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RESEARCH ARTICLE

Forest heterogeneity outweighs movement costs by enhancing hunting success and reproductive output in California spotted owls

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Abstract

Context The concept of landscape heterogeneity is central to species conservation; yet understanding the processes by which heterogeneity affects species can be challenging in practice. Complex and sometimes difficult-to-measure responses of species may reflect the outcome of life-history trade-offs shaped by different landscape properties.

Objectives We tested the hypothesis that a mosaic of forest stand types affected hunting and breeding success for California spotted owls (*Strix occidentailis occidentalis*).

Methods We integrated high-temporal-resolution GPS tags, video monitoring of nest sites, long-term assessments of reproductive status, and high-resolution remotely sensed vegetation data in a mixed-ownership landscape in the Sierra Nevada, California to test our hypothesis.

Results Spotted owls made shorter nocturnal movements in homogenous territories with large areas of medium-aged forest apparently because this forest type allowed direct movement paths to foraging sites. However, spotted owls delivered prey at a higher rate to nest sites when they had more forest edge in their territory, which presumably provided greater access to large-bodied woodrat (*Neotoma* spp.) prey. Further, spotted owl reproductive output was relatively high in heterogenous territories containing a mix of mature and open forest.

Conclusions The benefits heterogenous forests provide to hunting success appeared to outweigh costs associated with additional commuting distance to foraging sites and provided potential fitness benefits to spotted owls. We suggest that the effects of landscape heterogeneity can vary not only among,

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but also within, species and can reflect the outcome of trade-offs among different life history activities. Understanding the effects of landscape properties on biological communities will benefit from additional empirical and mechanistic studies of individual species.

Keywords Habitat fragmentation · Habitat heterogeneity · Hunting success · Movement · Reproductive output · Spotted owl

Introduction

Landscape heterogeneity is a fundamental concept in basic ecology and promoting landscape heterogeneity is often a guiding principle in applied conservation science (Rosenzweig 1995; Katayama et al. 2014). Landscape heterogeneity can be often defined as the occurrence of multiple habitat types distributed in a mosaic of patches with different characteristics (Turner and Gardner 2015). Such mosaics can promote the persistence of species using different habitat and thus benefit species diversity (MacArthur 1958; MacArthur and MacArthur 1961). Moreover, individual species can also benefit from heterogenous environments, particularly when individuals use different habitat types for different life-history needs such as breeding, foraging, and concealment (Vickery and Arlettaz 2012).

Responses to landscape heterogeneity, however, will depend on the size, configuration, and the juxtaposition of patch types (Tilman et al. 1997; Hanski et al. 2013; Loke et al. 2019) and will vary both within and among species (Stein et al. 2015; Wilson et al. 2016; Crooks et al. 2017; Chesson 2018). While some life-history traits can influence a species' responses in predictable ways (Cote et al. 2016), the manner in which the arrangement of habitat types influences individual fitness and populations may be the result of complex outcomes involving interactions between landscape properties and a suite of traits. Indeed, trade-offs can occur where one trait responds positively and another responds negatively to a specific landscape feature, with the nature of trade-offs differing among landscape features (Hanski et al. 2006). Consequently, there is a need for more empirical, mechanistic studies evaluating how life-history traits—and particularly potential trade-offs among traits—are shaped by landscape properties to understand how anthropogenic habitat change affects species. An enhanced focus on responses by individual species to landscape patterns may reveal mechanisms that contribute to a greater understanding of community-level responses (Jones and Tingley 2022).

The California spotted owl (*Strix occidentalis occidentalis*) provides a high profile example of the challenges associated with understanding how landscape heterogeneity and changes to landscape heterogeneity impacts a species. Spotted owls—which are a major consideration in the management planning of many western forests—typically nest and roost in large patches of mature forest and some studies have found that fitness components and territory occupancy benefit from extensive relatively contiguous areas of closed canopy and mature forests in their home ranges (Tempel et al. 2014, 2016; Jones et al. 2018). Moreover, the Humboldt flying squirrel (*Glaucomys oregonsis*), a primary prey species for many spotted owl populations (Munton et al. 2002), is often associated with dense canopy cover in mature forests (Meyer et al. 2005; Smith and Person 2007). However, in some parts of their range, spotted owls also forage in landscapes characterized by a mix of mature, young, and open forests (Waters and Zabel 1995; Irwin et al. 2007; Williams et al. 2011; Atuo et al. 2019; Gallagher et al. 2019; Zulla et al. 2022). Notably, woodrats (*Neotoma* spp.), on average are more energetically profitable than flying squirrels (1205 kJ versus 592 kJ; Weathers et al. 2001), can achieve higher densities in open/younger forests (Lee and Tietje 2005; Innes et al. 2007; Slowik 2015), and may be particularly accessible to owls along the edges of mature and open/younger forests where the combination of prevalent perching structures and dense prey create favorable hunting conditions (Sakai and Noon 1997). Both the consumption of woodrats and presence of open/young forest that promote woodrat populations, when intermixed with more mature forest (i.e., spotted owl nesting habitat), have been shown to benefit spotted owl populations in some studies (Franklin et al. 2000; Hobart et al. 2019a, b). Nevertheless, the dispersion of more mature forests created by the interspersion of open and younger forests could increase travel distances for spotted owls while foraging given that owls often tend to prefer mature forest during nocturnal activities (Atuo et al. 2019; Blakey et al. 2019; Kramer et al. 2021a), and thus may be restricted to such forests when commuting to more heterogenous foraging areas. Potential increases in movement distances in heterogeneous forests could both increase the energetic costs of foraging and the risk of nest predation while adults are hunting, thus reducing reproductive output. To date, however, studies linking spotted owl population metrics, habitat, and prey conditions are typically coarse in scale and correlational—with no mechanistic, integrative assessments of the behavioral, trophic, and fitness consequences of the potential trade-offs associated with different arrangements of forest types.

Here, we tested the hypothesis that the benefits to California spotted owls (henceforth spotted owl) of capturing larger prey (such as woodrats) outweigh the costs of potentially greater nocturnal movements when their mature forest foraging habitat is patchily distributed or intermixed with open forest and younger forest within their home ranges. We developed several predictions that, if supported, would provide evidence for this hypothesis. First, we predicted that spotted owls would travel farther distances to foraging sites when habitat characteristics were more patchily distributed within their home ranges (prediction 1). Second, we predicted that spotted owls would deliver prey items and biomass to nests at higher rates when their home ranges encompassed greater forest heterogeneity and edge (prediction 2). Finally, we predicted that spotted owl reproductive success would be related to the degree of forest heterogeneity and edge in home ranges as a consequence of these trade-offs (prediction 3). Understanding these potential trade-offs and the effects of landscape properties on spotted owls is particularly important given that much of their habitat occurs in mixed-ownership landscapes experiencing commercial timber harvesting and planting, and secondly, that forest managers are attempting to promote more heterogeneous forest conditions to create more resilient landscapes and reduce large severe wildfires in a region experiencing unprecedented change (Jones et al. 2020, 2021; Koontz et al. 2020).

Materials and methods

Study system

Our study took place in the northern and central Sierra Nevada, California (Fig. 1). Field work was conducted in a mix of private and public land to characterize spotted owl space use, trophic ecology, and fitness consequences across a gradient of composition and configuration of forested stands of different ages. Specifically, we studied spotted owls in and adjacent to (1) the Eldorado Demography Study Area (EDSA; all predictions); (2) Sierra Pacific Industries' (SPI) Stirling Study Area (SSA; all predictions), and (3) within SPI's five Watershed Study Areas (WSAs; prediction 3 only; Hobart et al. 2019b). All of these areas were characterized by mixed coniferous forests containing both patches of mature forest dominated by large trees and forests where the selective harvesting of large trees has produced relatively homogenous stands dominated by medium-aged trees (Fig. 2). Forests where selective harvest had occurred typically contained high densities of trees resulting from over a century of fire suppression (Parsons and Debenedetti 1979). Other forest types in the study areas included patches of open (often times containing a brushy understory) naturally regenerating young forests, and timber plantations (primarily on private land; Fig. 2). Past wildfires also shaped forest structure in our study areas and ranged from mixed severity fires that created a mosaic of forest types across the landscape to primarily large, severe fires that created extensive areas of snag forest (see also below). The vegetation was typical of Sierran mixed-conifer forest dominated by Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurens*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), and California black oak (*Quercus kelloggii*). Tanoak (*Lithocarpus densiflorus*) formed a dense understory in some areas. Mountain whitethorn (*Ceanothus cordulatus*), common manzanita (*Arctostaphylos manzanita*), and sierra gooseberry (*Ribes roezlii*) are commonly found in open areas across the landscape as well.

