



Older forests function as energetic and demographic refugia for a climate-sensitive species

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Abstract

More frequent and extreme heat waves threaten climate-sensitive species. Structurally complex, older forests can buffer these effects by creating cool microclimates, although the mechanisms by which forest refugia mitigate physiological responses to heat exposure and subsequent population-level consequences remain relatively unexplored. We leveraged fine-scale movement data, doubly labeled water, and two decades of demographic data for the California spotted owl (*Strix occidentalis occidentalis*) to (1) assess the role of older forest characteristics as potential energetic buffers for individuals and (2) examine the subsequent value of older forests as refugia for a core population in the Sierra Nevada and a periphery population in the San Bernardino Mountains. Individuals spent less energy moving during warmer sampling periods and the presence of tall canopies facilitated energetic conservation during daytime roosting activities. In the core population, where tall-canopied forest was prevalent, temperature anomalies did not affect territory occupancy dynamics as warmer sites were both less likely to go extinct and less likely to become colonized, suggesting a trade-off between foraging opportunities and temperature exposure. In the peripheral population, sites were more likely to become unoccupied following warm summers, presumably because of less prevalent older forest conditions. While individuals avoided elevated energetic expenditure associated with temperature exposure, behavioral strategies to conserve energy may have diverted time and energy from reproduction or territory defense. Conserving older forests, which are threatened due to fire and drought, may benefit individuals from energetic consequences of exposure to stressful thermal conditions.

Keywords Climate change · Energetics · Forest · Occupancy · Refugia

Introduction

Broad scale, extreme temperature events associated with modern climate change threaten a myriad of species. A species' vulnerability to these events is mediated by exposure to extreme conditions, sensitivity to those conditions, and their ability to adapt to novel environments (Peterson 2003; Parmesan and Yohe 2003; Moritz and Agudo 2013). While temperatures approach and exceed thermal thresholds for

climate-sensitive species, pockets of suitable habitat space, or refugia, can act as buffers to the consequences of extreme weather (Keppel et al. 2015). Individual organisms often exhibit preference for habitats and structures that create cooler microclimates during heat waves (Wolff et al. 2020; Varner et al. 2016; Briscoe 2015). However, changes in land-cover due to anthropogenic activities can degrade such refugia (De Frenne et al. 2021), leaving some individuals and populations vulnerable to challenging thermal environments.

In the absence of thermal refugia, exposure to extreme temperatures increases the amount of energy an organism must expend to maintain homeostasis (Tucker 1970; Schulte 2015). Many endotherms are particularly vulnerable to extreme heat, and behaviors that increase heat dissipation require physiological trade-offs, leading to elevated energetic expenditure, losses in body mass, and reduced fitness (McKechnie and Wolf 2010). In response to changing abiotic environments, some animals alter their behavior to either

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accommodate elevated energetic expenditure or avoid exposure entirely (Moyer-Horner et al. 2015). Birds in particular are expected to experience thermoregulatory costs due to warming and drying conditions (Riddell et al. 2021). The physiological and demographic consequences of exposure manifest in species' range shifts and population declines, especially when warm temperature events are longer and have greater influence on more widespread declines (Conradie et al. 2019; Cunningham et al. 2013; Zuckerberg et al. 2018; McKechnie and Wolf 2010; Both et al. 2006).

While warm temperatures threaten many climate-sensitive species, well distributed and effective thermal refugia should shield individuals from heat exposure and ultimately slow or prevent population declines stemming from increasingly unsuitable temperatures (Morelli et al. 2020). For example, high canopy cover, large trees, and vertical complexity in overstories reduce solar radiation and maintain stable temperatures (De Frenne et al. 2021). Hence, older forests in western North America create microclimates that are relatively buffered from regional temperatures to the benefit of several bird species (Frey et al. 2016). As such, forests have variable thermal properties and capacity to buffer climate-sensitive species from warm temperatures. The potential value of suitable forest conditions to old-forest associated species could increase as heat events are projected to become more frequent and extreme (Cayan et al. 2008; Hulley et al. 2020). Although more complex forest structure can reduce the negative effects of warming on some avian populations (Betts et al. 2018), we have yet to understand the mechanisms by which cool microclimates created by older forest characteristics can mitigate potential physiological consequences of rising temperatures and subsequent effects on distribution and abundance.

