figure 5A). Accordingly, flying squirrel biomass was similar in heterogeneous ($\bar{x} = 2705.9$ g/month) versus homogeneous ($\bar{x} = 2553.6$ g/month) home ranges. Further, while spotted owls consumed an additional 1000 g/month of other prey in homogeneous ($\bar{x} = 3176.1$ g/month) versus heterogeneous ($\bar{x} = 2139.6$ g/month) home ranges (Figure 5B), this difference was not enough to compensate for the 2.5 times greater consumption of woodrat biomass in heterogeneous ($\bar{x} = 6055.6$ g/month) versus homogeneous ($\bar{x} = 2485.8$ g/month) home ranges. Specifically, owls delivered total biomass at a rate 1.3 times greater (2685.6 more g/month) in heterogeneous ($\bar{x} = 10,901.1$ g/month) versus homogeneous ($\bar{x} = 8215.5$ g/month) home ranges (Figure 5B).

DISCUSSION

We demonstrated that landscape-scale heterogeneity in vegetation types including young forest refuges increased the abundance and availability of woodrats that, in turn, provided energetic and potentially reproductive benefits to mature forest-associated spotted owls, thus providing strong empirical support for the hypothesis that prey refuges can benefit predators in heterogeneous landscapes. While previous theoretical and laboratory-based research suggested that landscape heterogeneity including patches of prey refuges could profoundly affect predator-prey dynamics, these approaches typically involved highly simplified conditions, were used at the patch rather than landscape scale, or failed to account for alternative prey (Juliano et al., 2022; Ryall & Fahrig, 2006). Thus, our findings provide some of the first evidence from natural systems that promoting landscape heterogeneity may