Owl surveys

We surveyed for owls from March 15 to August 31, 2013–2020 in all three study areas. EDSA and WSA territory locations were part of a long-term monitoring program (Tempel et al. 2016; Roberts et al. 2017). Owls were located during call-back surveys at night and found during dusk or dawn surveys the following day to determine their reproductive status and roost and nesting locations (Franklin et al. 1996). Owls

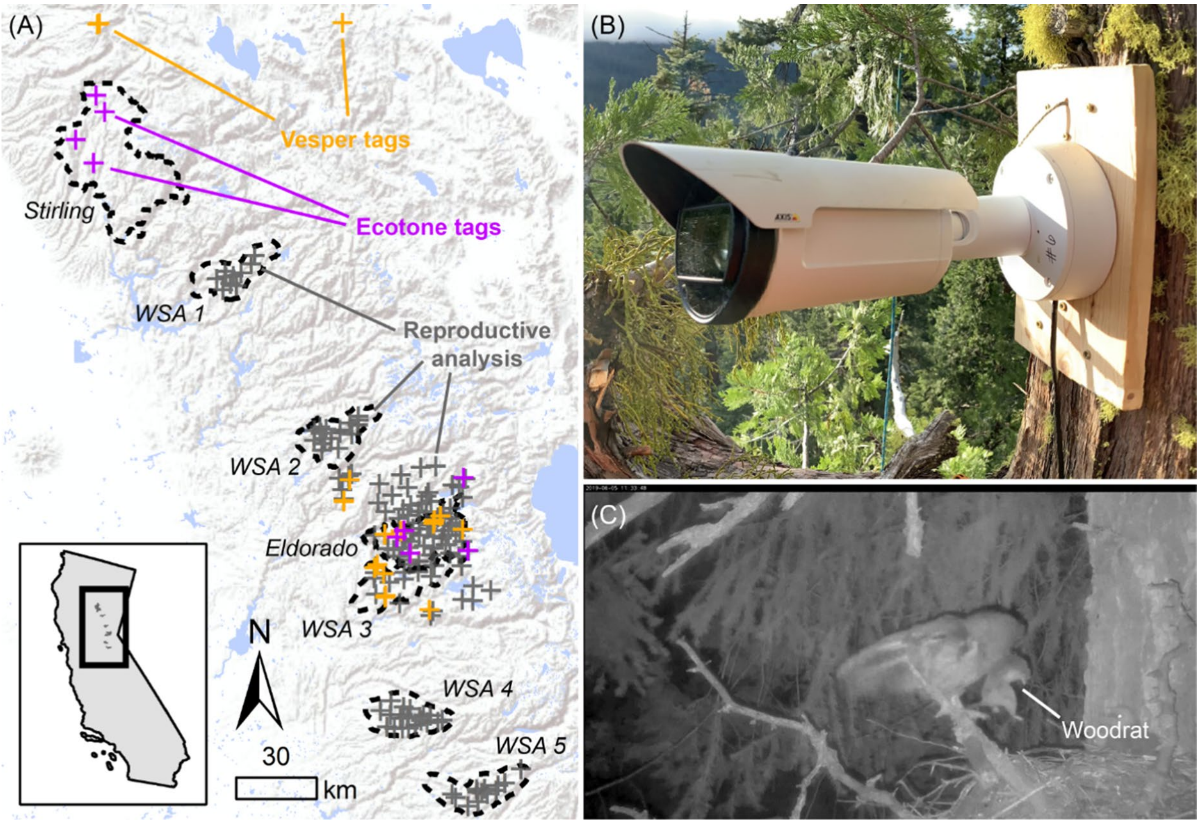

Fig. 1 **A** Map of Sierra Nevada, USA depicting locations of California spotted owl territories sampled in the study. **B** Video camera adjacent to a spotted owl nest. **C** Prey delivery of dusky-footed woodrat (*Neotoma fuscipes*) recorded on the video camera

were fed live mice during follow-up surveys to determine nesting status and number of juveniles fledged (Franklin et al. 1996).

GPS tagging

We captured 31 spotted owls (24 males and 7 females) for GPS tagging in 2019 and 2020, using noose poles, pan traps and hand capture methods (Wood et al. 2021). Owls were selected opportunistically for tagging based on the accessibility of the nest for video-monitoring (see below) and the likelihood of recapture to remove transmitters. We affixed GPS tags (Alle-300, Ecotone, Poland, 10 g) to 15 of these owls as tail mounts following methods in previous research (Kramer et al. 2021a, b). We affixed a different tag model (Vesper 3.2 tag manufactured by ASD, Haifa, Israel; 11.6 g) to the remaining 16 individuals also as tail mounts. The second set of tags collected vocalization data as part of another study in addition to the GPS data (Reid et al. 2022). Ecotone tags averaged a 45 m median spatial error and Vesper tags averaged a 23 m median spatial error when tested in various forested conditions (open, medium-aged, and mature forest; Kramer and Whitmore, *unpublished data*). For Ecotone GPS units, we removed locations below 3.7 voltage because they typically have greater positional error; and with Vesper GPS we removed locations with horizontal dilution of precision (HDOP) < 10 and satellites < 6 (S. Whitmore *unpublished data*). We programmed tags to collect locations at two-minute intervals throughout the nocturnal foraging period (2000 to 0600 Pacific Daylight Time) to characterize spotted owl movements during the nestling period in May and early June. Following the final deployment, we attempted to recapture all owls to remove GPS tags. Two individuals were not recaptured but were expected to molt during that season or the following, thus shedding the GPS tag.

