The effects of spatial heterogeneity on predators, prey, and their interactions

By

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Dedication

To Zoë.

More than you will ever know.

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Dissertation Abstract

Habitat changes and prey depletion are among the most prominent drivers of near-global declines in predator populations. In particular, landscape homogenization - driven by climate change, anthropogenic land use, and management policies - can destabilize essential trophic interactions and represents a continuing threat to biodiversity and ecosystem function. Many predator and prey species occur, and likely evolved, in complex landscapes with heterogeneously distributed resources that shape many of their ecological interactions. A growing body of research has explored the role of spatial heterogeneity in predator-prey interactions, suggesting that heterogeneous landscapes containing prey refuges can decouple prey availability from abundance, with consequences when any one habitat type predominates. However, most of these studies are theoretical or lab-based, limited to controlled settings and by simplifying assumptions. Moreover, many studies of natural predator-prey systems are conducted at limited spatial scales, do not involve mobile predators, or fail to consider the role of alternative prey. As a result, our understanding of spatial heterogeneity - and the consequences of landscape simplification - remain limited by the available literature. This dissertation seeks to reduce key uncertainties and assess the emergent consequences of environmental change and landscape simplification on wildlife populations.

Chapter 1 (Kuntze et al., 2024; *Journal of Mammalogy*) leveraged a 13-year monitoring dataset, stable isotope analysis, and high-resolution climate and habitat imagery to evaluate demographic responses of an isolated and endangered distinct population segment of fishers (*Pekania pennanti*) to rapid environmental change in the southern Sierra Nevada, California, USA. Fisher survival was sensitive to both biotic and abiotic factors, although the strength and direction of these effects were ultimately mediated by age and sex. These findings suggest that continued climate change will likely have consequences for Fishers through both incremental stressors and extreme weather events but increasing forest heterogeneity may help to buffer against the impacts of such change. Further, this study illustrates the importance of disentangling the effects of intrinsic

and extrinsic factors on survival, especially among species with distinct sexual or ontogenetic differences.

Chapter 2 (Kuntze et al., 2023; *Ecological Applications*) is the first of three that focuses on predator-prey dynamics between the spotted owl (*Strix occidentalis*) - an iconic old-forest species at the center of forest management planning in western North America - and one of its principal prey species, the dusky-footed woodrat (*Neotoma fuscipes*) - a younger forest species. This chapter explores the hypothesis that heterogeneous landscapes can create sources or spatial refuges for prey that ultimately benefit predator and prey populations when each are associated with different habitats. Here, we combined mark-recapture and survival monitoring of woodrats with direct observations of prey deliveries by spotted owls, and found that (1) woodrat abundance was higher within spotted owl home ranges defined by a heterogeneous mix of mature forest, young forest, and open areas, (2) woodrat mortality rates were low across all forest types (although all observed owl predation occurred within mature forests) and did not differ between heterogeneous and homogeneous owl home ranges, (3) owl consumption of woodrats increased linearly with woodrat abundance, and (4) consumption of alternative prey could not reconcile the deficit of reduced woodrat captures in homogeneous home ranges, as owls in heterogeneous landscapes delivered 30% more total prey biomass - equivalent to the energetic needs of producing one additional young. These findings represent some of the first empirical evidence from natural systems that promoting landscape heterogeneity can provide co-benefits to both predator and prey populations and constitute an effective strategy for conserving endangered predator populations.

Chapter 3 (in review at *Journal of Animal Ecology*) contrasts foraging strategies within the context of a primary and secondary prey species to experimentally evaluate whether the magnitude of perceived risk, and in turn, the nature and strength of anti-predator investment, is governed by both predation intensity and the setting in which an encounter takes place. We studied the effects of spotted owls on two species experiencing asymmetrical predation pressures: dusky-footed woodrats (primary prey) and deer mice (*Peromyscus* spp., alternative prey). Woodrats exhibited behavioral responses to both background and acute risk at each stage of the foraging process, while deer mice only responded to acute risk. This suggests that prey may conform to or depart from the risk allocation hypothesis (i.e., that background risk modulates responses to immediate cues of predation risk) depending on relative predation risk from a shared predator. Furthermore, woodrats and deer mice employed time allocation and apprehension in different manners and under opposing circumstances, highlighting that primary and secondary prey can exhibit profound differences in both how risk is *perceived*, as well as how it is *managed*.

Finally, **Chapter 4** (prepared for *Forest Ecology and Management*) characterizes patterns in woodrat site occupancy at site-, patch-, and landscape-scales within landscapes where forest heterogeneity was created by even-aged timber management. Woodrats were more likely to occupy sites with greater canopy cover, understory cover, and hardwoods - particularly tanoak (*Notholithocarpus densiflorus)* - and smaller patches of young forest. Woodrats were also more likely to occur in mature forests in close proximity to younger forest, suggesting that high-quality habitat patches can produce dense populations that recruit into adjacent, lower-quality patches. These findings highlight the benefit of multiscale studies and provide insight into management activities that may benefit species conservation without compromising resilience in forest ecosystems.

These latter three chapters collectively demonstrate that heterogeneity in vegetation types including high-density young forests increased the abundance and availability of early-successional woodrats that, in turn, provided energetic and potentially reproductive benefits to mature forest-associated spotted owls. Overall, this dissertation provides empirical support for theoretical studies on the role of heterogeneity (and the mechanisms conferring co-benefits), as well as contingencies mediating anti-predator behaviors, fit to the appropriate spatial scales.

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Chapter 1: Sex and age mediate the effects of rapid environmental change for a forest carnivore, the Fisher (*Pekania pennanti*)

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Abstract

Rapid environmental changes—in climate, land use, and biotic interactions—are accelerating species extinctions and extirpations globally. Identifying the drivers that threaten populations is essential for conservation yet can be difficult given the variable nature of the response of an organism to biotic and abiotic stressors. We analyzed a long-term monitoring dataset to explore the demographic responses of fishers (*Pekania pennanti*) to rapid environmental change in the southern Sierra Nevada, California, USA. Fisher survival was sensitive to both biotic and abiotic factors, although the strength and direction of these effects were ultimately mediated by age and sex. Specifically, male survival was lower among young individuals and decreased with increasing temperatures and fungi consumption. Female survival was resilient to age effects and diet but increased with greater forest heterogeneity and decreased with increasing temperatures and snow depth. Our findings suggest that continued climate change will likely have consequences for fishers through both incremental stressors and extreme weather events, but increasing forest heterogeneity may help to buffer against the impacts of such change. Further, we illustrate the importance of disentangling the effects of intrinsic and extrinsic factors on survival, especially among species with distinct sexual or ontogenetic differences. As global drivers of environmental change intensify in strength and frequency, understanding these complex relationships will allow practitioners to best manage for population persistence and habitat resilience concurrently.

Keywords: Carnivore conservation, environmental change, Fisher, forest management, sex differences, stable isotopes

Introduction

Rapid changes in climate are altering habitat conditions and biotic interactions to drive species extinct globally (Bellard et al. 2012). Understanding the proximate mechanisms underlying species responses to environmental change is essential for effective management (Bellard et al. 2012; Newbold 2018). However, identifying the drivers that threaten individual species is difficult given the variable nature of exposure and sensitivity of an organism to changes in abiotic (e.g., temperature, precipitation) or biotic (e.g., vegetation cover, species interactions) conditions (Lenoir and Svenning 2015). Indeed, environmental stressors differ in space (Chen et al. 1999) and time (Trisos et al. 2020), while extreme weather events can trigger abrupt and unpredictable ecological responses (Harris et al. 2018). Multiple ecosystem stressors may have additive or even synergistic properties (Brook et al. 2008; Newbold 2018), and for populations that are genetically or geographically isolated, habitat loss, extreme weather, and decoupled trophic interactions may have unique consequences for persistence (Lenoir and Svenning 2015; Jones et al. 2018). Further confounding these relationships, organisms can exhibit great plasticity in morphology (Fox et al.

2019), physiology (Conradt et al. 2000), behavior (Chevin et al. 2010), and diet (Walsh and Tucker 2020), which can mediate adaptive capacity among conspecifics, especially in heterogeneous and changing environments (Chevin et al. 2010).

Intrinsic factors of the organism, such as sex and age, also facilitate different responses to environmental changes (Komoroske et al. 2014; Alonso et al. 2016). As an individual ages, ontogenetic differences in morphology and behavior can alter the strength and type of stressors encountered (Yang and Rudolf 2010; Komoroske et al. 2014). This is also true for sexually dimorphic species, for which differences in behavior and resource use (Barceló et al. 2022) can yield different responses to the same stressors (Fox et al. 2019). Thus, sex- or age-based differences may play a significant role in determining resilience to environmental change, with potential carry-over effects on population dynamics (Komoroske et al. 2014; Hangartner et al. 2022). However, quantifying the effects of age, sex, and biotic interactions concurrently with broad, regional-scale patterns in climate and habitat is logistically challenging and requires the tracking of a large number of individuals over broad spatiotemporal scales. As a result, few studies have addressed differences in sensitivity and responses to rapid environmental change for species with apparent sexual or ontogenetic trait variation.

Between 2012 and 2015, the Sierra Nevada mountains, California, experienced the most extreme drought of the last 1000 years (Crockett and Westerling 2018). This drought, in conjunction with an infestation of bark beetles, resulted in substantial forest mortality with up to hundreds of dead trees per square kilometer (Fettig et al. 2019). In contrast, even though average precipitation and annual snowpack have steadily decreased since the 1950s (Grundstein and Mote 2010), the region is also experiencing periods of extreme precipitation. Following the severe drought of 2012-2015, there was a record snowfall, with some areas receiving up to 186% of the statewide average (Hatchett et al. 2017). Such changes in climate and landscape composition will likely have numerous consequences for wildlife in the southern Sierra Nevada (Zielinski et al. 2013; Jones et al. 2018).

For carnivores in particular, climate extremes and habitat loss can alter prey availability and mediate unique responses, including niche expansion and increasing dietary overlap among competing species (Manlick and Pauli 2020).

The Fisher (*Pekania pennanti*) is a mesocarnivore associated with dense, multi-layered forests throughout North America (Zielinski et al. 2004), and occurs as a geographically and genetically isolated and federally endangered population in the southern Sierra Nevada (Tucker et al. 2012; USFWS 2020). Although fishers would have historically existed in a landscape with diverse topography and land cover (including natural openings and constrictions in forest cover), under current conditions there is concern that geographic barriers and habitat fragmentation may restrict connectivity and spatial recovery (Tucker et al. 2014; Thompson et al. 2021a), while mortalities from predation, disease, and anthropogenic threats including toxicants, incidental trapping, and vehicle collisions could limit population growth (Sweitzer et al. 2016a; Lewis et al. 2022). Fishers also possess relatively high foot loadings that can constrain movement in deep, uncompacted snow (Renard et al. 2008; Suffice et al. 2020), which exerts an energetic cost limiting occupancy and dispersal (Pauli et al. 2022). Fishers in this region have a complex history of dietary constraints; while fishers typically consume large-bodied Snowshoe Hare (*Lepus americanus*) and Porcupine (*Erethizon dorsatum*) across much of their distributional range (Kirby et al. 2018; Pauli et al. 2022), Fisher diet in the southern Sierra Nevada is primarily limited to small mammals (e.g., voles, mice, pocket gophers, tree and ground squirrels) and other forage such as reptiles, fungi, insects, and fruit (Zielinski et al. 1999). Recent work found that fishers in the southern Sierra Nevada exhibit a wide diversity of diet including non-trivial amounts of insects and especially fungi in addition to vertebrates (Smith et al. 2022). Increasing consumption of atypical or lower-calorie forage may affect the resilience of this endangered population to continued environmental change and has been suggested as a potential reason for reduced fecundity, recruitment, and juvenile survival rates relative to populations in the rest of their range (Green et al. 2018).

Sexual dimorphism among adult fishers, particularly within western populations, is striking, with males being up to 50% larger than females (Wengert et al. 2014). Male fishers also possess home ranges up to three times larger than females (Furnas et al. 2017; Kordosky et al. 2021). Differences in morphology, behavior, and energetic demands may present different risks for males and females. For example, while the predominant predator of fishers in this region are mountain lions (*Puma concolor*), females are also killed by smaller mammalian carnivores including bobcats (*Lynx rufus*) and coyotes (*Canis latrans*), likely a result of their reduced body size (Wengert et al. 2014). Alternatively, mortality risk from disease, starvation, toxicants, and vehicle strikes is higher for males (Sweitzer et al. 2016a). Therefore, males typically exhibit lower survival rates than females across their distributional range (Sweitzer et al. 2016b; Lewis et al. 2022). Survival may also vary by age (Sweitzer et al. 2016b)—fishers disperse from natal areas before they reach sexual maturity (Matthews et al. 2013), and dispersal can have unique consequences for individual fitness. Younger carnivores typically have lower survival rates than adults (Farias et al. 2005; Manlick et al. 2017), although our knowledge of ontogenetic variation in responses to individual stressors remains limited (Sweitzer et al. 2015). Given the unique biotic and abiotic factors that threaten Fisher persistence in the southern Sierra Nevada, coupled with the potential for age- and sex-specific responses, it is important to consider both intrinsic and extrinsic factors when determining resilience to environmental stressors.

Herein, we explored whether age and sex mediate the demographic responses of fishers to rapid environmental change. We combined stable isotope analysis of diet with high-resolution climate and habitat data, along with spatial information collected from Fisher monitoring, to evaluate the proximate mechanisms driving spatiotemporal variation in Fisher survival. We hypothesized that the effects of environmental change—along both biotic and abiotic axes—affect Fisher persistence in the southern Sierra Nevada, but that the relative strength and direction of stressors are mediated by sex and age. First, we predicted that individuals within territories containing more features typical of Fisher habitat (i.e., dense, multi-layered, late-successional forest) would exhibit high survival (Suffice et al. 2020). Second, we predicted that survival would decrease with increasing drought severity and forest mortality. We also predicted that survival would decrease with increasing snow depth (Suffice et al. 2020; Pauli et al. 2022), and that this effect would be stronger for males as larger body size, home range, and foot loading impose greater energetic costs (Renard et al. 2008). Finally, we predicted that increasing consumption of atypical foods, especially the consumption of fungi, would decrease survival for both males and females (Green et al. 2018; Kirby et al. 2018).

Methods

Study system

This study was conducted as part of ongoing research with the Kings River Fisher Project (KRFP) by the U.S. Forest Service, Pacific Southwest Research Station (PSW). The study area was located on the western slope of the southern Sierra Nevada, California and encompassed roughly 435 km^2 of the Sierra National Forest (Fig. 1). The climate features warm, dry summers and cool, wet winters and the region is topographically complex, marked by steep slopes and river canyons. Most fieldwork occurred within elevation ranges of 915-2385 m, within the primary range of Fisher occurrence in the area (Zielinski et al. 2004; Green et al. 2018). Here, mosaics of mixed pine, mixed fir, and montane hardwood forests are interspersed with pockets of chaparral, grasslands, and rocky outcrops throughout (Fites-Kaufman et al. 2007).

Field methods

For monitoring and sample collection, we trapped, handled, and collared fishers following established KRFP protocols (outlined in Green et al. 2018). We captured fishers in baited steel mesh traps (model 108; Tomahawk Live Trap Company, Hazelhurst, Wisconsin, USA) outfitted with wooden cubbies. Trapping occurred primarily during the fall and winter; we checked traps each morning and replenished bait when necessary. At capture, fishers were sedated with ketamine (22.5 mg/kg) mixed with Diazepam or Midazolam (0.125 mg/kg). We classified individuals by sex and age based on examination of genitalia, molar cusps, definition of sagittal crest—and for females, state of teats to provide evidence of breeding (Sweitzer et al. 2016b; Green et al. 2018). New individuals were marked with passive integrated transponder (PIT) tags (Biomark, Boise, Idaho, USA). During processing, we collected hair samples from both nape and tail. We fit fishers with VHF collars (Holohil model MI-2M, 31g; Holohil Systems Ltd, Carp, Ontario, Canada or Advanced Telemetry Systems model 1920, 38g, ATS, Inc., Insanti, Minnesota, USA) or GPS collars (Lotek model LiteTrack 40, 45g or model LiteTrack 60, 63g; Lotek Wireless Inc., Newmarket, Ontario, Canada; Thompson et al. 2012). All collars were equipped with handmade breakaway devices to allow for growth and to avoid injuries. Captures were done under a combination of authorizations and permits over the years including California Department of Fish and Wildlife (Permit SC-2730), using techniques approved by the Institutional Animal Care and Use Committee of the University of California, Davis (IACUC #18022), and following guidelines of the American Society of Mammalogists (Sikes et al. 2016).

We initiated monitoring on the week of 3 June 2007, and recorded status (alive, dead, missing, or dropped collar) of all radio collared fishers. Status was recorded from the first capture to either death, disappearance (collar drop or failure), or the end of the study (7 March 2020). We typically triangulated collared fishers 1-3 times per week by ground or air. Fishers that were missing or whose status was not recorded for > 2 consecutive weeks were right-censored in our encounter histories. If these individuals were recaptured or regular monitoring was continued, they were added back to the data set from that point. We censored 39 individuals from our dataset that were not recaptured; it is common for fishers to avoid detection for extended periods of time, and our approach follows previous studies (Sweitzer et al. 2016a; Lewis et al. 2022).

Quantifying environmental covariates

We incorporated a set of spatially and temporally explicit environmental covariates classified into three subgroups: forest structure; landscape composition; and climate (Table 1; Supplementary Data SD1-SD3). To calculate these, we first created 95% Kernel Density Estimates (KDEs) of annual home ranges for individuals with a minimum of 16 relocations (158 individuals) obtained from captures, telemetry locations, and GPS fixes collected during our population year starting 1 June and ending 31 May the following year (Börger et al. 2006; Pauli and Peery 2012). After filtering out locations with suspect accuracy (i.e., for GPS relocations a threshold of 10 HDOP; for telemetry relocations a minimum of three bearings at least 20 degrees apart from each other), we generated these using the R package ‘adehabitatHR’ (Calenge and Fortmann-Roe 2013). For individuals with < 16 relocations (18 individuals), we buffered an area equal to the median adult activity area (46.08 km^2 males; 17.95 sq km^2 females) around the centroid of recorded locations of that individual from that year. We then extracted all environmental variables from these home ranges relative to the population year.

For climate, we used PRISM data to estimate monthly values for mean precipitation, as well as monthly and annual values for maximum and minimum temperature, averaged within individual annual home ranges (PRISM Climate Group; Oregon State University). We estimated mean and maximum land surface temperature in Fisher home ranges during summer (21 June – 21 Sep) at 30 m resolution (Ermida et al. 2020). We included values of mean and average maximum snow depth at 1 km resolution from 1 Nov until 30 April of the following year, obtained from the Snow Data Assimilation System (SNODAS; National Operational Hydrologic Remote Sensing Center) and calculated mean snow depth averaged over yearly (Nov 1 – Apr 30) and monthly timescales. Finally, we quantified annual and monthly drought conditions using the Palmer Drought Severity Index (PDSI; Palmer 1965; Mukherjee et al. 2018). For habitat, we included hardwood basal area, canopy cover, understory cover, and covariates of forest age class (open, young, medium, and mature) estimated within yearly Fisher home ranges from gradient-nearest-neighbor (GNN) maps (LEMMA Lab; Oregon State University, Corvallis, OR, USA). We also quantified yearly drought-mediated tree mortality from 2015-2018 from the Southern Sierra Nevada Fractional Land Cover Dataset (McGregor et al. 2021). For landscape composition, we included tree diameter diversity index and calculated forest heterogeneity (Shannon's diversity index) and patch adjacency (Interspersion and Juxtaposition Index) of our forest age classes, as well as dispersion (standard deviation) and disorderliness (entropy) of image texture pixel values from Enhanced Vegetation Index (EVI) composites. For additional information on data sources and covariates, see Supplementary Data SD4.

Diet analysis

To quantify Fisher diet, we analyzed samples for $\delta^{13}C$ and $\delta^{15}N$ ratios via stable isotope analysis following established protocols (outlined in Pauli et al. 2009 and Smith et al. 2022). We used Bayesian mixing models to quantify population- and individual-scale proportional diet of fishers in program MixSIAR (Stock et al. 2018). To represent source items in our mixing models, we used samples collected and analyzed during a previous study in the southern Sierra Nevada (Smith et al. 2022), then divided functionally similar dietary source items into four *a priori* categories (plants, fungi, insects, and vertebrates) and verified isotopic independence of these groups using a K nearest-neighbor analysis (Rosing et al. 1998). We accounted for digestibility and elemental concentration for each source item (Smith et al. 2022), and addressed trophic discrimination by correcting for the digestibility of carbon and nitrogen by forage items ($\delta 13C \pm SD = 2.6‰ \pm 0.09$; $\delta 15N \pm SD = 3.4‰ \pm 1.2$; Supplementary Data SD5; Smith et al. 2022).

To evaluate individual diet, we ran a set of MixSIAR models with our four dietary source categories and an individual-year variable as a fixed factor. For each model, we used informative priors derived from a previous diet study that spatially overlapped with our study area (Smith et al. 2022; fungi 0.47, vertebrates 0.13, plants 0.16, insects 0.24) and ran three Markov chains (length = 1,000,000; burn-in = 500,000; thinning rate = 500). We also ran a second model set with uninformative priors (uniform across all source groups) to compare the influence of our priors on our dietary estimates. We confirmed model convergence by checking that Gelman-Rubin diagnostic values were < 1.05 and < 5% of Geweke diagnostics were outside +/- 1.96 for each chain. We also calculated measures of individual specialization (Newsome et al. 2012)—the specialization index (ε) represents how much a consumer concentrates on a specific diet category, relative to the number of other diet items. Hair samples capture the period of isotopic incorporation during molting and hair growth (June–October; Pauli et al. 2009). Therefore, our estimates best represent the assimilated diet of fishers in our study area from summer through fall.

Survival analysis

We estimated survival rates of fishers by constructing known-fate models in Program MARK (White and Burnham 1999), with a staggered entry design to allow introduction of individuals throughout the study. We used encounter histories from 3 June 2007 until 7 March 2020 and defined our population year from 1 June to 31 May the following year. We set 1 June as the start date to best align with the beginning of isotopic incorporation captured by Fisher hair growth (Pauli et al. 2009).

We analyzed two sets of models to explore interactions between demographic and environmental covariates. First, we constructed candidate models for all individuals including only demographic and seasonal effects. Here, we introduced covariates for sex, season (summer [1 May-31 October]; winter [1 November-30 April]), and age class with either two (young [<24 months]; adult [≥24 months]) or three (juvenile [<12 months]; subadult [12-24 months]); adult [≥24 months]) groups. We used the structure from the top model(s) in our first set (Table 2) to inform construction of our second model set. We derived estimates of monthly survival from our top-performing models and projected rates of annual survival relative to age and sex and 6-month survival relative to season.

We employed a secondary candidate set strategy (Morin et al. 2020) and constructed separate univariate model sets for males and females to compare covariates grouped within our environmental and diet subgroups (Table 1). We ranked models using Akaike Information Criterion adjusted for small sample sizes (AIC_C) and carried forward any covariate that outperformed the null and was within 2 ΔAIC_C of the top model (White and Burnham 1999; Morin et al. 2020). We considered other viable covariates (i.e., 95% CIs of coefficient estimates did not cross zero) if they were within 5 ΔAIC_C of the top model and were not correlated with other competitive variables. Given differences in morphology, life history events, and survival of fishers as a function of age, sex, and season (Wengert et al. 2014; Sweitzer et al. 2016b; Green et al. 2018), we also tested each univariate covariate with additive effects of age class and season. If the age- or season-additive form of a covariate outperformed the null model, the univariate form, and the univariate age or season model, it was also carried forward into the next stage of model construction. We also evaluated season interactions for several climate covariates and carried these forward if they were competitive.

With the top-ranking covariates from the univariate subgroups, we then constructed a set of *a priori* multivariate models for both males and females. We tested independent variables for collinearity using Spearman's rank coefficient and did not include highly correlated covariates ($r_s \geq |0.7|$) in the same model (Dormann et al. 2012). To evaluate temporal trends and effects, we modeled survival as either constant (.) or varying by categorical year (t), while the relative effect of our time-varying covariates was kept constant. Coefficients from our top-ranking and competitive models in both sets were examined and statistical significance was determined from 95% confidence intervals.

Results

Between 3 June 2007 and 7 March 2020, we collared and tracked 170 fishers (91 females; 79 males). We compiled a total of 3,616 monthly monitoring records (2262 females; 1354 males). The number of monitoring months per individual ranged from 1 to 114 (females 1-114; males 2-67). We confirmed 84 mortalities over the course of our study (47 females; 37 males). Individual consumption of fungi, insects, and vertebrates was relatively equal across the population, with low overall consumption of plants (Supplementary Data SD6) and with moderate variability between and among years (Supplementary Data SD7).

Demographic and seasonal drivers of Fisher survival

Fisher survival was associated with sex, age class, and season. The most supported model included an interaction between sex and age class, as well as an interaction between sex and season (Table 2). As we found more support for the age class covariate with two groups, we did not carry the age class covariate with three groups forward in the second stage of model construction. Yearly female survival ($\hat{s} = 0.781$; 95% *CI* [0.720, 0.831]) was greater than male survival ($\hat{s} = 0.717$; 95% *CI* [0.632, 0.786]), and this difference was greater when comparing survival of young females ($\hat{s} = 0.832$; 95% *CI* [0.7173, 0.903]) and males ($\hat{s} = 0.643$; 95% *CI* [0.521, 0.741]) to adult females ($\hat{s} = 0.759$; 95% *CI* [0.683, 0.820]) and males ($\hat{s} = 0.803$; 95% *CI* [0.680, 0.883]; Fig. 2A). Seasonal trends also differed by sex (Table 2). For females, seasonal (6-month) survival during the summer ($\hat{s} = 0.842$; 95% *CI* [0.784, 0.886]) was lower than winter survival ($\hat{s} = 0.923$; 95% *CI* [0.878, 0.952]), but for males, summer survival ($\hat{s} = 0.897$; 95% *CI* [0.822, 0.942]) was greater than winter survival ($\hat{s} = 0.807$; 95% *CI* [0.731, 0.865]; Fig. 2B).

Extrinsic drivers of Fisher survival

The top model for female survival included the effects of maximum monthly temperature, mean winter snow depth, and Shannon's Diversity Index (SHDI) of forest cover types (Table 3).

Survival increased with greater forest heterogeneity (β = 2.08; 95% *CI* [0.06, 4.11,]; Fig. 3A). For climate, survival decreased with increasing mean winter snow depth (β = -0.004; 95% *CI* [-0.005, -0.002]; Fig. 3B), as well as increasing minimum monthly temperature (β = -0.06; 95% *CI* [-0.11, -0.02]; Fig. 3C) and maximum monthly temperature (β = -0.05; 95% *CI* [-0.09, -0.02]; Fig. 3D). While understory cover (β = -0.03; 95% *CI* [-0.17, 0.10]) and canopy cover (β = -0.02; 95% *CI* [-0.07, 0.03]) were represented among competitive models, they did not affect survival.

The top model for male survival included the effect of season, age class, minimum monthly temperature, and the consumption of fungi (Table 4). Interestingly, survival decreased with increasing individual consumption of fungi (β = -.15; 95% *CI* [-0.29, -0.01]; Fig. 4A). For climate, survival decreased with increasing minimum monthly temperature (β = -0.10; 95% *CI* [-0.19, -0.02]; Fig. 4C) but not maximum monthly temperature (β = -0.05; 95% *CI* [-0.14, 0.04]). However, when paired with a season interaction, survival decreased with increasing maximum monthly temperature in winter (β = -0.13; 95% *CI* [-0.25, -0.004]; Fig. 4D) but not in summer (β = -0.001; 95% *CI* [-0.12, 0.12]; Fig. 4D). Other variables from competitive models, including mean forest mortality (β = 0.04; 95% *CI* [-0.002, 0.09]), mean basal area of hardwoods (β = -0.17; 95% *CI* [-0.35, -0.001]), young forest (β = -0.91; 95% *CI* [-5.72, 3.91]), and PDSI (β = 0.047; 95% *CI* [-0.09, 0.18]), did not affect survival.

Discussion

Our work reveals that environmental factors associated with climate, habitat, and biotic interactions were important drivers of survival, but the direction and magnitude of individual responses were mediated by age and sex. Survival of male fishers was lower among young individuals and sensitive to changes in biotic and abiotic factors related to temperature and diet. Female fishers were vulnerable to changes in temperature, snow depth, and landscape composition, yet more resilient to diet and age effects. Our study adds to a growing body of literature emphasizing the importance of considering age and sex when assessing the impacts of environmental change (Yang and Rudolf 2010; Komoroske et al. 2014; Hangartner et al. 2022).

Temperature was a key determinant of Fisher survival, and the only covariate to affect both sexes. Survival of females decreased with both increasing minimum and maximum monthly temperature, while male survival decreased with increasing minimum monthly temperature and maximum monthly winter temperature. During hot, dry periods, increasing temperatures compound the effects of heat stress and water loss (Alonso et al. 2016). Conversely, during cold winter months increasing temperatures should, in theory, benefit fishers by expediting snow melt (Grundstein and Mote 2010), and reducing energetic costs associated with locomotion and thermoregulation (Martin et al. 2020). However, increasing winter temperatures can also constrain availability of key prey. For example, fishers may change their diet in response to resource availability (Zielinski et al. 1999; Kirby et al. 2018), and mammal consumption typically peaks in winter when many other food groups are unavailable (Zielinski et al. 1999). For snow-adapted small mammals, winter conditions drive population cycles (Scott et al. 2022) and warmer ambient temperatures can reduce the insulating properties of the subnivium (Thompson et al. 2021b), with cascading effects for abundance and diversity (Scott et al. 2022). In turn, declines in seasonal prey resources resulting from warming winter temperatures can have consequences for Fisher persistence.

While decreasing annual snowpack may negatively impact Fisher survival via prey abundance, so too can events of extreme precipitation, which are likely to increase in frequency and severity with climate change (Hatchett et al. 2017; Harris et al. 2018). Snow can exert variable effects on organisms, mediated by physical characteristics such as depth, density, and surface hardness (Pozzanghera et al. 2016; Pauli et al. 2022). Indeed, while modest snowfall at regular intervals typically creates dense compacted snow, periods of heavy snowfall can create areas of deep, fluffy snow that limit occupancy and dispersal of many carnivore species (Pozzanghera et al. 2016). Among fishers, high foot loading is theorized to compound the energetic cost of movement through deep snow (Pauli et al. 2022), and male fishers exhibit a foot load up to 43% greater than females (Renard et al. 2008). However, while increasing snow depth had a negative effect on female survival, male survival was unaffected—which ran counter to our predictions. This suggests that morphology alone does not explain the relationship between snow and survival, and life history may also mediate differential demographic responses. It is possible that increased energy expenditure caused by higher foot loading could be offset by energy intake if males are able to forage on a food resource that females cannot, or that differences in body condition allow males to better survive these extreme weather events (Bright Ross et al. 2021). Parturition among female fishers typically occurs in late winter or early spring (Green et al. 2018), coinciding with periods of high snow accumulation. The energetic demands of reproduction, lactation, and foraging for dependent offspring may expose females to increased risk (Powell and Leonard 1983; Green et al. 2018), and this has been corroborated by findings of reduced female survival from spring through summer (Sweitzer et al. 2016b). Therefore, even if movement through snow incurs a greater energetic cost for males, the ultimate impact may be stronger for females by compounding the effects of existing stressors. A baseline level of snow can benefit Fisher survival by increasing seasonal prey abundance (Scott et al. 2022) or reducing encounters with larger intraguild predators (Jensen and Humphries 2019), but during periods of extreme precipitation or reproductive stress, the net effect appears to be negative. Further, increasing winter temperatures may amplify the demographic consequences of deep snow by mediating the physical characteristics of snowpack. Specifically, by preventing the formation of an ice crust on snow surface, locomotion may be increasingly costly for fishers forced to move through deep, soft snow (Suffice et al. 2020; Pauli et al. 2022).We found that female survival increased with forest heterogeneity, highlighting the importance of both landscape composition and configuration. Heterogeneous landscapes increase niche availability (MacArthur 1972), which can promote prey diversity (Walsh and Tucker 2020) or facilitate carnivore coexistence (Manlick et al. 2020). In the southern Sierra Nevada, Sweitzer et al. (2016a) found that intraguild predation accounted for 67% of Fisher mortalities, and anthropogenic change in forest structure driving increased interspecific contact may be responsible for high predation rates (Wengert et al. 2014). Intraguild predation generally decreases in habitats with greater structural complexity (Janssen et al. 2007), while female fishers are vulnerable to a more diverse predator guild (Wengert et al. 2014)—which may help explain the relationship between survival and forest heterogeneity unique to females. Heterogeneity also increases the availability of microclimatic refugia (Chen et al. 1999), which can dampen the effects of inclement or extreme weather (Latimer and Zuckerberg 2021). As both female and male fishers use a variety of habitat microsites as refugia throughout the year (e.g., tree cavities, hollows in logs; Green et al. 2019), habitat heterogeneity may help to buffer from the effects of both biotic and abiotic stressors.

Male fishers that consumed more fungi exhibited lower survival. In contrast, female survival was unaffected by diet. Mesopredators exhibit considerable dietary plasticity, both locally and across their distributional ranges (Manlick and Pauli 2020; Walsh and Tucker 2020), which is cited as a driver of resilience and contemporary range expansions (Prugh et al. 2009). However, reliance on atypical resources can incur fitness consequences, and among predators increasing consumption of low-quality forage has been linked to changes in space use (Hobart et al. 2019) and reproduction (Chevallier et al. 2020), although linking individual diet to survival is difficult for mesopredators given their ability to occupy multiple trophic levels (Prugh et al. 2009; Colborn et al. 2020). Diet limitations among fishers in the southern Sierra Nevada may explain small litter sizes (Green et al. 2018), and elsewhere reductions in preferred prey have been identified as a potential driver of poor body condition and population decline (Kirby et al. 2018). A modest level of fungi consumption may benefit Fisher persistence by providing nutrients and water during food shortages or periods of protracted drought (Claridge and May 1994; Smith et al. 2022). However, fishers have a relatively simple gut morphology (McGrosky et al. 2016), and in the absence of specialized digestive pathways or microbial communities, their digestive efficiency of fungi may be limited by enzymatic reactions (Claridge and May 1994). We found no differences in proportional diet between males and females, which corroborates prior findings (Kirby et al. 2018; Smith et al. 2022). Still, morphology, territory size, and life history strategies such as dispersal (Matthews et al. 2013), may drive increased energy expenditure and caloric requirements among male fishers—which was reported for closely related male Pacific martens (*Martes caurina*; Martin et al. 2020). Therefore, the risk of gut satiation, energetic deficiency, and associated demographic consequences may be greater for males consuming more fungi. Notably, our estimates of diet best reflect trends from summer and fall, which does not align with parturition or weaning among females (Green et al. 2018) or mate searching among males (Matthews et al. 2013). Given the potential for temporal changes in energy expenditure and food availability (Zielinski et al. 1999; Scott et al. 2022), we also recommend that future work quantify seasonal changes in Fisher diet and incorporates these estimates into demographic studies.