The California spotted owl (*Strix occidentalis occidentalis*, Xántus de Vesey, 1860) is a climate-sensitive, old-forest species that provides novel opportunities to examine the extent to which the spatial distribution and structure of forests buffer energetic and fitness costs of a warming climate. Spotted owls are less heat tolerant than other birds and exhibit behavioral signs of heat stress while roosting and elevated resting metabolic rates under moderate increases in daytime temperatures (Barrows et al. 1981; Ganey et al. 1993; Weathers et al. 2001). Generally, birds benefit from complex forest structure and vegetation diversity (Kim et al. 2022), but forest structure varies considerably in western North America because of management history (e.g., timber harvesting), wildfire, drought-related tree mortality, and natural variation in floristics and growing conditions, which can have disparate effects on forest species (Brunk et al. 2023; Gutiérrez et al. 2017). Spotted owls often respond negatively to major landcover change (Gutiérrez et al. 2017), particularly at the southern extent of the species' range, where territories that lack the older forest component of large trees

at lower, warmer elevations are less likely to be occupied (Tempel et al. 2022). While this species typically nests and roosts in tall forests with high canopy cover (Gutiérrez et al. 2017), the extent to which such forest characteristics provide temperature refugia for spotted owls during heat events is uncertain. Therefore, it is essential to understand the spatial extent and structure of forests needed to create effective temperature refugia to develop strategies to conserve, not only spotted owls, but a host of other old-forest species.

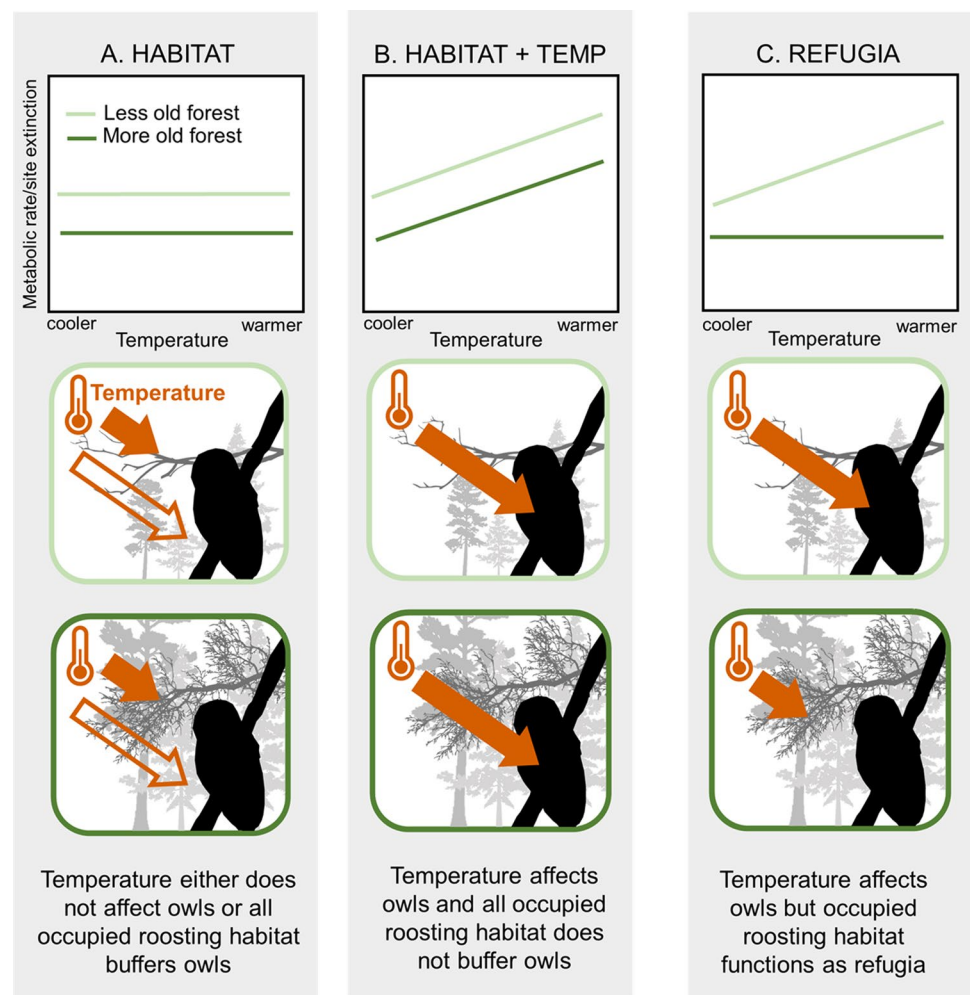
Here, we assessed how forest structure and prevalence of older forest characteristics influence the potential consequences of rapidly changing thermal conditions on this iconic old-forest species. We did so by measuring the effects of temperature on individual field metabolic rates, spatial behaviors, and dynamic territory occupancy rates across individual owl territories and broader geographic regions along a gradient of forest and temperature conditions. Under this framework, metabolic rates and spatial behaviors reflect the individual-level responses to heat exposure and occupancy reflects population-level responses to heat events. We proposed three alternative hypotheses for how forest structure and warm temperatures affect energetics and occupancy (Fig. 1). (1) If only habitat affects energetics and occupancy, then either warm temperatures do not have a direct impact on spotted owls, or all occupied habitat is sufficient temperature refugia regardless of forest structure or the prevalence of older forest in a territory (Fig. 1a). (2) If both habitat and temperature affect energetics and occupancy, and these effects operate independently, then older forest structure does not function as sufficient temperature refugia (Fig. 1b). (3) If habitat and temperature interact such that the effects of warmer temperatures are buffered by older forests, then older forest structure functions as temperature refugia (Fig. 1c). To evaluate these three competing hypotheses, we estimated spotted owl field metabolic rates, collected high-resolution movement data from GPS-tagged owls, and developed multi-season occupancy models across a range of climate conditions and habitat characteristics.