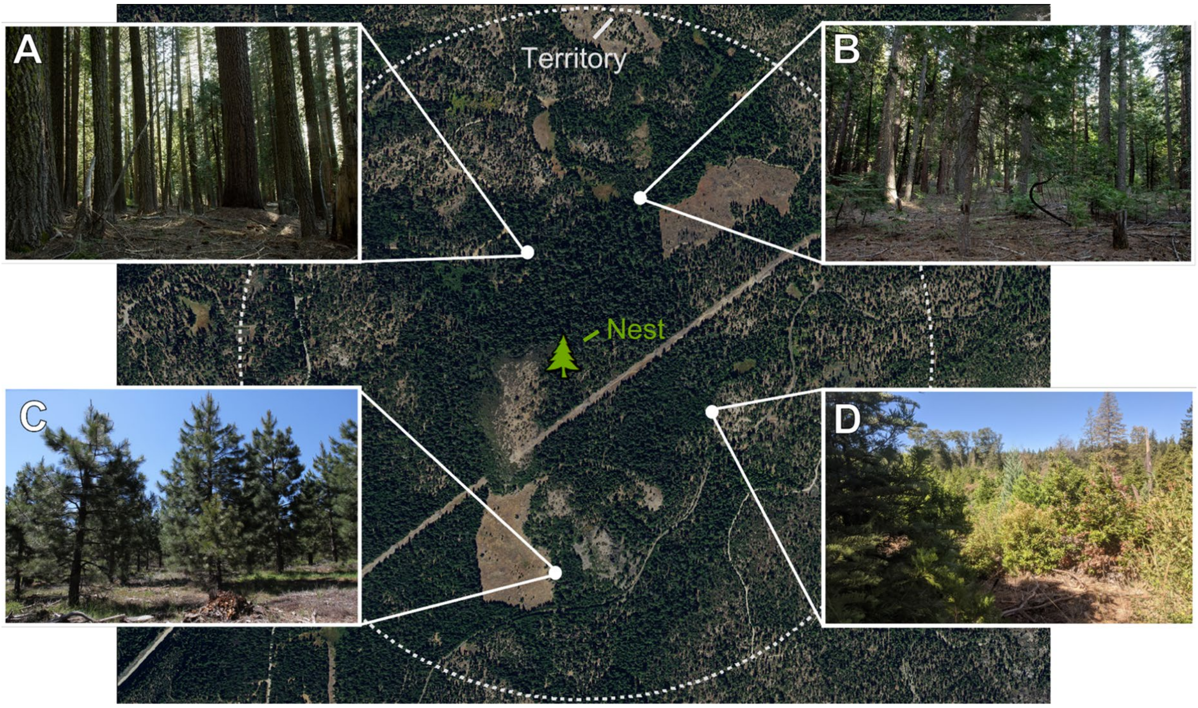

Fig. 2 Example images of vegetation types used in analyses (refer to Table 1 for definitions) overlayed on top of a spotted owl territory. **A** mature forest, **B** medium-aged forest, **C** young forest, and **D** open forest

Nest video monitoring

We monitored prey deliveries using infrared (IR) video cameras placed at the nest sites of 15 GPS-tagged males concurrent with the collection of GPS locations. To do so, we climbed a nearby adjacent tree (10–50 m from the nest tree) using a single rope technique and secured a video camera across from the nest tree. We monitored nests using AXIS Q1786—LE 4 megapixel outdoor infrared video cameras that continuously recorded high quality images throughout the nocturnal foraging period (2000 to 0630 Pacific Daylight Time). The video cameras were powered by a deep cycle lithium battery, both the battery and the video camera were connected to a Power over Ethernet (PoE) switch. The camera was programmed (using AXIS Companion manufactured by Canon Inc., Lund, Sweden) to specify image quality and recording period. Video recordings were saved to an onboard SD card, downloaded, and reviewed to detect and identify prey delivered to each nest.

Characterizing habitat composition and configuration

To understand the effects of habitat composition and configuration on spotted owl movements and prey deliveries, we characterized vegetation conditions within individual GPS-tagged spotted owl home ranges as well as in a large number of spotted owl home ranges in our study to understand effects on reproductive output (see below). For each GPS-tagged owl, we estimated the home range using 95% kernel density estimators (KDE) with all GPS location points (Seaman and Powell 1996). This unbiased method of home range estimation does not represent an individual's total territory nor its total home range size, as that would require months of tracking each individual owl (Forsman et al. 1984). Instead, the 95% KDE provides a relative measure of space use during the 2-to-15-night tracking period. Additionally, this method generates a utilization distribution that estimates the amount of time an owl spends in one location and then creates the smallest area containing 95% of the distribution. Within the calculated home range, we characterized the landscape into measures of both habitat composition (forest stand type) and configuration (spatial arrangement of forest stand types).

We classified habitat composition based on four forest stand types: mature, medium-aged, young, and open forest (Table 1) based on canopy cover and quadratic mean diameter thresholds consistent with previous work on owl-prey relationships (Hobart et al. 2019b). We defined open forest as areas where canopy cover was less than 40% and divided other forested areas with a canopy cover of 40% or greater into several classes based on tree sizes: (i) mature forest, where the quadratic mean diameter (QMD) of dominant and codominant trees was at least 60 cm, (ii) medium-aged forest, when QMD was between 30 and 60 cm, and (iii) young forest, when QMD was less than 30 cm. We then calculated the proportional area of each habitat class within each 95% KDE home range.

Our classification was based on 30 m resolution gradient nearest neighbor (GNN) data, which interpolates information from an extensive forest-inventory plot network across the landscape using Landsat imagery at a resolution of 30 m (Ohmann and Gregory 2002). Given that owl data spanned from 2013–2020, we used GNN data from an intermediate date of 2017. While timber harvesting did occur in some territories both before and after 2017, temporal changes in habitat composition based on remotely-sensed data were very small (on average < 1% of territories) relative to the degree of spatial variation in habitat composition among territories (Table 1; Tempel et al. 2016; Jones et al. 2018) and our analyses were focused on variation in owl behavior, diet, and reproduction that occurred among territories. Our study area experienced a large, severe fire in 2014 (the King fire) which substantially changed habitat conditions in several territories. However, on average, less than 1% of the area of the 95% KDE home range

Table 1 Metrics used to characterize habitat composition and configuration within individual spotted owl home ranges

Metric	Data source	Definition	Mean (SD)	Min–max
Mature forest	GNN	Proportion of home range with forests with QMD ≥ 60 cm and canopy cover ≥ 40%	0.09 (0.08)	0.00–0.43
Medium-aged forest	GNN	Proportion of home range with forests with QMD 30–60 cm and canopy cover ≥ 40%	0.55 (0.16)	0.08–0.90
Young forest	GNN	Proportion of home range with forests with QMD < 30 cm and canopy cover < 40%	0.19 (0.10)	0.02–0.74
Open forest	GNN	Proportion of home range with forests with < 40% canopy cover	0.14 (0.15)	0.00–0.78
Medium/mature patch distance*	CFO	Mean distance to nearest neighboring patch, for each medium/mature core forest patch (height > 20 m). To delineate each medium/mature core forest patch (i) identify all areas of medium/mature forest, (ii) remove all area within 50 m of young or open forest patches (of > 3600 m^2), and (iii) delineate patches using the 4-neighbor rule, and removing patches ≤ 3600m^2	71.8 (40.3)	2–141
Woodrat-prevalent edge	CFO	Relative woodrat-prevalent edge area in each territory, where edge is defined as the area between forests with 2–10 m canopy height and > 20 m canopy height (classified using a 90 m moving window across 10 m CFO-generated canopy height)	0.013 (0.010)	0–0.058
Forest heterogeneity	CFO	Canopy texture (SD of SD, using a 90 m moving window across 10 m CFO-generated canopy height)	0.80 (0.19)	0.23–1.29

Habitat composition metrics were derived from 30 m resolution 2017 Gradient Nearest Neighbor (GNN) data (Ohmann and Gregory (2002) and habitat configuration metrics were calculated using 10 m 2017 California Forest Observatory data [CFO; California Forest Observatory (2020)]

QMD quadratic mean diameter, *SD* standard deviation

*Some territories lacked medium/mature patches, which prevented computation of this variable because patch distance was greater than home range size. In these cases, we estimated patch distance as the maximum observed value plus one standard deviation for each of the 15 tagged spotted owls included in the movement and prey delivery analyses was affected by severe fire since 1986 and less than 4% of open forests in spotted owls 95% KDE home ranges overlapped with severe fire. Thus, the vegetation features in the home ranges of GPS tagged owls (including measures of spatial configuration described below) were mostly created by forest management on private lands rather than by severe fire.