Our findings suggest that both biotic and abiotic factors are responsible for driving changes in Fisher survival, but individual responses are mediated by age and sex. We found that rapidly changing climate may impact Fisher survival directly, by mediating temperature and snow depth, as well as indirectly, by shaping habitat conditions and resource availability. This work also highlights potential co-benefits in managing for Fisher persistence and forest resilience, objectives that have been viewed as complicated and at times, even diametrically opposed (Collins et al. 2010). Traditionally, wildfire has been a natural factor of the historical disturbance regime, maintaining habitat heterogeneity and creating complex, critical habitat elements (Steel et al. 2015). However, recent fires have both burned outside the natural range of variability and homogenized large sections of forest, removing many of the features that fishers depend on (Crockett and Westerling 2018; Green et al. 2019). While we did not explicitly consider fire effects in this study, recent work on Fisher use of postfire landscapes found avoidance of areas dominated by high-severity fire, with greater use of low-severity or unburned islands (Thompson et al. 2021a). Therefore, future management designed around low-severity fire regimes, forest heterogeneity, and habitat connectivity may represent a solution that limits the risk of megafires while promoting Fisher survival. As the biotic and abiotic consequences of rapid environmental change threaten extinctions and extirpations globally, disentangling the intrinsic and extrinsic factors that mediate species responses will be critical in guiding effective conservation strategies.

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Table 1: Covariates included in known fate models to quantify changes in survival for fishers (*Pekania pennanti*) in the southern Sierra Nevada, California, USA.

Category	Variable	Ecological description
Forest structure	Young forest	Proportion of home range with forest Quadratic Mean Diameter (QMD) < 30 cm and canopy cover > 40%
	Medium forest	Proportion of home range with forest with QMD 30-61 cm and canopy cover > 40%
	Mature forest	Proportion of home range with forest with QMD > 61 cm and canopy cover > 40%
	Open area	Proportion of home range with canopy cover < 40%
	Hardwood basal area	Mean basal area of hardwoods (m^2/ha)
	Understory cover	Percent of understory cover (between 2-4 m)
	Canopy cover	Percent of canopy cover
	Mean tree mortality	Percent of tree mortality within home range, averaged across 30 m pixels
Landscape composition	Interspersion and juxtaposition index	Evenness of patch adjacencies - represents intermixing of the four forest types (young, medium, mature, open)
	Forest heterogeneity	Shannon's Diversity Index calculated from the four forest types
	Entropy	Disorderliness in spatial distribution of image texture pixels from Enhanced Vegetation Index (EVI) data
	Standard deviation	Dispersion of image texture pixels from EVI data
	Diameter diversity index	Measure of forest structural diversity based on densities of different tree size classes. Increases with stand age
Climate - annual	Mean snow depth	Average snow depth in the winter (Nov 1 – Apr 30)
	Maximum snow depth	Maximum snow depth in the winter, averaged across all pixels at 1 km resolution
	Drought	Average yearly Palmer Drought Severity Index (PDSI) value at 4 km resolution
	Land surface temperature	Mean and maximum summer (Jun 21- Sep 21) land surface temp (LST) in Kelvin (K) at 30 m resolution
Climate - monthly	Minimum temperature	Average monthly minimum temperature, averaged across all pixels at 30 m resolution

	Maximum temperature	Average monthly maximum temperature, averaged across all pixels at 30 m resolution
	Snow depth	Average monthly snow depth, averaged across all pixels at 1 km resolution
	Drought	Average monthly PDSI value at 4 km resolution
	Precipitation	Average monthly precipitation, averaged across all pixels at 30 m resolution
Demography	Sex	Sex of individual. Two groups: male and female
	Age - A	Age class of individual. Three groups: juvenile (< 12 months), subadult (12-24 months), adult (≥ 24 months)
	Age - B	Age class of individual. Two groups: young (< 24 months), adult (≥ 24 months)
Diet	Fungi	Estimated dietary contribution from fungi (%)
	Specialization index	The degree to which an individual concentrates on a functional prey group

Table 2: Top models (≤2 ΔAIC_C) for the first model stage of Fisher (*Pekania pennanti*) survival between 2007-2019 in the southern Sierra Nevada, California, USA. 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). Predictor variables shown include sex, age class (young [<24 months]; adult [≥24 months]), and season (summer [1 May-31 October]; winter [1 November-30 April]).

Covariate(s)	AIC_C	ΔAIC_C	*w*	k
Sex*Season + Sex*Age	795.93	0	0.30	6
Sex*Season	796.16	0.22	0.27	4
Sex*Season + Age	797.73	1.79	0.12	5
Sex*Season + Age*Season	797.75	1.82	0.12	6
Null	802.30	6.36	0.01	1

Table 3: Top models (≤2 ΔAIC_C) for female Fisher (*Pekania pennanti*) survival between 2007-2019 in the southern Sierra Nevada, California, USA. 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). Predictor variables shown include max monthly temp (maximum monthly temperature), snow depth (mean winter snow depth), SHDI (forest heterogeneity, estimated with Shannon's Diversity Index of forest cover types), understory (mean understory cover), min monthly temp (minimum monthly temperature), and canopy (mean canopy cover).

Covariate(s)	AIC_C	ΔAIC_C	*w*	k
Max monthly temp + Snow depth + SHDI	448.21	0	0.20	4
Max monthly temp + Snow depth	449.39	1.17	0.11	3
Max monthly temp + Snow depth + SHDI + Understory	449.73	1.51	0.09	5
Min monthly temp + Snow depth + SHDI	449.98	1.77	0.08	4
Season + Max monthly temp + Snow depth + SHDI	450.22	2.01	0.07	5
Max monthly temp + Snow depth + SHDI + Canopy cover	450.221	2.011	0.07	5
Null	461.11	12.90	0	1

Table 4: Top models (≤2 ΔAIC_C) for male Fisher (*Pekania pennanti*) survival between 2007-2019 in the southern Sierra Nevada, California, USA. 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). Predictor variables shown include season, min monthly temp (minimum monthly temperature), age (age class), fungi (proportional consumption of fungi), tree mortality (proportion of tree mortality), PDSI (drought conditions), hardwoods (mean hardwood basal area), and young (proportion of young forest).

Covariate(s)	AIC_C	ΔAIC_C	*w*	k
Season + Age + Min monthly temp + Fungi	333.208	0	0.14	5
Season + Age + Min monthly temp + Tree mortality	333.210	0.002	0.13	5
Season + Age + Min monthly temp + Fungi + Hardwoods	334.46	1.25	0.07	6
Season + Age + Min monthly temp + Fungi + PDSI	334.74	1.53	0.06	6
Season + Age + Min monthly temp + Fungi + Tree mortality + Hardwoods	334.79	1.58	0.06	7
Season + Age + Fungi + Hardwoods	334.82	1.61	0.06	5
Season + Fungi + Hardwoods	334.87	1.67	0.06	4
Season + Age + Min monthly temp + Fungi + Tree mortality + Young	335.05	1.84	0.05	7
Age + Fungi + Hardwoods	335.24	2.03	0.05	4
Null	341.38	8.17	0	1

Fig. 1: Kings River Fisher Project study area visualized with forest class variables in the southern Sierra Nevada, California, USA, for monitoring Fisher (*Pekania pennanti*) diet and survival between 2007-2019. The inset map demonstrates an example of a typical 95% kernel home range for one female Fisher with a red outline.

Fig. 2: Estimated survival rates (±95% CI) for male and female fishers (*Pekania pennanti*) between 2007-2019 in the southern Sierra Nevada, California, USA. Survival is shown relative to (A) age class (young [<24 months], adult [≥24 months]); and (B) season (summer [1 May-31 October], winter [1 November-30 April]). Survival rates were transformed from monthly model-derived estimates into (A) yearly and (B) seasonal 6-month rates.

Fig. 3: Fitted values (±95% CI) representing monthly survival of female fishers (*Pekania pennanti*) between 2007-2019 in the southern Sierra Nevada, California, USA. Survival is shown relative to (A) forest heterogeneity, estimated with Shannon's Diversity Index (SHDI) of forest cover types, (B) mean winter snow depth, (C) maximum, and (D) minimum monthly temperature (°C). Values were derived from the top-ranked model for each covariate, with additional variables held constant at mean observed values.

Fig. 4: Fitted values (±95% CI) representing monthly survival of male fishers (*Pekania pennanti*) between 2007-2019 in the southern Sierra Nevada, California, USA. Survival is shown relative to (A) dietary contribution of fungi (%), (B) minimum monthly temperature (°C), and (C) maximum monthly temperature (°C) with a season interaction during summer and winter. Values were derived from the top-ranked model for each covariate, with additional variables held constant at mean observed values.

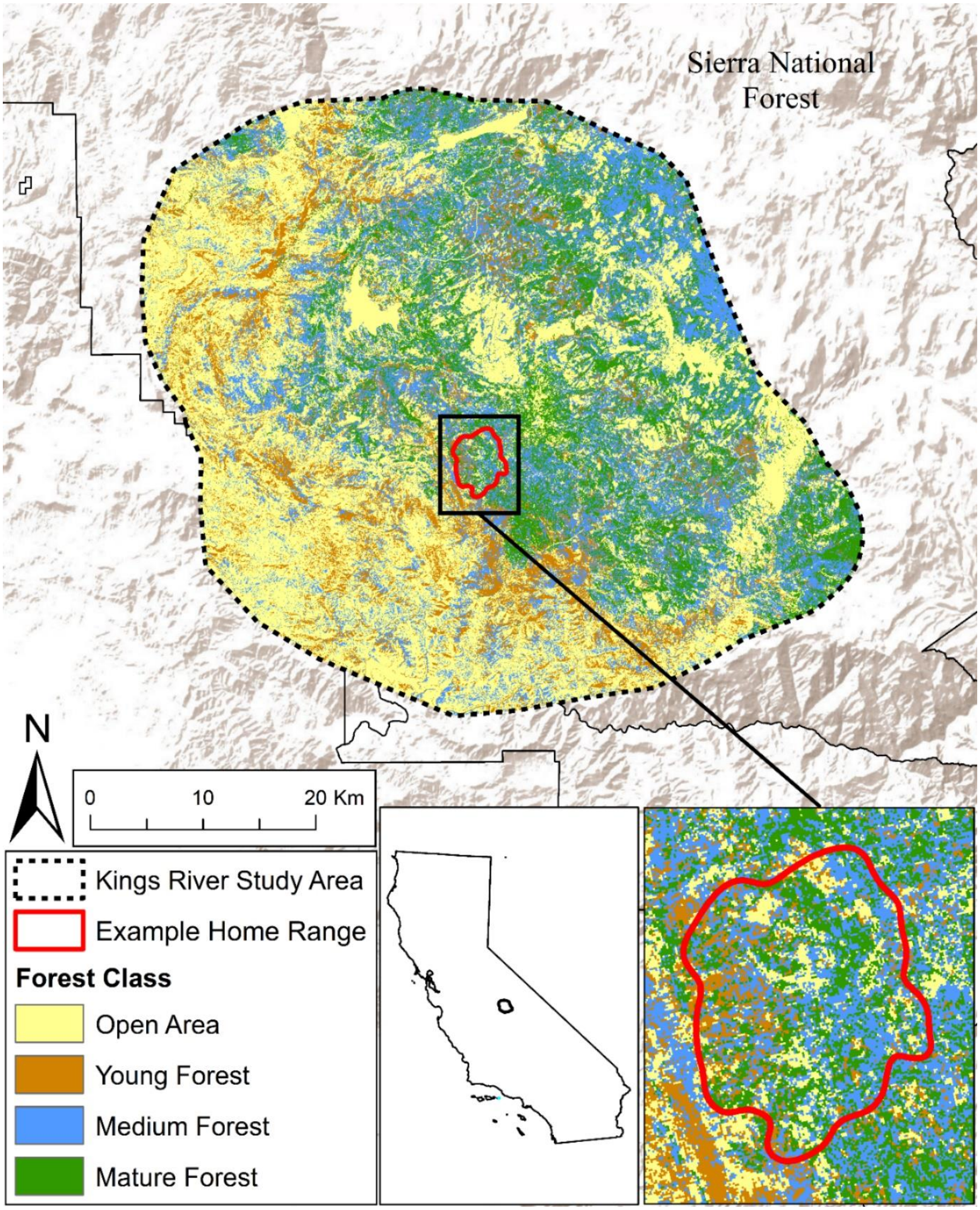

Sierra National Forest
N
0
10
20 Km
Kings River Study Area
Example Home Range
Forest Class
Open Area
Young Forest
Medium Forest
Mature Forest

Fig. 1

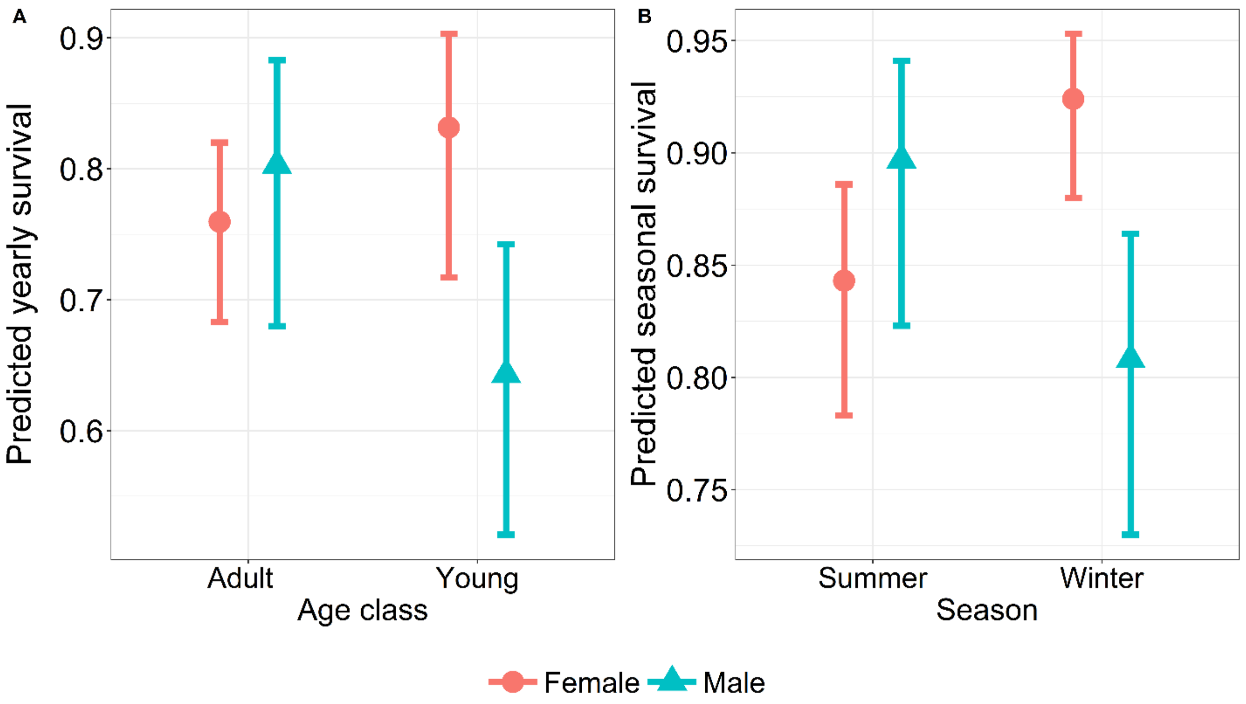

A
Predicted yearly survival
0.9
0.8
0.7
0.6
Adult
Young
Age class
B
Predicted seasonal survival
0.95
0.90
0.85
0.80
0.75
Summer
Winter
Season
● Female
▲ Male

Fig. 2.

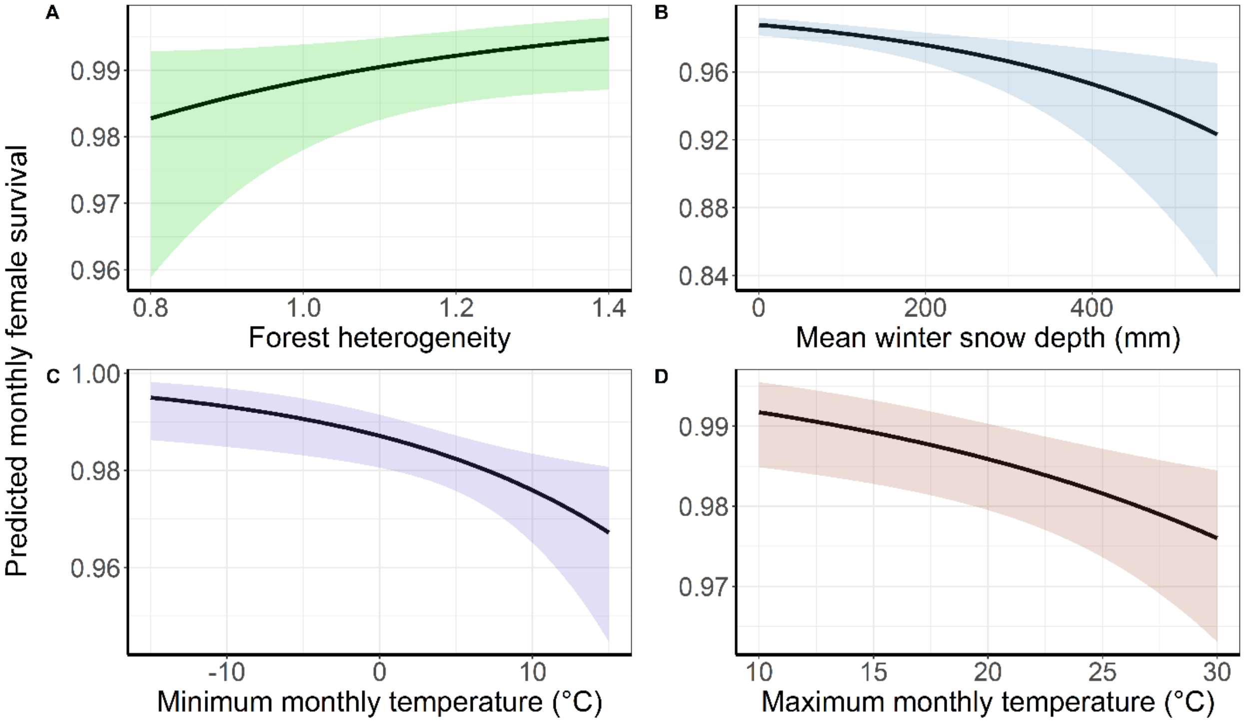

A
0.99
0.98
0.97
0.96
0.8
1.0
1.2
1.4
Forest heterogeneity
B
0.96
0.92
0.88
0.84
0
200
400
Mean winter snow depth (mm)
Predicted monthly female survival
C
1.00
0.98
0.96
-10
0
10
Minimum monthly temperature (°C)
D
0.99
0.98
0.97
10
15
20
25
30
Maximum monthly temperature (°C)

Fig. 3.

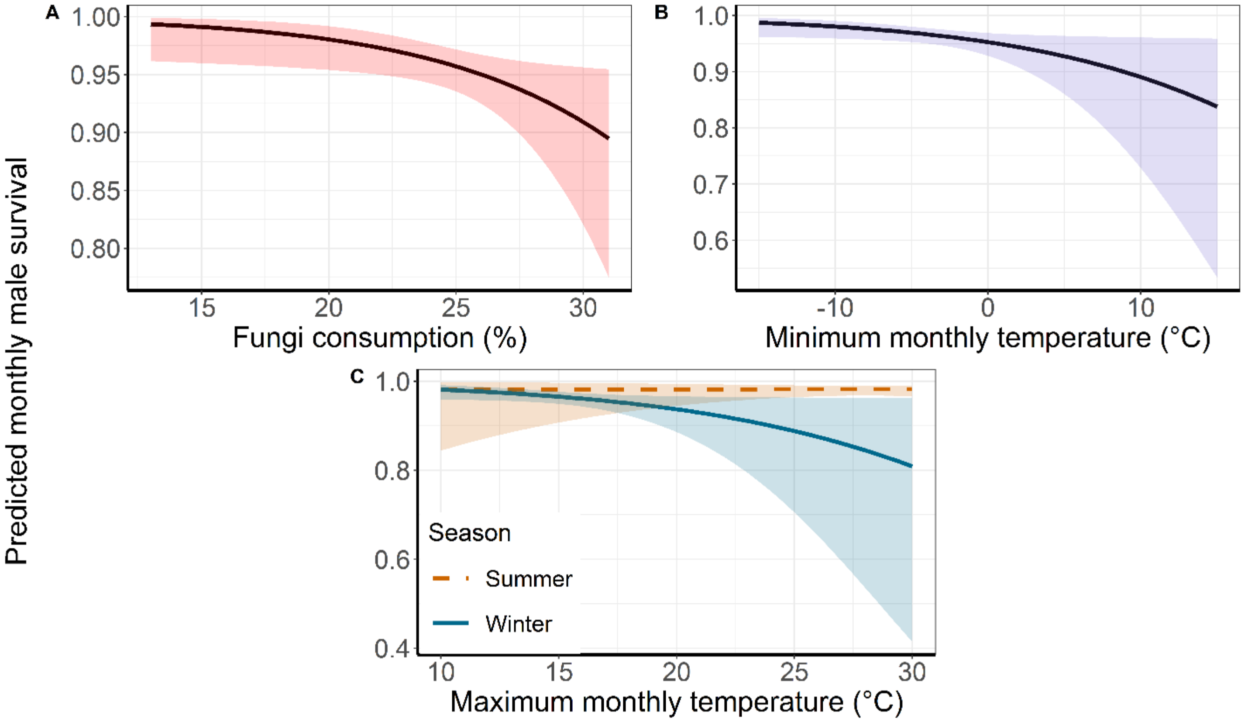
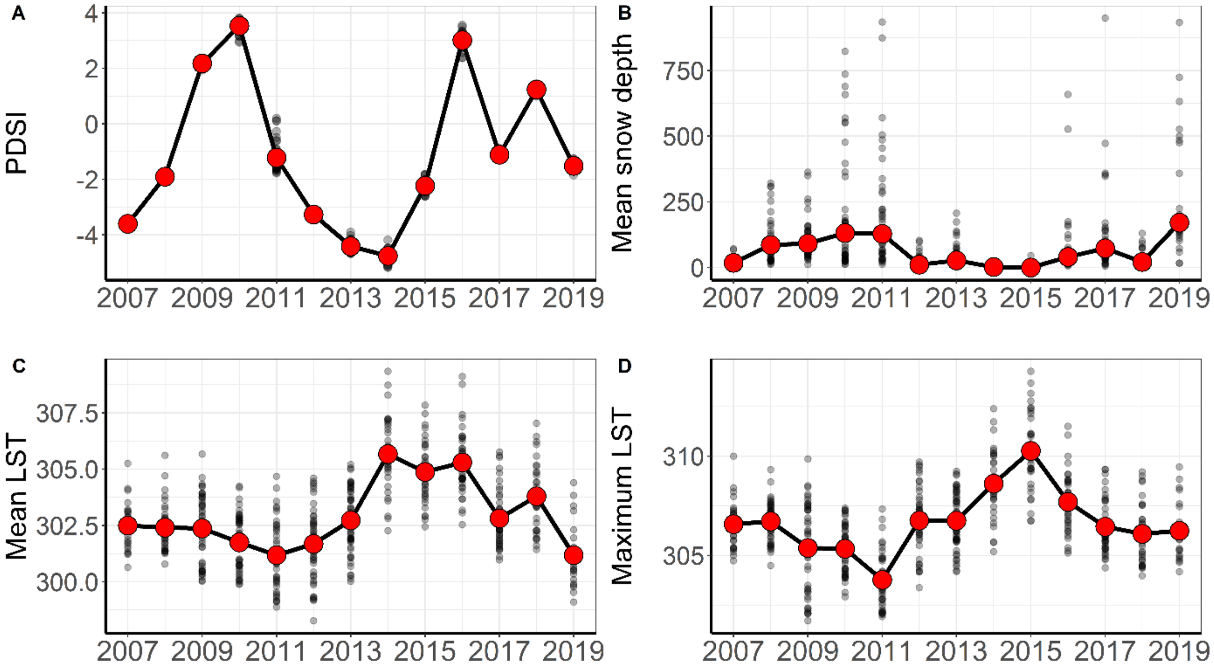
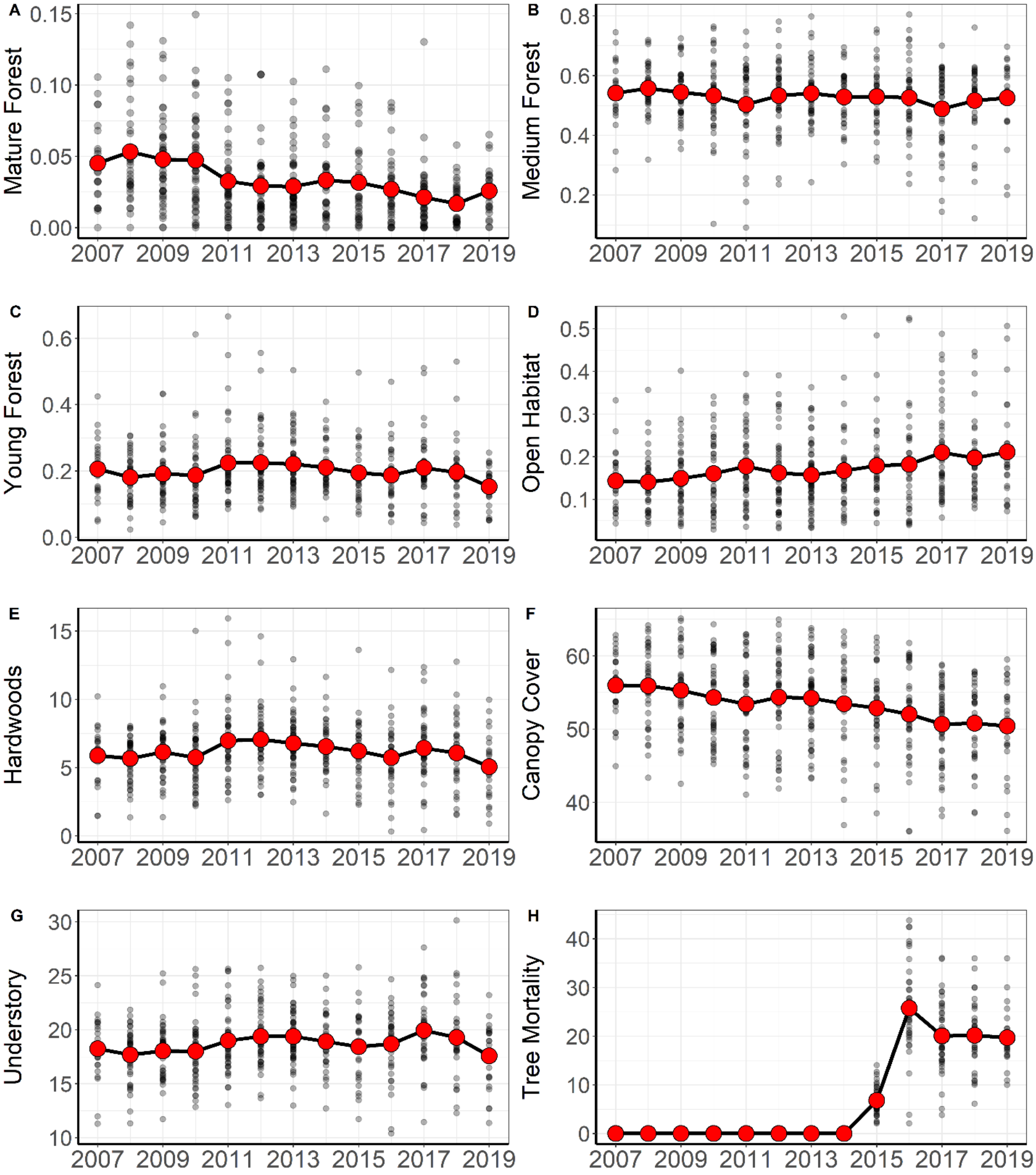

A
B
C
Predicted monthly male survival
1.00
0.95
0.90
0.85
0.80
15
20
25
30
Fungi consumption (%)
1.0
0.9
0.8
0.7
0.6
-10
0
10
Minimum monthly temperature (°C)
1.0
0.8
0.6
0.4
10
15
20
25
30
Maximum monthly temperature (°C)
Season
Summer
Winter

Fig. 4.

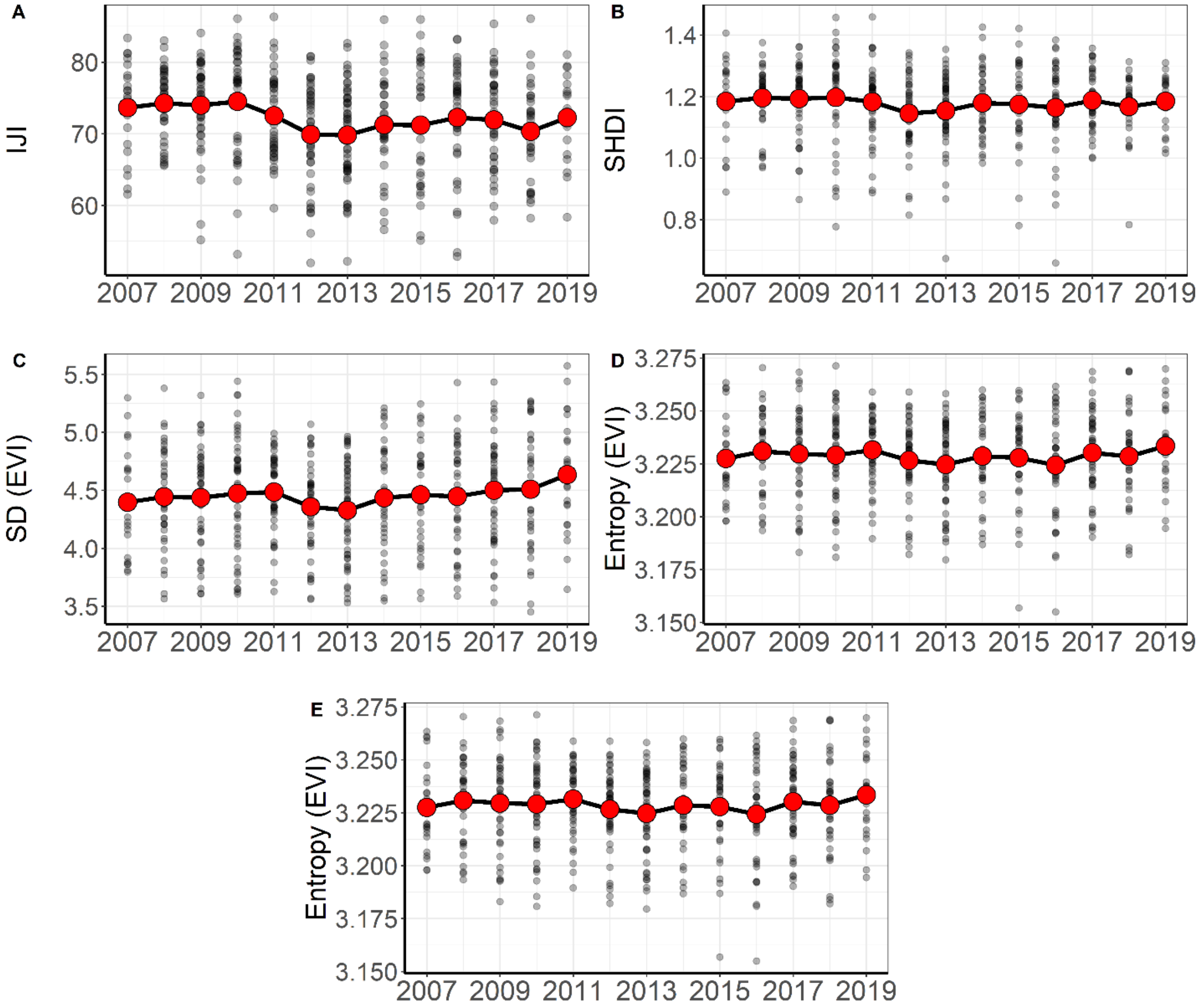
Supporting Information



Supplementary Data SD1.—Spatial and temporal variation in climate variables. Figures represent climate variables averaged within an annual Fisher (*Pekania pennanti*) home range, including (A) Palmer Drought Severity Index (PDSI), (B) mean winter snow depth (mm), (C) mean summer land surface temperature (LST; °K), and (D) maximum summer land surface temperature (LST; °K). Gray circles represent values calculated within individual territories, whereas red circles and black lines represent yearly means and relationships.



Supplementary Data SD2.—Spatial and temporal variation in forest structure variables. Figures represent proportion of an annual Fisher (*Pekania pennanti*) home range containing (A) mature forest, (B) medium forest, (C) young forest, and (D) open habitat, as well as mean (E) hardwood basal area (m^2/ha), (F) canopy cover, (G) understory cover, and (H) percent of tree mortality. Gray circles represent values calculated within individual territories, whereas red circles and black lines represent yearly means and relationships.



Supplementary Data SD3.—Spatial and temporal variation in landscape composition variables. Figures represent composition of an annual Fisher (*Pekania pennanti*) home range quantified by (A) Interspersion and Juxtaposition Index (IJI), (B) forest heterogeneity calculated from Shannon's Diversity Index (SHDI) of forest cover types (mature, medium, young, and open), (C) standard deviation (SD) and (D) entropy of image texture pixels from EVI data, and (E) diameter diversity index (DDI). Gray circles represent values calculated within individual territories, whereas red circles and black lines represent yearly means and relationships.

Supplementary Data SD4. — Additional information on the specific environmental covariates used in known fate models for fishers (*Pekania pennanti*) in the southern Sierra Nevada, California, USA, including data sources, estimation methods, and spatial resolution.