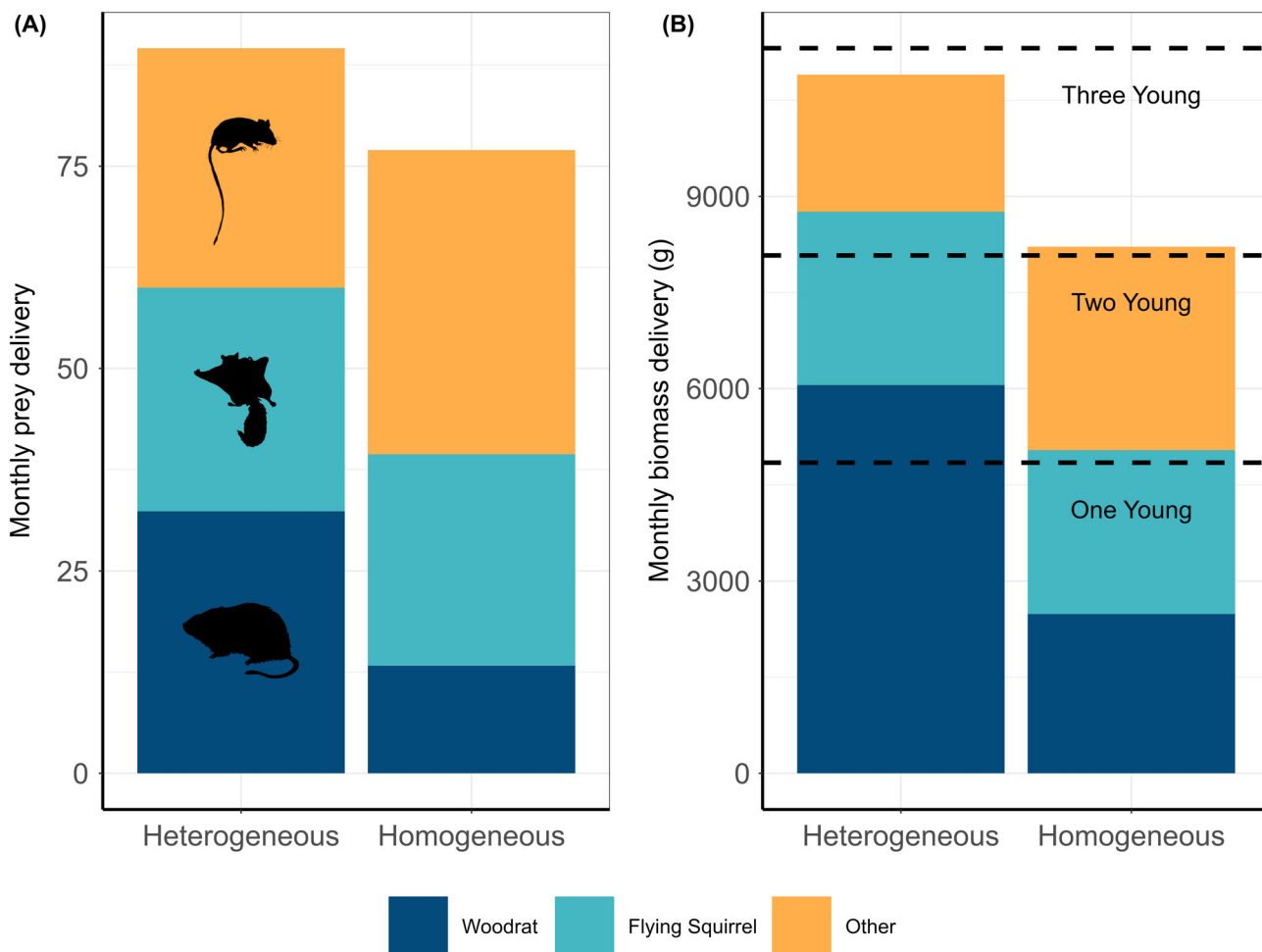


FIGURE 5 Estimated monthly prey delivery rate by prey species (A) and biomass (B) in 2019 and 2020 by spotted owls (*Strix occidentalis*) within heterogeneous and homogeneous home ranges within the central and northern Sierra Nevada, California, USA. Horizontal dashed lines in (B) represent the estimated metabolic cost to produce and raise one, two, or three young for a nesting owl pair, derived from Ward Jr. et al. (1998) and Weathers (1996).

provide co-benefits to both predator and prey populations and constitute an effective strategy for conserving endangered predators.

Young forests promote woodrat abundance within heterogeneous landscapes

As predicted, woodrat abundance was ~2.5 times greater in heterogeneous than homogeneous spotted owl home ranges, in large part because of the greater woodrat densities in young forests that were more prevalent in heterogeneous home ranges. While sample sizes of spotted owl home ranges were modest in our abundance and prey delivery analyses, the effects of landscape composition on these measures were large and occurred in directions consistent with our a priori understanding of the system—such that we do not believe limited sample size compromised our inferences. The finding that woodrat densities in young forests were considerably greater than in mature forests was consistent with previous studies (Sakai & Noon, 1993; Ward Jr et al., 1998), as were low densities in open areas with little vegetation cover (Cranford, 1977). Young forest likely confers benefits to woodrat populations by providing higher-quality food resources owing to a greater diversity and abundance of flora (Carraway & Verts, 1991; Sakai & Noon, 1993), a more stable microclimate (Atsatt & Ingram, 1983), structures and materials required for nest building (Innes et al., 2007), and cover that reduces predator risk (Sakai & Noon, 1997). In particular, while black oak acorns represent a preferred food item (Innes et al., 2007), woodrats consume a variety of fruits, nuts, and fibrous woody plants—many of which occur in greater densities within young forest and are not subject to inconsistent mast production (Carraway & Verts, 1991; McEachern et al., 2006). High woodrat densities in young forest, whether the result of resource availability or reduced predation, may have supported woodrat populations in nearby mature forests as evidenced by the 2.3 times greater densities we estimated for mature forests within heterogeneous compared to homogeneous home ranges (Figure 3). Indeed, high densities and associated intraspecific competition in young forest patches may lead to increased dispersal from these source populations that recruit into lower-density mature forest patches (Hansen et al., 2019; Sakai & Noon, 1997), a process expected to be weaker in homogeneous spotted owl home ranges containing less young forest.