We characterized three metrics of spatial configuration of forests within owls 95% KDE home ranges: (i) the distance between patches of medium-aged and mature forest (medium/mature patch distance), (ii) relative amount of edge where woodrats would likely be prevalent (woodrat prevalent edge; Sakai and Noon 1993, 1997), and (iii) forest heterogeneity (Table 1). We did so using finer-scale 2017 California Forest Observatory data [CFO; California Forest Observatory (2020)] describing vegetation height and canopy cover at 10 m resolution because fine-scale habitat configuration may be driving prey abundance and ease of capture. To calculate medium/mature patch distance, we first defined the core patch area as patches (defined using the four-neighbor rule; Turner & Gardner 2015) of at least 3600 m^2 in area where canopy height was over 20 m and which were located at least 50 m from shorter forest patches (defined as patches at least 3600 m^2 in area and with canopy height at or below 20 m; see Fig. 3). We then calculated the average distance between these patches within each 95% KDE home range. We approximated woodrat-prevalent edge as areas where shorter vegetation (small trees and brushy areas that we presumed to be woodrat source habitat; Sakai and Noon 1993, 1997) was in close proximity to tall vegetation (where woodrats may have been less abundant but easier to capture by owls because of more perching locations for owls and less cover for woodrats). We calculated this metric using a 90 m moving window to identify all pixels where at least 30% of pixels within the moving window were between 2 and 10 m in height [where 10 m was the maximum vegetation heigh in the woodrat abundant younger forest considered by Sakai and Noon (1997)] and at least 30% of the remaining pixels were over 20 m in height (see Fig. 3). Finally, we estimated forest heterogeneity using the standard deviation of vegetation height. We first calculated the standard deviation of canopy height within a 90 m moving window. In heterogeneous forests composed of a patchwork of clear cuts and mature forest, this produced a raster with both very high values (on clear cut edges) and very low values (within clear cuts or in even-aged stands), whereas in homogeneous forests that were more contiguous, values were mostly intermediate. While this delineation differentiated between these landscapes visually, a summary statistic could not capture this pattern. Thus, we measured the standard deviation of the standard deviation raster using another 90 m moving window. As shown in Fig. 3, this clearly resulted in values that were higher in heterogeneous areas and lower in more homogeneous forests.

Estimating distance travelled

We used sequential GPS locations to estimate the total nocturnal flight distance each night for each individual owl. Because energetic cost is strongly correlated to distance traveled, we considered this estimate likely to be a reasonable proxy for nightly energy expenditure (Shepard et al. 2013). To account for GPS error (again 45 m and 23 m median spatial error for the Ecotone and Vesper tags, respectively; Kramer and Whitmore, *unpublished data*) we removed any point that was farther from both the previous and subsequent points than the distance between the previous and subsequent points, a process that removed 10% of the GPS points. We then smoothed the line using a polynomial approximation with an exponential kernel algorithm to better approximate the actual distance flown by each owl each night. Finally, we calculated the mean nightly distance travelled for each tagged individual for analyses of movements in relation to habitat conditions, as described in more detail below.

Estimating prey and biomass delivery rates

For each nest monitored with video recorders, we estimated both the mean nightly prey delivery rate (number of prey items delivered per hour) and the mean nightly biomass delivery rate (grams delivered per hour) based on prey deliveries identified from the nest video data. Calculating prey biomass delivery rate required that we estimate the body mass of each prey item delivered. For the largest and most common prey, dusky-footed woodrats and Humboldt flying squirrels, we assumed that the mean

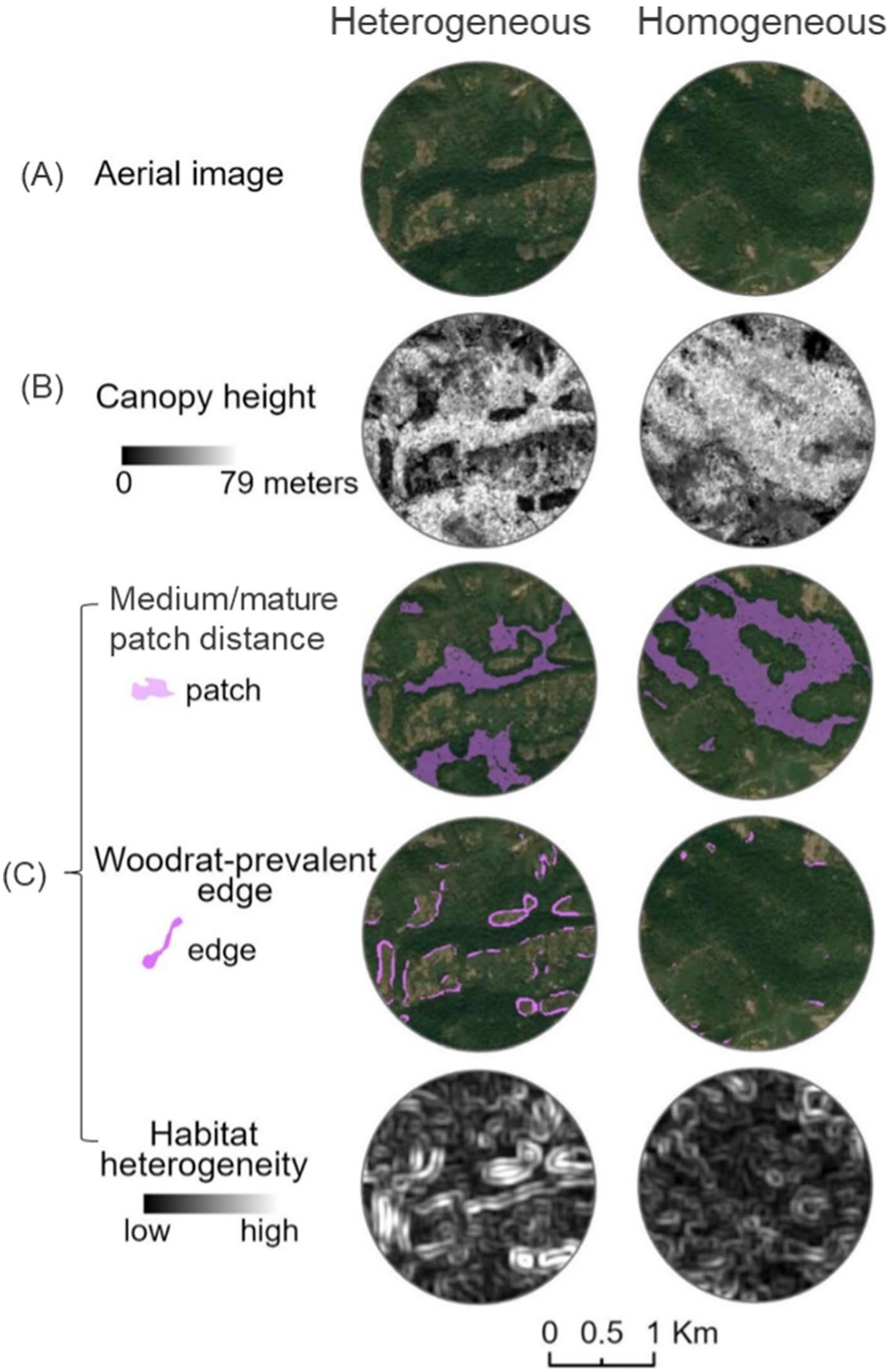

Fig. 3 **A** NAIP imagery for a heterogenous and homogenous spotted owl territory. **B** Canopy heights for the same two territories based on 2017 California of Forest Observatory (CFO) data. **C** Derived measures of habitat configuration for these territories calculated from CFO tree height data

body mass of individuals delivered to nests were equal to the body mass of individuals consumed by spotted owls as ascertained from regurgitated pellets that we collected as a part of previous field work in these areas (Peery, *unpublished data*). To calculate the mean body mass of these two species in spotted owl pellets, we collected at least one and up to six skull and mandible measurements (depending on the condition of the prey remains) from 26 flying squirrel and 31 dusky-footed woodrat skulls or skull fragments (Table S1). We then collected the same measurements from museum specimens using available mass measurements from the University of Washington's Burke Museum for flying squirrels ($n=86$) and the University of California, Berkeley's Museum of Vertebrate Zoology for woodrats ($n=50$). For the museum specimens, we developed predictive relationships between body mass and skull and mandible measurements using a set of univariate linear regressions of body mass against the skeletal measurements. We did not use a multiple regression approach as measurements could not be taken on all skull and mandible parts for all museum specimens or pellet samples. We estimated body mass for remains within pellets based on these predictive relationships and measurements of skull and mandible parts in museum specimens (Table S1). For each of the two species, we averaged body mass estimates from each prediction to determine an average mass. Using this approach, we estimated that the mean body mass of woodrats and flying squirrels consumed by spotted owls was 187.4 g (range 110.9 to 271.2 g) and 98.8 g (range: 80.2 to 117.2 g), respectively. We estimated the mass of the secondary and generally smaller species delivered to nests according to the midpoint of body mass ranges for species presented in the literature (Reid 2006). For example, if an owl delivered a mouse (body mass range 15–25 g) to their nest, the assigned body mass would be 20 g. When we were unable to identify the species delivered, we assigned the body mass based on the observed size class (large, medium, small, or extra small). Thus, in the small class that included mice (15–25 g), montane voles (30–80 g), and passerines (20–120 g), the prey mass estimate was 47.5 g. In instances where we were able to identify that there was indeed a prey delivery but were unable to estimate the size of the prey item due to the view being obstructed by the owl or an object in frame, we used the mean body mass of all other prey deliveries at that territory. To calculate the mean nightly biomass delivery rate and the mean nightly delivery rates, we averaged nightly values of these rates for each tagged spotted owl.