Climate variables — We used PRISM data to estimate monthly values for mean precipitation, as well as monthly, seasonal, and annual values for maximum and minimum temperature, averaged within individual annual home ranges (PRISM Climate Group; Oregon State University). We also estimated mean and average maximum land surface temperature in Fisher home ranges during summer (21 June – 21 Sep) at 30 m resolution (Ermida et al. 2020). We included values of mean and average maximum snow depth at 1 km resolution from 1 Nov until 30 April of the following year, obtained from the Snow Data Assimilation System (SNODAS; National Operational Hydrologic Remote Sensing Center) and calculated mean snow depth averaged over seasonal and monthly timescales. We estimated annual and monthly drought conditions using the Palmer Drought Severity Index (PDSI; Palmer, 1965; Mukherjee et al., 2018).

Habitat variables — We calculated most forest structure metrics using gradient-nearest-neighbor (GNN) maps, which were created by the Landscape Ecology, Modeling, Mapping, and Analysis team (LEMMA Lab; Oregon State University, Corvallis, OR, USA). These employ Landsat imagery at 30 m resolution, and included four forest age class classifications, mean diameter diversity index (DDI), mean basal area of hardwoods (BAH), and mean canopy cover (Ohmann and Gregory 2002). Forest age classifications (open, young, medium, and mature) were defined by canopy cover and quadratic mean diameter (QMD) of dominant and codominant trees. Diameter diversity index represents a unitless measure of forest structure diversity, which increases with stand age and densities of different tree size classes. GNN data were available from 2007-2017; for 2018 and 2019, we used data from 2017, given forest structure variables did not dramatically change among those years. We quantified tree mortality using data from the Southern Sierra Nevada Fractional Land Cover Dataset (McGregor et al. 2021). This dataset models fractional land cover by training random forest classification models on RapidEye satellite spectral imagery (Planet Labs Inc.), then classifying land cover into categorical groups. Therefore, our values for tree mortality represent the percentage of a 30m pixel covered by dead, standing trees, averaged across a territory. Mortality data were available from 2015-2018; prior to 2015, forest mortality in our study area was low in comparison so we set values for 2007-2014 to 0 (Fettig et al. 2019). Conversely, forest mortality reached a relative plateau after 2018, so we used 2018 values of tree mortality for our 2019 covariates (Fettig et al. 2019). Finally, we used remotely sensed habitat data from California Forest Observatory (CFO; Salo Sciences) to estimate mean understory cover from 2016 and 2018 at 10 m resolution.

Landscape Composition Variables — We used FRAGSTATS to calculate indices of Shannon's diversity (H) and Interspersion and Juxtaposition (IJI) of the four forest age classes within each home range (McGarigal et al. 2012). We estimated additional variables of landscape composition by evaluating metrics of image texture from Enhanced Vegetation Index (EVI) composites for the continental US (Farwell et al. 2021). We included both first order (standard deviation) and second order (entropy) measures of texture; standard deviation represents the dispersion of image texture pixel values, while entropy represents the disorderliness in the spatial distribution of pixel values (Farwell et al. 2021).

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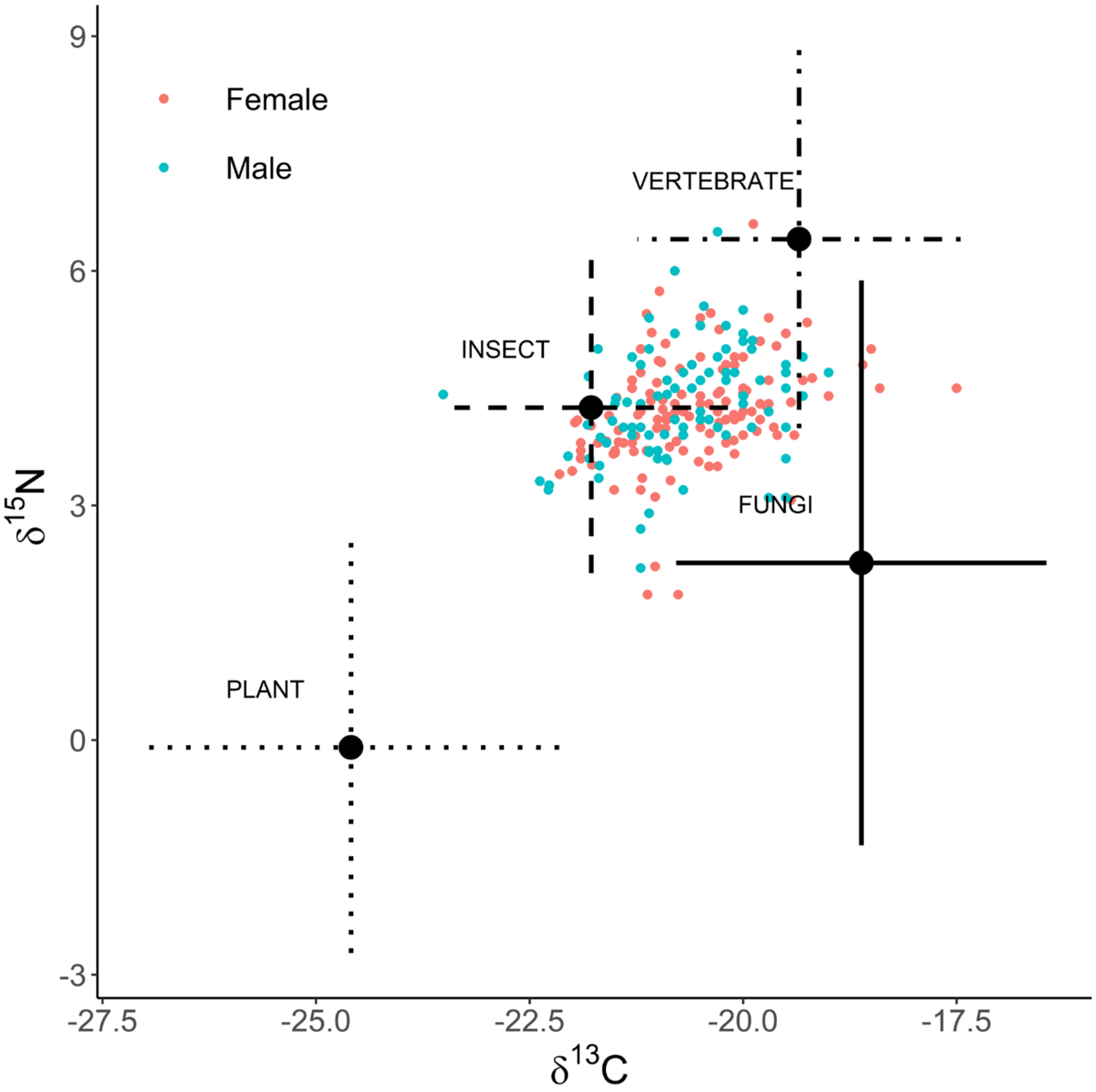
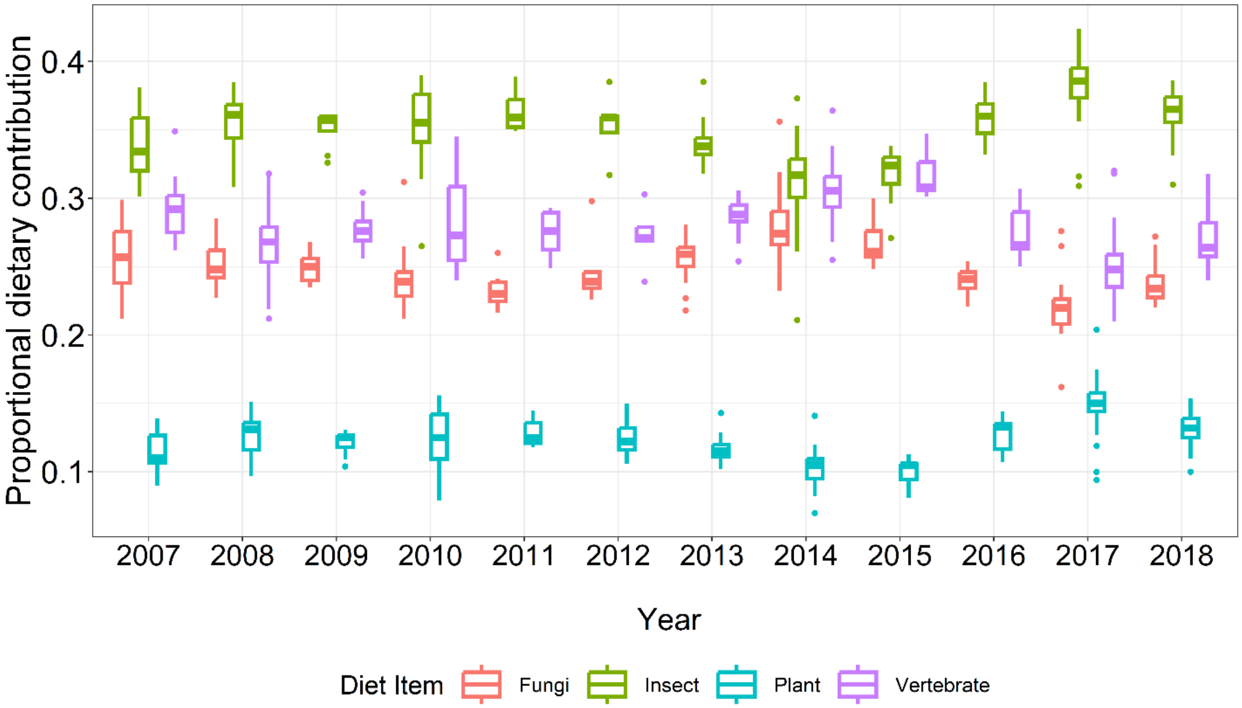


Supplementary Data SD5.—Isotopic signatures of individual fishers (*Pekania pennanti*; females are shown as red points and males are shown as blue points) and trophic-corrected dietary source groups (means are shown as black points ±95% CI).

Supplementary Data SD6. — Estimated means of proportional dietary contribution (95% credible intervals) for each functional prey group, plus specialization index (ε) among individual fishers (*Pekania pennanti*) in the southern Sierra Nevada, California, USA. Estimates are shown for all sampled individuals.

Dietary Variable	**Total Population**
Fungi	0.25 (0.20-0.30)
Insects	0.35 (0.29-0.41)
Vertebrates	0.28 (0.22-0.34)
Plants	0.12 (0.08-0.16)
Specialization Index	0.20 (0.18-0.22)



Supplementary Data SD7.—Estimated dietary contribution by source group and year among individual fishers (*Pekania pennanti*) in the southern Sierra Nevada, California, USA. Estimates are shown for all sampled individuals.

Chapter 2: Landscape heterogeneity provides co-benefits to predator and prey

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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 VHF tracking with direct observations of prey deliveries to dependent young by owls in both heterogeneous and homogeneous home ranges. Woodrat abundance was approximately 2.5x higher in owl home ranges (1,412 hectares) 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 approximately 2.5x 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-prey, predator conservation, 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 and Price 1992, Wiens 1995). Among these, the composition and configuration of habitat patches can mediate predator-prey interactions, with consequences on population dynamics for both predator and their prey (Schmitz 1998, Fahrig et al. 2011, 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 and Reynolds 1995) in predator-prey systems (Layman et al. 2007, Bullock et al. 2022). However, to date most studies of 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 and 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 and 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 (Holling 1959, Coulson et al. 2006), 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 – i.e., 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 (Huffaker et al. 1963, Coulson et al. 2006), 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 and 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 needed are studies conducted across a gradient of heterogeneity in natural systems – i.e., 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 et al. 2019a). Spotted owls use mature forest for nesting, roosting, and foraging (Gutierrez et al. 1992, Moen and Gutiérrez 1997), while woodrats are predominantly associated with younger, brushier forests and large oaks (Williams et al. 1992, Sakai and Noon 1993) that are traditionally viewed as less suitable habitat for foraging owls (Atuo et al. 2019, Kramer et al. 2021a). Despite this purported mismatch between predator and prey habitat, in lower-elevation forests of the Sierra Nevada, USA, woodrats can comprise 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 from 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 et al. 2019a), 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 examine (i) the mechanisms driving increased woodrat consumption by spotted owls and (ii) 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 (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 (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, CA, USA, within and adjacent to the Eldorado Demography Study Area (EDSA; Figure 1), a long-term spotted owl monitoring site encompassing roughly 355 km^2 of the Eldorado National Forest (Jones et al. 2021). Elevation in the EDSA ranged from 366 to 2,257 m, although we concentrated our woodrat trapping efforts within approximately 1,000 to 1,500 m, a range that can contain dense woodrat 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 less stand features generally found in older forests, such as large snags and logs (Stewart et al. 2016). 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 and Noon 1993). Spotted owls nest and forage on both ownership types (Roberts et al. 2017, Hobart et al. 2019b, Atuo et al. 2019).

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 conducted 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 ones 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 (1,412 ha) from previous studies (Jones et al. 2016, Atuo et al. 2019, 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 away from other home ranges we considered sampling, above elevations with high woodrat densities (>1,500 m) and below elevations where owls are commonly found in our study landscape (<1,000 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 9 home ranges (5 homogeneous; 4 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 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 4 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 8x8 or 4x16 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 edge 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 either 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) or passive integrated transponder (PIT) tag (Avid Identification Systems, Norco, CA). All captures were done with approval by the Institutional Animal Care and Use Committee of the University of Wisconsin, Madison (IACUC #A006173-A01), and followed guidelines from the American Society of Mammalogists (Sikes et al. 2019).

We estimated abundance using Huggins closed-capture models in program MARK (White and 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 (AICc) and AICc 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 and Parmenter 2015). We estimated ETA (in km^2) 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 its respective ETA (Schwemm et al. 2018). Given that dispersal from patches of adjacent young forest may facilitate increased woodrat densities (Sakai and 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). We calculated standard error 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 their 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 (3 homogeneous; 4 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 120g with VHF collars (Lotek model TW-5, 10g; Lotek Wireless Inc, Newmarket, Ontario, Canada or Telenax model TXE-116C, 6g; 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 every collared individual 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 on the week of 14 June and in 2021 on the week of 11 May. We located collared woodrats 1-2 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 their 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 was 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 of 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 Program MARK (White and 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, 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 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 (Roberts et al. 2017, Hobart et al. 2019b, Zulla et al. 2022), and 15 nesting males were captured and GPS tagged (5 in 2019; 10 in 2020). Infrared video cameras (AXIS Q1786-LE 4; Axis communications AB, Lund, Sweden) were placed at 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 PDT). 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 (number delivered per hour) and scaled these to monthly estimates with bootstrapped confidence intervals. 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 above-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 standard error and 95% confidence intervals 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 (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 187.4g (range 110.9 - 271.2) and flying squirrels was 98.8 g (range 80.2 - 117.2). Other prey species were assigned a mass based on the midpoint of mass ranges in the literature (e.g., mouse 20g; Reid 2006). Finally, if species of a prey delivery could not be determined, then it was assigned to a size class (extra small; 5.3g, small; 47.5g, medium; 175g, large; 205g) with 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 (g delivered per hour) and scaled these to monthly estimates. We also conducted two-sample Welch's *t*-tests to determine if 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 (4 heterogeneous, 4 homogeneous) for a total of 8,448 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/km^2; 95% CI: 156.0, 359.0) and mature forest in heterogeneous home ranges (134.2 woodrats/km^2; 95% CI: 97.9, 220.0), followed by mature forest in homogeneous home ranges (57.8 woodrats/km^2; 95% CI: 42.0, 95.7), with the lowest densities in open area (9.5 woodrats/km^2; 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 approximately 2.5x higher ($t_6 = 14.92$, $p < 0.001$) in heterogeneous home ranges ($\hat{N}_H = 1{,}805.0$ woodrats; range: 1,662.3 – 1,897.8) than homogeneous home ranges ($\hat{N}_O = 727.3$ woodrats; range: 648.9 – 817.9).

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 8 owl home ranges (4 heterogeneous; 4 homogeneous) and compiled a total of 1,030 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: 3 from avian (and presumably spotted owl) predation, 3 from mammalian predation, and 6 from non-predation 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 uninformative parameters (Arnold 2010) so 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 (2 mature-heterogeneous; 1 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 hours). 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., 4 voles, 2 pocket gophers, 2 moles, 1 bird, and 1 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, 9 were extra small, 19 were small, 9 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 heterogeneous home ranges (see above), we found no effect of landscape composition on the delivery frequency of flying squirrels ($t_{12} = 0.14$, $p = 0.89$) or all other alternate 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 (x̄ = 2553.6 g/month) home ranges. Further, while spotted owls consumed an additional 1,000 g/month of other prey in homogeneous (x̄ = 3,176.1 g/month) versus heterogeneous (x̄ = 2,139.6 g/month) home ranges (Figure 5B), this difference was not enough to compensate for the 2.5x greater consumption of woodrat biomass in heterogeneous (x̄ = 6,055.6 g/month) versus homogeneous (x̄ = 2,485.8 g/month) home ranges. Specifically, owls delivered total biomass at a rate 1.3x greater (2,685.6 more g/month) in heterogeneous (x̄ = 10,901.1 g/month) versus homogeneous (x̄ = 8,215.5 g/month) home ranges (Fig 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 has suggested that landscape heterogeneity including patches of prey refuges can profoundly affect predator-prey dynamics, these approaches typically involve highly simplified conditions, are conducted at patch rather than landscape scales, or fail to account for alternative prey (Ryall and Fahrig 2006, Juliano et al. 2022). Thus, our findings provide some of the first evidence from natural systems that promoting landscape heterogeneity may 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 approximately 2.5x greater in heterogeneous than homogeneous spotted owl home ranges, in large part because of 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 and Noon 1993, Ward Jr et al. 1998), as were low densities in open areas with little vegetation cover (Cranford 1977). Young forest confers likely benefits to woodrat populations by providing higher quality food resources owing to a greater diversity and abundance of flora (Carraway and Verts 1991, Sakai and Noon 1993), a more stable microclimate (Atsatt and Ingram 1983), structures and materials required for nest building (Innes et al. 2007), and cover that reduces predator risk (Sakai and 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 and 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 2.3x 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 (Sakai and Noon 1997, Hansen et al. 2019), 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 and 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: 1 in mature homogeneous and 2 in mature heterogeneous – similar to observations by Sakai & 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 et al. 2019a). 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 2.5x more woodrats in heterogeneous home ranges, which themselves contained a 2.5x 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 (Stephens and Krebs 1986, Sih 2005). 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 (Ruiz-Olmo and Jiménez 2009, Moorhouse-Gann et al. 2020). 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 (Wendland 1984, Coulson et al. 2006, Hobart et al. 2019b).

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 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 et al. 2019b) 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 and 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 (McLauchlan et al. 2020, Hoffman et al. 2021). 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 (Sakai and Noon 1993, Innes et al. 2007). 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 forest (Sakai and Noon 1997, Kramer et al. 2021b, Zulla et al. 2022); (2) consume a greater proportion of woodrats in more heterogeneous landscapes based on stable isotope analyses (Hobart et al. 2019a); (3) have smaller home ranges, higher territory occupancy rates, and higher densities in areas where they consume more woodrats (Zabel et al. 1995, Hobart et al. 2019a); 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 et al. 2019b).

As such, our findings, in conjunction with these 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 (Tempel et al. 2014, Conner et al. 2016). 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 which regenerate into future young forest following planting or natural re-seeding, 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 (Steel et al. 2022, Gaines 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 fuels 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 (Schulte et al. 2007, Collins et al. 2017, Sapkota et al. 2021). 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 is increasingly recognized as a global threat to biodiversity and ecosystem function, particularly among species adapted to naturally complex ecosystems (Riley et al. 2003, Anile et al. 2019). For predators, landscape simplification can cause declines in prey diversity and abundance (Cramer and Willig 2002, Benedek and Sîrbu 2018), 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 and 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.

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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. Information includes model covariates for initial capture probability (*p*) and recapture probability (*c*), ranked by AICc (Akaike's Information Criterion adjusted for small sample size), and compared by ΔAICc (difference in AICc between a model and the top-ranked model), *w* (model weight), and k (number of parameters).

Covariate(s)	**AICc**	**ΔAICc**	***w***	**k**
p(.), c(.)	1535.607	0.000	0.260	2
p(year), c(.)	1536.610	1.003	0.158	3
p(.), c(t)	1536.775	1.168	0.145	6
p(.), c(year)	1537.439	1.831	0.104	3
p(t) = c(t)	1537.517	1.909	0.100	6

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. Information includes model covariates, ranked by AICc (Akaike's Information Criterion adjusted for small sample size), and compared by ΔAICc (difference in AICc between a model and the top-ranked model), *w* (model weight), and k (number of parameters).

Covariate(s)	**AICc**	**ΔAICc**	***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

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 & 2) were estimated in 2020 and 2021. Landscape composition is depicted by red (heterogeneous) and green (homogeneous) circles.

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) NAIP imagery and (B) habitat type (mature, young, and open), and (C) at the scale of a trapping grid visualized with NAIP imagery.

Figure 3: Estimated density (±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 km^2 in open habitat, young forest, and mature forest within home ranges classified as heterogeneous and homogeneous.

Figure 4: Estimated monthly consumption rate (±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.

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 on (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).

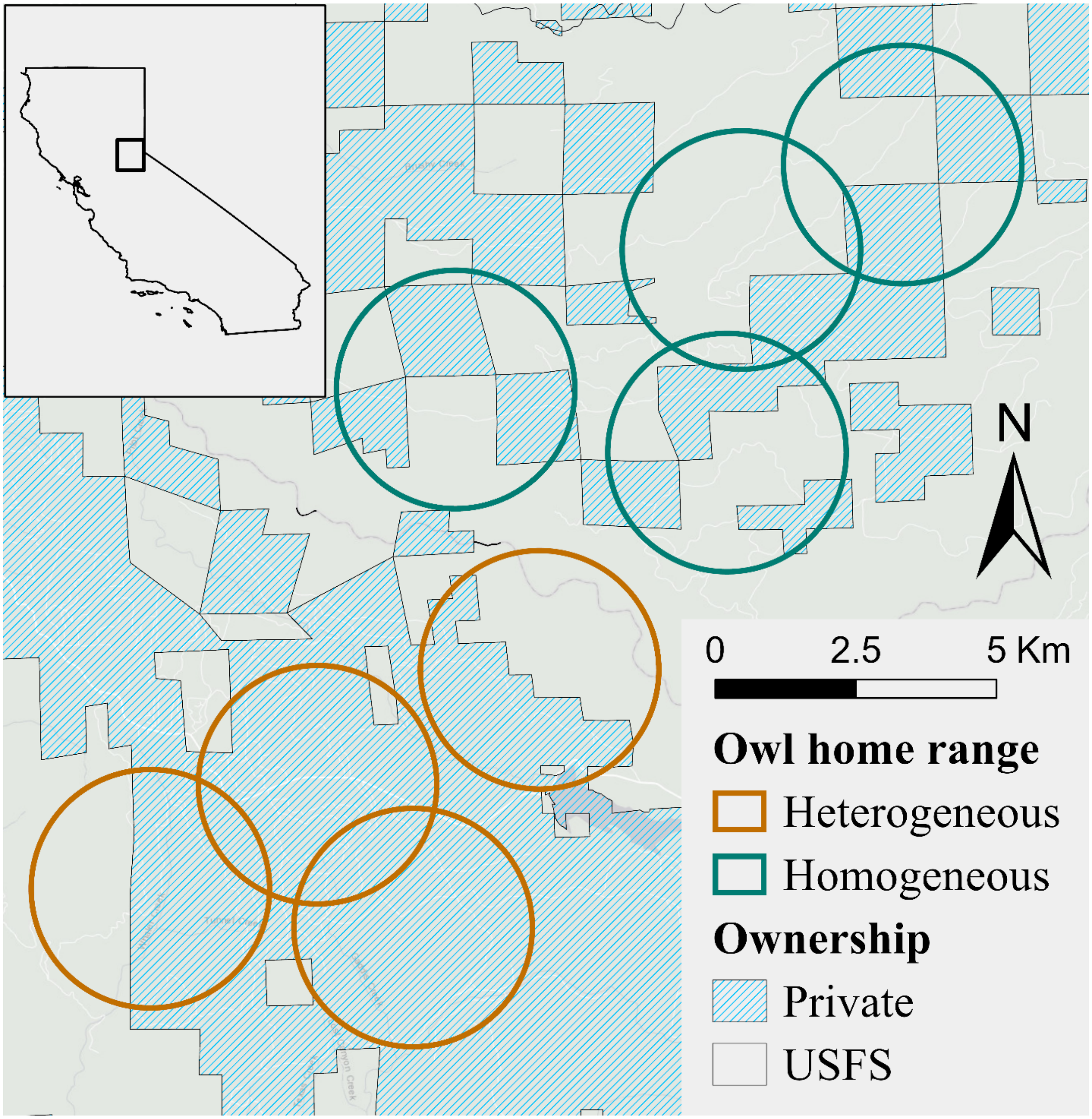
N
0
2.5
5 Km
Owl home range
Heterogeneous
Homogeneous
Ownership
Private
USFS

Figure 1

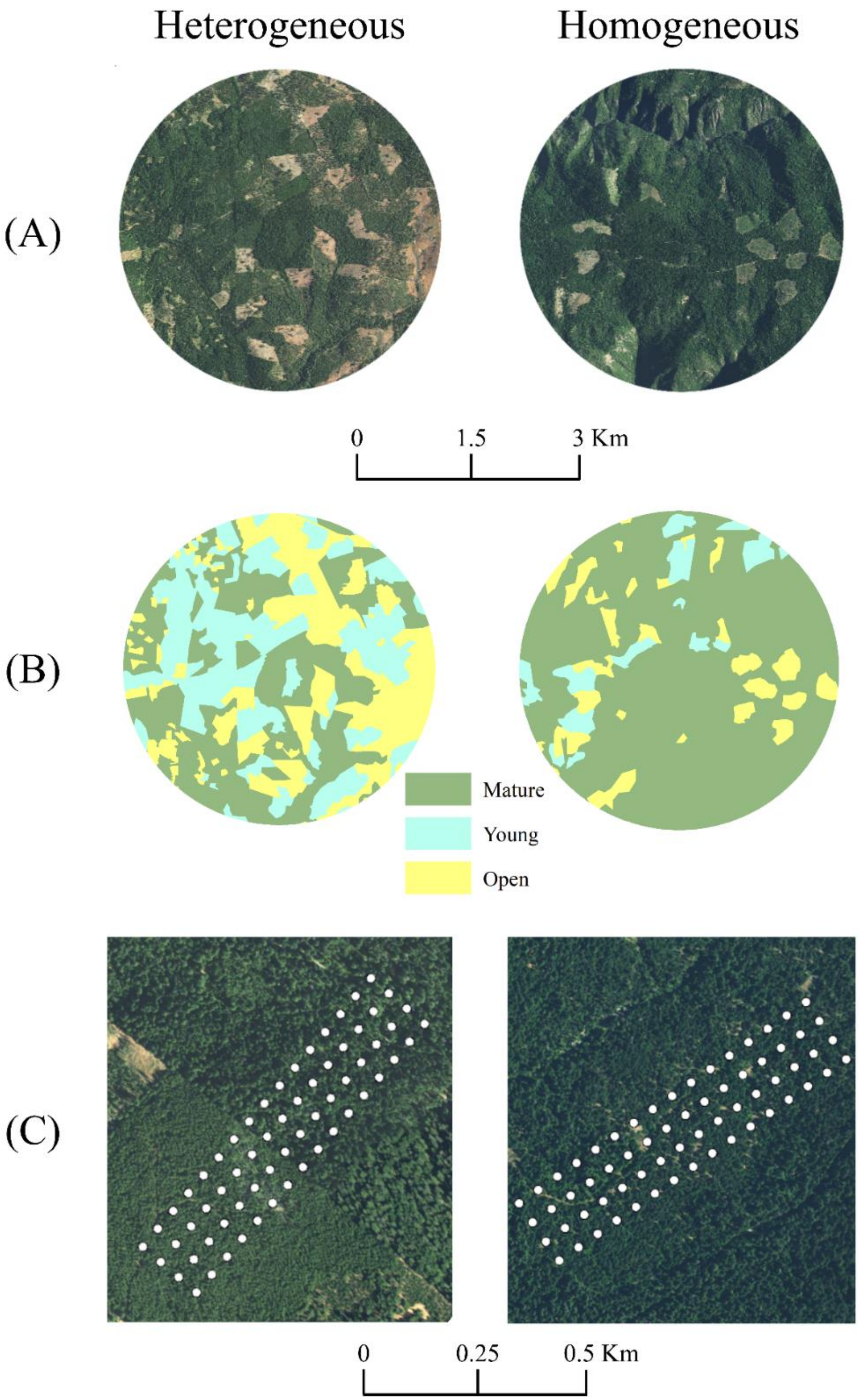
Heterogeneous
Homogeneous
(A)
0
1.5
3 Km
(B)
Mature
Young
Open
(C)
0
0.25
0.5 Km

Figure 2.

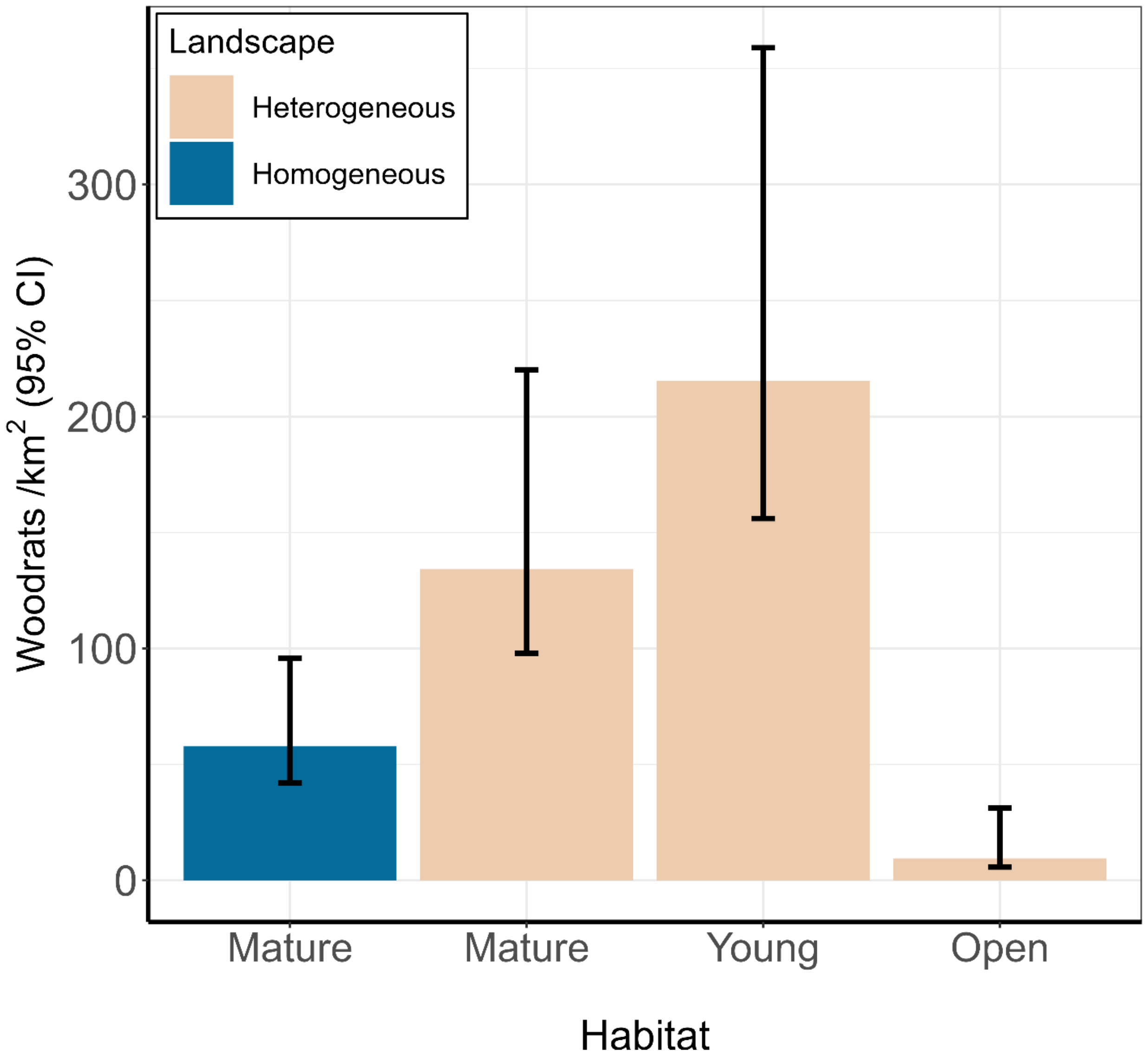
Landscape
Heterogeneous
Homogeneous
Woodrats /km^2 (95% CI)
0
100
200
300
Mature
Mature
Young
Open
Habitat