Methods

Study areas and field work

Our study took place in the core distribution of the California spotted owl in the Sierra Nevada, California, USA, and at the southern periphery of the species' distribution in the San Bernardino Mountains, which harbors the largest spotted owl population in southern California (Verner et al. 1992). In the Sierra Nevada, spotted owls defend territories between ~800 and 3000 m in elevation in mixed-conifer forest with woodlands at lower elevations (Verner et al. 1992). The average proportion of forest with canopy cover over 70%

Fig. 1 Alternative hypotheses for the role of roost/nest habitat as temperature refugia. Light green indicates characteristics associated with younger, more open forests and dark green indicates characteristics typical of older forests like closed canopies, tall trees, and vertical complexity. We show predictions for individual metabolic rate and the probability of site extinction. Predictions for spatial behaviors and colonization are equal but opposite in direction. Arrows in the figure indicate the negative effects of warm temperatures for spotted owls (solid) or lack thereof (hollow)



in a territory in the Sierra Nevada is 0.43 (SE=0.03) and the average proportion of forest with canopies over 20 m tall is 0.35 (SE=0.03). In the San Bernardino Mountains, spotted owls occupy territories between 1000 and 2500 m elevation (Smith et al. 1999). However, at higher elevations, their habitat mainly consists of mixed-conifer forests; whereas at lower elevations, their habitat is restricted to drainages that contain large conifers and deciduous trees surrounded by shrubs and chaparral (LaHaye et al. 2004). In San Bernardino Mountains, the average proportion of forest with canopy cover over 70% in a territory is 0.08 (SE=0.01) and the average proportion of forest with canopies over 20 m tall is 0.01 (SE=0.002). Regional maximum temperatures in spotted owl territories range from 25 to 33 °C in the Sierra Nevada and from 21 to 32 °C in the San Bernardino mountains.