Estimating reproductive output

We related reproductive success estimated from spotted owl surveys conducted from 2013 to 2020 to the metrics of vegetation composition and configuration in Table 1. This analysis included the same 151 spotted owl territories used in Hobart et al. (2019b) but over a longer time period (Fig. 1). We treated the number of juveniles fledged (0, 1, 2, or 3) as the response variable where territorial pairs that did not attempt to nest were excluded such that 0 young fledged in this case represented the outcome of failed nesting attempts. Our rationale for this approach was that analyses of prey delivery rates to nests (i.e., prediction 2) were, by definition, constrained to pairs that attempted to nest and our objective was, collectively, to understand how the habitat-mediated variation in prey deliveries influenced the number of young fledged.

Because we lacked GPS tagging data for spotted owls within all of 151 territories considered in reproductive analyses, we calculated measures of vegetation composition and configuration (2017 GNN and CFO vegetation data) within circular areas approximating the size and location of owl territories. We calculated the geometric center for each territory based on the geometric mean of nest and roost locations over the study period following Hobart et al. (2019b). We then calculated the ½ nearest-neighbor distance for each territory (1.12 km) to create a radius centered on the territory's activity center and subsequently summarized the vegetation data within the circle.

We excluded reproductive data from the breeding seasons of 2013 and 2014 (pre-fire) to ensure that there were no substantial temporal mismatches between mapped vegetation conditions and owl data collection. Almost all of these severely burned territories remained unoccupied for the remainder of our study (2015–2020) and therefore generated no reproductive data. We included one territory in our reproductive analysis that experienced > 50% of severe burn and remained an occupied territory post fire. However, we did exclude pre-fire reproductive data for this territory because the mapped vegetation conditions did not reflect those present prior to the King Fire.

Statistical analyses

We used generalized linear models (GLMs) and generalized linear mixed-effects models (GLMMs) to evaluate our three predictions in program R with the packages 'glmulti' version 1.0.8 (Calcagno and de Mazancourt 2010) and 'lme4' version 1.1-27 (Bates et al. 2015). We selected the most parsimonious model for each prediction using an all-subsets approach in which all combinations of covariates in Table 1 were evaluated as competing models and did not consider interactions among variables (but see below). All covariates were z-standardized to improve model fitting routines and interpretation (Schielzeth 2010). We selected models using Akaike's information criterion with sample size correction (AICc). Models within 2 AICc of the top model were considered competitive (Burnham and Anderson 2002). Models containing pairs of variables with correlation coefficients greater than 0.70 were not considered. We report the 85% confidence interval for model coefficients because this interval is more compatible with AIC approaches than a 95% confidence interval (Arnold 2010). We estimated a pseudo-R^2 for GLMs and GLMMs using a corrected likelihood ratio-based approach (Nagelkerke 1991) with the R package 'rsq' version 2.2 (Zhang 2021). All-subsets selection was conducted using package 'glmulti' for GLMs and the 'dredge' function in the package 'MuMIn' version 1.43.17 (Barton 2020) for GLMMs. For each prediction, we selected the distributional family a priori before model fitting and selection. All models were fitted using maximum likelihood estimation.

For prediction 1 (mean nightly distance traveled as a function of patchiness; $n=31$), we specified a Gamma distribution with a log link. For the sake of parsimony, prior to considering the habitat covariates in Table 1, we first modeled "nuisance" effects that included sex, reproductive status, and tag type (because of differences in locational precision) as categorical fixed effects without any random effects. We then included supported terms from this modeling stage in all models incorporating habitat covariates in a second modeling stage. For prediction 2 (mean nightly prey biomass and mean nightly prey item delivery rates as a function of patchiness; $n=15$) we specified a Gamma distribution with a log link. Similar to prediction 1, this model contained only fixed effects. For prediction 3 (reproductive output), we specified a Gaussian distribution. The number of young fledged followed a positive discrete distribution ranging from 0 to 3. Although the data distribution for young fledged was not Gaussian, applying normal regression procedures (or a GLM procedure with Gaussian error) was less biased than GLM alternatives that followed positive discrete error distributions, such as Poisson (McDonald and White 2010). Territories were repeatedly visited across 8 years, so we treated 'territory' as a random effect. Reproductive output can also vary substantially among years in spotted owls (Franklin et al. 2004), so we treated 'year' as a random effect.

Results

Distance travelled

We acquired 33,056 usable nocturnal locations from the 15 spotted owls tagged with Ecotone GPS units and an additional 45,460 usable nocturnal GPS locations from the 16 spotted owls tagged with Vesper GPS units. We also deleted any partial nights from the estimates of distance travelled for both GPS tags. For analyses purposes, we collected a mean of 1466 locations per owl (range 553–4327) over a mean of 5.3 nights (range 2–15). The average size of the 95% KDE for these 31 individuals was 400 ha (SD = 377).

Our "nuisance" analysis suggested that the mean nightly distance travelled differed as a function of breeding status and tag type, but not sex or month—and we therefore carried over the former two effects into the second stage of modelling that included habitat covariates. Based on this model, spotted owls travelled shorter distances when there was more medium-aged forest available within their territory ($\beta_{\text{medium-aged forest}} = -0.14$, 85% CI $[-0.20, -0.08]$) based on the top model following all-subsets selection in the second stage (AICc = 115.88; pseudo-$R^2 = 0.87$; Table 2). Breeding owls traveled over twice as far as non-breeders (breeders mean nightly distance = 7375 m and non-breeders mean nightly distance = 3648 m; Fig. 4). Models containing measures of configuration (medium/mature patch distance, woodrat prevalent edge, or forest heterogeneity) all received relatively little support (ΔAICc = 0.267 to 3.07) and, indeed, all three measures were considered uninformative parameters (Table 2).