Figure 3

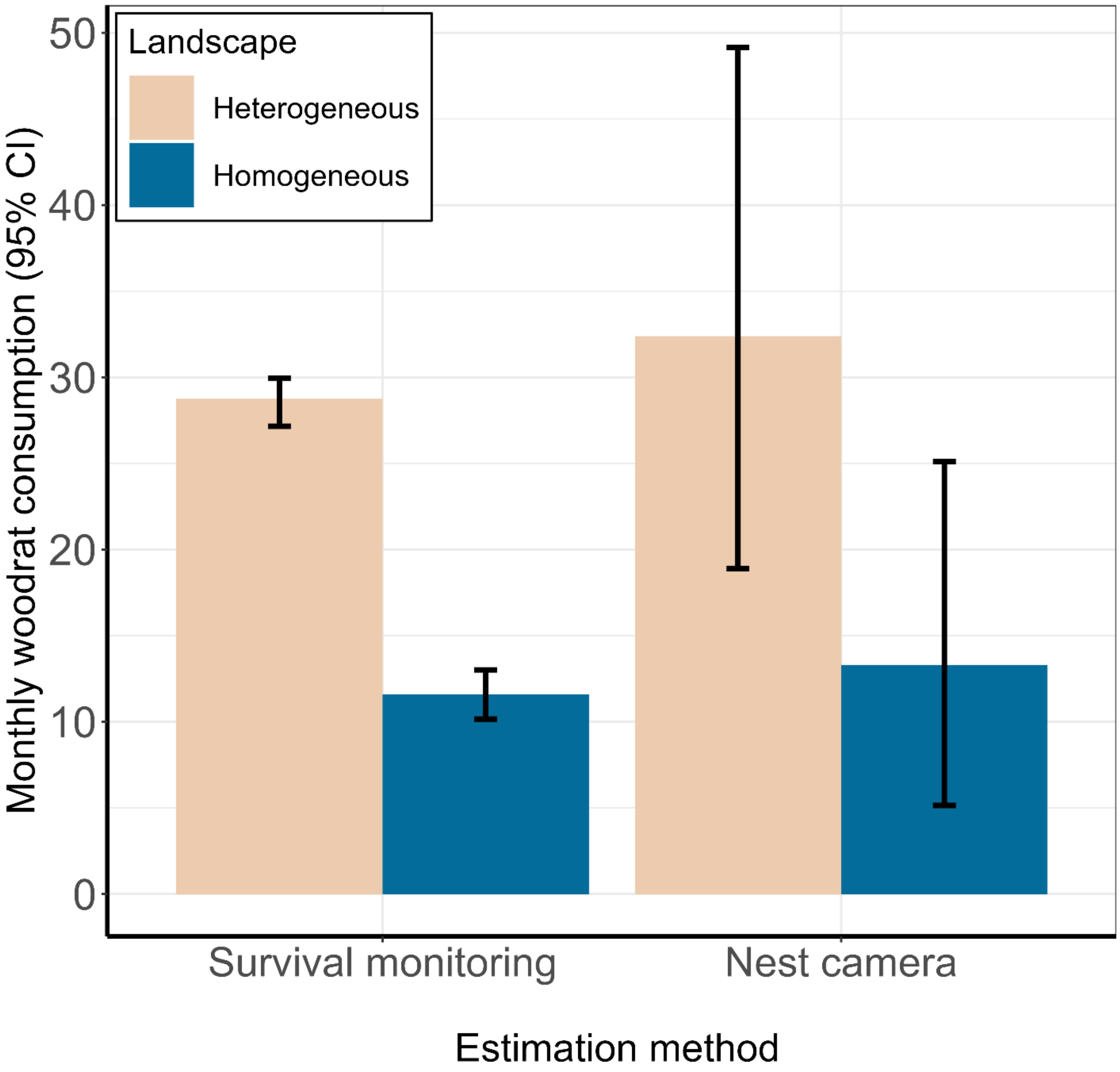
Landscape
Heterogeneous
Homogeneous
Monthly woodrat consumption (95% CI)
0
10
20
30
40
50
Survival monitoring
Nest camera
Estimation method

Figure 4

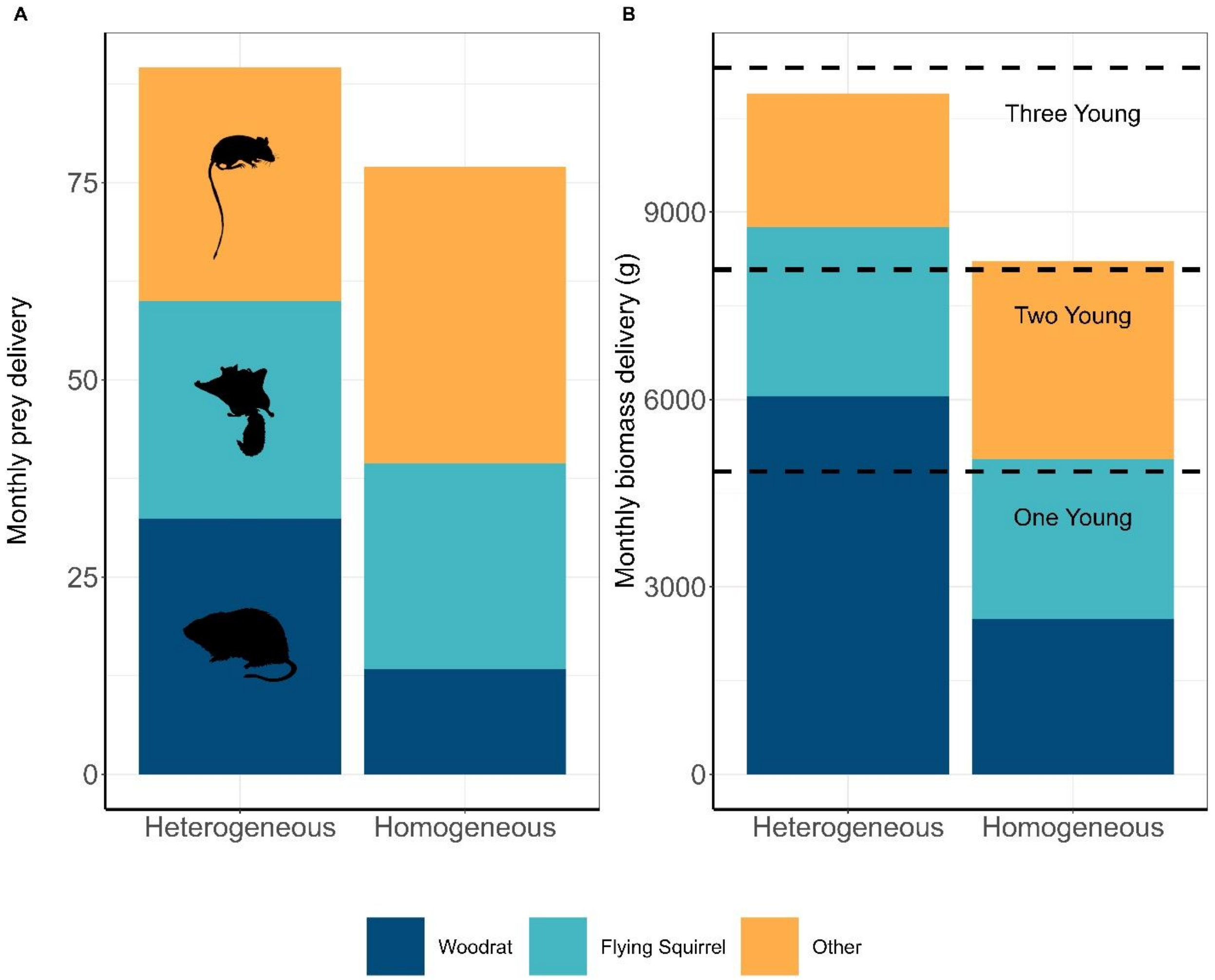
A
B
Monthly prey delivery
0
25
50
75
Heterogeneous
Homogeneous
Monthly biomass delivery (g)
0
3000
6000
9000
Three Young
Two Young
One Young
Woodrat
Flying Squirrel
Other

Figure 5

Supporting Information

Appendix S1: Estimating woodrat abundance within spotted owl home ranges

We obtained estimates for woodrat abundance within homogeneous ($\hat{N}_H$) and heterogeneous ($\hat{N}_E$) home ranges by multiplying our estimates of density by habitat type (woodrats per km^2; Figure 3) by the total area of open (A_O), young (A_Y), and mature (A_M) forest within each home range using the equations:

$$N_H = (57.8 * A_M) + (215.3 * A_Y) + (9.5 * A_O)$$

(Equation S1)

$$N_E = (134.2 * A_M) + (215.3 * A_Y) + (9.5 * A_O)$$

(Equation S2)

then averaged values for each group to estimate mean abundance across homogeneous ($\hat{N}_H$) and heterogeneous ($\hat{N}_E$) home ranges in our study area. To calculate the standard error for these values, we used the delta method (Powell 2007, Marques et al. 2013). This method estimates the variance of a parameter (i.e., abundance) that is derived from multiple other variables (i.e., density by habitat type) that each have their own variances.

Appendix S2: Exploring fitness outcomes of biomass delivery rates

To explore the potential fitness outcomes of a 1.3x increase in biomass delivery rates among owls in heterogeneous home ranges (Figure 5), we followed a similar approach to Ward Jr et al. (1998) and Weathers (1992, 1996) and approximated the energetic contribution of prey and costs of reproduction, metabolic maintenance, and fledgling growth. In short, we estimated monthly metabolic cost (in kJ and prey biomass) to a male spotted owl providing food for itself, a nesting mate, and one, two, or three young using:

(1) An average mass of 580g and 665g for adult male and female northern spotted owls, respectively

(2) An experimentally determined basal metabolic rate (BMR) value for Mexican spotted owls (*Strix occidentalis lucida*) of 0.84 ccO_2 g^{-1} hr^{-1} from Ganey et al. (1993)

(3) A conversion of 1.7BMR for daily maintenance costs from King (1973)
   a. 397.3 kJ/day for males
   b. 342.4 kJ/day for females

(4) A one-time cost of 252 kJ for production of one egg calculated from methods in Walsberg (1983)

(5) An allometric equation from Weathers (1992) for calculating total metabolic cost of producing one fledgling (hereafter TME) derived from its mass (M) and total growth time (t_{fl}), calculated with both the mean (Equation S3) and upper 95% confidence limit (Equation S4) of the intercept and exponents for M and T_{fl}:
   a. $TME = 6.65M^{0.852}\ t_{fl}^{0.710}$

(Equation S3)

   b. $TME = 10.09M^{0.9206}\ t_{fl}^{0.8924}$

(Equation S4)

(6) An average energy equivalent of 18.4 kJ g^{-1} for prey

(7) An estimated 75% metabolic efficiency for an owl (Wijnandts 1984)

We presented values from the model using the upper 95% confidence limit of TME, which estimated greater energetic (and biomass) costs associated with producing young. We chose this value to account for the fact that our model did not include the costs of foraging or other activities for the male beyond daily maintenance. We ultimately estimated monthly costs of 66,845 kJ (4,844g prey), 111,488 kJ (8,079g prey), and 156,130 kJ (11,314g prey) for producing one, two, and three fledglings, respectively.

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Chapter 3: Asymmetrical predation intensity produces divergent antipredator behaviors in primary and secondary prey

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Abstract

It is widely recognized that predators can influence prey through both direct consumption and by inducing costly antipredator behaviors, the latter of which can produce nonconsumptive effects that cascade through trophic systems. Yet, determining how particular prey manage risk in natural settings remains challenging as empirical studies disproportionately focus on single predator-prey dyads. Here, we contrast foraging strategies within the context of a primary and secondary prey to explore how antipredator behaviors emerge as a product of predation intensity as well as the setting in which an encounter takes place. We studied the effects of spotted owls (*Strix occidentalis*) on two species experiencing asymmetrical risk: dusky-footed woodrats (*Neotoma fuscipes;* primary prey) and deer mice (*Peromyscus* spp.; alternative prey). Woodrats are most abundant within young forest, but predominantly captured by owls foraging within mature forest; in contrast, deer mice occur in high densities across forest types and seral stages and are consumed at lower per-capita rates overall. We deployed experimental foraging patches within areas of high and low spotted owl activity, created artificial risky and safe refuge treatments, and monitored behavior throughout the entirety of prey foraging bouts. Woodrats were more vigilant and foraged less within mature forest and at riskier patches, although the effect of refuge treatment was contingent upon forest type. In contrast, deer mice only demonstrated behavioral responses to riskier refuge treatments while forest type had no effect on perceived risk or the relative effect of refuge treatment – suggesting that prey may conform to or depart from the risk allocation hypothesis contingent on relative predation from a shared predator. Our findings show that asymmetrical predation can modulate both the magnitude of perceived risk and the strategies used to manage it, thus highlighting an important and understudied contingency in risk effects research. Evaluating the direct and indirect effects of predation through the paradigm of primary and secondary prey may improve our understanding of how nonconsumptive effects can extend to population- and community-level responses.

Keywords: Antipredator behavior, asymmetrical predation, habitat domain, hunting mode, optimal foraging, risk management

Introduction

Predator-prey interactions can be likened to an adaptive foraging game where each participant strives to outwit the other (Brown et al., 2001; Kotler, 2016). In this context, the success of the predator is determined by the ability to encounter and subdue their prey, while the success of prey is determined by the ability to avoid and escape their predators (Brown et al., 2001; Wolf & Mangel, 2007). Prey species have honed their strategies to navigate this high-stakes arena through morphological, behavioral, and physiological defenses (Brown & Kotler, 2004; Schmitz & Trussell, 2016). While these adaptations increase the likelihood of immediate survival of prey, they often involve nonconsumptive effects (NCEs), or trade-offs with other consequences that influence fitness (Preisser et al., 2005; Wirsing et al., 2021) – the most fundamental being the balance between food and safety (Brown & Kotler, 2004). The implications of NCEs are not confined to the predator-prey dyad; the propagation of these risk effects are now widely recognized for their ability to drive higher-order interactions that can rival or even exceed consumptive effects in terms of their impact on ecosystem structure and function (Donadio & Buskirk, 2016; Wirsing et al., 2021).

Antipredator behaviors emerge from complex spatiotemporal dynamics as the outcome of both background and immediate levels of perceived risk (Lima & Bednekoff, 1999; Moll et al., 2017). For prey, the immediate risk of predation is typically driven by direct cues from predators that inform the likelihood of encounter or capture (Creel, 2011; Lima & Dill, 1990). This acute risk may increase with proximity or activity levels of predators (Kohl et al., 2019), while the presence of conspecifics among prey may attenuate risk through cooperative vigilance, defense, or dilution effects (Alexander, 1974; Carthey & Banks, 2015). In contrast, prey often lack the ability to directly detect the presence or densities of their predators (Lima & Dill, 1990), and rely on indirect cues to evaluate chronic background risk (Gaynor et al., 2019). This gives rise to the 'landscape of fear', which can generate spatiotemporal variability in trait responses and NCEs within prey communities (Gaynor et al., 2019; Laundré et al., 2014). The risk allocation hypothesis suggests that the ultimate responses to immediate cues of predation risk may vary according to background levels of risk (Lima and Bednekoff, 1999). Therefore, prey manage these complex risk dynamics by adopting both proactive and reactive strategies (Lima & Bednekoff, 1999; Wirsing et al., 2021). This can be seen in foraging behaviors, as prey balance the tradeoffs between food and safety with behavioral titrations (Brown & Kotler, 2004; Kotler & Blaustein, 1995), including patch selection, time allocation, and apprehension (Brown & Kotler, 2004; Kotler et al., 2010). For example, some animals prioritize foraging within patches with greater food availability or with lower risk (Brown & Kotler, 2004), while others may practice vigilance to increase safety at the cost of foraging efficiency (Kotler et al., 2010). Understanding these decisions can help us assess how foragers behave optimally by balancing the marginal costs and benefits of foraging (Kotler & Blaustein, 1995).

Investigations of risk effects have largely centered around spatiotemporal properties of the environment that influence the likelihood of predator-induced mortality; however, a growing body of literature suggests that properties of the organisms involved may also contribute to the nature and magnitude of antipredator behavior (Schmitz & Trussell, 2016; Wirsing et al., 2021). Within diverse prey communities, perceived risk can also vary with the presence or absence of other prey and relationships with the predators themselves (Holt & Lawton, 1994; Wilson et al., 2022). For example, by specializing on one or several preferred species from a pool of potential prey, dietary preferences among predators can drive differences in predation intensity between these 'primary' and alternative 'secondary' prey species (Holt & Lawton, 1994). Within the context of multi-prey systems, this interplay between primary and secondary prey species introduces more complexity that further modulates risk beyond morphology, state dependencies, or spatiotemporal variation within the landscape of fear (Gaynor et al., 2019). While the ecological consequences of shared natural enemies have been explored in the context of consumptive effects and apparent competition (Holt & Lawton, 1994), empirical studies on risk effects disproportionately focus on single predator-prey pairings and provide an incomplete picture of contingencies in NCEs (Sheriff et al., 2020; Wirsing et al., 2021). A few notable studies have explored these dynamics in multi-predator or multi-prey systems (e.g., Dröge et al. 2017, Dellinger et al. 2019, Kachel et al. 2023). For example, Dellinger et al. (2019) found that two different species of deer (*Odocoileus* spp.) exhibited divergent strategies of space use to terrain suiting their respective running gaits when exposed to grey wolf (*Canis lupus*) predation, demonstrating how prey escape mode can drive spatial variability in the effectiveness of antipredator strategies among sympatric species (Wirsing et al., 2010). However, still missing are empirical studies within multi-prey systems that A) consider how dietary specialization by a predator can modify risk between a primary and secondary prey species (*sensu* Holt and Lawton 1994), and B) examine how differential predation intensity can drive risk management through foraging behaviors.

To explore how properties of predator, prey, and their environment interact to determine perceived risk from a relatively specialized predator, we studied the effects of spotted owls (*Strix occidentalis*) on two prey species that experience differing predation intensities – dusky-footed woodrats (*Neotoma fuscipes* – primary prey) and *Peromyscus* spp. (alternative prey). Woodrats are the largest-bodied and most energetically profitable prey for spotted owls, and when present, typically comprise the majority of spotted owl diet in both quantity and total biomass (Kuntze et al., 2023; Zulla et al., 2022). Accordingly, the consumption of woodrats has been linked to benefits in fitness, occupancy, and space use for spotted owls (Hobart et al., 2019; Kuntze et al., 2023). In contrast, smaller-bodied secondary prey such as *Peromyscus* spp., voles (*Microtus* spp.), moles (*Scapanus* spp.), and gophers (*Thomomys* spp.) are less important to spotted owls in terms of both number and biomass, although *Peromyscus* spp. are the most frequently consumed among these secondary prey species. *Peromyscus* spp. are also up to 30x more abundant than woodrats (Fraik et al., 2023; Kelt et al., 2017), suggesting that per-capita predation rates on woodrats are far greater than any alternative prey. Further, while *Peromyscus* spp. are habitat generalists and occur in high densities across different forest types and seral stages (Kelt et al., 2017), woodrats and spotted owls exhibit divergent habitat preferences that should, in theory, limit encounter rates between these two species. Specifically, spotted owls typically nest, roost, and forage in larger patches of mature forest (Jones et al., 2018), while woodrats are associated with – and reach greatest densities within – younger, brushier forests (Kuntze et al., 2023; Sakai & Noon, 1993), traditionally viewed as less suitable habitat for foraging owls.

Using spotted owls, woodrats, and *Peromyscus* spp. in a spatially heterogeneous environment featuring variable predation intensity, we contrasted foraging behaviors within the hierarchy of a primary and secondary prey species. Here, we tested whether woodrats and

Peromyscus spp. perceive risk from spotted owl predation differently and explored the strategies used to manage risk. We hypothesized that the nature and strength of risk experienced by prey – and in turn, the amount of antipredator investment – is governed by both the dietary preferences of the predator and the setting in which an encounter takes place. We predicted that perceived risk would follow spatial patterns of actual risk; that is, we expected that antipredator behavior would increase in mature versus young forests. We predicted that both prey species would manage risk through behavioral changes at distinct stages of the foraging process (Figure 1A) but expected that the actual strategies employed would differ between the two. Specifically, we predicted that woodrats would exhibit a greater overall antipredator response and that they would manage risk predominantly through decisions on where and how to forage (i.e., patch selection, apprehension, and patch quitting), while *Peromyscus* spp. would reduce the frequency and duration of patch visitations. To test these predictions, we deployed experimental foraging patches within areas of high and low spotted owl hunting activity, created artificial risky and safe microhabitat conditions, then monitored woodrat and *Peromyscus* spp. behavior throughout the entirety of foraging bouts. By systematically exploring these predictions through each stage of the foraging process, we provide further insights into risk perception and contingencies in NCEs by exploring properties of both predator and prey, as well as the environment in which these interactions occur.

Methods

Study system

We conducted this study within and adjacent to the Eldorado Demography Study Area, a long-term spotted owl monitoring site that encompasses approximately 355 km^2 of the Eldorado National Forest on the western slope of the central Sierra Nevada, CA, USA. *Peromyscus* spp. here could be one of two species, *P. maniculatus* or *P. boylii*; we hereafter refer to them as deer mice. This study area has been described in detail elsewhere (Kuntze et al., 2023; Zulla et al., 2022), but briefly, land use practices have created a landscape with distinct spatial variation in forest structure and configuration. Here, relatively homogeneous stands of mature mixed-conifer trees are interspersed with a mosaic of stand types and seral stages – including patches of brushy young forest. The differential use of this landscape among spotted owls, woodrats, and deer mice likely affects these primary and secondary prey differently, further modulating perceived risk and concomitant response.

Field methods

In summer 2021, we conducted foraging experiments within five known and presently occupied spotted owl home ranges (Figure 1B). Our field methods, particularly site selection, were focused on woodrats due to their status as the primary prey species of spotted owls and their patchy distribution (Kuntze et al., 2023; Sakai & Noon, 1993). Deer mice occurred ubiquitously and at high densities throughout the area. Therefore, our study was designed with the assumption that effective selection of woodrat habitat would effectively include deer mice as well.

We captured and uniquely marked woodrats, then selected a subsample of these individuals (*n* = 73) to fit with VHF collars equipped with onboard mortality sensors (details in Appendix S1 – Supplementary Methods). Within 2 days of collar deployment, we tracked woodrats to their middens. We assigned each midden to one of two forest types based on canopy cover and size of dominant trees in the area: mature forest (>40% canopy cover and trees >12 inches diameter at breast height [DBH]; Figure 1C) or young forest (>40% canopy cover and saplings or trees <12 inches DBH; Figure 1D). Additional forest types were grouped into the 'other' category and not considered in this study, although open area (<40% canopy cover) accounted for the majority of the ‘other’ category. From these, we selected sites (*n* = 31) within young (*n* = 14) and mature (*n* = 17) forests to capture a gradient of local habitat features, minimize proximity to water or human activity, and allow adequate separation between stations (>150m) to ensure independence (Figure

1B). Woodrats demonstrate midden fidelity and small home ranges (Sakai & Noon, 1997), which we confirmed by GPS collaring individuals during pilot work in Summer 2019. Further, we confirmed that none of the individuals in our study moved during the course of the study by VHF monitoring outside of the midden every 1-2 days.

At each site, we placed a foraging station consisting of two foraging patches – spaced 5m apart – 10m from a midden that was presently occupied by a collared woodrat. To construct each patch, we first placed a plastic tray in a shallow hole so that the top lip was approximately level with the ground. One patch was randomly chosen as the risky treatment (Figure 1E), while the other was chosen as the safe refuge treatment (Figure 1F). For the risky patch, we cleared all brush <2m tall from within 1m of the tray. For the refuge patch, we created a 0.5 x 0.5m wooden structure over the tray covered with black netting that stood approximately 40cm from the ground and mimicked natural cover by thoroughly covering this structure with cut brush. By creating vertical but not horizontal cover at refuge patches, we provided protection from the risk of avian predation but not from mammalian or other cursorial predators (Embar et al., 2014; Makin et al., 2017). We filled each tray with 5L of sifted sand and 20g of shelled, halved peanuts; this specific food resource and ratio was determined after field testing to ensure consumption and avoid saturation or depletion following one night of foraging.

We allowed for two days of acclimation in which trays were placed and refilled, but data was not collected. After this, we collected data for a minimum of four consecutive days. Risk perception – and consequent response – may be sensitive to temporally variable conditions (e.g., Prugh & Golden, 2014); we controlled for this by only collecting data on nights with high lunar illumination (>0.5), minimal cloud cover, and no measurable precipitation. Data was collected daily; every morning, sand from each tray was sieved and recovered food items were dried, cleaned of debris, and then weighed to the nearest centigram (0.01g). At dusk, a new matrix of 20g peanuts and 5L sand was placed within each tray.

Each tray was monitored with infrared, motion-sensing video cameras (Campark IP66), which recorded at continuous 30-second intervals until movement ceased. In addition to providing data on visitation and behavior within the patch, cameras helped address a number of shortcomings associated with traditional approaches to quantifying foraging behavior (Bedoya-Perez et al., 2013). Specifically, they provided a reliable method to confirm patch visitation by target individuals and account for the effect of nontarget foragers. In addition, for woodrats, by conducting experiments exclusively on collared individuals we could identify multiple foragers, even when visitation was not concurrent.

We first removed data from nights where the camera malfunctioned or the tray was disturbed by nontarget species such as black bear (*Ursus americanus*) or gray fox (*Urocyon cineroargenteus*). We inspected all footage to see whether a patch was visited on a given night by either species, then quantified behavior at foraging patches using program BORIS (Friard & Gamba, 2016). For each experimental night, we recorded the number of patch visits and the cumulative visit duration – hereafter patch residence time (PRT) – by target woodrats and deer mice. We also recorded whether a patch was visited, the number of patch visits, and PRT for all nontarget (i.e., uncollared) woodrats. For target woodrats we further quantified patch behavior by recording the duration of time spent foraging (e.g., digging, exploring the patch, and handling food), vigilant (i.e., paused foraging with head up and clear inspection of surroundings), and other (e.g., grooming or interacting with other organisms). We did not quantify these behaviors for deer mice because the mean visit duration was short ($\bar{x}$ = 14.7s ± 0.76 SE) compared to woodrats, which had average patch visitations that were approximately four times as long ($\bar{x}$ = 57.8s ± 3.97 SE; Figure S1).

Following data collection, we conducted vegetation sampling at every foraging station. We centered circular plots with a radius of 12.5m at the midpoint between paired trays, within which we recorded canopy cover using a densitometer and understory with a visual estimation of the proportion of ground obscured by brush <2m height. Finally, for each tree within our plot, we recorded species, DBH, and condition (live, dead), then estimated total basal area.

Analytical methods

We explored several response variables for the foraging process, separated into four principal stages (Figure 1A). These included patch visitation probability (Stage 1), number of patch visits and PRT (Stage 2), foraging behavior (Stage 3), and patch quitting (Stage 4). For each, we evaluated the effect of forest type (young, mature) and patch treatment (refuge, risky) targeted as part of our study design, plus a number of predictor variables related to local habitat features and biotic interactions (Table S1). For woodrats, we also included covariates for among-individual differences in age, sex, and body condition. To quantify body condition, we used residuals from a regression of body mass against hind foot length (Schulte-Hostedde et al., 2005) for all woodrats captured during the field season (n = 195). We also evaluated several *a priori* interactions derived from our study design and prior literature highlighting habitat features important to woodrats (Fraik et al., 2023; Sakai & Noon, 1993, 1997).

For patch visitation probability (Stage 1), we created a binary response variable for whether each foraging patch was visited (1) or not (0) during a given experimental night. We constructed mixed effects logistic regression models and included predictor variables for habitat, intrinsic, and binary variables for visitation by nontarget species and/or nontarget foragers (Table S1).

For each response variable in stages 2-4, we used two statistical approaches. First, we explored only the *a priori* relationships between refuge treatment and forest type that were targeted as part of our study design. Here we compared the differences between risky and safe refuge treatments within mature and young forest. Next, we constructed separate linear mixed effects models (LMMs). Within each model set, we included all predictor variables from stage 1, as well as covariates for the frequency and duration of nontarget foraging by woodrats and/or deer mice (Table S1).

To quantify foraging behavior, we divided the duration of time spent exercising vigilance by PRT to get the percentage of time that a woodrat spent vigilant. To avoid outliers from nights with brief visitation, we only included nights in which PRT was >90 seconds. As stated previously, we did not describe foraging behavior for deer mice.

We quantified patch quitting using the giving-up density approach (GUD; Brown 1988) – testing a response variable for the amount of food (g) remaining in a patch after an experimental night in which the target individual visited (i.e., nights without visitation were not included in the dataset). To address the effect of foraging by nontarget species on the value of remaining food, we calculated values for the total and proportional PRT by the target and nontarget species relative to all foragers for each night. If the nontarget species foraged for >90 seconds or made up >10% of total PRT, then we removed this night from our dataset. Therefore, we also excluded any predictor variables for deer mice in woodrat models of giving-up density, or any variables for woodrats in deer mice models.

We conducted analyses in R (R Core Team, 2023) using package lme4 and lmerTest for model construction and package sjPlot for visualization of effect sizes and relationships. We standardized all continuous variables and included a unique site ID for foraging station as a random effect in all models. To address multicollinearity, we excluded highly correlated covariates ($|r| > 0.6$) from the same model (Dormann et al., 2013). For each response variable, covariates were tested univariately, then combinations of competitive covariates were determined from *a priori* hypotheses in a final model set. We ranked models using Akaike Information Criterion adjusted for small sample sizes (AICc). Any model that outperformed the null and was within 2 ΔAICc of the top model (Morin et al., 2020) was deemed competitive. In the results, we report effect sizes and coefficient estimates from the top-performing models. We followed the same methodology for both species, save for excluding stage 3 and several predictor variables for deer mice; specifically, as we could not differentiate between individuals from camera data, we omitted variables for conspecific foraging, sex, age, and body condition from model sets.

Behavioral analysis: Harvest rate curve

With values for GUD and PRT at each patch we estimated quitting harvest rates (QHR) and plotted harvest rate curves *sensu* Kotler & Brown (1990) and Kotler et al. (2010). We used PRT and giving-up density data for values of the total time spent in a patch (t), plus initial (N_0) versus remaining (N_f) resource density. With video data from foraging individuals, we directly observed and estimated average handling times (h; time [g s^{-1}] required by the forager to process and consume food) for both woodrats (6s g^{-1}) and deer mice (16s g^{-1}). We subset the data into groups relative to each of our categorical predictor variables (e.g., forest type, treatment, and the interaction of forest type and treatment) and produced values of attack rate (a; food encounter rate), mean GUD, and characteristic QHR for comparison.

Finally, we plotted harvest rate curves for each species and forest type-treatment combination using the appropriate estimate of attack rate from each group and the overall value of h. The harvest curve characterizes patch depletion and summarizes risk management strategies; different slopes correspond to distinct levels of apprehension, while the location of the average GUD on the curve represents the characteristic QHR and corresponds to time allocation (Kotler & Brown, 1990). For example, steeper slopes indicate faster harvesting of equal food densities, meaning foragers prioritize harvesting over predator detection, corresponding to less apprehensive animals, whereas lower GUDs on the harvest rate curve represent greater time allocation to feeding.

Results

We collected 356 experimental tray-nights of data. After removing 82 nights that were disturbed, occurred during cloudy and rainy periods, or had camera-related issues, we ultimately evaluated 274 experimental tray-nights across 28 foraging stations (i.e., 56 unique trays). These were relatively evenly split among forest type (mature = 146; young = 128) and treatment (refuge = 138; risky = 136).

Stage 1: Patch selection

Woodrats visited foraging patches during 202 tray-nights. Patch visitation probability was greater among females (β_{male} = -3.11 [95% CI = -5.83, -0.40]), on nights where a tray was visited by another woodrat ($\beta_{nontarget}$ = 1.07 [0.10, 2.05]), and greater at safe versus risky patches in mature forest (β_{refuge} = 1.87 [0.70, 3.03]), but lower at safe versus risky patches in young forest ($\beta_{young:refuge}$ = -2.82 [-4.66, -0.98]; Figure S2, Table S2). Deer mice visited foraging patches during 156 tray-nights. The top model was the intercept model while no other covariates were informative (Table S3), suggesting that patch visitation probability was unaffected by any tested predictor variables.

Stage 2: Patch visitation

Woodrats visited patches more frequently in young versus mature forest (Figure 2A). Further, the number of nightly visits was greatest at safe patches in young forest, followed by similar visitation frequencies at risky patches in young forest and safe patches in mature forest; risky patches in mature forest were visited the least (Figure 2A). Deer mice most frequently visited safe patches in mature forest, with little difference between risky patches in mature forest and either treatment in young forest (Figure 2B). Among woodrats, the number of patch visits increased at refuge treatments (β_{refuge} = 1.98 [0.79, 3.17]), with increasing understory ($\beta_{understory}$ = 0.88 [0.09, 1.68]), canopy cover in young forest ($\beta_{young:cover}$ = 2.18 [0.45, 3.90]), and conspecific PRT ($\beta_{nontarget\_prt}$ = 0.96 [0.31, 1.61]; Figure 2C; Table S2). For deer mice, visitation frequency was greater at safe patches within mature forest ($\beta_{mature:refuge}$ = 10.37 [4.05, 16.68]) but lower in young forests ($\beta_{young:refuge}$ = -9.69 [-19.08, -0.29]), while understory had opposite effects between treatments; specifically, visitation increased with increasing understory at safe patches ($\beta_{refuge:understory}$ = 5.36 [0.58, 10.14]), but decreased at risky patches ($\beta_{risky:understory}$ = -4.15 [-8.03, -0.27]; Figure 2C; Table S3).

Woodrats spent the most time at safe patches in young forest, with no significant difference in PRT between risky patches in young forest and either treatment in mature forests (Figure 3A). Deer mice spent nearly 3x longer at safe versus risky patches in mature forests, while there was no difference between treatments in young forests (Figure 3B). Among woodrats, PRT increased with conspecific PRT($\beta_{nontarget\_PRT}$ = 72.65 [32.62, 112.69]), canopy cover within young forests ($\beta_{young:cover}$ = 140.29 [30.53, 250.04]), and at safe patches within young forests ($\beta_{young:refuge}$ = 153.29 [8.59, 297.99]; Figure 3C; Table S2). For deer mice, the top model for PRT only included the interaction between forest type and treatment, as individuals spent more time in safe patches within mature forest ($\beta_{mature:refuge}$ = 388.81 [255.13, 522.48]), but less time in young forests ($\beta_{young:refuge}$ = -312.50 [-509.15, -115.84]; Figure 3C; Table S3).

Stage 3: Patch behavior

Woodrats allocated almost twice as much proportional time to vigilance within mature versus young forests (β_{young} = -8.96 [-12.05, -5.88]; Figure 4A) and were more vigilant at risky versus safe patches in mature forest ($\beta_{mature:refuge}$ = -5.35 [-8.16, -2.54]; Figure 4B; Table S2), but not young forest. Woodrats also increased vigilance with increasing frequency of patch visits by other woodrats ($\beta_{nontarget\_visits}$ = 1.59 [0.76, 2.42]).

Stage 4: Patch quitting

Woodrat GUDs were double in mature versus young forest; further, woodrats exploited safe patches more within mature but not young forests (Figure 5A). Deer mice followed a similar pattern, as they foraged more at safe than risky patches in mature forests but not within young forests (Figure 5B). In addition to young forests ($\beta_{young} = -3.99$ [-6.72, -1.26]) and safe versus risky patches in mature forests ($\beta_{young:refuge} = -3.34$ [-5.73, -0.96]), woodrat GUDs decreased with increasing conspecific PRT ($\beta_{nontarget\_prt} = -1.70$ [-2.68, -0.72]) and canopy cover within young forests ($\beta_{young:cover} = -5.99$ [-8.42, -3.55]; Figure 5C; Table S2). For deer mice, GUDs were lower at safe versus risky patches ($\beta_{refuge} = -3.64$ [-5.62, -1.67]; Figure 5C; Table S3).