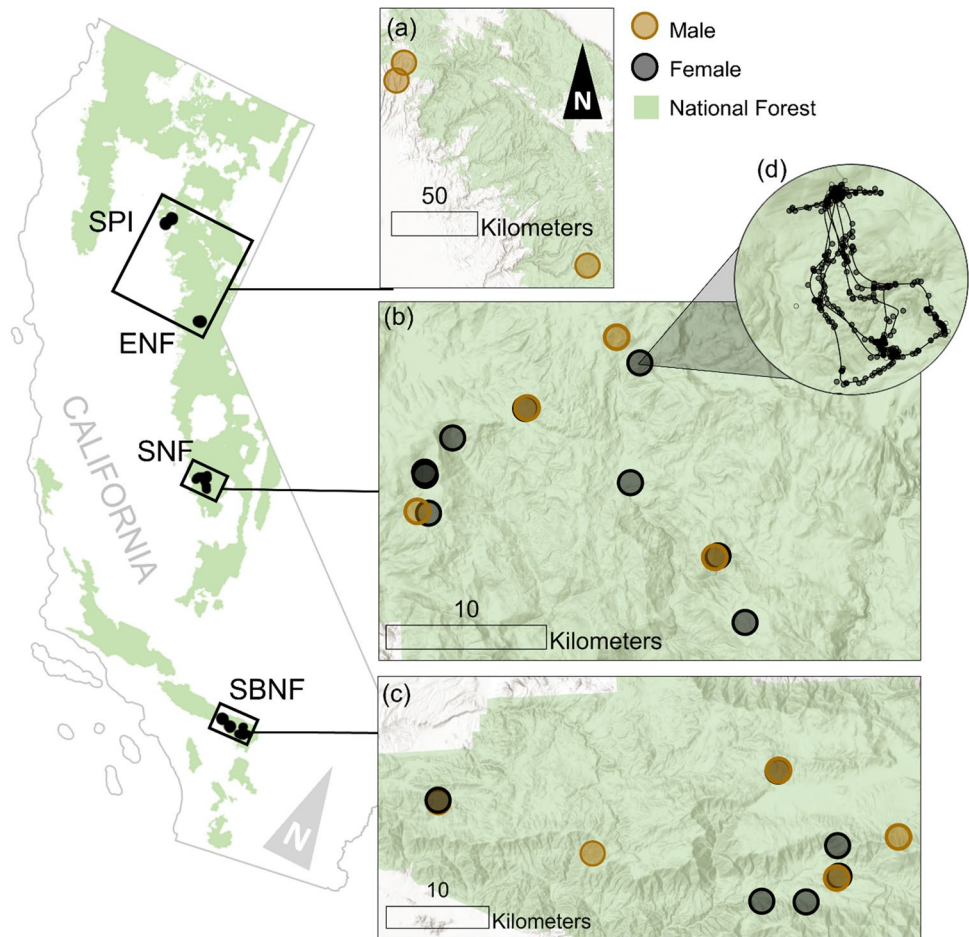
We captured, tagged, and obtained doubly labeled water samples from 27 California spotted owls between 2019 and 2021 from SPI (Sierra Pacific Industries, $n=2$), ENF (Eldorado National Forest, $n=1$), SNF (Sierra National Forest, $n=13$), and SBNF (San Bernardino National Forest, $n=11$,

Fig. 2a–c). Individuals were located by imitating their territorial four-note calls in territories identified as part of long-term demographic and other studies (Berigan et al. 2019; Tempel et al. 2016; Jones et al. 2016). We targeted owls strategically to maximize our chance of recapture and obtain a sample from a large elevational gradient and corresponding temperature conditions. Individuals were initially captured using a hand-grab technique that minimizes stress, maximizes the likelihood of recapture, and decreases confounding factors that could affect metabolic rate (Zulla et al. 2022). Recaptures were performed using a hand-grab technique, snare-pole, or pan-trap (Zulla et al. 2022).

Isotope enrichment for field metabolic rate

To measure field metabolic rate (FMR), we used a single-sample DLW approach (Speakman 1993; Schultner et al. 2010) over a 2–8-day period on all 27 owls (July 2019–July 2022). Following initial capture, a maximum of 200 µL blood sample was drawn from the metatarsal vein to determine background levels of ^{18}O and ^2H isotopes expenditure

Fig. 2 Study areas and territories where we tagged individual spotted owls. We tagged 13 males (brown) and 14 females (black) between the years 2019–2021. Field work was conducted in the **a** Eldorado (ENF), **b** Sierra (SNF) and **c** San Bernardino (SBNF) National Forests and **a** two samples for individual analyses were obtained from the Sierra Pacific Industries' Stirling study area (SPI). We tagged each bird with a GPS unit and obtained distance traveled per day and average velocity using **d** locations from GPS devices



(Nagy 1983). Using 25-gauge needles and 5 mL syringes, we administered a dose of DLW into the pectoral muscle ($\sim 1.10 \text{ g } ^{18}\text{O kg}^{-1}$ total body water, or TBW, $0.48 \text{ g } ^2\text{H kg}^{-1}$ TBW). We calculated the mass of each dose immediately prior to and after injection. We aimed to recapture individuals after a minimum of one-half ^{18}O half-life (Nagy 1983). Sterile 25-gauge needles and 1 mL syringes were used for all blood samples, and blood was collected in 100 μL micro-hematocrit capillary tubes, which were initially sealed with medical grade clay sealant and eventually flame-sealed to prevent fractionation of blood sampled (Martin et al. 2020). Blood samples were refrigerated at 3°C until we had access to a lab for distillation and isotope analyses.