Prey biomass and prey delivery rates

Based on the video recordings, we observed 348 potential prey deliveries by spotted owls to their 15 nests. Of these, 62.6% were identified to species, 18.7% were identified according to size, 6.4% were of unknown species and size, and it was uncertain

Table 2 Most supported generalized linear models from each of three predictions

Model	AICc	ΔAICc	*w*	K
Prediction 1				
"Nuisance" analysis for distance traveled				
Breeding + tag type	122.07	0.00	0.433	3
Breeding + tag type + nights	123.46	1.38	0.217	4
Sex + breeding + tag type	124.89	2.81	0.106	4
Breeding + tag type + month tag deployed	124.91	2.83	0.105	4
Sex + breeding + tag type + nights	126.20	4.12	0.055	5
Breeding + tag type + nights + month tag deployed	126.45	4.37	0.049	5
Distance traveled				
Breeding + medium-aged forest + tag type	115.88	0.00	0.247	4
Breeding + medium-aged forest + mature + tag type	118.52	2.64	0.066	5
Breeding + medium-aged forest + young forest + tag type	118.55	2.66	0.065	5
Breeding + medium-aged forest + woodrat prevalent edge + tag type	118.56	2.67	0.065	5
Breeding + medium-aged forest + medium/mature patch distance + tag type	118.73	2.85	0.059	5
Breeding + open forest + medium forest + tag type	118.94	3.06	0.053	5
Breeding + medium-aged forest + heterogeneity + tag type	118.95	3.07	0.053	5
Prediction 2				
Prey biomass without potential influential territory				
Open forest + woodrat prevalent edge	107.66	0.00	0.167	3
Open forest	108.25	0.58	0.125	3
Open forest + woodrat prevalent edge + medium/mature patch distance	108.46	0.79	0.112	4
Open forest + medium/mature patch distance	109.67	2.00	0.061	3
Intercept-only	110.01	2.34	0.052	1
Prey biomass with potential influential territory				
Heterogeneity	131.85	0.00	0.194	2
Intercept-only	132.84	0.98	0.118	1
Mature forest	133.93	2.07	0.069	2
Woodrat prevalent edge	134.46	2.60	0.053	2
Young forest	134.55	2.69	0.050	2
Prey delivery rate				
Intercept-only	− 11.07	0.00	0.190	1
Heterogeneity	− 10.34	0.73	0.131	2
Woodrat prevalent edge	− 9.54	1.53	0.088	2
Mature forest	− 8.68	2.39	0.057	2
Young forest	− 8.56	2.51	0.054	2
Prediction 3				
Reproductive success*				
Mature forest + open forest + mature forest * open forest	543.2	0	0.135	6
Mature forest + open forest	543.4	0.14	0.126	5
Mature forest	543.8	0.6	0.100	4
Medium-aged forest + young forest	544.7	1.47	0.065	5
Woodrat prevalent edge + mature forest + open forest	544.8	1.59	0.061	6

AICc Akaike information criterion, *ΔAIC* difference between AIC and the top model in the set, *w* Akaike weight, *K* number of parameters. Depending on the degree of model selection uncertainty, we display models within 2 (denoted with *) or 5 AICc of the top model. Intercept-only (null) models were included in each set. K for Prediction 3 includes two random effects (year and territory)

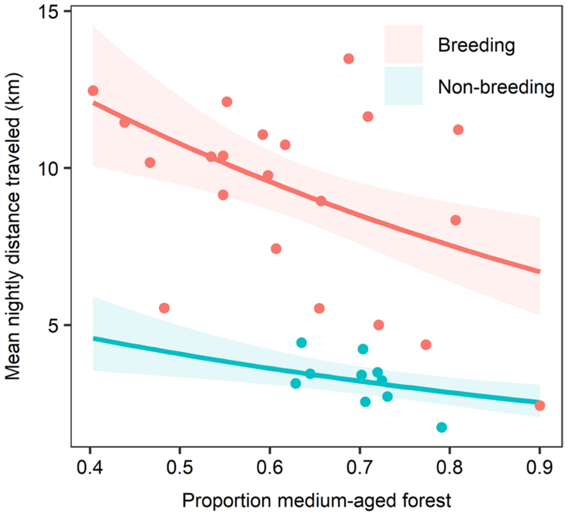

Fig. 4 Mean nightly distanced moved for breeding and non-breeding owls as a function of the proportion of their home range containing medium-aged forest

whether prey was delivered in 12.3% of cases. We identified eight different species delivered to nests, of which dusky-footed woodrats and Humboldt flying squirrels were the most common (41.5% and 40.2%, respectively). The less common species were bats (*Myotis* spp., 0.4%), mice (*Peromyscus* spp., 13.8%), montane voles (*Microtus montanus,* 1.8%), Townsend's mole (*Scapanus townsendii,* 0.9%), pocket gophers (*Thomomys* spp., 0.9%) and passerines (*Passeriformes* (order), 0.4%).

The null model for the mean number of prey *items* delivered per night, (AICc = −11.08) outperformed all other models indicating that delivery rates by spotted owls were unrelated to the measures of vegetation composition and configuration we considered (Table 2). The top model for the mean nightly prey biomass delivery analysis (AICc = 107.7; pseudo-R^2 = 0.50) suggested that spotted owls delivered prey biomass at a slower rate when there was a higher proportion of open forest within their 95% KDE home range ($\beta_{open} = -0.16$, 85% CI [−0.26, −0.07]; Fig. 5A) and at a higher rate to nests when more woodrat-prevalent edge occurred within their 95% KDE home range ($\beta_{woodrat\text{-}prevalent\ edge} = 0.12$, 85% CI [0.04, 0.21]; Fig. 5B). This relationship was derived after excluding a single observation with a high rate of biomass delivery (117 g per hour) at a nest for which we only collected 10.5 h of data before the juveniles fledged and for which a relatively high proportion of prey (8 of 9 deliveries) were not identified to species. Including this data point, spotted owls delivered prey biomass at a faster rate to nests when their territories contained more heterogeneous forest conditions ($\beta_{habitat\ heterogeneity} = 0.22$ [0.05, 0.41]); based

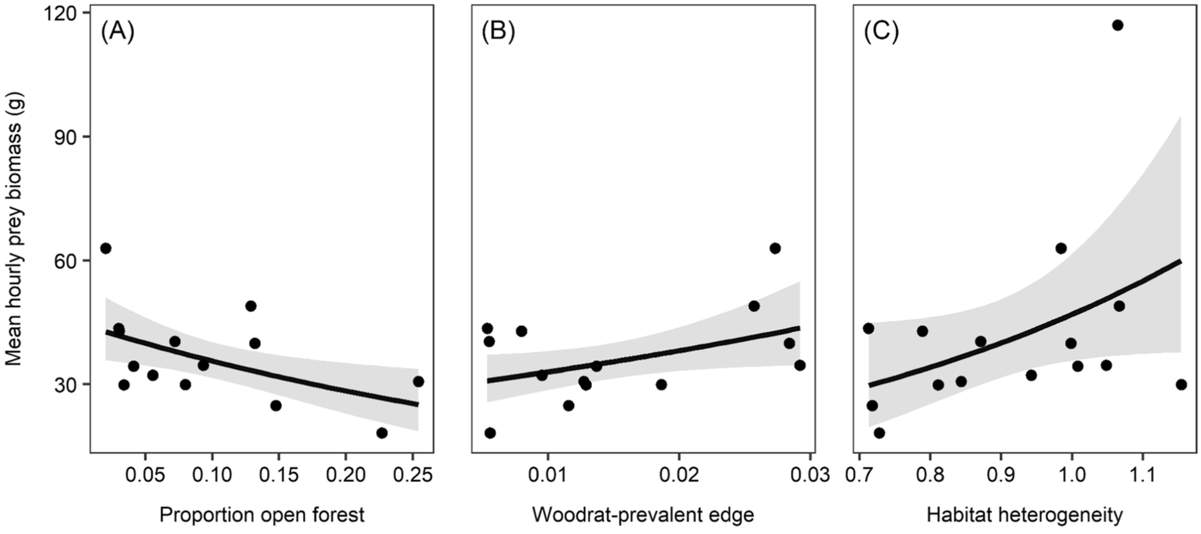

Fig. 5 Effects of habitat composition and configuration on prey biomass delivery rates to nests by spotted owls in the Sierra Nevada, California

on the top model (AICc = 131.9; pseudo-$R^2 = 0.24$; Fig. 5C); this was the only model to outperform the null model (AICc = 132.8).