Harvest rate curves

Woodrat QHRs were significantly different between forest type-refuge treatment combinations ($F_{3,134} = 40.04$, $p < 0.0001$). The QHR slope was steepest and the attack rate highest at safe patches in mature forest (0.046 g/s), followed by approximately equal slopes and attack rates at both safe (0.016 g/s) and risky (0.014 g/s) patches in young forest, with shallowest QHR slopes and lowest attack rates at risky patches in mature forests (0.003 g/s; Figure 6A), indicating that the rate of harvest was quickest at safe patches in mature forest (i.e., apprehension is employed less as an antipredator strategy), while at mature-risky combinations woodrats foraged slowly and attentively. Accordingly, woodrats exhibited a characteristic QHR (i.e., QHR at mean GUD values) pattern of: Mature-safe (0.127g s^{-1}) > young-safe (0.063g s^{-1}) = young-risky (0.062g s^{-1}) > mature-risky (0.030g s^{-1}) and mean GUD pattern of: Mature-risky (14.45g) > mature-safe (11.55g) > young-risky (7.20g) > young-safe (6.19g).

Among deer mice, QHRs between forest type-refuge treatment combinations were also significantly different ($F_{3,78} = 7.378$, $p < 0.001$), yet followed different patterns than woodrats. QHR slopes were steepest and attack rates highest at safe patches in both young (0.030 g/s) and mature (0.025 g/s) forests, followed by considerably shallower slopes and lower attack rates at risky patches within mature (0.010 g/s) and young (0.088 g/s) forests (Figure 6B). Characteristic QHRs followed a different pattern of: Young-risky (0.056g s^{-1}) > young-safe (0.043g s^{-1}) = mature-safe (0.040g s^{-1}) = mature-risky (0.039g s^{-1}), and a mean GUD pattern of: Mature-risky (10.10g) > young-risky (5.75g) > mature-safe (4.85g) = young-safe (4.68g).

Discussion

We found that asymmetrical predation on a primary and secondary prey precipitated differences between the two species both in terms of risk perception and consequent strategies used to manage risk. Woodrats (primary prey) demonstrated behavioral responses to both forest type and refuge treatment at each stage of the foraging process, while deer mice (alternative prey) only exhibited behavioral responses associated with refuge treatment. Moreover, while refuge treatments decreased perceived risk among deer mice regardless of forest type, for woodrats its importance was contingent upon the specific forest type in which it was located. These findings highlight how background risk mediates the relative perception of immediate risk and how these interactions can vary between primary and secondary prey.

Habitat structure is frequently used as a proxy for risk perception (Gaynor et al., 2019). Given that spotted owls predominantly forage within mature forests (Zulla et al., 2022), we expected that primary prey would perceive and respond to elevated risk within those areas. Throughout the foraging process, woodrats consistently exhibited behavioral responses (A) within mature forests and (B) at refuge treatments within mature forests, but not within young forests. Together, these findings support the risk allocation hypothesis (Lima & Bednekoff, 1999); notably, that antipredator behavior is a product of both acute and background predation risk. In our study, refuge treatment modulated acute risk while forest type determined background risk, and woodrats responded to both. In contrast, deer mice responded only to cues of acute risk and rarely responded to background risk. More importantly, among deer mice the relative effect of refuge treatment on acute risk was not dependent on the level of background risk, suggesting then that secondary prey do not conform to the risk allocation hypothesis. Empirical support for the risk allocation hypothesis in natural settings has been mixed to-date (Ferrari et al., 2009), due in part to contingencies such as state dependencies (Matassa & Trussell, 2011; Moll et al., 2017). We show that even within the same community featuring a shared predator, prey may conform to or depart from the risk allocation hypothesis according to whether they are primary or secondary prey. Therefore, the spatiotemporal pattern of risk experienced by prey is an emergent outcome between not only the properties of the predator or the setting in which the encounter may take place, but also the magnitude of predation relative to the overall prey community (Sheriff et al., 2020; Wirsing et al., 2021).

Consumptive effects of predators on primary and secondary prey have received considerable attention in ecological research (Holt & Lawton, 1994). Predator-mediated apparent competition can yield various outcomes, from competitor exclusion to increased predator densities (Bonsall & Hassell, 1997; Wilson et al., 2022). In systems with a clear prey hierarchy, targeted consumption of primary prey can relieve secondary prey from predation pressure, increasing secondary prey abundance while simultaneously decreasing overall prey biomass (Holt & Lawton, 1994; Moran & Hurd, 1997). A small number of studies have linked antipredator behavior to factors such as the effectiveness of risk management strategies (Dellinger et al., 2019), community composition (Prasad & Snyder, 2006), or baseline risk prior to the addition of a novel predator (Makin et al., 2018). However, nonconsumptive effects within multi-prey systems, particularly within the paradigm of primary and secondary prey, still remain largely overlooked. The interactions between consumptive and nonconsumptive effects can vary in strength and nature (Matassa & Trussell, 2011) and increases in perceived risk can drive countervailing effects between lethal and nonlethal impacts (Prasad & Snyder, 2006). We found that primary – but not secondary – prey exhibit stronger antipredator behaviors that closely mirror actual patterns of risk.

Therefore, in addition to experiencing stronger consumptive effects, our findings suggest that primary prey invest more in antipredator strategies than secondary prey, resulting in greater nonconsumptive effects, particularly when background risk is high. Thus, the demographic consequences of nonconsumptive effects may also indirectly benefit alternative prey by decreasing competitor abundance in a manner similar to consumptive effects (Laundré et al., 2014; Moran & Hurd, 1997). Nevertheless, there may also be consequences for alternative prey. Asymmetrical and spatially accurate risk management by primary prey can indirectly affect the community by reducing the ratio of available prey and thereby increasing relative predation pressure on naive secondary species (Bonsall & Hassell, 1997). We contrasted the benefit of risk dilution and competitive release with the potential cost of enemy-mediated competition by testing whether the presence of interspecific foragers modulated perceived risk. However, none of our variables (i.e., presence, number of visits, or PRT) affected any stage of the foraging process for either woodrats or deer mice. In contrast, among woodrats conspecific activity influenced nearly every stage of the foraging process, underscoring the effect of group foraging on perceived risk and the value of a resource patch (Alexander, 1974; Carthey & Banks, 2015). While the loss or addition of species can have far-reaching trophic effects (Holt & Lawton, 1994) – and in some invertebrate systems may also have non-trophic effects (Moran & Hurd, 1997; Steffan & Snyder, 2010) – we did not find evidence for this in our system. Therefore, asymmetrical risk management may come at a cost to primary prey by elevating nonconsumptive effects with little to no net benefit to predators or secondary prey.

Beyond predation intensity, our study highlights additional drivers of NCE contingencies that arise from properties of predator and prey (Schmitz, 2007), especially predator hunting mode and the relative overlap of habitat domains between predator and prey (Gaynor et al., 2019; Schmitz et al., 2017). When prey are mobile and have broad domains, they typically select predator-free spatial refuge to minimize the likelihood of encounter (Dellinger et al., 2019; Wirsing et al., 2021). Conversely, when predator hunting domains overlap or exceed those of their prey – as with spotted owls – prey must rely more on behavioral adjustments and use local space in a manner that facilitates their evasion strategies (Schmitz et al., 2017). Predator hunting mode (e.g., active versus ambush predation) can also influence risk management strategies (Makin et al., 2017; Preisser et al., 2007). Ambush predators have a relatively continuous and spatially predictable presence (Brown, 1999; Zulla et al., 2022), which creates a heterogeneous pattern of background risk across their home range (Gaynor et al. 2019). While there were other predators within our study area, we do not believe this affected our results as we A) designed our refuge treatment to target avian predation, and B) only sampled within known, occupied spotted owl home ranges – although additional avian predators would likely reinforce, rather than diminish, any behavioral responses. Indeed, studies on small mammals have found that foraging under protective cover may reduce the risk of avian predation (Verdolin, 2006), but simultaneously increase the risk of predation from snakes or mammals (Embar et al., 2011). This may explain why the presence of vertical cover at a patch was only important in mature forests among woodrats. The decision to forage more at the “safe” patch within ostensibly “riskier” mature forest but not within young forest suggests that from a woodrat’s perspective, refuge treatments may represent islands of relative safety in a sea of risky forest (Embar et al., 2014). In contrast, for deer mice, changes in antipredator behavior relative to refuge treatment but not forest type suggest that outside of the immediate vicinity, perceived risk is relatively homogeneous by forest type and agnostic of the actual risk of encounter.

Evaluating the specific behavioral tools used to manage risk can refine our understanding of risk perception beyond GUDs and foraging time in the context of how organisms resolve the tradeoff between food and safety. Indeed, while the foraging cost of predation is a product of the magnitude of risk and the forager’s state (Kotler et al., 2010), the strategies used to manage it can vary by species, sensory modality, or even the relative investment in one strategy over another

(Kotler et al., 2010; Wirsing et al., 2021). By quantifying the relationship between foraging success and resource density, the slope and shape of the harvest curve illustrate how prey alter their use of time allocation and vigilance to manage risk under varying foraging conditions (Brown, 1999; Kotler et al., 2010). Through these, we show that within young forests woodrats use a combination of strategies to manage risk regardless of refuge treatment at the foraging patch. Yet, while woodrats responded to increased risk in mature forests with a lower average harvest, the manner by which they reached higher GUDs differed between refuge treatments. Specifically, woodrats at risky patches predominantly used vigilance to manage risk – as evidenced by shallower slopes – while at safe patches they mostly abandoned vigilance – resulting in steeper slopes. As a result, while time allocation was comparable between refuge treatments, at safe patches the quitting harvest rate was higher and GUD was lower. These reveal a nuanced response wherein vigilance is used to manage risk within ‘risky’ environments but is largely abandoned in the presence of a ‘safe’ refuge treatment. This may be a result of vigilance no longer being effective or necessary as the presence of vertical cover (Embar et al., 2011; Verdolin, 2006) reduces the acute risk of avian predation. In contrast, deer mice had comparable slopes, quitting harvest rates, and GUDs at safe patches regardless of forest type, suggesting that risk management strategies were predominantly affected by conditions at the foraging patch. However, we did detect differences between risky patches relative to forest type: in the absence of refuge within young forests, deer mice were more vigilant and harvested less food overall; in the absence of refuge in mature forests, they harvested more food but spent less time foraging and quit the patch even when the rate of return was high. Taken together, these results demonstrate a behavioral approach wherein vigilance and time allocation are used to manage risk by both primary and secondary prey, but in different manners and under at times, opposing circumstances. For woodrats, our findings align with previous studies that demonstrate that vigilance is used more in locations where background risk is high and when acute risk is also high, but not when acute risk is low (Dröge et al., 2017; Embar et al., 2011). In contrast, deer mice used vigilance more where acute risk was high and when background risk was low, but not when background risk was high. These results also then suggest that primary prey are responsive to and manage for both background and acute threats whereas secondary prey primarily rely upon managing acute threats to mitigate risk.

Our findings provide some of the first empirical evidence that among a diverse prey guild within a spatially heterogeneous environment, asymmetrical predation can modulate not only the magnitude of antipredator behaviors, but also the specific strategies used to manage risk. These behavioral differences between primary and secondary prey have implications for both the species involved as well as the community when contrasted with the direct effects of asymmetrical predation. Consumptive effects impose costs only on those animals actually consumed, which translate to direct benefits for the predator (Ives & Dobson, 1987), while the costs of NCEs are paid by the entire prey population and do not benefit (or lead to more) predators (Ives & Dobson, 1987; Wirsing et al., 2021). Further, antipredator behaviors produce feedbacks in predation rates and the predator population more rapidly than feedback from direct consumption (Ives & Dobson, 1987), which may stabilize oscillations in predator and prey densities (Laundré, 2010). The presence of multiple prey species – particularly when one is disproportionately targeted – adds additional complexity to these dynamics. While primary prey experience greater consumptive effects (i.e., per-capita mortality rates) than secondary prey, we show that the relative difference in nonconsumptive effects between the two is even greater when background risk is high, yet reduced when background risk is low. Thus, if risk-induced fitness consequences have an additive rather than compensatory effect on prey, these differences can alter population size, and in turn, community assemblages (Donadio & Buskirk, 2016). Amidst a growing literature of NCEs, there is a drive to understand how risk influences population size and the manner in which species are represented in a given environment (Sheriff et al., 2020). Here, we highlight an important and understudied contingency in how predation risk effects among prey may extend to population- and community-level responses.

These differences may have emergent consequences for predator populations as well. Optimal foraging theory suggests that a predator should select the most beneficial prey in terms of net energy gain relative to searching and handling time (Stephens & Krebs, 1986). When primary prey exhibit stronger antipredator behavior that accurately reflects background risk, the tradeoff between biomass and naivete may influence patterns in dietary specialization. Spotted owls benefit from selecting prey that most efficiently balance foraging costs with energetic returns (Hobart et al., 2019; Stephens & Krebs, 1986). As such, woodrats often dominate owl diets in occurrence and biomass (Hobart et al., 2019), although in many parts of their range owls still consume a sizable number of alternative prey including deer mice (Kuntze et al., 2023; Zulla et al., 2022). Increasing consumption of larger-bodied woodrats has emergent benefits for spotted owl occupancy and fitness (Hobart et al., 2019; Kuntze et al., 2023). However, overreliance on risk-averse species may increase energetic expenditures associated with prey searching, particularly when primary prey abundance is low (Balme et al., 2020; Ives & Dobson, 1987), highlighting a potential benefit of consuming naïve deer mice. Asymmetrical predation is not uncommon among prey guilds with shared predators (Holt & Lawton, 1994). Therefore, these findings have conservation implications for both predators and prey beyond the ones studied here. While high-quality prey are typically the prominent driver of population dynamics among relatively specialized predators (Hobart et al., 2019; Kuntze et al., 2023), we suggest that the naivete of alternative prey may allow individuals to better exploit this resource base and meet energetic demands during periods of low primary prey availability or within highly impacted ecosystems (Balme et al., 2020). Evaluating consumptive and nonconsumptive effects through the paradigm of primary and secondary prey may improve predator conservation as well as our understanding of how NCEs propagate through complex communities.

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Figure 1: Overview of the study design for exploring antipredator behavior among dusky-footed woodrats (*Neotoma fuscipes*) and deer mice (*Peromyscus* spp.) within the central Sierra Nevada, CA, USA. The conceptual diagram (A) outlines the response variables quantified at each stage of the foraging process and the harvest rate curve which synthesizes behaviors and values from stages 2-4. Also shown are the average mass and specific foraging stages explored for both woodrats (left) and deer mice (right). The locations of foraging stations (B) are shown within 95% kernel home ranges (colored outlines) of GPS-tagged spotted owls *(Strix occidentalis*) relative to mature (C; green) and young (D; turquoise) forests. Each foraging station consisted of two individual patches with either a risky (E) or refuge treatment (F).

Figure 2: Number of nightly patch visits by dusky-footed woodrats (*Neotoma fuscipes*) and deer mice (*Peromyscus* spp.). Figures represent raw values and relationships relative to forest type and refuge treatment for woodrats (A) and deer mice (B), and coefficient estimates (C) from each best-supported LMM and their associated 95% confidence intervals with significance denoted by solid circles. The reference level for categorical modalities are ‘mature’ for forest type, ‘risky’ for treatment, and ‘female’ for sex.

Figure 3: Cumulative patch residence time (PRT) by dusky-footed woodrats (*Neotoma fuscipes*) and deer mice (*Peromyscus* spp.) during an experimental night. Figures represent raw values and relationships relative to forest type and refuge treatment for woodrats (A) and deer mice (B), and coefficient estimates (C) from each best-supported LMM and their associated 95% confidence intervals, with significance denoted by solid circles. The reference level for categorical modalities are ‘mature’ for forest type and ‘risky’ for treatment.

Figure 4: Percentage of nightly patch residence time allocated to vigilance behavior among dusky-footed woodrats (*Neotoma fuscipes*). Figures represent raw values and relationships relative to forest type and refuge treatment (A), and coefficient estimates (B) from the best-supported LMM and associated 95% confidence intervals with significance denoted by solid circles. The reference level for categorical modalities are ‘mature’ for forest type and ‘risky’ for treatment.

Figure 5: Giving-up densities (GUD) for dusky-footed woodrats (*Neotoma fuscipes*) and deer mice (*Peromyscus* spp.). Figures represent raw values and relationships relative to forest type and refuge treatment for woodrats (A) and deer mice (B), and coefficient estimates (C) for both species from each best-supported LMM and their associated 95% confidence intervals with significance denoted by solid circles. The reference level for categorical modalities are ‘mature’ for forest type, ‘risky’ for treatment, and ‘subadult’ for age.

Figure 6. Harvest rate curves for dusky-footed woodrats (*Neotoma fuscipes*; A) and deer mice (*Peromyscus* spp.; B) within four combinations of forest type and refuge treatment: mature/refuge, mature/risky, young/refuge, and young/risky. Estimates of quitting harvest rates appear as functions of food density within the foraging patch. Curves are created by estimating attack rates and handling times from foraging data and fitting them to Holling’s disc equation. For each combination, we plot the estimated quitting harvest rate (QHR) derived from GUD values and the disc equation. Red circles represent the characteristic QHR at mean GUD values for each group. Shallower slopes correspond with higher levels of vigilance; giving-up densities lying closer to the origin correspond with greater time allocation to foraging.

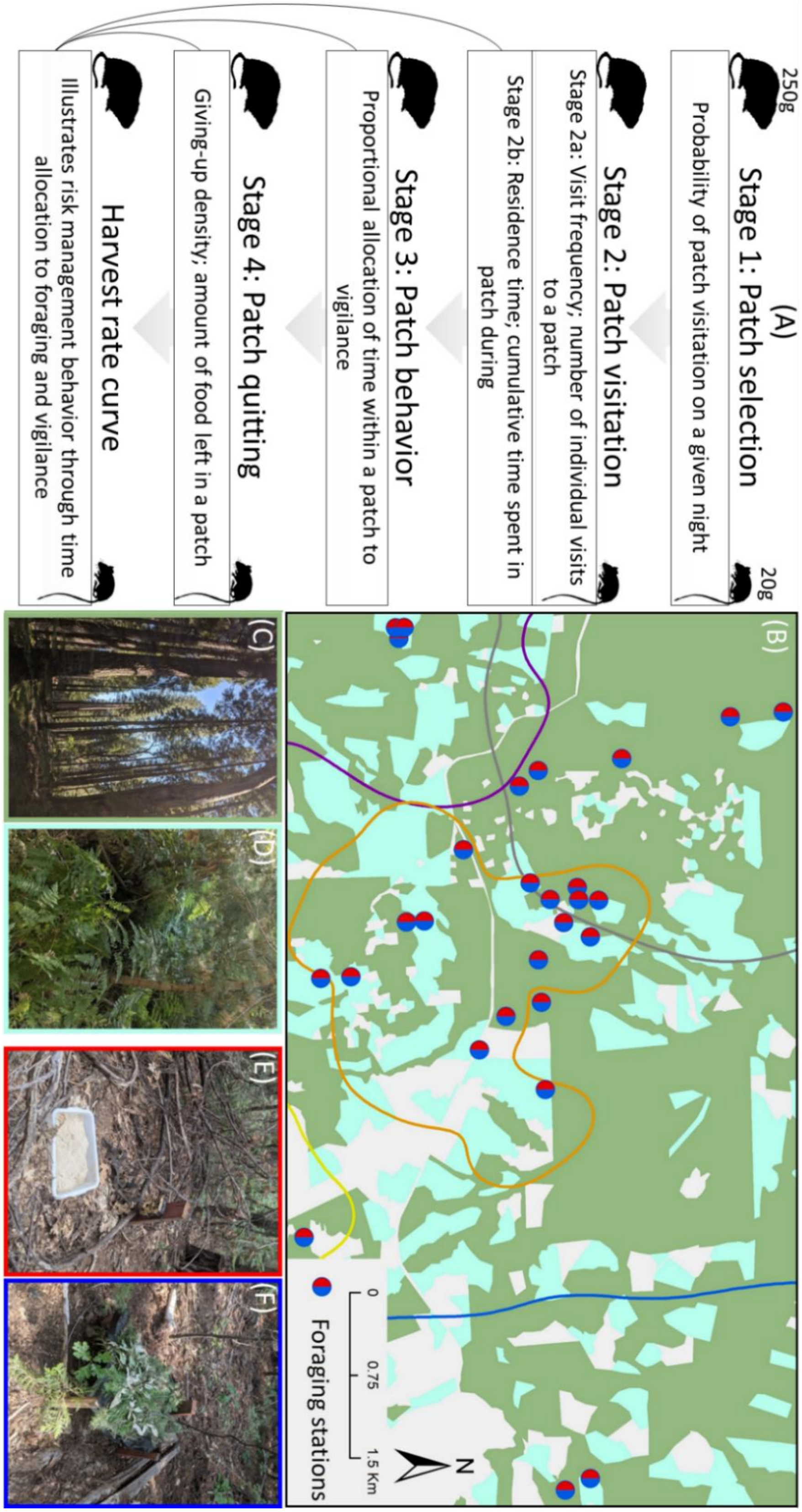
(A)
250g
20g
Stage 1: Patch selection
Probability of patch visitation on a given night
Stage 2: Patch visitation
Stage 2a: Visit frequency; number of individual visits to a patch
Stage 2b: Residence time; cumulative time spent in patch during
Stage 3: Patch behavior
Proportional allocation of time within a patch to vigilance
Stage 4: Patch quitting
Giving-up density; amount of food left in a patch
Harvest rate curve
Illustrates risk management behavior through time allocation to foraging and vigilance
(B)
0
0.75
1.5 Km
N
Foraging stations
(C)
(D)
(E)
(F)

Figure 1

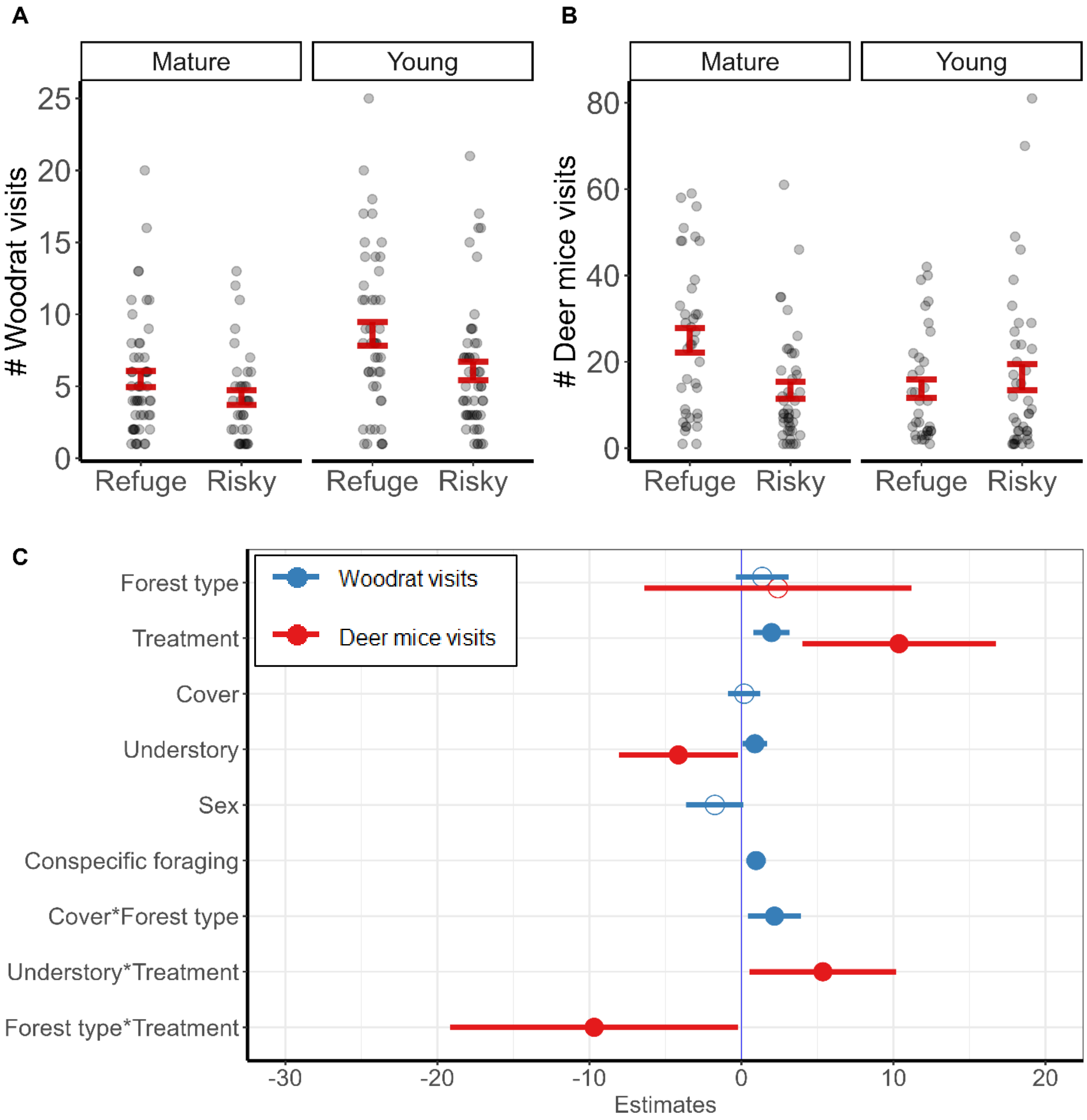
A
Mature
Young
Woodrat visits
0
5
10
15
20
25
Refuge
Risky
Refuge
Risky
B
Mature
Young
Deer mice visits
0
20
40
60
80
Refuge
Risky
Refuge
Risky
C
Woodrat visits
Deer mice visits
Forest type
Treatment
Cover
Understory
Sex
Conspecific foraging
Cover*Forest type
Understory*Treatment
Forest type*Treatment
-30
-20
-10
0
10
20
Estimates

Figure 2

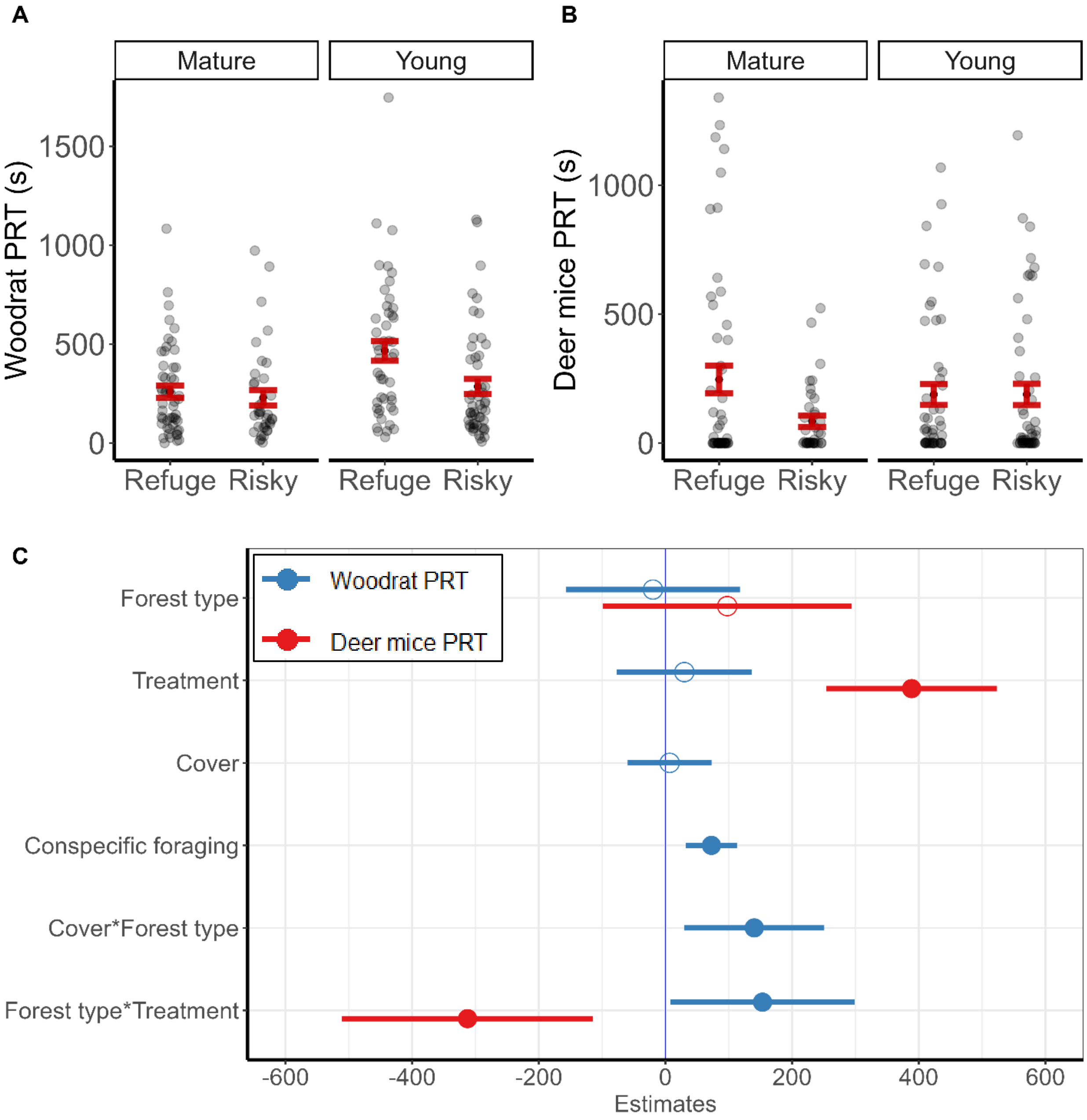
A
Mature
Young
Woodrat PRT (s)
1500
1000
500
0
Refuge
Risky
Refuge
Risky
B
Mature
Young
Deer mice PRT (s)
1000
500
0
Refuge
Risky
Refuge
Risky
C
Woodrat PRT
Deer mice PRT
Forest type
Treatment
Cover
Conspecific foraging
Cover*Forest type
Forest type*Treatment
-600
-400
-200
0
200
400
600
Estimates

Figure 3

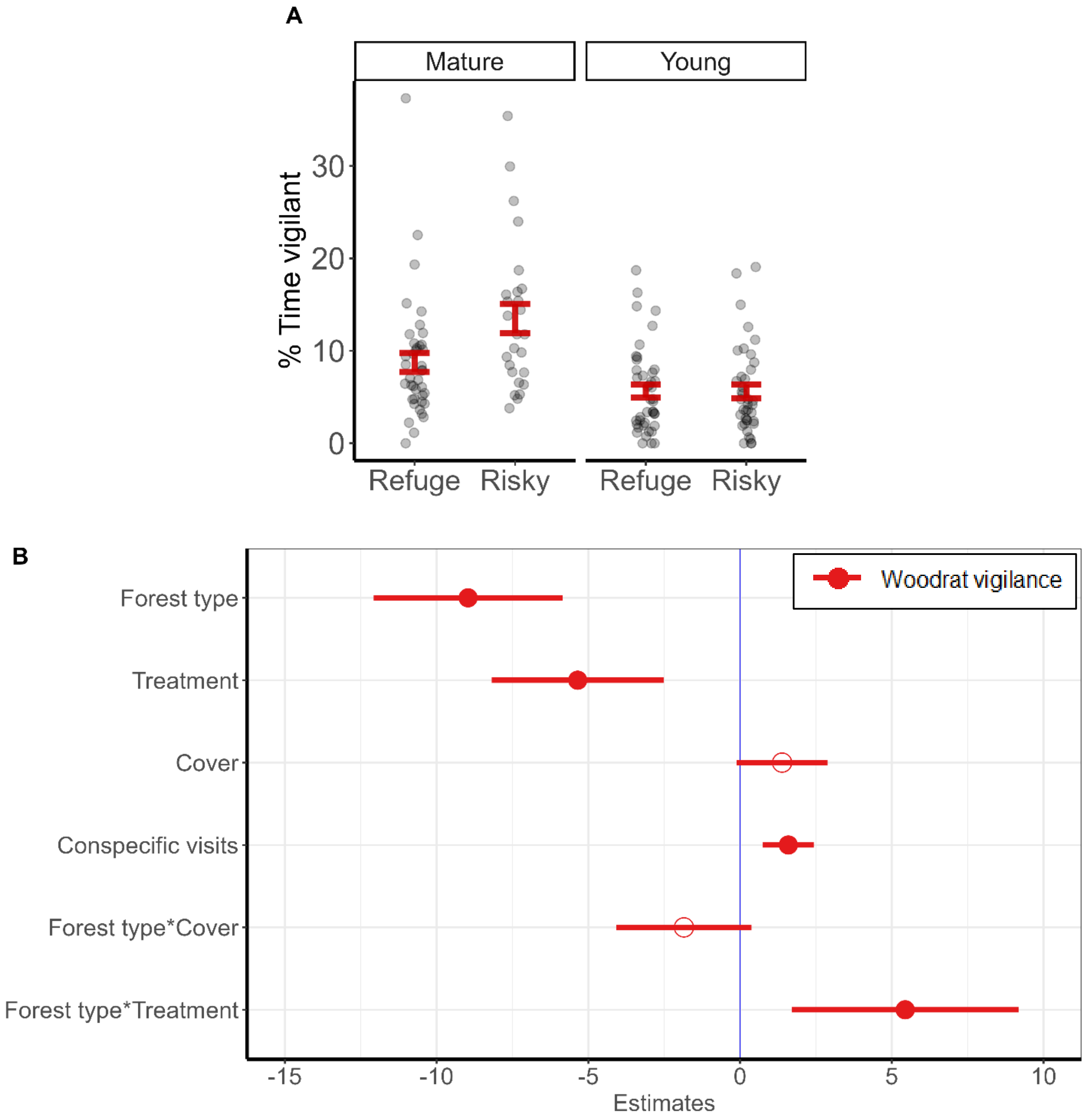
A
Mature
Young
% Time vigilant
0
10
20
30
Refuge
Risky
Refuge
Risky
B
Woodrat vigilance
Forest type
Treatment
Cover
Conspecific visits
Forest type*Cover
Forest type*Treatment
-15
-10
-5
0
5
10
Estimates