We vacuum distilled blood samples and analyzed distillate to determine levels of ^{18}O and ^2H (Nagy 1983). We analyzed samples at the University of Wisconsin–Madison using gas source isotope ratio mass spectrometry to measure isotope ratios of $^{18}\text{O}:^{16}\text{O}$ and $^2\text{H}:^1\text{H}$. We ran samples collected in the field alongside standard samples for $^2\text{H}_2^{18}\text{O}$, serial dilutions, and background water, and we obtained estimates of daily energetic expenditure from isotope enrichments using the single-pool model for animals $< 5 \text{ kg}$ (Speakman 1997). Rates of CO_2 production, water influx,

and water efflux were calculated according to single-sample methods defined in Speakman (1997). CO_2 production rates were converted to field metabolic rates (FMR, kJ day^{-1}) using caloric equivalents calculated from the assumption that energy expended was derived from ingested food (0.72 for uricotelic carnivores, Gessaman and Nagy 1988). Total energetic expenditure was calculated from O^{18} elimination respective to H^2 elimination. We used a single-sample approach to estimate initial isotope enrichment based on the relationship of initial isotope enrichment and body mass, which required the assumption that all individuals have approximately the same proportion of body water and that total body water remains constant throughout the measurement interval (0.617 , Webster and Weathers 1989; Speakman 1993; Schultner et al. 2010). We scaled our estimates of field metabolic rate to account for body mass (mass-specific; $\text{kJ day}^{-1} \times \text{kg}^{0.71}$; Hudson et al. 2013).

Estimating distance traveled and average velocity

Following initial injections, we tagged individuals with one of two types of GPS tags (Pinpoint-120, SWIFT, Lotek, US and Alle-300, Ecotone, Poland) via tail mounts (Kramer

et al. 2021) to estimate distance and velocity of owl movements. We tagged 22 birds with Pinpoint tags (~6.7 g), which had relatively shorter battery life, and 5 birds with Ecotone tags (~10 g), which had longer battery life (~6 days) and were used in collaboration with two separate projects (Zulla et al. 2022; Wilkinson et al. 2022). All tags regardless of type were programmed to record a location every 2–3 min for 10 h each night (2000–0600 PDT) over the life of the tag (3–8 nights). Pinpoints were additionally programmed to record one location every hour during the day to obtain an estimate of operative temperature. We standardized all final nocturnal data so that each tag effectively recorded a location every three minutes. We filtered all GPS points obtained with Pinpoints by horizontal dilution of precision (<5) and the number of satellites involved in the fix (>5), which were both correlated with error in initial testing ($r_{\text{HDOP}}=0.42$, $r_{\text{SATS}}=-0.16$). We filtered points obtained with Ecotones by battery life (>3.7 V; Zulla et al. 2022).

To calculate distance each bird traveled per night, we removed any location that was farther from both the previous and subsequent locations than the distance between the previous and subsequent points (Online Resource 1: Fig. S1), an approach that eliminated 10% of GPS locations. We then smoothed the line using polynomial approximation with exponential kernel algorithm to better approximate the actual distance flown by each owl (Fig. 2d). We calculated average nightly distance traveled by dividing the total distance each individual traveled by the total time each individual was tagged with a live GPS unit. We measured average nightly velocity each bird traveled by calculating the distance between finalized locations, dividing by the time interval between fixes, and averaging the speed of all nightly movements for each bird.

Covariates for energetic analyses

All temperature covariates were computed using daily, gridded estimates of surface temperature data from a 1 km grid, which are interpolated and extrapolated meteorological observations from weather stations (Daymet et al. 1840). We computed two temperature covariates for the time birds were tagged (3–7 days): mean daily maximum (T_{max}) and mean daily average temperatures (T_{mean}) for the period birds were tagged (3–7 days). We additionally defined a binary covariate (T_{30}) that indicates whether an individual was exposed to temperatures above 30 °C for at least an hour. This threshold is related to the temperature at which spotted owls begin to show thermoregulatory behaviors (Weathers et al. 2001).