Counter to our predictions that woodrat survival rates would be greater in young forests and heterogeneous (prey-dense) home ranges, we observed no difference in survival among vegetation or landscape types, either overall or from presumed spotted owl predation. This result

contrasts with a previous study that found lower survival within mature forest patches, likely due to higher predation rates from spotted owls (Sakai & Noon, 1997). However, mortality rates were uniformly very low, both overall and from spotted owl predation, which may have limited our ability to detect differences in survival rates among vegetation or landscape types statistically. Of note, all presumed spotted owl predation events observed in this study occurred in mature forest: one in mature homogeneous and two in mature heterogeneous—similar to observations by Sakai and Noon (1997). As such, the balance of evidence indicates that young forests, to a degree, act as woodrat refuges from spotted owl predation. However, young forests almost certainly harbored relatively high woodrat densities primarily because they provided greater resource availability given the marked difference in densities yet similar predation rates among habitat types. Spotted owl predation exerted little to no top-down pressure on woodrat populations given the very low estimated per-capita predation rates, even in mature forests—suggesting that high densities in young forests are driven as much, and likely more, by bottom-up processes.

Landscape heterogeneity promotes woodrat consumption by spotted owls

Spotted owls consumed more woodrats in heterogeneous than homogeneous landscapes, presumably because of greater woodrat abundance—with nest video monitoring and population-based approaches yielding very similar estimates of woodrat consumption rates. This finding supports previous analyses via stable isotopes that the proportion of woodrats present in spotted owl diets increases with forest heterogeneity (Hobart, Jones, et al., 2019). Spotted owls in our study exhibited a type I functional response (i.e., prey consumption rate increases linearly with prey density; Holling, 1959) given they consumed 2.5 times more woodrats in heterogeneous home ranges, which themselves contained a 2.5 times greater abundance than homogeneous territories. The 1:1 relationship between woodrat consumption and abundance suggests that spotted owls are consuming more woodrats in heterogeneous home ranges because of higher encounter rates rather than kill rates. Regardless of the mechanism, the linear functional response indicates that vegetation management promoting woodrat populations can, under appropriate conditions, lead to direct increases in woodrat acquisition by spotted owls.