Figure 4

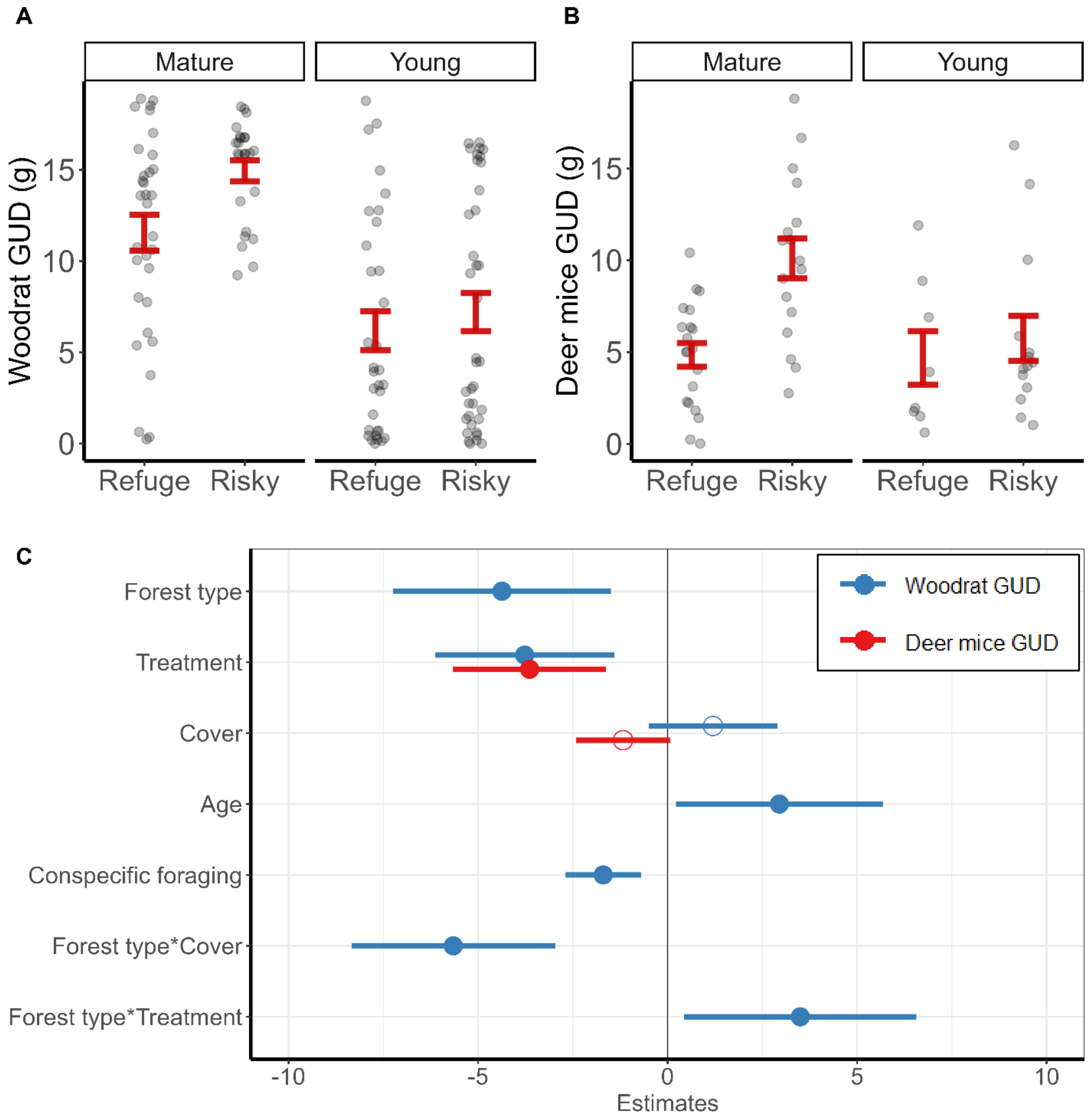
A
B
Mature
Young
Mature
Young
Woodrat GUD (g)
Deer mice GUD (g)
0
5
10
15
Refuge
Risky
Refuge
Risky
Refuge
Risky
Refuge
Risky
C
Forest type
Treatment
Cover
Age
Conspecific foraging
Forest type*Cover
Forest type*Treatment
Woodrat GUD
Deer mice GUD
-10
-5
0
5
10
Estimates

Figure 5

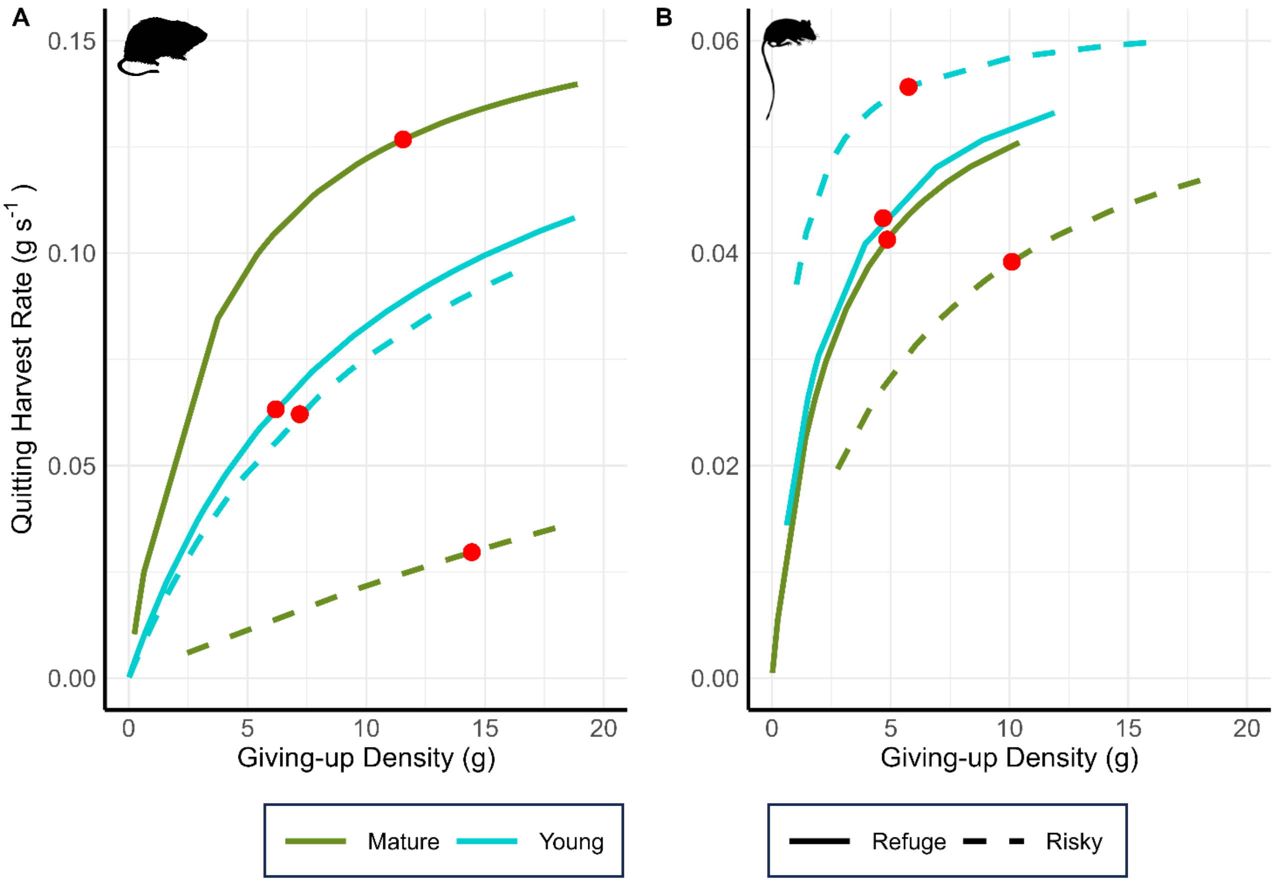
A
B
Quitting Harvest Rate (g s^{-1})
0.15
0.10
0.05
0.00
0.06
0.04
0.02
0.00
0
5
10
15
20
Giving-up Density (g)
Mature
Young
Refuge
Risky

Figure 6

Supporting Information

Appendix S1 – Supplementary methods

Field methods for capturing and monitoring woodrats

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. Individuals were ear punched and marked with a unique ear tag (Model 1005-1; National Band & Tag Company, Newport, KY) or passive integrated transponder (PIT) tag (Avid Identification Systems, Norco, CA). A subsample of these individuals (*n* = 73) weighing above 120g were fit with VHF collars (Lotek model TW-5, 10g; Lotek Wireless Inc, Newmarket, Ontario, Canada or Telenax model TXE-116C, 6g; Titley Scientific, Columbia, Missouri, USA) equipped with onboard activity sensors, which allowed us to monitor movement patterns and detect mortality events shortly after they occurred. All captures were done with approval by the Institutional Animal Care and Use Committee of the University of Wisconsin, Madison (IACUC #A006173-A01), and followed guidelines from the American Society of Mammalogists (Sikes et al. 2016).

Literature Cited

Sikes, R. S. and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Table S1. Model covariates used for quantifying foraging behavior of dusky-footed woodrats (*Neotoma fuscipes*) and deer mice (*Peromyscus* spp.) in the Sierra Nevada, California, USA.

Category	**Variable**	**Description**
Habitat	Forest type	Forest structure designation defined by canopy cover and quadratic mean diameter of dominant trees (mature, young)
	Treatment	Presence/absence of artificial cover structure at foraging patch (risky, refuge)
	Canopy cover	Proportion of sky obscured by canopy >2m height within 12.5m
	Basal area	Total basal area (m^2) of all live and dead standing trees <2m height within 12.5m
	Understory	Proportion of ground obscured by vegetation <2m height within 12.5m
Intrinsic (Woodrat only)	Body condition	Residuals from the regression of body mass against hind foot length; positive values represent individuals in better body condition while negative values represent poor body condition
	Age	Age class of target individual (adult, subadult)
	Sex	Sex of target individual (female, male)
Other foragers (Stage 1-4)	Conspecifics	Presence/absence of additional woodrats beyond the target individual (yes, no; woodrat only)
	Woodrat	Presence/absence of woodrats (yes, no; deer mice only; not included in patch quitting)
	Deer mouse	Presence/absence of deer mice (yes, no; woodrat only; not included in patch quitting)
Other foragers (Stages 2-4)	Nontarget visits	Number of visits to a patch in one of four forms: A) all woodrats, B) nontarget woodrats, C) deer mice, or D) nontarget woodrats and deer mice
	Nontarget foraging	Cumulative time spent in patch (s) in one of four forms: A) all woodrats, B) nontarget woodrats, C) deer mice, or D) nontarget woodrats and deer mice

Table S2. — Results of (generalized) logistic and linear mixed effects models quantifying foraging behavior for dusky-footed woodrats (*Neotoma fuscipes*) in the central Sierra Nevada, California, USA. Significant relationships are bolded at α = 0.05 and italicized at α = 0.1.

Variable	Visitation		# Patch visits		Patch residence		Vigilance		GUD	
	β ± SE	*p*	β ± SE	*p*	β ± SE	*p*	β ± SE	*p*	β ± SE	*p*
Intercept	0.96 ± 1.06	0.368	3.63 ± 0.78	**<0.001**	190.59 ± 52.44	**<0.001**	14.57 ± 1.23	**<0.001**	13.17 ± 1.13	**<0.001**
Forest type	2.76 ± 1.43	*0.054*	1.37 ± 0.88	0.14	-19.69 ± 69.61	0.778	-8.96 ± 1.57	**<0.001**	-3.99 ± 1.39	**0.008**
Treatment	1.87 ± 0.59	**0.002**	1.98 ± 0.61	**<0.001**	29.86 ± 53.98	0.581	-5.35 ± 1.43	**<0.001**	-3.34 ± 1.22	**0.007**
Cover			0.18 ± 0.54	0.735	6.66 ± 33.54	0.844	1.38 ± 0.76	*0.069*	1.33 ± 0.81	0.116
Understory			0.88 ± 0.4	**0.044**						
Sex	-3.11 ± 1.38	**0.025**	-1.75 ± 0.96	*0.084*						
Age									2.73 ± 1.29	*0.051*
Nontarget woodrat	1.07 ± 0.50	**0.031**								
Nontarget woodrat PRT			0.96 ± 0.33	**0.004**	72.65 ± 20.43	**0.001**			-1.78 ± 0.51	**<0.001**
# Nontarget woodrat visits							1.59 ± 0.42	**<0.001**		
Forest type * Cover			2.18 ± 0.88	**0.024**	140.29 ± 56.00	**0.018**	-1.85 ± 1.13	0.103	-5.99 ± 1.24	**<0.001**
Forest type * Treatment	-2.82 ± 0.94	**0.003**			153.29 ± 73.83	**0.039**	5.44 ± 1.89	**0.005**	2.98 ± 1.59	*0.064*

Effects (β) and their standard error (SE) are displayed as well as *p* values from model comparisons. All continuous variables have been standardized. The reference level for categorical modalities are mature for forest type, risky for treatment, female for sex, 'adult' for age class, and no for visitation by nontarget woodrat. Variables that are present on Table 1 but missing here were still tested; covariates that were not present in any final model sets are not included on this table for easier interpretability.

Table S3. — Results of (generalized) logistic and linear mixed effects models quantifying foraging behavior for deer mice (*Peromyscus* spp.) in the central Sierra Nevada, CA, USA. Significant relationships are bolded at α = 0.05 and italicized at α = 0.1.

Variable	Visitation		# Patch visits		Patch residence		GUD	
	β ± SE	*p*	β ± SE	*p*	β ± SE	*p*	β ± SE	*p*
Intercept	0.08 ± 0.52	0.874	13.22 ± 2.91	**<0.001**	160.41 ± 64.91	0.018	7.91 ± 0.86	**<0.001**
Forest type			2.4 ± 4.44	0.592	97.55 ± 99.21	0.333		
Treatment			10.37 ± 3.22	**0.002**	388.81 ± 68.2	**<0.001**	-3.64 ± 1.01	**0.001**
Cover							-1.17 ±0.62	*0.099*
Understory			-4.15 ± 1.98	**0.042**				
Forest type * Treatment			-9.69 ± 4.79	**0.045**	-312.5 ± 100.33	**0.002**		
Treatment * Understory			5.36 ± 2.44	**0.030**				

Effects (β) and their standard error (SE) are displayed as well as *p* values from model comparisons. All continuous variables have been standardized. The reference level for categorical modalities are 'young' for forest type and 'safe' for treatment. Variables that are present on Table 1 but missing here were still tested; covariates that were not present in any final model sets are not included on this table for easier interpretability.

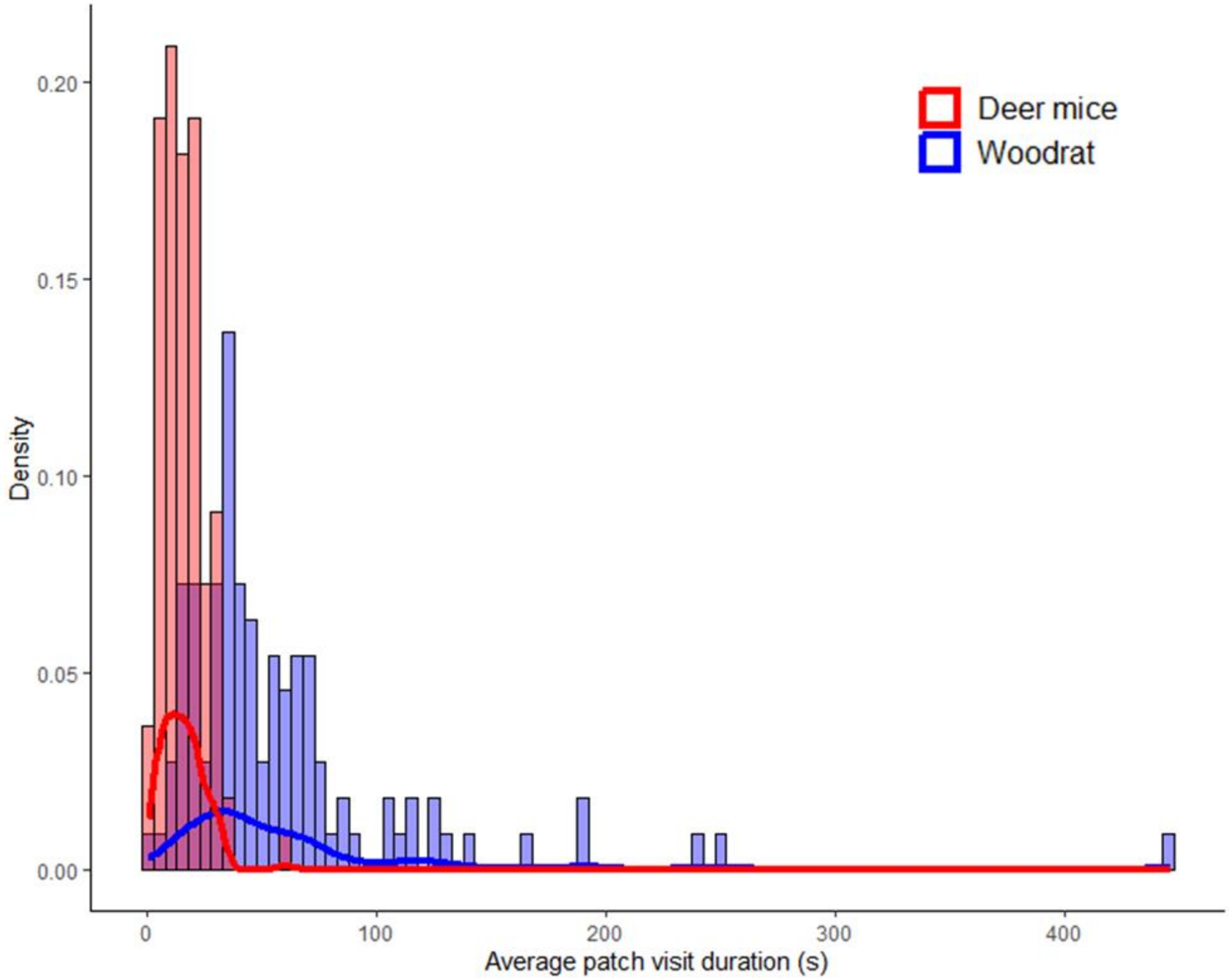

Figure S1: Distribution of nightly values for average patch visit duration among dusky-footed woodrats (*Neotoma fuscipes*) and deer mice (*Peromyscus* spp.).

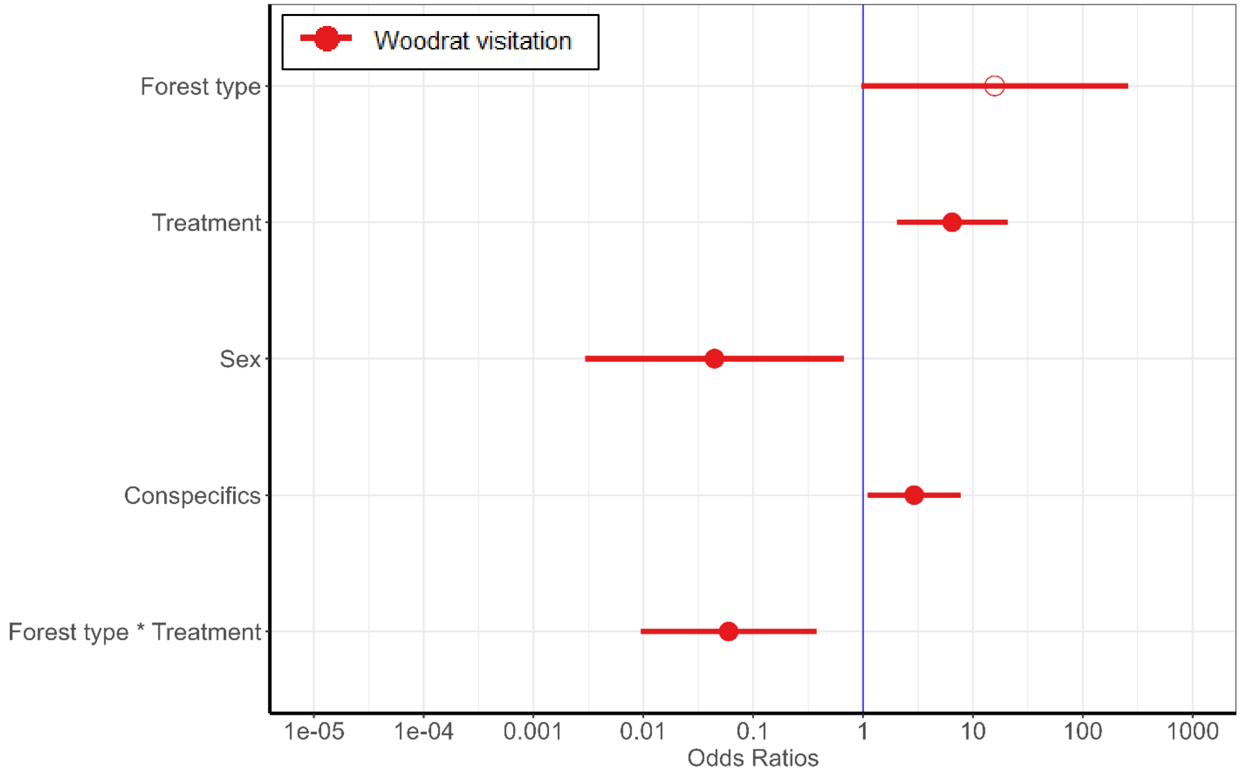

Figure S2: Odds ratios for patch visitation probabilities (Stage 1) among dusky-footed woodrats (*Neotoma fuscipes*) from the best-supported mixed effects logistic regression model and associated 95% confidence intervals with significance denoted by solid circles. The reference level for categorical modalities are ‘mature’ for forest type, 'risky' for treatment, 'female' for sex, and 'no' for visitation by nontarget woodrat. Odds ratios for deer mice (*Peromyscus spp.*) visitation are not displayed because the top model was the intercept model.

Chapter 4: Multi-scale forest heterogeneity promotes occupancy of dusky-footed woodrats in the Sierra Nevada

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In preparation for *Forest Ecology and Management*

Abstract

Forested landscapes are naturally heterogeneous, with the distribution of resources influencing animal habitat selection at multiple spatial scales. However, anthropogenic activities and changing disturbance regimes have reorganized how forests are structured from fine- to landscape scales, including creating more homogeneous dry forest ecosystems devoid of small patches of early-successional patches – generally with unknown consequences to forest-associated wildlife. As forest management aims to improve forest resilience to extreme fire and drought by restoring historical disturbance regimes, there is a need for studies that evaluate how animals respond to forest heterogeneity at multiple scales. Here, we characterized occupancy patterns relative to forest structure and composition at site-, patch-, and landscape-scales for the dusky-footed woodrat (*Neotoma fuscipes*), an important prey species for a variety of forest predators including the

California spotted owl (*Strix occidentalis occidentalis*), within landscapes where forest heterogeneity was created by even-aged timber management. Woodrats were more likely to occupy sites with greater canopy cover, understory cover, and hardwoods - particularly tanoak (*Notholithocarpus densiflorus)* - and smaller patches of young forest. Woodrats were also more likely to occur in mature forests in close proximity to younger forest, suggesting that young forest patches with more favorable local conditions can produce populations that recruit into adjacent, lower-quality mature forests. Finally, we developed a habitat suitability model for woodrats using remotely-sensed data that will help managers predict how forest management activities affect woodrat occurrence across much of the Sierra Nevada. Our results suggest that creating small (~2 ha) patches of high-quality woodrat habitat (i.e., young forests with dense understory and hardwoods) could provide foraging opportunities for spotted owls and support higher woodrat densities in surrounding mature forests managed for fuels – thus helping to meet both spotted owl conservation and forest resilience objectives. More broadly, we highlight the benefits of multi-scale studies and demonstrate that restoring landscape heterogeneity, including the creation of small early successional forests, may benefit species conservation without compromising efforts to improve resilience in forest ecosystems globally.

Keywords: Forest management, heterogeneity, multi-scale occupancy modeling, Sierra Nevada, spotted owl, woodrat

Introduction

Forested landscapes are naturally heterogeneous (Wiens, 1995), characterized by patterns in vegetation structure, composition, and configuration that vary at multiple spatial scales (Bullock et al., 2022; Gauthier et al., 2010). Accordingly, habitat selection by forest-associated animal species represents a scale-dependent, hierarchical process (Holland et al., 2004; Orrock et al., 2000; Mayor et al., 2009). At a local scale, individuals select for vegetation features that provide foraging opportunities, concealment from predators, and den or nest sites (McMahon et al., 2017; Schooley, 2006), which collectively determine the quality of a habitat patch (Wiens, 1989). Patch characteristics (e.g., area, perimeter, isolation) and the juxtaposition of patch types within the surrounding landscape can shape spatial structure in populations through metapopulation and source-sink dynamics (Freckleton et al., 2005; Ritchie, 1997). Landscape and patch features may also mediate competitive and predator-prey interactions between species that perceive or use the environment at divergent spatial scales (Sollman et al., 2016; Zulla et al., 2022; Kuntze et al., 2023). Thus, scale-dependent ecological processes can have emergent consequences for the distribution and abundance of forest-associated species (Andrén, 1994; Boyce et al., 2003). Understanding how species select habitat across spatial scales is essential for predicting population responses to landscape changes and designing evidence-based conservation strategies (Bowyer and Kie, 2006; Rettie and Messier, 2000; Schweiger et al., 2021). However, in practice consideration of scale is rarely intuitive (Levin, 1992), and often driven by logistics rather than theory – resulting in studies limited by a focus on *priori*-selected scales or specific habitat features (Schweiger et al., 2021).

Rapid environmental changes and anthropogenic activities are redefining the structure, function, and composition of forest landscapes worldwide (Bullock et al., 2022; Seastedt et al., 2008), with some of the most pronounced changes occurring in forests shaped by natural disturbance processes (Collins et al., 2017; Steel et al., 2022). In dry forest ecosystems, spatial heterogeneity was historically maintained by wildfires that varied in frequency, severity, and size (McLauchlan et al., 2020; North et al., 2017; Steel et al. 2015). These produced a landscape mosaic of mature, large tree-dominated forests interspersed with patches of early successional, younger forest that supported high biodiversity (Boisramé et al., 2017). However, widespread fire suppression and the elimination of Indigenous burning practices, coupled with selective logging of large trees, has created denser, more homogeneous forests with fewer large trees and early successional patches on many public lands (North et al., 2017; Steel et al., 2015). As a result, ecological processes are changing too, often at the expense of species that occur and evolved within these naturally complex ecosystems (Devictor et al. 2008; Henle et al. 2004). Early-successional habitats, such as young forests, are an important component of many forest ecosystems as they have distinctive characteristics and can sustain high species diversity, including numerous early-successional obligates (Allen et al., 2022; Fontaine et al., 2009). Forest management that removes or artificially restores these disturbed forest areas can therefore have significant consequences for the species and processes that rely on them (Franklin et al., 2002; Swanson et al., 2011). For predators, the elimination of these early-seral stages can reduce prey diversity and abundance (Benedek and Sîrbu, 2018; Ehrlén and Morris, 2015), which in turn can reduce fitness or increase the frequency of antagonistic competitive interactions (Davies et al. 2021; Parsons et al. 2022). Therefore, understanding scales of habitat selection is essential for understanding not only the distribution and abundance of focal taxa, but may also be important for understanding the distribution and abundance of their predators.

A number of forest management approaches seek to restore the historical processes of disturbance-prone dry forests (Bullock et al., 2022; Gaines et al., 2022; Steel et al., 2022). However, it can be challenging to recreate ecosystems that resemble historical conditions as these processes developed under a different time, climate, and environment (Watts et al., 2020). Contemporary timber management and prescribed or managed fire use may emulate a natural mosaic of vegetation types by creating patches of early successional habitat that regenerate following planting and natural reseeding (Collins et al., 2017; Gaines et al., 2022), but evidence is mixed as to whether animals respond similarly to manufactured versus natural disturbances (Farrell et al., 2019; Zimmerling et al., 2017). Studying habitat selection and species interactions within forested landscapes managed for timber production and that contain earlier successional patches can provide valuable insights into how to recreate historically heterogeneous forests and meet biodiversity objectives (Arroyo-Rodríguez et al., 2020; Bullock et al., 2022). This is particularly important as managers seek to improve forest resilience to extreme fire and drought by reintroducing low-to-moderate disturbance events (Collins et al., 2017; Steel et al., 2022), highlighting the need for studies that allow us to extrapolate across scales and identify mutually beneficial strategies (Bullock et al., 2022).

The dusky-footed woodrat (*Neotoma fuscipes*) is an early-successional species in the Sierra Nevada, California, USA, that represents one of the largest and most energetically profitable prey for a range of forest predators (Ward Jr et al., 1998; Weathers, 1996) including the California spotted owl (*Strix occidentalis occidentalis*). Woodrat consumption is linked to emergent population benefits for mature forest-associated spotted owls (Franklin et al., 2000; Hobart et al., 2019), yet woodrats themselves are typically associated with younger forests and local forest conditions (e.g., structural complexity and dense understory cover) on timber-managed landscapes that can run counter to some fuels reduction goals (Carraway and Verts, 1991; Fraik et al., 2023). Patch and landscape characteristics also play a role in facilitating these crucial predator-prey interactions. Spotted owls capture and consume more woodrats with increasing young forest and forest heterogeneity at a home-range-scale (Hobart et al., 2019; Kuntze et al., 2023; Wilkinson et al., 2023) – which may be driven by higher woodrat abundances in young forests or increased capture opportunities of dispersing woodrats along the edge between mature and young forests (Sakai and Noon, 1997; Zulla et al., 2022). However, while these studies suggest that multi-scale processes may be important to woodrat populations, they typically occur at limited spatial scales or are predominantly designed around spatial scales or habitat features most salient to spotted owls most salient to spotted owls. While this is advantageous for understanding predator foraging patterns, this perspective may make it difficult to discover nuance in the linkages between prey and forest management. Further, we lack a mechanistic understanding of the underlying processes—such as source-sink dynamics—that can mediate woodrat population dynamics from a landscape context. Therefore, studies that evaluate patterns and processes across multiple spatial scales will improve our ability to develop management approaches that increase woodrat availability to spotted owls without compromising overall forest resilience.

Herein, we characterized patterns in woodrat site occupancy within a heterogeneous landscape defined by a mosaic of stand ages created by even-aged timber management, hypothesizing that woodrats respond to forest composition and structure at site-, patch-, and landscape-scales. At the site scale, we predicted that occupancy would increase when dense understory and masting hardwoods were more prevalent because of greater protective cover and resource availability. At the patch scale, we anticipated that woodrat occupancy would be highest in young forests owing to greater resource availability and lower risk of predation. At the landscape scale, we predicted that occupancy would be high when heterogeneity in forest types was high and, in mature forests, when more young forests occurred in proximity because of dispersal from these high-density patches. Finally, we developed a habitat suitability model for woodrats across much of the Sierra Nevada using high resolution remotely-sensed data to help assess how forest management activities might affect this key prey species. While many studies on small mammal populations focus on local habitat features, environmental processes and forest management decisions often occur at patch- and landscape-scales. Therefore, understanding how habitat features that vary at different scales can affect occupancy may both improve our knowledge of woodrat ecology and help inform best management practices for forest restoration and spotted owl conservation.

Methods

Study area

Our study took place on the western slope of the central Sierra Nevada, California, USA (Fig. 1), primarily within the Eldorado Demography Study Area (EDSA), a long-term spotted owl monitoring region that encompasses ~355 km^2 of the Eldorado National Forest. Elevation in this region ranges from 366-2257 m, although our work primarily took place within ~1,000 to 1,500 m, a range that was most likely to contain abundant woodrat populations (Innes et al., 2007). Here, differences in forest management practices over time and among landownership types have formed a landscape defined by a spatially heterogeneous mix of forest conditions described in detail elsewhere (Kuntze et al., 2023; Zulla et al., 2022; Jones et al. 2021). Briefly, within public forests, a legacy of fire suppression coupled with the selective removal of large trees since the late 19th century has created contiguous and spatially homogeneous stands of mature trees (Stephens et al., 2015). In comparison, on private lands frequent, even-aged timber harvesting has created a mosaic of patches that vary in size and successional stage, producing forests that are on average 30-40 years younger with less vertical structure than those on public lands (North et al. 2017).

The predominant forest type was Sierran mixed-conifer and primary vegetation included ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), and several hardwood species including California black oak (*Quercus kelloggii*) and tanoak (*Notholithocarpus densiflorus*). Both of these hardwood species seldom occupy entire stands and are typically found as single trees or in small clumps among conifer associates (McDonald, 2002); this was particularly true for tanoaks, which were patchily distributed throughout the study area (Fites-Kaufman et al., 2007). Further, while black oak and tanoak each have a shrub form that allows for growth in poorer sites and at higher elevations (McDonald, 2002), in our study area the majority of tanoaks existed as dense clusters of stems emerging from a single base while black oaks predominantly existed as larger trees. Primary understory species included saplings of the aforementioned conifer and hardwood species in addition to deerbrush (*Ceanothus integerrimus*), mountain whitethorn (*C. cordulatus*), manzanita (*Arctostaphylos manzanita*), and young Pacific dogwood (*Cornus nuttallii*).

Woodrat trapping surveys

To characterize patterns in occupancy, we live-trapped woodrats between May and August in 2020 and 2021. We deployed grids of 64 traps spaced 50m apart in 8x8 or 4x16 configurations within eight occupied spotted owl home ranges (Fig. 1). These home ranges were created by centering circular buffers around the most recent known nest or roost site for the respective spotted owl pair with a 2.12 km radius – equal to the median home range of all males tagged for a minimum of 25 days (14.12 km^2) from previous studies (Atuo et al., 2019; Zulla et al., 2022). To determine grid placement within home ranges, we first used imagery from the National Agricultural Imagery Program (NAIP) to manually digitize patches of relatively uniform vegetation conditions within ArcGIS following protocols described in Tempel et al. (2014). We defined three predominant forest types 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 area (<40% canopy cover). Then, we classified home ranges with predominantly mature forest in large, contiguous stands as 'homogeneous' (n = 4) and home ranges with a more even mixture of forest types and patch sizes as 'heterogeneous' (n = 4). These designations were supported with estimates of Shannon's diversity index, wherein forest types were more uniformly represented within heterogeneous home ranges ($\hat{H}$ = 0.92, range = 0.79 – 1.05; mean areas = 58.8% mature, 27.9% young, and 12.2% open) compared to homogeneous ones ($\hat{H}$ = 0.65, range = 0.57 – 0.71; mean areas = 78.6% mature, 9.9% young, and 11.5% open; Kuntze et al., 2023). Within homogeneous home ranges, we randomly placed grids in large contiguous stands of mature forests; within heterogeneous home ranges, we used ArcGIS and stratified trapping grids by forest type. Specifically, we centered our trapping grids along edges of (i) young and mature forest or (ii) open and mature forest to ensure adequate representation of core and edge for each forest type. As part of this process, we constrained grid locations in heterogeneous home ranges to contain at least 30% of mature forest and 30% of either young forest or open area.