Reproductive output

Reproductive output was lower for owls in territories with more mature forest ($\beta_{\text{mature forest}} = -0.11$, 85% CI [−0.19, −0.04]) and open forest ($\beta_{\text{open}} = -0.17$, 85% CI [−0.33, −0.02]) based on the most supported model (AICc = 543.4; Table 2). However, given that edges (or heterogeneity in vegetation conditions) increased biomass delivery rates to nests (prediction 2), we also examined a post-hoc model to explore a potential interaction between mature and open forest. This post hoc model (AICc = 543.2) was slightly more supported than the additive model and indicated that the effect of mature forest on reproductive output was conditional on the amount of open forest in a territory ($\beta_{\text{mature forest*open}} = 0.27$, 85% CI [0.01, 0.54]). Specifically, the benefits of mature forest on reproductive output were only realized when territories also had a high proportion of open forest (Fig. 6). Collectively, open forest, mature forest, and their interaction explained 33% of the variance in reproductive output among territories following the variance components approach of Franklin et al. (2000).

Discussion

Improved understanding of the mechanisms by which species respond behaviorally and demographically to landscape heterogeneity is needed to mitigate the potential effects of land use change and develop informed conservation plans. Here, we demonstrate that the effects of habitat configuration on a species considered to be a barometer of mature forest conditions are complex, where (i) the prevalence of medium-aged forest reduced nocturnal movements, (ii) edges between older and younger forests increased rates of biomass delivered to nests; and (iii) a mixture of mature and open forest increased reproductive output. Medium-aged forests may help reduce energy expenditures during nocturnal activities that include foraging, but a mixture of forest types provide the greatest benefit to prey acquisition and ultimately fitness (as measured by reproductive output). These findings are broadly consistent with previous studies demonstrating that heterogenous forest conditions can, in some circumstances, benefit spotted owl fitness by increasing the abundance or availability of

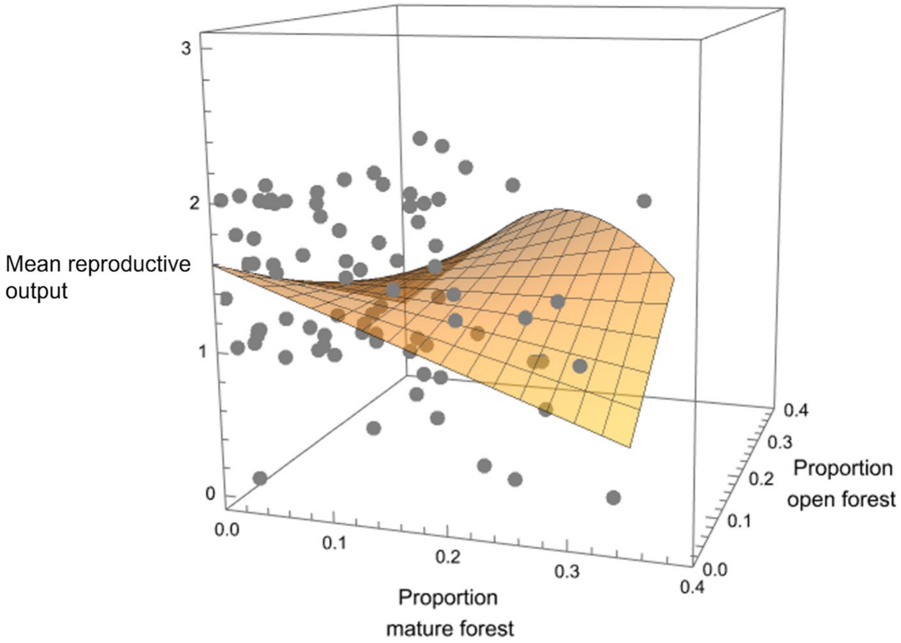

Fig. 6 Mean reproductive output as a function of interacting effects of the proportion of mature and the proportion of open forest within territories for nesting spotted owls in the Sierra Nevada, California

prey (Franklin et al. 2000; Hobart et al. 2019a). We provide a mechanistic and integrative explanation of how habitat configuration benefits spotted owls by shaping their movement patterns, prey capture success, and fitness.

Spotted owls made shorter nightly movements when there was more medium-aged forest available within their 95% KDE home range. This presumably resulted in lower energetic expenditures for owls when more medium-aged forest was available. While movement distances were not associated with the medium-aged and mature forest patch distance or other measures of habitat configuration we considered, the negative association between movement distance and medium-aged forest was generally consistent with our expectation that heterogeneity might increase movement distances. Medium-aged forest was the most prevalent forest type within spotted owl 95% KDE home ranges, on average exceeding half of the 95% KDE home range area (Table 1), such that 95% KDE home ranges containing a high portion of this forest type can be considered relatively homogenous. We suggest that high proportions of medium-aged forest afforded more direct paths to foraging sites at more heterogenous locations (Fig. 7) and potentially more direct paths to locations used to meet other life history demands such as territorial defense (Wood et al. 2019). Our previous work suggests that successful prey capture sites, particularly for woodrats, often occur in more open and heterogenous areas (Zulla et al. 2022). Further, spotted owls often selected medium-aged forests (and mature forests) for nocturnal activities based on GPS and VHF tagging agnostic to activity (Atuo et al. 2019; Kramer et al. 2021b). The frequent use of this forest type in our study may reflect commuting to more high-quality foraging sites while providing concealment from predators associated with open habitats such as great-horned owls (*Bubo virginianus*). While medium-aged forests reduced nightly movement distances in general, we note that spotted owl 95% KDE home ranges with large areas of this forest type have the potential to increase commuting distances to edges with open/younger forests where owls tend to capture woodrats. In addition, breeding individuals exhibited greater nightly movement distances than non-breeders, likely because of the additional movement necessary to deliver prey from foraging sites to nests (Zulla et al. 2022). However, breeding status and medium-aged forest were not correlated (r = − 0.30), such that tests of these two effects in the most supported model should have been independent.

While medium-aged forests reduced nocturnal movements and potentially benefited spotted owls energetically, edges between older forests (typically considered spotted owl habitat) and younger forests (more likely to constitute woodrat habitat) increased the rate at which adults (Fig. 5B) delivered prey to

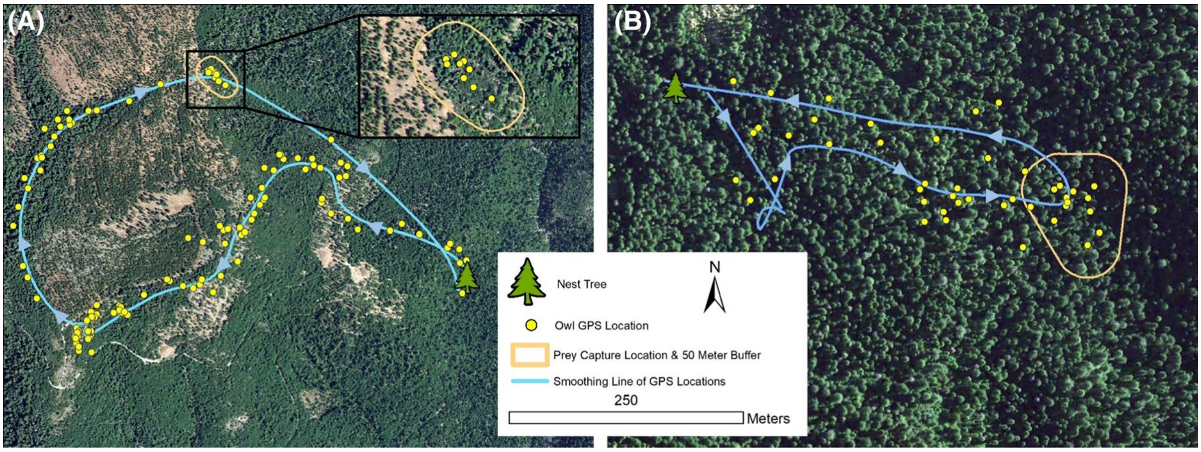

Fig. 7 Two examples of spotted owl movement paths away from and back to nest sites following successful prey captures in the Sierra Nevada, California. **A** a more circuitous path in areas with less medium-aged forest and **B** a more direct path in areas with more medium-aged forests. Note the prey capture sites are shown with tan shaded polygons (see Zulla et al. 2022 for methods)