As expected, lower delivery rates of woodrats by spotted owls to their nests in homogeneous home ranges containing fewer woodrats reduced overall biomass delivery rates (Figure 5B). Further, owls in homogeneous

home ranges only partially reconciled the deficit of decreased woodrat deliveries with alternative prey (Figure 5A). Thus, the “reduction” in mature forest spotted owl habitat in heterogeneous landscapes did not come at a cost to, but rather benefited, spotted owl prey acquisition. Spotted owls likely attempt to maximize energy gain by selecting prey that most efficiently balance foraging costs with the benefits of prey consumption (Sih, 2005; Stephens & Krebs, 1986). Reliance on smaller and less dense prey, such as flying squirrels, or very small species, such as mice, may incur costs, including increased energetic expenditures associated with prey searching or reduced biomass delivery rates (Moorhouse-Gann et al., 2020; Ruiz-Olmo & Jiménez, 2009). In contrast, consuming a greater proportion of larger-bodied and densely distributed prey such as woodrats can reduce these costs (McNab, 1963) or increase biomass delivery rates, with benefits for occupancy, space use, and even population growth (Coulson et al., 2006; Hobart, Roberts, et al., 2019; Wendland, 1984).

To explore potential fitness outcomes associated with increased biomass delivery rates in heterogeneous home ranges, we estimated the energetic cost of a nesting spotted owl pair to produce and raise one, two, or three young and converted this into monthly prey biomass values based on Ward Jr et al. (1998) and Weathers (1996) (Appendix S1: Section S2). Based on these calculations, we estimated that spotted owls GPS-tagged in homogeneous landscapes captured and delivered enough biomass to produce and raise approximately two young, whereas owls in heterogeneous landscapes met the energetic costs of raising approximately three young (Figure 5B). While we were not able to assess whether greater prey biomass delivered to nests translated directly to fitness benefits in this study population given our sample size and the uncertainty surrounding estimates drawn from a number of variables, food supplementation has increased reproductive performance in many avian species, including owls, in controlled experiments (Korpimäki, 1992; Ruffino et al., 2014). Thus, we consider it likely that prior observations of higher spotted owl reproduction in heterogeneous home ranges (Franklin et al., 2000) and home ranges containing more young forest and hardwoods (Hobart, Roberts, et al., 2019) were the result of greater woodrat abundance and consumption by owls, as suggested by these authors.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Spotted owls depend on mature forests for nesting (Moen & Gutiérrez, 1997; North et al., 2000) and often

forage within forests characterized by large trees (Zulla et al., 2022). Nevertheless, our results suggest that promoting landscape heterogeneity could benefit spotted owl populations in parts of their range where woodrats are important prey. Heterogeneity is a natural feature of many dry forest ecosystems occupied by spotted owls and was maintained historically by frequent and predominantly low- to moderate-severity fires and smaller high-severity burned areas resulting from natural and Indigenous sources (Hoffman et al., 2021; McLauchlan et al., 2020). These forests, then, were typically characterized by larger stands of comparatively open but large-tree-dominated forests interspersed with smaller patches of early successional shrub and young forest (Boisramé et al., 2017) that presumably harbored dense woodrat populations (Innes et al., 2007; Sakai & Noon, 1993). However, more than a century of fire suppression coupled with the historic selective logging of large trees has created denser, more homogeneous forests with fewer early successional patches and large trees (North et al., 2017). While our landscape classification did not include old-growth forest as a standalone category, our results suggest that the homogenization of these forests has reduced the abundance of woodrats and their consumption by spotted owls—and come at a cost to overall prey acquisition and potentially reproductive success. This conclusion is supported by a constellation of previous studies indicating that spotted owls (1) forage and capture woodrats at the edge of young and mature forests (Kramer, Jones, Kane, et al., 2021; Sakai & Noon, 1997; Zulla et al., 2022); (2) consume a greater proportion of woodrats in more heterogeneous landscapes based on stable isotope analyses (Hobart, Jones, et al., 2019); (3) have smaller home ranges, higher territory occupancy rates, and higher densities in areas where they consume more woodrats (Hobart, Jones, et al., 2019; Zabel et al., 1995); and (4) can have higher reproductive rates in heterogeneous landscapes (Franklin et al., 2000), including those that contain a relatively high proportion of young forest with hardwoods (Hobart, Roberts, et al., 2019).