We deployed traps for six consecutive days using a paired approach in which two grids were sampled concurrently – one each within a heterogeneous and homogeneous home range. We captured woodrats in steel mesh traps (model #105; Tomahawk Live Trap Company, Hazelhurst, Wisconsin, USA) baited with a mixture of birdseed, dried fruit, and peanuts. At the initial capture, we recorded age, sex, mass (g), and hind foot length of all individuals. All captures were conducted with approval from the Institutional Animal Care and Use Committee of the University of Wisconsin, Madison (IACUC #A006173-A01), and followed guidelines from the American Society of Mammalogists (Sikes et al., 2019).

Sampling environmental features and defining covariates

We conducted vegetation sampling at every trap location with a woodrat detection as well as an additional 480 locations without woodrat captures. For non-capture sites, we selected every other or every third trap location in a grid for vegetation sampling. We measured slope and aspect and confirmed the forest type assigned from NAIP imagery. We then centered circular plots with a radius of 12.5m around sampled trap locations, within which we recorded canopy cover with a densitometer, and understory cover using a visual estimation of the proportion of ground obscured by vegetation <2m height. For each tree within a plot, we recorded species, DBH, and condition (live, dead). We measured downed woody debris by counting the number of logs and snags within our plot >1m in length with >10 cm DBH. We then walked a 12.5m line-transect from the center and counted every stick that crossed the line; this provided us with a representative sample of midden-construction materials in the area. Finally, we determined whether there was a source of water within 25m of the trap location.

At each individual site where vegetative surveys were collected, we considered covariates defined at three spatial scales: landscape, patch, and site (Table 1). Landscape covariates were estimated based on patterns in forest type (i.e., mature, young, open). For these, we first assigned a categorical variable for whether a trap was located within a ‘heterogeneous’ or ‘homogeneous’ spotted owl home range as defined by our sampling design. Next, we derived estimates of forest composition from circles of 100m centered around each individual site (Fig. 2). This buffer size represented areas equal to the average reported area of woodrat home ranges (Innes et al., 2009; Sakai and Noon, 1997). We estimated the percentage of mature forest (Mature100), young forest (Young100), and open area (Open100) within each buffered area. Proportions were highly correlated, so while all were considered in the initial stages of model construction, we only carried forward the covariate for Young100 forward in our final model set. Further, to explore our prediction that source-sink dynamics from young forest would drive increased occupancy rates in adjacent mature forest specifically, we tested an interaction of this variable with forest type and ultimately report the proportion of young forest within 100m for sites within mature forest only. Patch-scale covariates included forest type and patch area (Fig. 2). Similar to the approach for Young100, we tested an interaction of patch area with forest type and only report parameter estimates for those traps within young forests. Site-scale covariates were collected during vegetative surveys and estimated within a circular plot with a radius of 12.5m centered around each trap location. These were outlined in the 'field methods' section and predominantly represented local metrics of forest characteristics (e.g., canopy cover, basal area), protective cover (understory, downed woody debris), and resource availability (hardwoods, tanoaks, sticks).

Multi-stage occupancy modeling framework

We employed a stepwise, multi-stage approach to model woodrat occupancy as a function of environmental conditions at the three spatial scales while incorporating detection probabilities to account for imperfect detection (MacKenzie et al., 2017; Morin et al., 2020; Pavlacky Jr. et al., 2012). We used the unmarked package (Fiske and Chandler, 2011; Kellner et al., 2023) in program R (R Core Team, 2023) to fit single-species, single-season occupancy models and estimate the probabilities of detection (p) and occupancy (ψ). We treated each trap-night as a sampling period, and recorded whether a woodrat was detected (1) or not detected (0), or if a trap was not functional from disturbance or bycatch (NA), in which case we censored that night's observation. Occupancy models assume closure where there is no immigration, emigration, or mortality (Royle and

Dorazio, 2008). Given the small home ranges, limited dispersal, and low mortality rates of this population (Kuntze et al., 2023; Sakai and Noon, 1997), as well as the short duration (6 days) of each trapping survey, we considered this assumption likely satisfied. At each stage, we constructed model sets for all combinations of relevant variables, then progressed covariates from the best model structure forward to be tested within the final stage. All continuous variables were standardized. To address multicollinearity, we excluded highly correlated covariates ($|r| > 0.6$) from the same model (Dormann et al., 2013). We ranked models using Akaike Information Criterion (AIC; Burnham and Anderson, 2002), and considered any model that outperformed the null and was within 2 ΔAIC of the top model to be competitive (Morin et al., 2020; White and Burnham, 1999). Our staged approach was as follows:

Stage 1. Determine model structure for detection. In this stage, we held ψ constant while p was allowed to vary based on covariates. We included a set of spatially independent covariates (sampling year, secondary sampling period, Julian date, and lunar illumination; Table 1) in these models in addition to the patch-scale forest type covariate for each trap-location. We chose to include this latter variable because woodrats exhibit behavioral differences (i.e., foraging and apprehension) between young and mature forests (Kuntze et al., *in review*), which may also affect detection probabilities. In all subsequent stages, we fixed the best-supported model for detection while ψ was allowed to vary based on covariates.

Stage 2. Test physiographic covariates. Prior to inclusion of scale-specific variables within our model sets, we tested the potential influence of physiographic, scale-independent covariates for elevation, slope, and water (Table 1) on ψ.

Stage 3. Test scale-specific covariates. We modeled the effects of covariates quantified at three distinct spatial scales on ψ by constructing separate model sets for landscape- (Stage 3.1), patch- (Stage 3.2), and site-scale (Stage 3.3) variables.

Stage 4. Combine sub-stages and interactions. We carried forward all covariates included in the top models from Stage 2 and each sub-stage in Stage 3 to construct a final model suite. In this stage, we also included a number of *a priori* interactions (Table S1) between covariates within and across scales, even if one or both covariates were not supported within model sets from Stage 3. We determined the best overall model(s) for ψ and reported the associated coefficients with significance based on 85% confidence intervals as recommended by Arnold (2010).

Modeling habitat suitability

Next, we incorporated our trapping data with remotely-sensed forest structure and landownership metrics to project habitat suitability for woodrats across a wider geographic area. We obtained measures of forest characteristics from California Forest Observatory (CFO; 2020) for four national forests (Stanislaus, Eldorado, Tahoe, and Plumas) in the Sierra Nevada. CFO data constitutes 10m resolution raster layers for canopy cover, canopy height, canopy base height, canopy layer count, canopy bulk density, ladder fuel density, and surface fuels (Table S2). Data were available for 2016 to 2020; we only used data from 2020 to best reflect conditions during our two trapping seasons. We also considered elevation, as well as a derived measure of forest heterogeneity following protocol outlined in Zulla et al. (2023) from CFO data. Briefly, we calculated the standard deviation of canopy height within a 90m moving window, then again calculated the standard deviation of these pixels using another 90m moving window. This created values that were distinctly higher in heterogeneous areas and lower in homogeneous forests (Zulla et al. 2023). Finally, to estimate habitat suitability relative to landownership we used federal boundary maps and classified all pixels within our sampling area as either ‘public’ (primarily USFS ownership) or ‘private’.

Woodrats exhibit elevational limits in their distribution; occurrence sharply declines above 1,600–1,800 m (Innes et al., 2009; Sakai and Noon, 1997), while occupancy can be variable below 900 m. Given this, we limited the spatial extent of our projections to sites between 914–1524 m, which also reflected the approximate spatial extent captured by our trapping grids. To further explore the potential effects of elevation within this band, we also stratified our habitat suitability estimates within discrete elevational bands of 914–1,219 m and 1,219–1,524 m, in addition to the combined sampling area. Large, severe wildfires across the Sierra Nevada have substantially changed habitat conditions; given a limited understanding of woodrat occupancy and recolonization following these fires, we chose to exclude any potential effects from recovering landscapes. We did so by first extracting shapefiles for all fires from the California Fire Perimeter Database (https://frap.fire.ca.gov/frap-projects/fire-perimeters/), then excluding any pixels that fell within the perimeter of fires that occurred between 1995–2020.

To model habitat suitability for woodrats, we followed a similar approach to that of other studies that employed presence/absence and occurrence probability data (e.g., Calderón et al., 2022; Chandler, 2019; Miranda et al., 2021). We fit a single-season occupancy model using the unmarked package in program R to our trapping data from all sites (n = 1,408), maintaining the earlier top detection structure from Stage 1 while incorporating covariates for all CFO metrics, forest heterogeneity, and elevation. No pairs of covariates were highly correlated ($|r| > 0.6$) and the distribution of covariate values in our model fitting process reflected those for the spatial extent of our projections (Table S3). Once our sampling area was defined, we used the lattice and terra packages in program R (Hijmans and Bivand, 2022; Sarkar, 2008) and our fitted occupancy model to predict the probability of habitat use (hereafter habitat suitability) at each pixel across this area.

Results

Over two field seasons we surveyed 22 grids of 64 traps each for a total of 8,448 trap-nights. In total, we recorded 460 detections of 236 individual woodrats. Woodrats were captured at 175 of 1,408 traps. In 2020, we collected 4,608 trap-nights of data (768 traps). Among those, we recorded 165 woodrat detections of 88 individuals (among 72 traps) and censored 334 trap-nights (among 237 traps). In 2021, we collected 3840 trap-nights of data (640 traps). Among those, we recorded 294 woodrat detections/occurrences of 148 individuals (among 105 traps) and censored 647 trap-nights (among 311 traps).

Multi-stage modeling

Stage 1: The top model for detection probability included the effect of habitat and secondary sampling period ($w_i = 0.43$; Table S4). Woodrat detection probability was greatest in young forests ($p = 0.58$ [0.53, 0.63]), followed by mature ($p = 0.43$ [0.30, 0.47]), with lowest detection probability in open areas ($p = 0.03$ [0.01, 0.08]). These two predictors were included in all occupancy models in subsequent stages. Competitive models (within 2 AIC) also included the effect of lunar illumination and Julian date, although these parameters were uninformative (Table S4).

Stage 2: The top model from Stage 2 indicated that among physiographic covariates, occupancy probability decreased with increasing elevation with no other models within 2 AIC ($w_i = 0.53$; Table 2; Table S5).

Stage 3: At the landscape-scale (Stage 3.1), occupancy probability was greater in heterogeneous home ranges and increased with proportion of young forest within a 100m buffer with no other models within 2 AIC (w_i = 0.75; Table 2; Table S5). At the patch-scale (Stage 3.2), occupancy probability was greatest within young forests, followed by mature forest and open areas. Occupancy also decreased with increasing young forest patch area with no other models within 2 AIC (w_i = 0.74; Table 2; Table S5). At the site-scale, occupancy probability increased with understory, tanoaks, canopy cover, and total basal area of all trees (w_i = 0.54; Table 2; Table S5), while a competitive model excluded the effect of basal area (w_i = 0.34; Table 2; Table S5).

Stage 4: The top overall model (w_i = 0.27; Table 3) indicated that woodrat occupancy was lower within homogeneous home ranges ($\beta_{homogeneous}$ = -0.43 [-0.80, -0.07]) and greater within young forest compared to open areas ($\beta_{young\text{-}open}$ = 3.59 [2.13, 5.04]; Figure 3A) and mature forests in homogeneous ($\beta_{young\text{-}mathom}$ = 1.99 [1.20, 2.79]]) – and to a lesser extent – mature forests in heterogeneous home ranges ($\beta_{young\text{-}mathet}$ = 1.56 [0.77, 2.35]). Occupancy probability was also greater in mature forests specifically within heterogeneous versus homogeneous home ranges ($\beta_{mathet\text{-}mathom}$ = 0.43 [0.07, 0.80]). Within young forests, occupancy decreased with increasing young patch area (β_{patch_area} = -0.50 [0.82, -0.19]; Fig. 3B). Occupancy probability at the site-scale increased with increasing understory ($\beta_{understory}$ = 0.73 [0.56, 0.91]; Fig. 3C), canopy cover (β_{canopy_cover} = 0.26 [0.05, 0.47]; Fig. 3D), basal area of all trees (β_{basal} = 0.25 [0.07, 0.43]; Fig. 3E), and basal area of tanoaks (β_{tanoak} = 1.24 [0.57, 1.92]; Fig. 3F). Competitive models (within 2 AIC; Table 3) excluded the effect of either landscape composition (w_i = 0.17) or canopy cover (w_i = 0.16); the values of the remaining parameters did not change notably in either. Additionally, other competitive models included the covariate for Young100 within mature forest, both with (w_i =

0.13) and without ($w_i = 0.12$) the effect of landscape composition, although this parameter was not informative in either model.

Habitat suitability

After removing all data outside of our elevational range (914–1,524 m) and within fire footprints from 1995-2020, we estimated woodrat habitat suitability across ~478 million 10x10m pixels. We found that 95% CLs for the beta coefficients of all covariates except canopy base height and surface fuels did not overlap 0 (Table S6). Specifically, probability of habitat use increased with canopy cover ($\beta_{cc} = 0.52$ [0.27, 0.77]), ladder fuels ($\beta_{lf} = 0.34$ [0.19, 0.50]), and forest heterogeneity ($\beta_{fh} = 0.37$ [0.24, 0.50]), while it decreased with increasing canopy height ($\beta_{ch} = 0.52$ [0.27, 0.77]), canopy bulk density ($\beta_{bd} = 0.52$ [0.27, 0.77]), canopy layer count ($\beta_{lc} = 0.52$ [0.27, 0.77]), and elevation ($\beta_{el} = 0.52$ [0.27, 0.77]). Across the entire sampling area, we estimated a mean habitat suitability of 0.215 (Fig. 4C). Relative to landownership, we found that mean habitat suitability across our sampling area was almost identical between public (0.2148) and private (0.2145) lands (Fig. 5). However, we did find differences once we accounted for our elevational groups; first, overall mean habitat suitability was more than double within our lower elevation (0.314) than higher elevation sites (0.145). Further, between 914–1,219 m elevation mean habitat suitability was greater in public (0.319) than private (0.302) lands while at 1,219–1,524 m it was greater in private (0.154) than public (0.141) areas.

Discussion

Large-scale forest management has the potential to affect animal habitat use in critical ways. We demonstrated that, within forest landscapes where spatial heterogeneity is created and maintained by even-aged timber management, woodrats select for forest structure and composition characteristics at multiple spatial scales. In particular, woodrat occupancy increased in association with elements of vegetation that provide food resources and protective cover, as well as within smaller patches of younger forests and with increasing forest heterogeneity. While studies on small mammals predominantly focus on local habitat features, environmental processes and forest management decisions often occur at broader spatial scales. By systematically evaluating multiple scales of observation within a hierarchical framework, our study provides a unique perspective on habitat selection and the mechanisms that influence the population dynamics of this key prey species within a local, patch, and landscape context.

Local characteristics

Woodrat occupancy increased in areas with dense understory and prevalent masting hardwoods, likely due to greater protective cover and resource availability (Carraway and Verts, 1991; Fraik et al., 2023), consistent with previous findings (Fraik et al., 2023; Hamm and Diller, 2009). The association with canopy cover has also been documented (Fraik et al., 2023; Hamm and Diller, 2009), although it is generally believed that this forest element does not have much standalone value to small mammals, and rather represents a proxy for areas with greater mast production or structural complexity (Sollmann et al., 2015).

In contrast to previous studies that found strong associations between woodrats and mast-producing black oaks (e.g., Fraik et al., 2023; Innes et al., 2007; Sakai and Noon, 1993) we demonstrated that prevalence of tanoaks was a key component of woodrat habitat in our study area as it far exceeded the explanatory power of all hardwoods combined (Table 2). Tanoaks have characteristics that may be particularly beneficial to woodrats – especially for the variety found within the Sierra Nevadas. While tanoaks along the Pacific coast (*N. densiflorus* var. *densiflorus*) can reach 20-25 m, dwarf tanoaks (*N. densiflorus* var. *echinoides*) occur at higher elevations - such as our study area - and frequently grow as a shrub less than 3 m tall (Griffin and Critchfield, 1976; Hickman, 1993). This variety of tanoak develops a multi-stem growth that produces a dense, structurally complex layer (Hickman, 1993; McDonald, 2002), that may provide dual benefits of protective cover and a foundation for midden construction at the base between stems. Under shady conditions young tanoak plants develop a more shrublike growth (McDonald, 2002; Tappeiner and Roy, 1990), suggesting that in shadier – and riskier – mature forests, the structure of tanoak provides even more protective cover when the threat of vertical predation is highest (Embar et al., 2011, Kuntze et al., *in review*). Tanoaks may also produce a more favorable food crop for woodrats. Despite the name, tanoaks are not a true oak species; while their acorn mast can vary annually, their flower and seed production is prodigious and no western 'oak' species produces acorns as consistently as tanoaks (McDonald, 2002; Tappeiner and Roy, 1990). Acorn production can start as early as 5 years (Tappeiner and Roy, 1990), and open-grown tanoaks produce larger crops than those in shade (McDonald, 2002), which may help woodrats colonize and occupy an area quicker following a disturbance - especially when large, masting black oaks are absent. However, despite their myriad benefits, our ability to extrapolate these findings across the woodrat distributional range may be limited as tanoaks require relatively high moisture levels and mild temperatures (Hickman, 1993), and have a relatively scattered distribution outside of lower, coastal areas (Griffin and Critchfield, 1976; Hickman, 1993). As such, woodrats and tanoak only overlap occasionally (Fig. S1), and outside of these areas the relative importance of other hardwoods (including black oak) and processes at other spatial scales may be greater.

Patch characteristics

Woodrat occupancy was greatest in young forest patches, reflecting previously reported patterns in density and abundance (Carraway and Verts, 1991; Kuntze et al., 2023; Sakai and Noon, 1993). The benefits of younger forest to woodrats are considered to be an emergent property of favorable local conditions, as younger forests contain a greater density and diversity of high-quality food resources (Carraway and Verts, 1991; Fontaine et al., 2009), unique microclimates (Swanson et al., 2011), nest-building structures and materials (Innes et al., 2007), and protective cover (Sakai & Noon, 1997; Kuntze et al., *in review*). While this is true to an extent, justifying patterns in patch-scale processes as a product of local conditions alone can fail to consider the effect of patch characteristics.

Counter to theoretical expectations, woodrat occupancy decreased within larger patches of young forests. Increasing patch area is commonly associated with beneficial intrinsic and extrinsic attributes that increase occupancy, such as resource availability, territory size, and habitat quality (Garda et al., 2013; Kitchener et al., 1980). However, studies on small mammals have also detailed neutral or positive responses to decreasing patch sizes (Foster and Gaines, 1991; Nupp and Swihart, 1996), attributed to competitive release from other species or denser populations in smaller patches (Dooley and Bowers, 1996; Foster and Gaines, 1991). Woodrats were the largest-bodied small mammal in our study area, and across their distributional range are competitively dominant (Grant, 1972), even over other *Neotoma* species (Cameron, 1971). While interspecific interactions have minimal effects on population dynamics, woodrats are semi-territorial and can aggressively defend core areas against same-sex conspecifics (Innes et al., 2009; Lynch et al., 1994). Yet, home range sizes also vary considerably among individuals (Innes et al., 2009; McEachern, 2005; Sakai and Noon, 1997), and in some cases can overlap with neighboring pairs

(Innes et al., 2007; Lynch et al., 1994). Home range size is often inversely related to population density among mammals (Sanderson, 1966); therefore, the increased occupancy probabilities observed in smaller patches may be a result of smaller, overlapping territories and greater woodrat densities.

In addition to being more likely to occupy younger forests, woodrat detection probability also varied with forest type and was 1.5x greater in young versus mature forests. Among prey species, forest structure can influence the perception of risk (Gaynor et al., 2019). In turn, spatial variation in predator activity can affect space use (Dellinger et al., 2019), foraging (Kotler and Blaustein, 1995), and population dynamics of prey (Ehlman et al., 2019; Garvey et al., 2020). Owls predominantly forage within mature forests (Atuo et al., 2019; Zulla et al., 2022), and woodrats occupying these areas exhibit behavioral differences (e.g., increased vigilance and decreased foraging time) compared to those in younger forests, independent of local-scale conditions including understory cover (Kuntze et al*., in review*). Higher woodrat detection in young forests supports the hypothesis that habitat selection by woodrats at patch-scales is driven, in part, by the avoidance of riskier areas in mature forests (Lima and Dill, 1990; Turkia et al., 2018).

Landscape characteristics

At a broader scale we found that spatial heterogeneity–driven primarily by the juxtaposition of mature and younger forests–drove patterns in woodrat occupancy observed or hypothesized in prior work on woodrat abundance within managed forest landscapes (Kuntze et al., 2023; Sakai and Noon, 1993). In heterogeneous systems, landscape-scale abundance is an emergent property of the composition of different habitat patches, with landscapes containing a greater area of high-quality habitat patches expected to have higher abundance (Holt, 1985; Iles et al., 2018). This likely translated to occurrence rates as we found that the probability of woodrat occupancy was 2.6x greater within spotted owl home ranges characterized by a heterogeneous composition of forest types, consistent with findings from Kuntze et al. (2023) that documented 2.5x greater total abundance in similar landscapes. Dispersal from high-density source patches can also increase occupancy or relative densities within lower-quality patches (Holt, 1985), and in some cases, landscape-scale abundance may even exceed the combined carrying capacity of all representative patches (Zhang et al., 2017). While previous studies have proposed a similar process driven by dispersal from high-quality young forest into the surrounding landscape (Innes et al., 2009; Kuntze et al., 2023; Sakai and Noon, 1997), empirical evidence for this mechanism has been limited by a lack of adequate sample sizes or perspectives from the appropriate spatial scales. We found that woodrat occupancy in mature forest patches was 2.8x higher in heterogeneous versus homogeneous spotted owl home ranges - slightly above but still in line with the 2.3x increase in density reported by Kuntze et al. (2023). Further, occupancy increased in mature forests with an increasing proportion of young forest within 100m (Fig. 6), with the greatest effect in model sets where patch- and landscape-scale conditions were exclusively considered. Thus, our findings suggest that high-quality young forest can produce dense woodrat populations that recruit into adjacent, lower-quality mature forests, decoupling local occupancy from habitat quality.

Habitat suitability modeling and fuels reduction implications

To combat the increasing frequency and severity of fires throughout the Sierra Nevada, proactive management and fuels reduction treatments are now being widely implemented (Fulé et al., 2012; Hessburg et al., 2021). However, uncertainty about how sensitive forest species will respond to these treatments has at times limited the scale and pace of efforts (Collins et al., 2010;

Jones et al., 2022). We found that woodrats selected for some features consistent with fuels reduction goals (e.g., decreasing canopy layer count and bulk density) but were also associated with increasing canopy cover and ladder fuels, which may increase the risk of severe wildfires. While treatments targeting ladder fuel reduction can improve fire resilience and benefit foraging spotted owls (Wright et al., 2023), they may negatively impact woodrat populations as a result. This poses a challenge for managers aiming to preserve owl habitat, increase prey populations, and reduce fuel loads simultaneously. Promoting spatial heterogeneity in fuels reduction treatments, including a mix of low and high ladder fuels (see also below), is likely to benefit both woodrats and spotted owls while facilitating increased interactions between the two species (Kuntze et al., 2023; Wilkinson et al., 2023; Wright et al., 2023).

Our findings of habitat suitability by landownership revealed an unexpected similarity between private and public lands within national forests. This contrasts with previous studies indicating that spotted owls consume significantly more woodrats on private lands and national parks compared to public national forests (Hobart et al., 2019). One possible explanation for this is that while private lands generally feature more high-quality young forests, they may also contain less vertical complexity and more open areas than public lands characterized by more contiguous mature forests (North et al., 2017; Stephens et al., 2015). As a result, while average habitat suitability may be unchanged for woodrats, the heterogeneous composition of forest types and woodrat densities in private lands may increase hunting opportunities for foraging spotted owls (Zulla et al. 2022, 2023).

Conservation implications and management suggestions

Forested landscapes worldwide are undergoing significant transformations in ecosystem structure, function, and composition due to climate change and land use practices (Bullock et al., 2022; Collins et al., 2017; Seastedt et al., 2008). Yet despite a growing call to restore forest processes and resilience, the implementation of effective strategies has been hindered in part by an incomplete understanding of the impacts of both disturbance and forest management on animal species and communities. Our study provides insight into two management activities occurring at different spatial scales that can benefit species conservation potentially without compromising resilience in forest ecosystems. First, timber harvesting and silvicultural practices that create landscape-scale heterogeneity–as a mosaic of mature forests, young forests, and open areas that naturally regenerate into younger forests–may foster higher woodrat occupancy within mixed-ownership landscapes like our study area. This, in turn, could increase woodrat abundance and availability to spotted owls with emergent benefits to fitness, occupancy, and space use (Conner et al., 2016; Hobart et al., 2019). This conclusion is supported by other studies that have demonstrated the benefits of promoting landscape heterogeneity on the scale of a spotted owl home range, especially in areas where woodrats represent a dominant prey species by biomass (Hobart et al., 2019; Kuntze et al., 2023; Zulla et al., 2023).

At a smaller scale, managers could employ silvicultural techniques such as group selection harvests to create small openings (~2 ha) on the landscape while managing the surrounding forests normally for fuels reduction goals. This size recommendation is supported by direct observations of commensurate young forest patches that contained ≥25 individuals. Following planting or natural reseeding, these openings would regenerate into patches of brushy young forest containing ideal conditions for early-successional woodrats. These small patches would then serve as ‘fishing holes’, or dense, self-sustaining populations of woodrats that disperse into the surrounding landscape, providing a critical food source for foraging spotted owls. While this approach may potentially help support spotted owl populations without compromising fuels reduction goals, effective implementation would benefit from additional research on 1) the effects of these management activities on forest resilience, 2) best practices for the quantity and distribution of ‘fishing holes’ within a forest landscape, and 3) whether smaller patches (≤1 ha) could sustain the same dense, self-sustaining woodrat populations as the ones we evaluated.

Our study also highlights the importance of ephemeral, early-successional habitats in sustaining key prey populations for sensitive species like spotted owls. Unlike late-successional forests, many attributes of early-successional ecosystems depend on time since disturbance and the type of disturbance (Donato et al., 2012; Swanson et al., 2011). These areas undergo structural and compositional changes beginning immediately post-disturbance (Bace et al., 2023), with different species, structures, and ecological processes often dominating throughout different sequences of forest stand development (Swanson et al., 2011). While we did not directly evaluate the effects of temporal heterogeneity, it likely represents an important component of our system as historically variable fire patterns in dry-forest ecosystems produced both spatially and temporally heterogeneous successional processes (McLauchlan et al., 2020). Within managed landscapes, timber harvest recurrently creates open patches of varying size that regenerate into early-successional habitat favored by woodrats, which may explain the high occupancy and abundance rates of woodrats in our study area reported here and in prior studies (Kuntze et al., 2023). Therefore, our findings suggest that promoting multi-scale forest heterogeneity by continuous, spatiotemporally variable timber harvesting can create and maintain crucial early-successional ecosystems as part of a diverse landscape.

Conclusions

In summary, forest research and management approaches that consider and incorporate ecological complexity and the hierarchical nature of habitat selection can provide valuable insights into how to recreate historically heterogeneous forests and meet biodiversity objectives. While restoring historical disturbance regimes remains a goal in forest ecosystems worldwide (Bullock et al., 2022; Gaines et al., 2022; Steel et al., 2022), it can be challenging – or even impossible - to replicate past conditions and processes (Watts et al., 2020). By grounding restoration policies and practices in the context of the modern environment while prioritizing an understanding of how ecological processes and community composition vary across spatial scales, we can foster consensus and progress among forest management goals.

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Table 1: Covariates included in models to explore occupancy patterns for dusky-footed woodrats (*Neotoma fuscipes*) in the Sierra Nevada, California, USA.

Category	Variable	Ecological description
Landscape	Forest heterogeneity	Categorical designation (homogeneous, heterogeneous) for landscape composition of patch-scale forest types targeted by sampling design.
	Mature100	Proportion of 100m circular buffer comprised of mature forest
	Young100	Proportion of 100m circular buffer comprised of young forest – for mature forest only
	Open100	Proportion of 100m circular buffer comprised of open area
Patch	Forest type	Forest type defined by NAIP imagery classification (mature, young, open)
	Patch area	Total area of the forest type patch (km^2) – for young forest only
Site	Canopy cover	Proportion of sky (%) obscured by vegetation >2m height within 12.5m
	Understory cover	Proportion of ground (%) obscured by vegetation <2m height within 12.5m
	Basal area	Total basal area (m^2; measured with DBH) of all live and dead standing trees <2m tall within 12.5m
	Hardwoods	Total live basal area of hardwoods within 12.5m
	Masting hardwoods	Total live basal area of hardwoods >28cm dbh within 12.5m
	Sticks	The number of sticks along a 12.5m line-transect from the center
	Downed woody debris	Number of logs and snags >1m length and >10cm dbh within 12.5m
Physiography	Slope	Average of upslope and downslope measurements (^{o}) from plot center along aspect
	Elevation	Elevation (m) at plot center
	Water	Presence of water within 25m as factor (yes, no)
Other	Julian date	Julian day of sampling night
	Lunar cycle	Phase of the lunar cycle during sampling night, measured by the number of days since a new moon (0; new moon – 15; full moon)
	Sampling season	Sampling year as factor (2020, 2021)
	Secondary sampling period	Sequential trapping night of a grid deployment (T; 1, first night – 6, final night)
	Home range ID	Individual ID for home range (unique owl pair)
	Grid ID	Individual ID for trapping grid

Table 2: Results from stages 2 and 3 for modeling dusky-footed woodrat (*Neotoma fuscipes*) occupancy in the central Sierra Nevada, California, USA. Models denoted by "." indicate the intercept-only (i.e., null) model. Covariates from the top model structure at each stage and substage were carried forward to all subsequent stages. Detection probability structure was held constant for all models at *p* (T, habitat).

Ψ	AIC	ΔAIC	K
Stage 2: Physiography			
Elevation	1860.75	0	6
Elevation + Slope	1861.3	0.56	7
Slope	1865.12	4.37	6
.	1869.96	9.21	5
Stage 3.1: Landscape			
Forest heterogeneity + Young100 (Mature)	1828.85	0	9
Forest heterogeneity	1831.15	2.3	6
Young100 (Mature)	1845.75	16.9	8
.	1869.96	41.1	5
Stage 3.2: Patch			
Habitat + Patch area (Young)	1839.12	0	9
Patch area (Young)	1841.21	2.09	8
Habitat	1855.2	16.08	7
.	1869.96	30.84	5
Stage 3.3: Local			
Understory + Basal + Canopy cover + Tanoaks	1748.27	0	9
Understory + Canopy cover + Tanoaks	1749.11	0.84	8
Understory + Basal + Tanoaks	1751.68	3.4	8
Understory + Tanoaks	1757.56	9.29	7
Basal + Tanoaks	1793.19	44.92	7
Tanoaks	1795.57	47.3	6
Understory + Basal	1795.95	47.67	7
Understory	1805.49	57.22	6
Hardwoods	1862.6	114.33	6
Basal	1865.31	117.04	6
Canopy cover	1868.16	119.88	6
.	1869.96	121.68	5
# Sticks	1870.04	121.77	6
Downed woody debris	1870.72	122.45	6

Table 3: Modeling results from stage 4 (combining substages and interactions) for dusky-footed woodrat (*Neotoma fuscipes*) occupancy in the central Sierra Nevada, California, USA. Covariates from the top model structure at each stage and substage were carried forward to this stage. The model denoted by "." indicates the intercept-only (i.e., null) model. Only competitive models (within 2 ΔAIC of the top model) are shown; variables from top models in earlier stages (i.e., Table 2) and interactions (i.e., Table S1) not shown here were still tested; noncompetitive models and covariates not present in any competitive models are not included on this table for easier interpretability. Detection probability structure was held constant for all models at *p* (T, Forest type).

Ψ	AIC	ΔAIC	K
Forest heterogeneity + Forest type + Patch area + Canopy cover + Understory + Tanoaks + Basal area	1737.22	0	13
Forest type + Patch area + Canopy cover + Understory + Tanoaks + Basal area	1738.10	0.88	12
Forest heterogeneity + Forest type + Patch area + Understory + Tanoaks + Basal area	1738.32	1.10	12
Forest heterogeneity + Forest type + Patch area + Young100 + Canopy cover + Understory + Tanoaks + Basal area	1738.67	1.45	14
Forest type + Patch area + Young100 + Canopy cover + Understory + Tanoaks + Basal area	1738.79	1.57	13
.	1869.96	132.74	5

Fig. 1: Locations of trapping grids within the central Sierra Nevada, CA, USA for studying dusky-footed woodrat (*Neotoma fuscipes*) occupancy within spotted owl (*Strix occidentalis*) home ranges designated as heterogeneous or homogeneous relative to patch-scale forest type.

Fig. 2: Example trapping grid for studying dusky-footed woodrat (*Neotoma fuscipes*) occupancy within the central Sierra Nevada, CA, USA relative to patch-scale forest type variables, with a visualization of the 100m buffer within which the proportion of young forest was estimated.

Fig. 3: Fitted values (±85% CI) representing estimates of occupancy probability for dusky-footed woodrats (*Neotoma fuscipes*) relative to (A) forest heterogeneity and forest type, (B) patch area in young forest, site-scale (C) understory cover, (D) canopy cover, (E) basal area of all trees, and (F) basal area of tanoaks within the central Sierra Nevada, California, USA. Values were derived from the top-ranked model with additional variables held constant at mean observed values.

Fig. 4: Study region and spatial predictions for habitat suitability of dusky-footed woodrats (*Neotoma fuscipes*) in the central and northern Sierra Nevada. Shown are (A) the four national forests surveyed relative to California, (B) the actual area surveyed within the four national forests after accounting for elevation and fires from 1995–2020 relative to landownership type, and (C) projected habitat suitability; warmer colors represent higher probability of habitat use.

Fig. 5: Habitat suitability for dusky-footed woodrats (*Neotoma fuscipes*) in the central and northern Sierra Nevada relative to landownership and elevation within higher (top half; 1,219–1,524 m) and lower (bottom half; 914–1,219 m) bands.

Fig. 6: Fitted values (± 85% CI) representing estimates of occupancy probability for dusky-footed woodrats (*Neotoma fuscipes*) in mature forest relative to the proportion of young forest within 100m. Values were derived from the top model in Stage 3.2 with additional variables held constant at mean observed values.