We obtained estimates for structural features of the forest, specifically the horizontal fraction occupied by tree canopies (canopy cover, CC), the distance between the ground and the top of the canopy (canopy height, CH), and the number of distinct canopy layers (vertical complexity,

VC). Canopy cover over 70%, trees over 20 m in height, and multiple canopy layers have been shown to positively affect spotted owls (Jones et al. 2016; Tempel et al. 2022; North et al. 2017). We averaged point estimates of CC, CH, and VC from all GPS locations acquired between 15 min prior to sunrise (estimated from a generic astronomy calculator) and 15 min after sunset (Online Resource 1: Fig. S2) using remotely sensed vegetation information. These are fine-scale estimates (10 m) created by imputing airborne lidar estimates of forest structure across the landscape using deep learning models that recognize forest structure patterns in satellite imagery, and they have been successfully implemented in other studies in this region (Brunk et al. 2023; Wilkinson et al. 2022; Herbert et al. 2022). We chose this dataset because of its very fine-scale resolution and personal observations of accuracy.

Covariates for occupancy analyses

We obtained estimates for the percentage of area in territories and nesting areas with CC over 70% and CH over 20 m, cover types that can increase territory colonization rates and reduce extinction rates (Tempel et al. 2014; 2022). Territory centers in both study areas were determined using (1) average coordinates of all nest locations, (2) average coordinates of all roost locations, or (3) the centroid of the Protected Activity Center designated by the USFS (Verner et al. 1992; Online Resource 1: Fig. S3). We measured occupancy covariates at two different scales: a nest/roost scale with a 135 m buffer around territory centers (CC_{nest} and CH_{nest}) and a territory scale with a 400 m buffer around territory centers (CC_{terr} and CH_{terr}). Chosen buffer distances reflect scales representative of nesting/roosting centers and territories, respectively (Jones et al. 2016). Covariates for occupancy analyses were considered as static and estimated using CFO-based representations of forest conditions in 2016. We did not consider territories in this analysis that experienced fire at any point during the sampling periods in each study area.

We defined two different temperature covariates for occupancy analyses: mean daily maximum temperature between July and August (T_{S}) and summer temperature anomalies (T_{A}). All individual- and population-level covariates and acronyms are in the Online Resource (Table S1).

Testing the effect of temperature on energetics

Velocity and distance were highly correlated ($r^2=0.96$), so we tested for the predicted relationship between velocity and energetic expenditure because it has been shown to be an important predictor for field metabolic rate in other species (Martin et al. 2020). We fit a linear regression model where mass-specific field metabolic rate was the response variable and average velocity was the fixed effect. We performed

this and all other regressions using package “lme4” in R (Bates et al. 2015). From this relationship, we examined residuals, which were normally distributed. These residuals reflected deviations from the expected relationship between movement and energetic expenditure, corresponding to “non-moving” energetic expenditure. We tested hypotheses about the potential buffering effect of forest conditions using the measure because spotted owls are exposed to hot day-time temperatures when they are roosting and effectively stationary.

To examine the potential buffering capacity of high-quality habitat on “non-moving” energetic expenditure, we first examined the effect of T_{mean} , T_{max} , and T_{30} on the residuals from the FMR-velocity regression. Because temperature covariates were highly correlated ($r_s = 0.96$), we examined their effect on residuals independently and used Akaike's information criterion corrected for small sample size (AIC_C) to compare models. We considered models within 2.0 AIC units of the top-ranked model to be competitive (Burnham and Anderson 2002). We then ran three models in which the predictors included a two-way interaction between a habitat covariate (CC, CH, and VC) and the best temperature covariate as well as the additive effects of each.

Finally, to examine potential “non-resting” behavioral responses to warm temperatures, we ran two linear regressions in which average nightly velocity and average nightly distance were the responses and maximum temperature and sex were the fixed effects. We included sex as an additional fixed effect because behavior varies between male and female spotted owls (Gutiérrez et al. 2017).