As such, our findings, in conjunction with those of previous studies, indicate that promoting landscape heterogeneity characterized by a mosaic of mature and young forests could help ameliorate the population declines observed in some areas by enhancing prey availability (Conner et al., 2016; Tempel et al., 2014). This condition could be achieved through active management that incorporates fire use and timber harvest strategies that mirror the fine-scale forest loss and recruitment events typically supported by historical disturbance regimes (Collins et al., 2017). Such strategies could continuously create small patches of open habitat that regenerate into future young forest following planting or

natural reseeded, emulating a natural mosaic of vegetation types. By mimicking historical processes of disturbance-prone forests, including those in western North America, the “managed dynamics” approach to conservation can maintain critical wildlife habitat (Gaines et al., 2022; Steel et al., 2022), although it requires continuous action to balance successional changes within regenerating patches (Steel et al., 2022). Our work demonstrating the benefits of heterogeneity to spotted owls, mediated by woodrat availability, was conducted in landscapes containing, in addition to national forests, privately owned lands managed for commercial timber production that yield a relatively high proportion of such young forests in patches tens of acres in size. While national forests are increasingly managed with an emphasis on fuel reduction intended to restore lower-severity fire regimes, this strategy can produce stands of younger forests in small, severely burned patches only if small high-severity patches are acknowledged and planned for as a desired outcome. Thus, the current emphasis on the restoration of historical fire regimes and historical forest structure (e.g., individual trees, clumps, and openings) from active harvest and burning strategies is likely to benefit spotted owl populations by creating high-density woodrat refuges adjacent to mature forest, while also reducing the risk of megafires that render large areas unsuitable for spotted owl foraging (Jones et al., 2016, 2020). Our work provides yet further evidence that the conservation of spotted owls and promotion of forest ecosystem resilience are compatible rather than conflicting objectives (Jones et al., 2022)—a perception that has constrained forest restoration in these highly vulnerable ecosystems (Collins et al., 2010).

We suggest that our findings have implications for species and ecosystems beyond the forests of western North America as historical and contemporary land-use practices have homogenized forests worldwide (Collins et al., 2017; Sapkota et al., 2021; Schulte et al., 2007). Human activities, including timber extraction, agricultural intensification, afforestation, and severe fires, have created ecological patterns without historical equivalent across all forest biomes (Seastedt et al., 2008). These departures from historical landscape conditions can alter the availability, predictability, and distribution of resources (Ullmann et al., 2018) and are increasingly recognized as a global threat to biodiversity and ecosystem function, particularly among species adapted to naturally complex ecosystems (Anile et al., 2019; Riley et al., 2003). For predators, landscape simplification can cause declines in prey diversity and abundance (Benedek & Sîrbu, 2018; Cramer & Willig, 2002), with consequences for behavior, space use, and demography (Parsons et al., 2022). However, despite the fact that

species at higher trophic levels may be most impacted by landscape-scale changes such as homogenization due to space and resource needs (Ripple et al., 2014), these effects have often been overlooked in studies of predators inhabiting human-altered environments (Ryall & Fahrig, 2006).

Here, we provide empirical evidence demonstrating the mechanisms whereby landscape-level processes alter prey availability to predators and explore a trophic-driven fitness consequence of landscape simplification. We recommend the promotion of management strategies that preserve and restore historical heterogeneity and also highlight the importance of considering spatial scale, habitat associations, and predator mobility in future studies on predator–prey interactions. There is a growing drive to understand and incorporate ecological complexity within conventional restoration approaches (Bullock et al., 2022), and our results show that understanding the role of landscape heterogeneity in predator–prey dynamics can benefit predator conservation worldwide.

AUTHOR CONTRIBUTIONS

Corbin C. Kuntze, M. Zachariah Peery, Jonathan N. Pauli, Ceeanna J. Zulla, Sarah C. Sawyer, Brian P. Dotters, Kevin N. Roberts, and John J. Keane conceived the ideas and designed the methodology. Corbin C. Kuntze and Ceeanna J. Zulla collected the data. Corbin C. Kuntze, M. Zachariah Peery, and Jonathan N. Pauli analyzed the data. Corbin C. Kuntze and M. Zachariah Peery led the writing of the manuscript, with key input from Jonathan N. Pauli. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Kuntze et al., 2023a) are available in Dryad at <https://doi.org/10.5061/dryad.4mw6m90g5>. Code (Kuntze et al., 2023b) is available in Zenodo at <https://doi.org/10.5281/zenodo.8011794>.