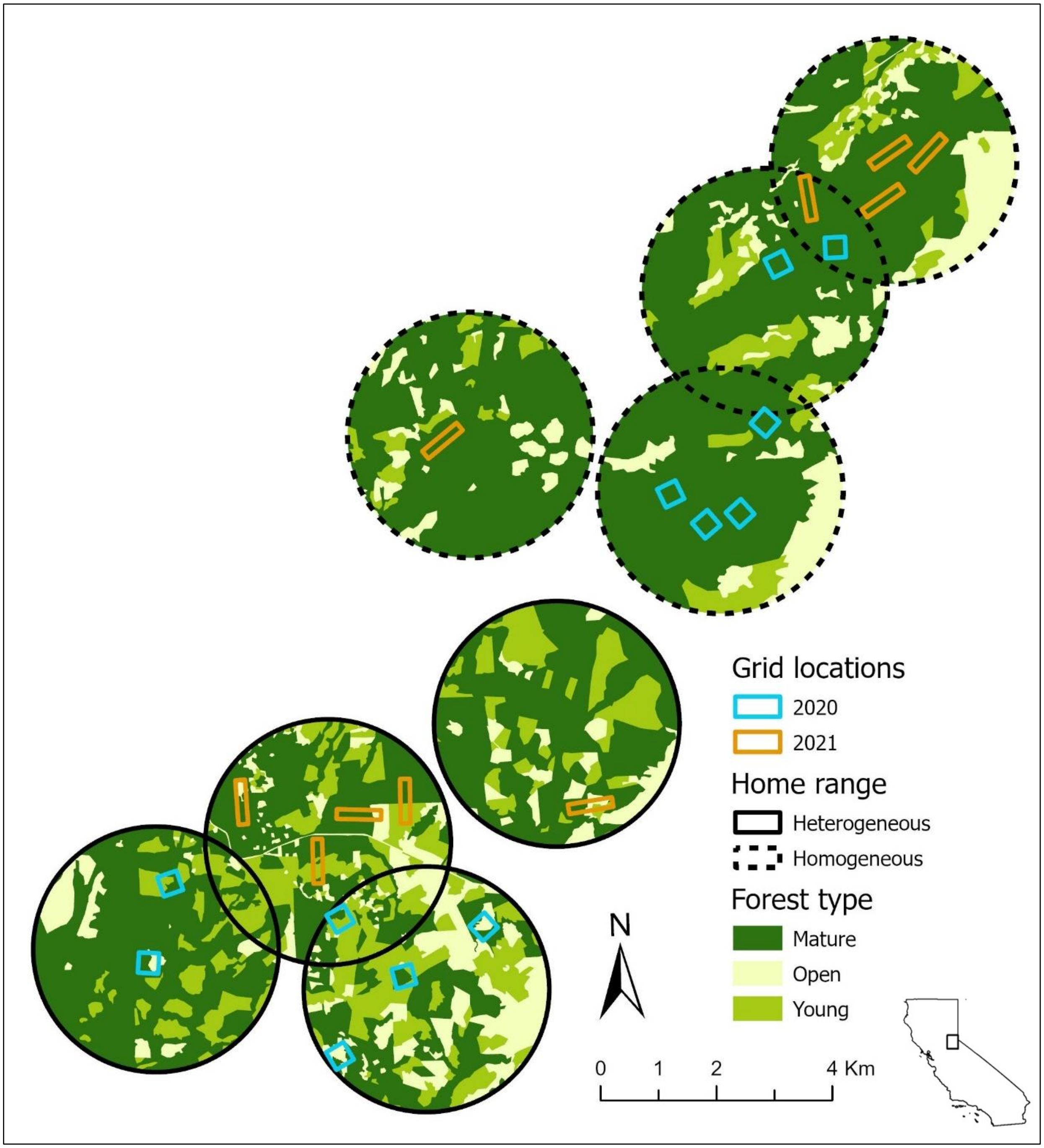
Grid locations
2020
2021
Home range
Heterogeneous
Homogeneous
Forest type
Mature
Open
Young
N
0
1
2
4 Km

Fig. 1

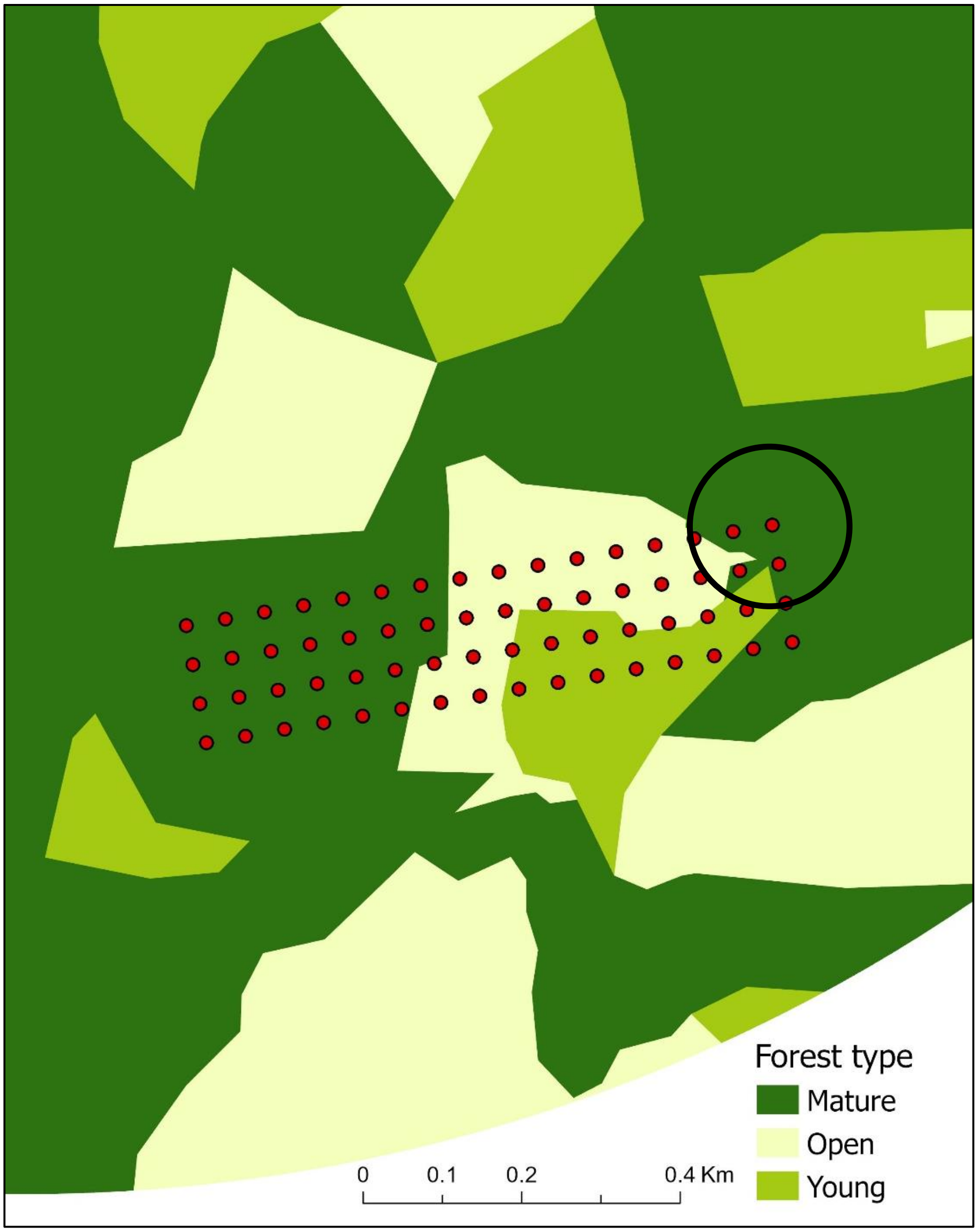

Fig. 2

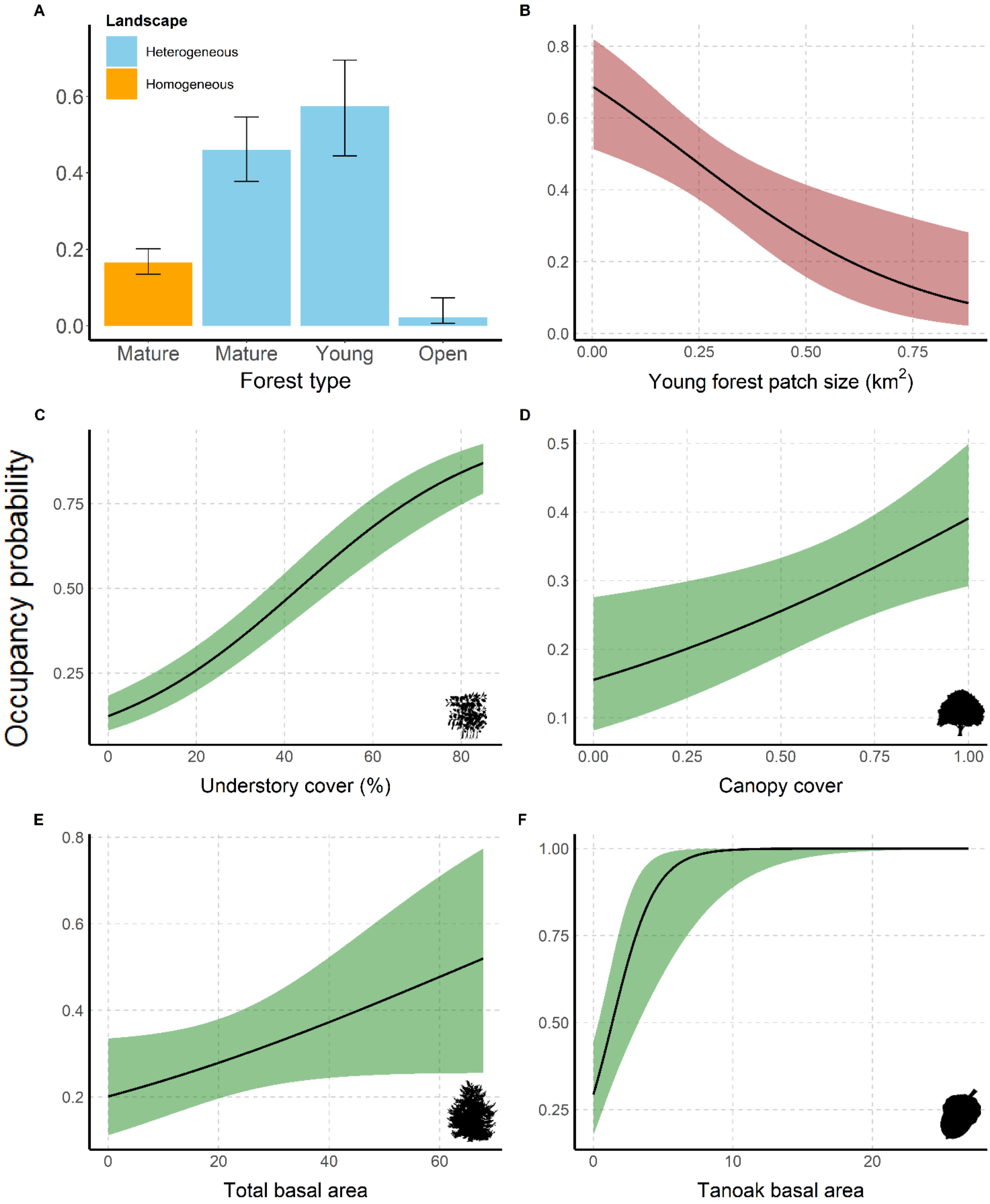
A
Landscape
Heterogeneous
Homogeneous
0.0
0.2
0.4
0.6
Mature
Mature
Young
Open
Forest type
B
0.0
0.2
0.4
0.6
0.8
0.00
0.25
0.50
0.75
Young forest patch size (km^2)
C
Occupancy probability
0.25
0.50
0.75
0
20
40
60
80
Understory cover (%)
D
0.1
0.2
0.3
0.4
0.5
0.00
0.25
0.50
0.75
1.00
Canopy cover
E
0.2
0.4
0.6
0.8
0
20
40
60
Total basal area
F
0.25
0.50
0.75
1.00
0
10
20
Tanoak basal area

Fig. 3

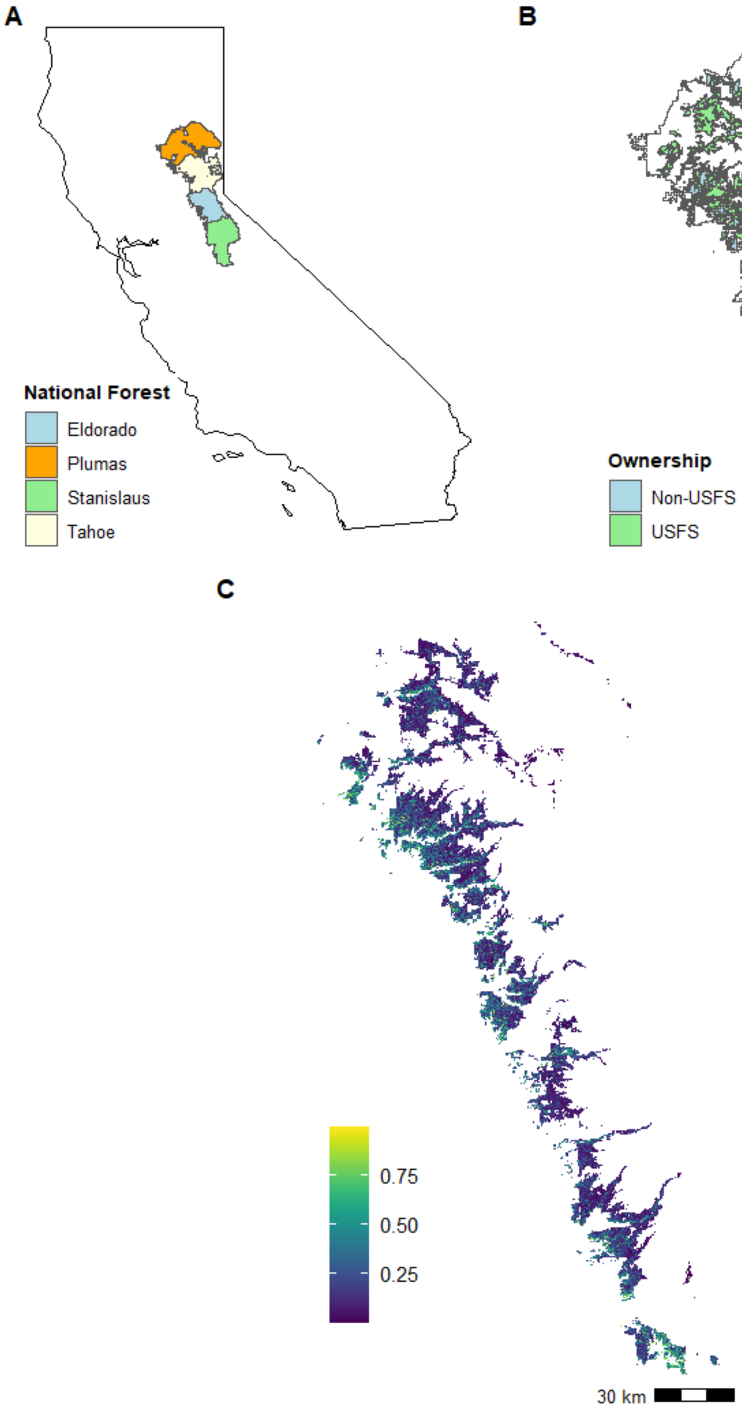
A
National Forest
Eldorado
Plumas
Stanislaus
Tahoe
B
Ownership
Non-USFS
USFS
C
0.75
0.50
0.25
30 km

Fig. 4

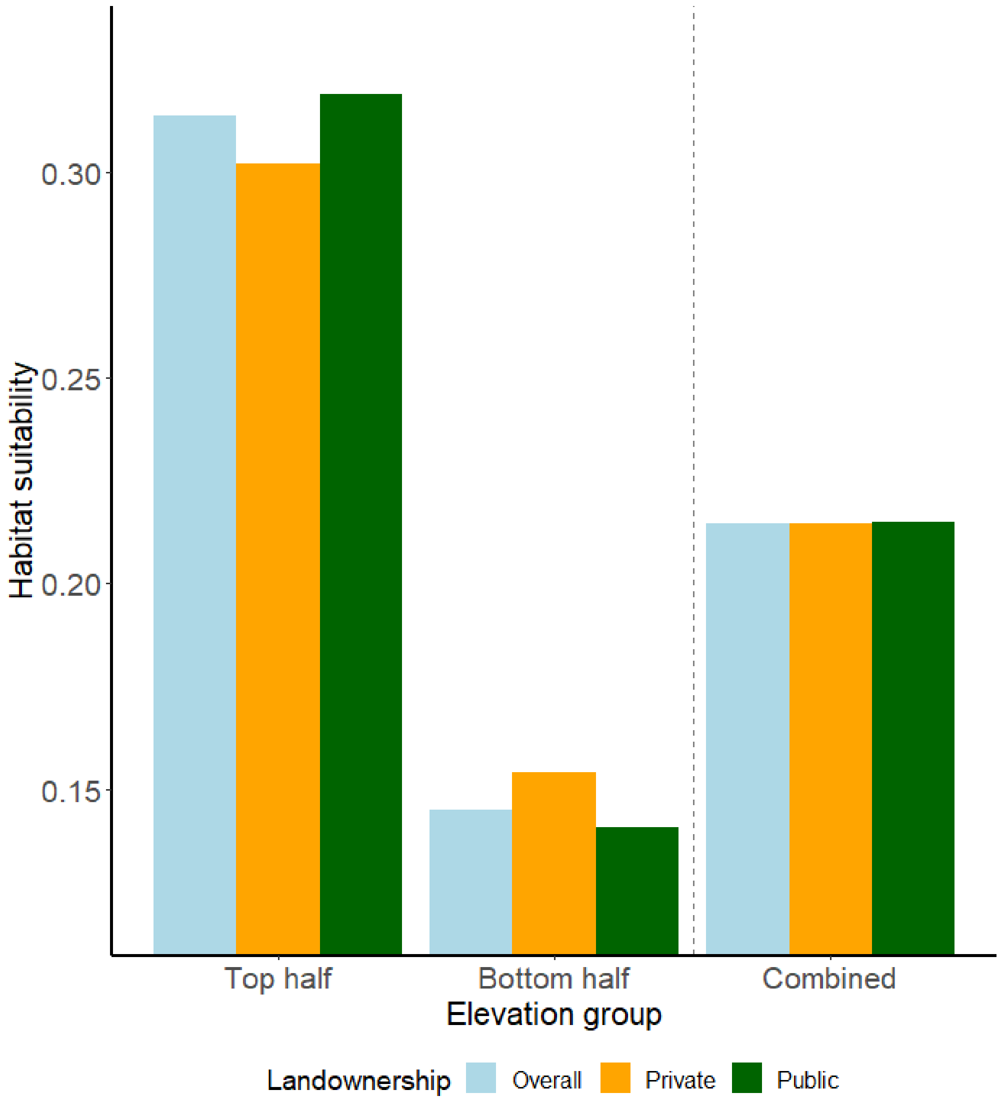
Habitat suitability
0.30
0.25
0.20
0.15
Top half
Bottom half
Combined
Elevation group
Landownership
Overall
Private
Public

Fig. 5

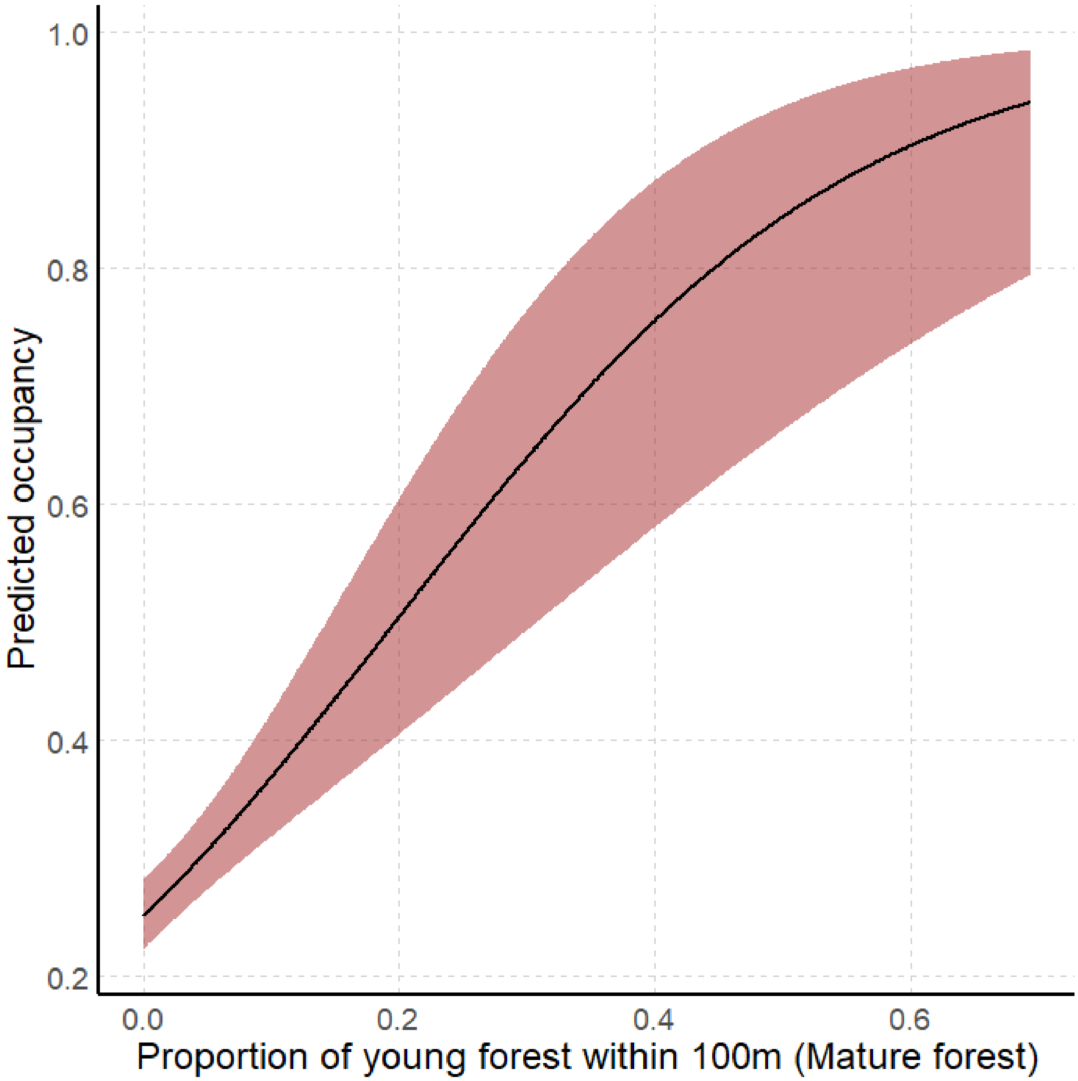
Predicted occupancy
1.0
0.8
0.6
0.4
0.2
0.0
0.2
0.4
0.6
Proportion of young forest within 100m (Mature forest)

Fig. 6

Supporting Information

Table S1: *A priori* interactions included in occupancy models for dusky-footed woodrats (*Neotoma fuscipes*) in the Sierra Nevada, CA, USA. Descriptors include the name (Interaction), covariates included (Covariates), and a brief prediction of the relationship or justification for including this interaction in occupancy models (Justification).

Interaction	**Covariates**	**Justification**
(1) Hard mast availability by forest type	Hardwoods * Forest type	We predicted that occupancy will increase with increasing basal area of masting hardwoods, particularly large black oaks. Further, this effect may be stronger within mature forest, where food availability from other sources is limited compared to young forests.
(2) Hard mast availability by year	Hardwoods * Sampling season	In addition to forest type, we may see an effect of year on the relationship between hardwood basal area and occupancy, as a year with low acorn production may limit the resources provided by masting trees, and in turn, the relative benefit of hardwoods.
(3a) Predation risk	Understory * Forest type	Understory cover is likely beneficial within all forest types - however, within young forest the latent risk of predation is lower so the relative effect of protective cover may be reduced.
(3b) Predation risk	Downed woody debris * Forest type	Increasing downed woody debris is likely beneficial within all forest types - however, within young forest the latent risk of predation is lower so the relative effect of protective cover may be reduced.
(4) Landscape composition and forest type	Forest heterogeneity * Forest type	Occupancy relative to forest type – particularly in mature forests may differ relative to the overall composition of a home range due to emergent effects of a greater proportion of high-density young forests.

Table S2: Covariates included in habitat suitability models for dusky-footed woodrats (*Neotoma fuscipes*) in the Sierra Nevada, California, USA.

Variable	**Ecological description**
Canopy cover	Horizontal cover (%) obscured by tree canopy.
Canopy height	Distance (m) between the ground and the top of the canopy.
Canopy base height	Distance (m) between the ground and the lowest branches of the canopy.
Canopy bulk density	Mass of canopy vegetation (e.g., leaves and small branches) divided by crown volume (kg/m^3).
Canopy layer count	Number (#) of distinct vertical canopy layers; reflects canopy complexity.
Ladder fuel density	Amount (%) of the understory floor covered with vegetation 1 - 4m height.
Surface fuels	Unitless metric derived from a model describing vegetation fuel type, size class, depth, and moisture and heat content.
Forest heterogeneity	Unitless metric of forest heterogeneity from Zulla et al. (2023). Estimated from the standard deviation of the standard deviation of canopy height using a 90m square moving window.
Elevation	Elevation (m) at center of a 10m pixel.

Table S3: Mean values (SD) for covariates included in habitat suitability modeling for dusky-footed woodrats (*Neotoma fuscipes*) in the Sierra Nevada, California, USA. Values shown reflect those from the model fitting process (Model fitting) and all pixels within the spatial extent of our habitat suitability projections (Model projection).

Variable	**Model fitting**	**Model projection**
Canopy base height	1.65 (0.99)	1.64 (0.95)
Canopy bulk density	0.026 (0.020)	0.025 (0.018)
Canopy layer count	1.89 (0.74)	1.99 (0.59)
Canopy cover	66.26 (21.7)	71.44 (18.16)
Canopy height	18.64 (10.07)	23.46 (9.2)
Surface fuels	169.03 (23.7)	173.04 (20.41)
Ladder fuels	19.82 (7.43)	19.50 (4.76)
Forest heterogeneity	0.86 (0.51)	0.93 (0.52)
Elevation	1254.58 (174.84)	1289.48 (87.42)

Table S4: Modeling results from stage 1 for dusky-footed woodrat (*Neotoma fuscipes*) detection in the central Sierra Nevada, California, USA. The model denoted by "." indicates the intercept-only (i.e., null) model. The top model was carried forward and fixed for detection in all models in subsequent stages. Occupancy probability structure was held constant for all models as the intercept-only form $\Psi(.)$.

p	AIC	ΔAIC	K
Stage 1:			
Secondary sampling period + Forest type	1869.96	0	5
Secondary sampling period + Forest type + Illumination	1871.03	1.07	6
Secondary sampling period + Forest type + Julian date	1871.73	1.77	6
Secondary sampling period + Forest type + Illumination + Julian date	1872.78	2.82	7
Secondary sampling period	1885.22	15.26	3
Habitat	1929.25	59.29	4
Illumination	1943.24	73.28	3
.	1944.35	74.39	2
Julian date	1945.34	75.38	2

Table S5: Effects (β) and standard error (SE) for the top-ranked model(s) from stages 1, 2 and 3 for dusky-footed woodrat (*Neotoma fuscipes*) detection (p) and occupancy (*Ψ*) probability in the central Sierra Nevada, California, USA. Bold font indicates that the respective 85% confidence interval did not overlap zero. Occupancy probability structure was held constant for the model in stage 1 as the intercept-only form *Ψ*(.), and detection probability structure was held constant for models at stage 2 and 3 at p (Secondary sampling period, Forest type).

Stage 1 (Detection)				
Intercept	Secondary sampling period	Forest Type (Open)	Forest Type (Young)	
-0.11 (0.09)	**0.54 (0.07)**	**-3.13 (0.66)**	**0.58 (0.17)**	
Stage 2 (Occupancy - Physiography)				
Intercept	Elevation			
-0.83 (0.09)	**-0.31 (0.09)**			
Stage 3.1 (Occupancy - Landscape-scale)				
Intercept	Forest heterogeneity (Homogeneous)	Yng100-Mature		
-0.48 (0.16)	**-0.94 (0.23)**	**0.27 (0.10)**		
Stage 3.2 (Occupancy - Patch-scale)				
Intercept	Patch area (Young)	Forest Type (Young)	Forest Type (Open)	
-1.15 (0.12)	**-0.65 (0.22)**	**2.21 (0.46)**	**-2.09 (0.75)**	
Stage 3.3A (Occupancy - Site-scale; $w_i = 0.54$)				
Intercept	Understory	Canopy cover	Tanoaks	Basal area
-0.81 (0.16)	**0.75 (0.11)**	**0.34 (0.15)**	**1.90 (0.58)**	**0.21 (0.12)**
Stage 3.3B (Occupancy - Site-scale; $w_i = 0.34$)				
Intercept	Understory	Canopy cover	Tanoaks	
-0.80 (0.16)	**0.74 (0.11)**	**0.43 (0.13)**	**1.88 (0.56)**	

All continuous variables have been standardized. The reference levels for categorical modalities were heterogeneous for landscape and mature for forest type (i.e., for both young and open). Variables from top models in earlier stages (i.e., Table 2) and interactions (i.e., Table S1) not shown here were still tested; covariates that were not present in any competitive models are not included on this table for easier interpretability.

Table S6: Parameter estimates, standard errors, and 85% confidence intervals of explanatory variables included in habitat suitability models for dusky-footed woodrats (*Neotoma fuscipes*) in the Sierra Nevada, California, USA.

Variable	**Estimate**	**SE**	**85% CI**
Intercept	0.186	0.817	-0.99, 1.362
Canopy cover	0.042	0.008	0.03, 0.054
Canopy height	-0.034	0.016	-0.057, -0.012
Canopy base height	0.085	0.123	-0.092, 0.262
Canopy bulk density	-0.251	0.092	-0.383, -0.119
Canopy layer count	-0.869	0.211	-1.172, -0.565
Surface fuels	-0.002	0.005	-0.009, 0.005
Ladder fuels	0.052	0.021	0.022, 0.083
Forest heterogeneity	1.112	0.157	0.887, 1.338
Elevation	-0.003	0.002	-0.001, -0.006

Detection probability structure was held constant during model construction at *p* (Secondary sampling period, Forest type).

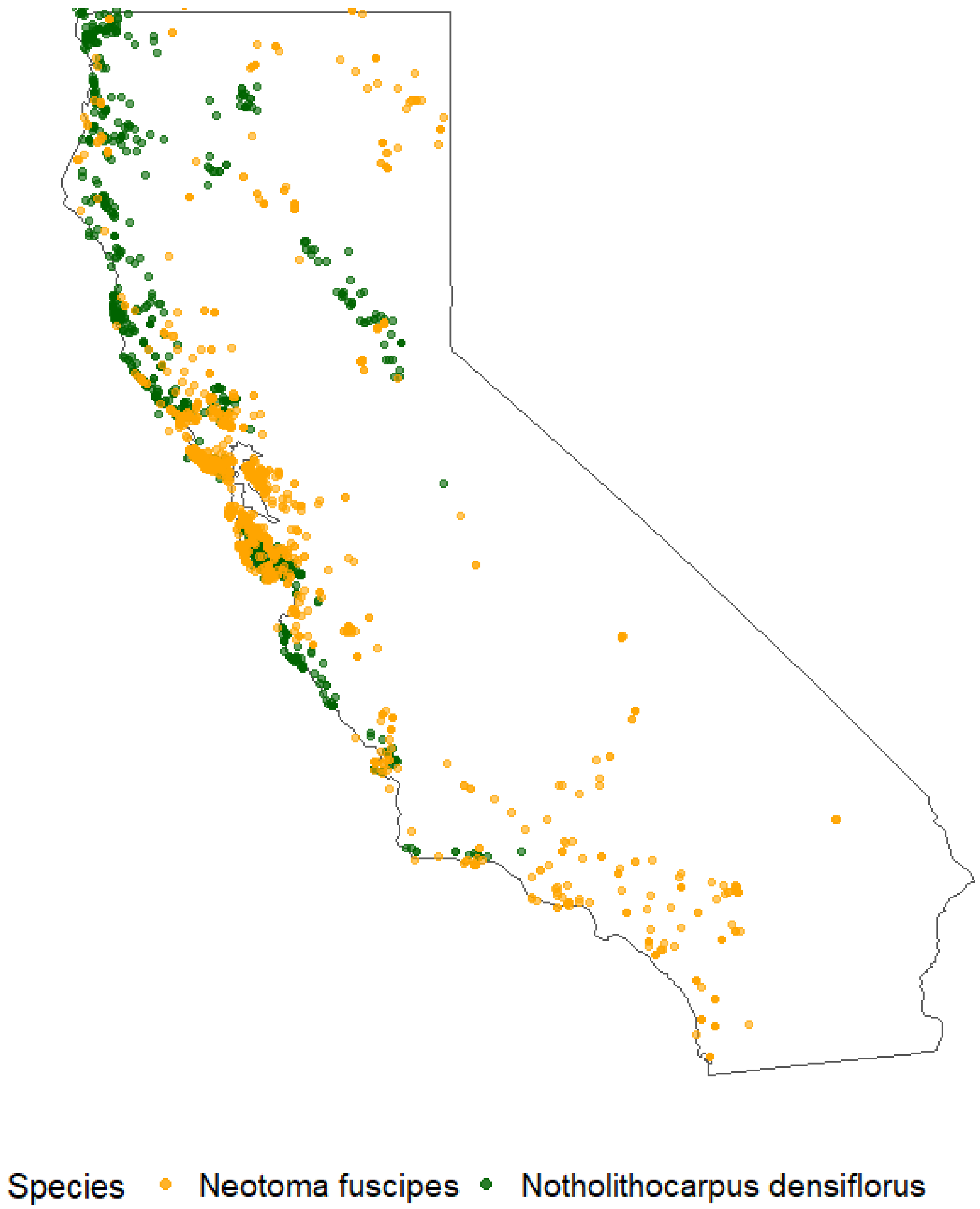

Fig. S1: Occurrence map of dusky-footed woodrats (*Neotoma fuscipes*) and tanoaks (*Notholithocarpus densiflorus*) within California, USA. Maps were created with point-of-occurrence data from the Global Biodiversity Information Facility (GBIF, www.gbif.org), which coalesces occurrence data from multiple datasets.

Fin.