nests. This result supports previous stable isotope work in the Sierra Nevada demonstrating that, in some mixed-ownership landscapes, heterogeneity can increase woodrat consumption in adult spotted owls, which in turn increases territory occupancy rates and landscape-scale population densities (Hobart et al. 2019a). This result is also consistent with spotted owls having higher fitness in territories characterized by higher levels of forest heterogeneity (Franklin et al. 2000), although we did not evaluate the mechanisms linking fitness and heterogeneity. Indeed, we provide long-sought support for the hypothesis that the juxtaposition of older forests and woodrat habitat promotes hunting success for spotted owls (Sakai and Noon 1993). The juxtaposition of these two habitats could both (i) promote the dispersal of individual woodrats from high-density populations in shorter (younger) forests into taller (more mature) forests, and (ii) allow spotted owls to capture woodrats at these ecotones (Sakai and Noon 1997). While we also found that spotted owls delivered prey biomass at a faster rate to nests when our measure of habitat heterogeneity was high, we caution that this result was strongly influenced by a single nest that was only monitored for a short period of time and for which it was unclear whether prey were delivered in several instances. While it may seem reasonable that fine-scale variation in forest age (as proxied by tree heights) could promote woodrat captures, we suggest that stronger evidence exists for the importance of edges between taller (older) and shorter (younger) forests. We note the edges promoting prey deliveries were typically the result of commercial timber management rather than wildfire in our study (e.g., Fig. 3C). None of the four territories with large values for edge in Fig. 5B experienced any recent severe fire. Importantly, however, the rate at which spotted owls delivered prey biomass to nests declined with the proportion of open forest in their territories (Fig. 5A). While some open areas, particularly those with substantial brush cover, likely harbor dense woodrat populations, large expanses are unlikely to be sources of prey to spotted owls unless sufficient taller (mature) forest is present in the vicinity.

Spotted owl reproductive output unexpectedly decreased with increasing proportions of mature forest and open forest, based on the most supported a priori model (Table 2). We expected that a greater proportion of mature forest would provide better opportunities for nest site selection, concealment from predators, and protection from inclement weather conditions (Franklin et al. 2000) particularly since this forest type constituted a relatively small proportion of spotted owl 95% KDE home ranges (0.09, Table 1). However, a *post-hoc* interactive model suggested that reproductive output was relatively high when territories contained greater proportions of *both* mature and open forests. In the absence of a positive main effect for mature forest, we suggest that a more likely explanation for higher reproductive output in territories containing a mix of mature and open forest involves enhanced foraging success—particularly considering the benefits of edge habitat to prey deliveries to nests. A faster rate of prey biomass delivery by adult spotted owls to nests afforded by greater edge between mature and open forests is likely to reduce nestling mortality and nest abandonment by breeding females. Although we acknowledge that woodrat-prevalent edge did not explain appreciable variation in reproductive output, we suggest that landscapes characterized by an interspersion of mature and open forest are likely to contain forest structural characteristics promoting the capture of woodrats, but we were unable to quantify these characteristics. Flying squirrels can be more abundant in mature forests, so that territories containing greater amounts of both forest types may harbor a greater diversity of prey types and overall prey availability. While the exact mechanism behind higher reproductive output in territories containing a mix of open and mature forest is uncertain, we suggest that enhanced prey access, hunting success, and deliveries to nests in territories with a mosaic of forest stand ages can lead to emergent benefits to spotted owl fitness in some ecological settings. Further, even if the association between reproductive output and mature and open forests were negative, as suggested by the top ranked a priori model, there was no evidence of greater commuting distances in territories with less medium-aged forest (and presumably greater heterogeneity).

Large scale loss and fragmentation of northern spotted owl (*S. o. caurina*) habitat from commercial timber harvesting appears to have contributed to population declines in the Pacific Northwest, where the Humboldt flying squirrel is the primary prey species (U.S. Department of Interior 1990). However, our results indicate that enhanced foraging opportunities in landscapes containing heterogenous forest conditions—with stands 10 s of ha in size—resulting largely from timber harvesting may benefit some fitness components (e.g., reproduction)—although we acknowledge that fire created some of this heterogeneity in 47 of the 151 territories (of these 47 territories, 33 were affected by less than 10% of fire across the territory). Previous work in the Sierra Nevada similarly suggested owls can have high reproduction and territory occupancy rates, as well as smaller home ranges, in such landscapes (Hobart et al. 2019a, b). Benefits of mosaics of forest of different ages are most likely to benefit spotted owls when younger and open forests retain the denser shrub cover and hardwood species (i.e., oaks) that promote dense woodrat populations. Moreover, there likely exists a threshold in terms of habitat modification where heterogeneous landscapes become fragmented by large expanses of open areas, reducing at least some fitness components and ultimately population density. However, further research is needed to understand the nature of such thresholds with respect to the composition and configuration of forest types not just within spotted owl home ranges, but at landscape scales as well. We also acknowledge that our results likely only apply to California spotted owls occurring in landscapes such as the low- to mid-elevation forests of the Sierra Nevada and higher elevation forests of southern California where woodrats can occur in high densities in younger forests and brushy open forests. Responses to changes in habitat composition and configuration are likely to differ in landscapes where flying squirrels are the primary prey of spotted owls, such as higher elevation forests in the Sierra Nevada (Hobart et al. 2019a). Finally, while our focus on reproductive output was appropriate given the tight linkage between prey availability and breeding often observed in owls (Dawson and Bortolotti 2000), other fitness components—such as individual survival and recruitment—can respond differently to habitat conditions (Franklin et al. 2000; Tempel et al. 2014). Nevertheless, while further work is needed to understand the relationship between habitat heterogeneity and spotted owl behavior, foraging success, and population dynamics in other forested landscapes, our study highlights new, integrative approaches (e.g., high temporal resolution GPS tags and nest video monitoring) that can yield novel insights into such questions.

Our results also have implications for the management of fire-suppressed forests on public land (i.e., national forests) where land managers are increasingly striving to reintroduce frequent, lower-severity fire regimes to promote forest heterogeneity and ultimately forest resilience to large, severe fires and droughts. While the benefits of forest heterogeneity to spotted owl foraging that we and previous studies have observed (e.g., Franklin et al. 2000; Atuo et al. 2019) was largely the result of commercial timber harvesting, lower-severity wildfire that creates fine-scale heterogeneity similarly benefits spotted owl foraging (Kramer et al. 2021a). In the evolutionary environment of spotted owls, patterns of forest heterogeneity were produced by fire, and owls appear to have become behaviorally adapted to such heterogeneity (Jones et al. 2020). Yet, from the perspective of the owl, the process generating heterogeneity may not be particularly critical. Hobart et al. (2019a) demonstrated using stable isotope analysis that spotted owl diets were similar (high proportion of woodrats) on both national parks and industrial timberlands, and that this similarity in diet was driven by landscape heterogeneity, albeit produced by different processes (fire and timber harvesting, respectively). Natural frequent-fire regimes create small patches of severely burned forests that become open (brushy) areas containing high woodrat densities in the early stages of regeneration (Converse et al. 2006); similar patterns of heterogeneity can be produced through forest management practices (North and Keeton 2008). Forest management that produces landscape heterogeneity, therefore, may result in the dual benefits of providing prey resources for spotted owls and increasing ecosystem resilience to drought and fire (North et al. 2021). Further research must downscale this broad generality to understand the landscape patterns, configurations, and scales that allow these two objectives to be achieved.

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Authors' contributions MZP, SCS, BPD, KNR, and JJK conceived the study; CJZ, RJG, BPD, and KNR led data collection, with contributions from KGK, WJB and SAW; CJZ, GMJ, HAK, JJK, and MZP designed the analysis; CJZ, GMJ, HAK, and MZP analysed the data; CJZ, GMJ, HAK and MZP wrote the manuscript. All authors provided critical feedback and gave final approval for publication.

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Data availability Data and R code is available from CJZ on request.

Declarations

Competing interests The authors declare no conflict of interest.

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