ORCID

Corbin C. Kuntze  <https://orcid.org/0000-0002-5059-0278>

REFERENCES

- Anile, S., S. Devillard, B. Ragni, F. Rovero, F. Mattucci, and M. L. Valvo. 2019. "Habitat Fragmentation and Anthropogenic Factors Affect Wildcat *Felis silvestris silvestris* Occupancy and Detectability on Mt Etna." *Wildlife Biology* 2019: 1–13.
- Arnold, T. W. 2010. "Uninformative Parameters and Model Selection Using Akaike's Information Criterion." *The Journal of Wildlife Management* 74: 1175–78.
- Atsatt, P. R., and T. Ingram. 1983. "Adaptation to Oak and Other Fibrous, Phenolic-Rich Foliage by a Small Mammal, *Neotoma fuscipes*." *Oecologia* 60: 135–142.
- Atuo, F. A., K. Roberts, S. Whitmore, B. P. Dotters, M. G. Raphael, S. C. Sawyer, J. J. Keane, R. J. Gutiérrez, and M. Zachariah Peery. 2019. "Resource Selection by GPS-Tagged California Spotted Owls in Mixed-Ownership Forests." *Forest Ecology and Management* 433: 295–304.
- Benedek, A. M., and I. Sirbu. 2018. "Responses of Small Mammal Communities to Environment and Agriculture in a Rural Mosaic Landscape." *Mammalian Biology* 90: 55–65.
- Boisramé, G. F. S., S. E. Thompson, M. Kelly, J. Cavalli, K. M. Wilkin, and S. L. Stephens. 2017. "Vegetation Change during 40 Years of Repeated Managed Wildfires in the Sierra Nevada, California." *Forest Ecology and Management* 402: 241–252.
- Bullock, J. M., E. Fuentes-Montemayor, B. McCarthy, K. Park, R. S. Hails, B. A. Woodcock, K. Watts, R. Corstanje, and J. Harris. 2022. "Future Restoration Should Enhance Ecological Complexity and Emergent Properties at Multiple Scales." *Ecography* 2022: e05780.
- Carraway, L. N., and B. J. Verts. 1991. "*Neotoma fuscipes*." *Mammalian Species* 386: 1–10.
- Collins, B. M., D. L. Fry, J. M. Lydersen, R. Everett, and S. L. Stephens. 2017. "Impacts of Different Land Management Histories on Forest Change." *Ecological Applications* 27: 2475–86.
- Collins, B. M., S. L. Stephens, J. J. Moghaddas, and J. Battles. 2010. "Challenges and Approaches in Planning Fuel Treatments across Fire-Excluded Forested Landscapes." *Journal of Forestry* 108: 24–31.
- Conner, M. M., J. J. Keane, C. V. Gallagher, T. E. Munton, and P. A. Shaklee. 2016. "Comparing Estimates of Population Change from Occupancy and Mark–Recapture Models for a Territorial Species." *Ecosphere* 7: e01538.
- Coulson, T., T. G. Benton, P. Lundberg, S. R. X. Dall, B. E. Kendall, and J. M. Gaillard. 2006. "Estimating Individual Contributions to Population Growth: Evolutionary Fitness in Ecological Time." *Proceedings of the Royal Society B: Biological Sciences* 273: 547–555.
- Cramer, M. J., and M. R. Willig. 2002. "Habitat Heterogeneity, Habitat Associations, and Rodent Species Diversity in a Sand–Shinnery–Oak Landscape." *Journal of Mammalogy* 83: 743–753.
- Cranford, J. A. 1977. "Home Range and Habitat Utilization by *Neotoma fuscipes* as Determined by Radiotelemetry." *Journal of Mammalogy* 58: 165–172.
- Ehrlén, J., and W. F. Morris. 2015. "Predicting Changes in the Distribution and Abundance of Species under Environmental Change." *Ecology Letters* 18: 303–314.
- Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, et al. 2011. "Trophic Downgrading of Planet Earth." *Science* 333: 301–6.
- Fahrig, L., J. Baudry, L. Brotons, F. G. Burel, T. O. Crist, R. J. Fuller, C. Sirami, G. M. Siriwardena, and J.-L. Martin. 2011. "Functional Landscape Heterogeneity and Animal Biodiversity in Agricultural Landscapes." *Ecology Letters* 14: 101–112.
- Fites-Kaufman, J. A., P. Rundel, N. Stephenson, and D. A. Weixelman. 2007. "Montane and Subalpine Vegetation of the Sierra Nevada and Cascade Ranges." In *Terrestrial Vegetation of California*, edited by M. Barbour, T. Keeler-Wolf, and A. A. Schoenherr, 456–501. Berkeley, CA: University of California Press.
- 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.
- Gaines, W. L., P. F. Hessburg, G. H. Aplet, P. Henson, S. J. Prichard, D. J. Churchill, G. M. Jones, D. J. Isaak, and C. Vynne. 2022. "Climate Change and Forest Management on Federal Lands in the Pacific Northwest, USA: Managing for Dynamic Landscapes." *Forest Ecology and Management* 504: 119794.
- Gerber, B. D., and R. R. Parmenter. 2015. "Spatial Capture–Recapture Model Performance with Known Small-Mammal Densities." *Ecological Applications* 25: 695–705.
- Gutiérrez, R. J., J. Verner, K. S. McKelvey, B. R. Noon, G. N. Steger, D. R. Call, W. S. LaHaye, B. B. Bingham, and J. S. Senser. 1992. "Habitat Relations of the California Spotted Owl." In *The California Spotted Owl: A Technical Assessment of its Current Status*. General Technical Report PSW-GTR-133, edited by J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, 79–98. Albany, CA: USDA Forest Service, Pacific Southwest Research Station.
- Hansen, N. A., C. F. Sato, D. R. Michael, D. B. Lindenmayer, and D. A. Driscoll. 2019. "Predation Risk for Reptiles Is Highest at Remnant Edges in Agricultural Landscapes." *Journal of Applied Ecology* 56: 31–43.
- Hastings, A. 1977. "Spatial Heterogeneity and the Stability of Predator–Prey Systems." *Theoretical Population Biology* 12: 37–48.
- Hebblewhite, M., E. H. Merrill, and T. L. McDonald. 2005. "Spatial Decomposition of Predation Risk Using Resource Selection Functions: An Example in a Wolf–Elk Predator–Prey System." *Oikos* 111: 101–111.
- 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. 2019. "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. 2019. "Site Occupancy and Reproductive Dynamics of California Spotted Owls in a Mixed-Ownership Landscape." *Forest Ecology and Management* 437: 188–200.
- Hoffman, K. M., E. L. Davis, S. B. Wickham, K. Schang, A. Johnson, T. Larking, P. N. Lauriault, N. Quynh Le, E. Swerdfager, and A. J. Trant. 2021. "Conservation of Earth's Biodiversity Is Embedded in Indigenous Fire Stewardship." *Proceedings of the National Academy of Sciences* 118: e2105073118.

- Holling, C. S. 1959. "Some Characteristics of Simple Types of Predation and Parasitism." *The Canadian Entomologist* 91: 385–398.
- Holt, R. D. 1985. "Population Dynamics in Two-Patch Environments: Some Anomalous Consequences of an Optimal Habitat Distribution." *Theoretical Population Biology* 28: 181–208.
- Hopcraft, J. G. C., A. R. Sinclair, and C. Packer. 2005. "Planning for Success: Serengeti Lions Seek Prey Accessibility Rather than Abundance." *Journal of Animal Ecology* 74: 559–566.
- Huffaker, C. B., K. B. Shea, and S. Herman. 1963. "Experimental Studies on Predation: Complex Dispersion and Levels of Food in an Acarine Predator-Prey Interaction." *Hilgardia* 34: 305–330.
- Hunter, M. D., and P. W. Price. 1992. "Playing Chutes and Ladders: Heterogeneity and the Relative Roles of Bottom-Up and Top-Down Forces in Natural Communities." *Ecology* 73: 724–732.
- Iles, D. T., N. M. Williams, and E. E. Crone. 2018. "Source-Sink Dynamics of Bumblebees in Rapidly Changing Landscapes." *Journal of Applied Ecology* 55: 2802–11.
- Innes, R. J., D. H. V. 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: 1523–31.
- Jones, G. M., R. Gutiérrez, D. J. Tempel, S. A. Whitmore, W. J. Berigan, 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. Clare, R. Gutiérrez, and M. Z. Peery. 2022. "Forest Restoration Limits Megafires and Supports Species Conservation under Climate Change." *Frontiers in Ecology and the Environment* 20: 210–16.
- Jones, G. M., H. A. Kramer, W. J. Berigan, S. A. Whitmore, R. J. Gutiérrez, and M. Z. Peery. 2021. "Megafire Causes Persistent Loss of an Old-Forest Species." *Animal Conservation* 24: 925–936.
- Jones, G. M., H. A. Kramer, S. A. Whitmore, W. J. Berigan, D. J. Tempel, C. M. Wood, B. K. Hobart, et al. 2020. "Habitat Selection by Spotted Owls after a Megafire Reflects their Adaptation to Historical Frequent-Fire Regimes." *Landscape Ecology* 35: 1199–1213.
- Juliano, S. A., J. A. Goughnour, and G. D. Ower. 2022. "Predation in Many Dimensions: Spatial Context Is Important for Meaningful Functional Response Experiments." *Frontiers in Ecology and Evolution* 10: 845560.
- Korpimäki, E. 1992. "Fluctuating Food Abundance Determines the Lifetime Reproductive Success of Male Tengmalm's Owls." *Journal of Animal Ecology* 61: 103–111.
- 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. 2021. "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, et al. 2021. "Elevational Gradients Strongly Mediate Habitat Selection Patterns in a Nocturnal Predator." *Ecosphere* 12: e03500.
- Kuntze, C. C., J. N. Pauli, C. J. Zulla, J. J. Keane, K. N. Roberts, B. P. Dotters, S. C. Sawyer, and M. Z. Peery. 2023a. "Landscape Heterogeneity Provides Co-benefits to Predator and Prey." Dryad, Dataset. <https://doi.org/10.5061/dryad.4mw6m90g5>.
- Kuntze, C. C., J. N. Pauli, C. J. Zulla, J. J. Keane, K. N. Roberts, B. P. Dotters, S. C. Sawyer, and M. Z. Peery. 2023b. "Landscape Heterogeneity Provides Co-benefits to Predator and Prey." Zenodo, Software. <https://doi.org/10.5281/zenodo.8011794>.
- Laundré, J. W. 2010. "Behavioral Response Races, Predator-Prey Shell Games, Ecology of Fear, and Patch Use of Pumas and their Ungulate Prey." *Ecology* 91: 2995–3007.
- Laundré, J. W., and L. Hernández. 2003. "Winter Hunting Habitat of Pumas *Puma concolor* in Northwestern Utah and Southern Idaho, USA." *Wildlife Biology* 9: 123–29.
- Layman, C. A., J. P. Quattrochi, C. M. Peyer, and J. E. Allgeier. 2007. "Niche Width Collapse in a Resilient Top Predator Following Ecosystem Fragmentation." *Ecology Letters* 10: 937–944.
- Li, H., and J. F. Reynolds. 1995. "On Definition and Quantification of Heterogeneity." *Oikos* 73: 280–84.
- McEachern, M. B., C. A. Eagles-Smith, C. M. Efferson, and D. H. Van Vuren. 2006. "Evidence for Local Specialization in a Generalist Mammalian Herbivore, *Neotoma fuscipes*." *Oikos* 113: 440–48.
- McLaughlan, K. K., P. E. Higuera, J. Miesel, B. M. Rogers, J. Schweitzer, J. K. Shuman, A. J. Tepley, J. M. Varner, T. T. Veblen, and S. A. Adalsteinsson. 2020. "Fire as a Fundamental Ecological Process: Research Advances and Frontiers." *Journal of Ecology* 108: 2047–69.
- McNab, B. K. 1963. "Bioenergetics and the Determination of Home Range Size." *The American Naturalist* 97: 133–140.
- Moen, C. A., and R. J. Gutiérrez. 1997. "California Spotted Owl Habitat Selection in the Central Sierra Nevada." *The Journal of Wildlife Management* 61: 1281–87.
- Moorhouse-Gann, R. J., E. F. Kean, G. Parry, S. Valladares, and E. A. Chadwick. 2020. "Dietary Complexity and Hidden Costs of Prey Switching in a Generalist Top Predator." *Ecology and Evolution* 10: 6395–6408.
- 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.
- North, M. P., M. W. Schwartz, B. M. Collins, and J. J. Keane. 2017. *Current and Projected Condition of Mid-Elevation Sierra Nevada Forests*. General Technical Report PSW-GTR-254, Vol. 254, 109–157. Albany, CA: US Department of Agriculture, Forest Service, Pacific Southwest Research Station.
- Parmenter, R. R., T. L. Yates, D. R. Anderson, K. P. Burnham, J. L. Dunnum, A. B. Franklin, M. T. Friggens, et al. 2003. "Small-Mammal Density Estimation: A Field Comparison of Grid-Based vs. Web-Based Density Estimators." *Ecological Monographs* 73: 1–26.
- Parsons, M. A., T. M. Newsome, and J. K. Young. 2022. "The Consequences of Predators without Prey." *Frontiers in Ecology and the Environment* 20: 31–39.

- Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. "Survival Analysis in Telemetry Studies: The Staggered Entry Design." *The Journal of Wildlife Management* 53: 7–15.
- Powell, L. A. 2007. "Approximating Variance of Demographic Parameters Using the Delta Method: A Reference for Avian Biologists." *The Condor* 109: 949–954.
- Reid, F. 2006. *A Field Guide to Mammals of North America*. North of Mexico: Houghton Mifflin Harcourt.
- Riley, S. P., R. M. Sauvajot, T. K. Fuller, E. C. York, D. A. Kamradt, C. Bromley, and R. K. Wayne. 2003. "Effects of Urbanization and Habitat Fragmentation on Bobcats and Coyotes in Southern California." *Conservation Biology* 17: 566–576.
- Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, and M. P. Nelson. 2014. "Status and Ecological Effects of the World's Largest Carnivores." *Science* 343: 1241484.
- Roberts, K. N., W. E. Hall, A. J. Shufelberger, M. A. Reno, and M. M. Schroeder. 2017. "California Spotted Owl Occupancy on Mixed-Ownership Lands in the Sierra Nevada of California, 2012 through 2016." *Northwestern Naturalist* 98: 101–116.
- Ruffino, L., P. Salo, E. Koivisto, P. B. Banks, and E. Korpimäki. 2014. "Reproductive Responses of Birds to Experimental Food Supplementation: A Meta-Analysis." *Frontiers in Zoology* 11: 1–13.
- Ruiz-Olmo, J., and J. Jiménez. 2009. "Diet Diversity and Breeding of Top Predators Are Determined by Habitat Stability and Structure: A Case Study with the Eurasian Otter (*Lutra lutra* L.)." *European Journal of Wildlife Research* 55: 133–144.
- Ryall, K. L., and L. Fahrig. 2006. "Response of Predators to Loss and Fragmentation of Prey Habitat: A Review of Theory." *Ecology* 87: 1086–93.
- 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.
- 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.
- Sapkota, R. P., K. Rijal, P. D. Stahl, B. Pyakurel, and A. P. Gautam. 2021. "Evidences of Homogenization in Species Assemblages of Restored Mixed *Shorea robusta* Forest Stands of Nepal." *Global Ecology and Conservation* 27: e01573.
- Schmitz, O. J. 1998. "Direct and Indirect Effects of Predation and Predation Risk in Old-Field Interaction Webs." *The American Naturalist* 151: 327–342.
- Schulte, L. A., D. J. Mladenoff, T. R. Crow, L. C. Merrick, and D. T. Cleland. 2007. "Homogenization of Northern U.S. Great Lakes Forests Due to Land Use." *Landscape Ecology* 22: 1089–1103.
- Schwemm, C. A., C. A. Drost, J. L. Orrock, T. J. Coonan, and T. R. Stanley. 2018. "Comparison of Estimators for Monitoring Long-Term Population Trends in Deer Mice, *Peromyscus maniculatus*, on the California Channel Islands." *Western North American Naturalist* 78: 496–509.
- Seastedt, T. R., R. J. Hobbs, and K. N. Suding. 2008. "Management of Novel Ecosystems: Are Novel Approaches Required?" *Frontiers in Ecology and the Environment* 6: 547–553.
- Sih, A. 1987. "Prey Refuges and Predator-Prey Stability." *Theoretical Population Biology* 31: 1–12.
- Sih, A. 2005. "Predator-Prey Space Use as an Emergent Outcome of a Behavioral Response Race." In *Ecology of Predator-Prey Interactions*, edited by P. Barbosa and I. Castellanos, 240–255. Oxford, UK: Oxford University Press.
- Sikes, R. S., T. A. Thompson, and J. A. Bryan. 2019. "American Society of Mammalogists: Raising the Standards for Ethical and Appropriate Oversight of Wildlife Research." *Journal of Mammalogy* 100: 763–773.
- Steel, Z. L., G. M. Jones, B. M. Collins, R. Green, A. Koltunov, K. L. Purcell, S. C. Sawyer, M. R. Slaton, S. L. Stephens, and P. Stine. 2022. "Mega-Disturbances Cause Rapid Decline of Mature Conifer Forest Habitat in California." *Ecological Applications* 33: e2763.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging Theory*. Princeton, NJ: Princeton University Press.
- Stephens, S. L., J. M. Lydersen, B. M. Collins, D. L. Fry, and M. D. Meyer. 2015. "Historical and Current Landscape-Scale Ponderosa Pine and Mixed Conifer Forest Structure in the Southern Sierra Nevada." *Ecosphere* 6: 1–63.
- Tempel, D. J., R. J. Gutiérrez, S. A. Whitmore, M. J. Reetz, R. E. Stoelting, W. J. Berigan, M. E. Seamans, and M. Z. Peery. 2014. "Effects of Forest Management on California Spotted Owls: Implications for Reducing Wild-fire Risk in Fire-Prone Forests." *Ecological Applications* 24: 2089–2106.
- Ullmann, W., C. Fischer, K. Pirhofer-Walzl, S. Kramer-Schadt, and N. Blaum. 2018. "Spatiotemporal Variability in Resources Affects Herbivore Home Range Formation in Structurally Contrasting and Unpredictable Agricultural Landscapes." *Landscape Ecology* 33: 1505–17.
- Ward, J. P., Jr., 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. 1996. "Energetics of Postnatal Growth." In *Avian Energetics and Nutritional Ecology*, edited by C. Carey, 461–496. New York: Chapman Hall.
- Wendland, V. 1984. "The Influence of Prey Fluctuations on the Breeding Success of the Tawny Owl *Strix aluco*." *Ibis* 126: 284–295.
- White, G. C., and K. P. Burnham. 1999. "Program MARK: Survival Estimation from Populations of Marked Animals." *Bird Study* 46: S120–S139.
- Wiens, J. A. 1995. "Landscape Mosaics and Ecological Theory." In *Mosaic Landscapes and Ecological Processes*, edited by L. Hansson, L. Fahrig, and G. Merriam, 1–26. Dordrecht: Springer Netherlands.
- Williams, D. F., J. Verner, H. F. Sakai, and J. R. Waters. 1992. "General Biology of Major Prey Species of the California Spotted Owl." In *The California Spotted Owl: A Technical Assessment of its Current Status*. General Technical Report PSW-GTR-133, edited by J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, 207–224. Albany, CA: USDA Forest Service, Pacific Southwest Research Station.
- Wilson, E. C., A. A. Shipley, B. Zuckerberg, M. Z. Peery, and J. N. Pauli. 2019. "An Experimental Translocation Identifies

- Habitat Features that Buffer Camouflage Mismatch in Snowshoe Hares.” *Conservation Letters* 12: e12614.
- Zabel, C. J., K. McKelvey, and J. P. Ward, Jr. 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: 433–39.
- Zhang, B., A. Kula, K. M. L. Mack, L. Zhai, A. L. Ryce, W. M. Ni, D. L. DeAngelis, and J. D. Van Dyken. 2017. “Carrying Capacity in a Heterogeneous Environment with Habitat Connectivity.” *Ecology Letters* 20: 1118–28.
- Zulla, C. J., H. A. Kramer, G. M. Jones, J. J. Keane, K. N. Roberts, B. P. Dotters, S. C. Sawyer, et al. 2022. “Large Trees and Forest Heterogeneity Facilitate Prey Capture by California Spotted Owls.” *Ornithological Applications* 124: duac024.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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