Testing the effect of temperature on site colonization and extinction

To test for the potential buffering capacity of older forest conditions on spotted owl occupancy rates, we conducted surveys at territories in the ENF ($n = 52$) and SBNF ($n = 162$) during the breeding season as part of demographic studies (Tempel et al. 2014, 2022). While surveys were conducted starting in the late 1980s in both study areas, we only included data from 2010 to 2021 in ENF and 2010–2019 in SBNF to reduce the effects of forest change prior to the first-year CFO-based vegetation data were available in 2016. We also only included data from sites that did not overlap with fire disturbance since 2010 to reduce confounding effects on occupancy (Online Resource 1: Fig. S3). Owls (singles or pairs) were detected at night by imitating owl vocalizations at call stations and along survey routes within owl territories. We then conducted diurnal/twilight surveys at territories with recent nocturnal detections to assess occupancy with visual sightings (LaHaye et al. 2004; Tempel et al. 2022). We included only diurnal/twilight detections in our detection histories

to reduce “false positive” responses from non-territorial floaters or individuals in neighboring territories (Berigan et al. 2019). Nocturnal detections of individual birds were only considered if they had occupied the territory during the previous year (i.e., if we resight color bands on previously captured birds) which we discerned by unique color banding of individuals. We determined reproductive status by feeding live mice to owls and observing if they took mice to an active nest or juvenile. Reproduction status required at least one definitive reproductive assessment.

We used dynamic occupancy models which contain parameters for initial occupancy (ψ_1), territory extinction (ϵ), territory colonialization (γ), and detection probabilities (p ; MacKenzie et al. 2003) implemented in the program PRESENCE (version 12.12; Hines 2006). Our primary sampling periods (i) were years and our secondary sampling periods (j) were 2-week sampling periods during the breeding season in ENF (April through August) and separate survey occasions during the breeding season in SBNF (March through July). Surveys needed to be at least 3 days apart to be included in separate surveys, and the total duration of the surveys with no detections needed to exceed 30 min in ENF and 15 min in SBNF. Surveys were designed so that territories were comprehensively surveyed. We truncated detection histories at no more than 6 surveys that occurred before June 30 to reduce the number of missing values and ensure detections occurred before the hottest months of the year.

We used Akaike's information criterion (AIC) to compare models at all stages of analysis and considered models within 2.0 AIC units of the top-ranked model to be competitive (Burnham and Anderson 2002). We did not include covariates that were highly correlated with one another in the same model (Spearman's rank coefficient, $r_s > 0.7$; Dormann et al. 2012). Modeling was performed separately for each study area to avoid testing for three-way interactions. In all models, we used within-year reproductive status (breeder vs. non-breeder; Tempel et al. 2014) and a year effect for detection probabilities, this consistently being the best model structure for detection probabilities in our datasets (Jones et al. 2016; Tempel et al. 2022). We first modeled the potential effects of habitat covariates on each parameter to define high-quality habitat (ϵ , γ ; “sub-models”; Online Resource 1: Table S3). We included a constant “null” sub-model and a sub-model with year effects for the target parameter. Non-target parameters were held constant with year effects to ensure convergence (Morin et al. 2020). After establishing habitat drivers (or lack thereof), we examined the effect of temperature covariates by building onto the best habitat models. Finally, we combined sub-models and examined potential interactions between habitat and temperature and ranked the final model set.

Results

Drivers of metabolic rates

We captured, tagged, and obtained energetic samples from 27 individual spotted owls. We used 25 individuals in analyses because two birds were recaptured before enough time elapsed to differentiate isotope elimination rates (Nagy 1983). All energetic and movement estimates are reported as means and 1 SE. The average daily energetic expenditure uncorrected for body mass was 269 kJ day^{-1} ($\text{SE} = 15.3$) and did not vary significantly from the previous estimate for this species (249 kJ day^{-1} , $\text{SE} = 26.7$; Weathers et al. 2001; $t = 0.65$, $df = 6.7$, $p = 0.53$).

Our initial linear model showed a positive relationship between average velocity and mass-specific FMR [$\beta_{\text{velocity}} = 162$, 85% CI (45, 278); Fig. 3a]. That is, for every 0.1 m s^{-1} increase in average velocity over the sampling period, predicted mass-specific FMR increased about

$16 \text{ kJ day}^{-1} \times \text{kg}^{0.71}$. We predicted that average “non-moving” metabolic expenditure was $140 \text{ kJ day}^{-1} \times \text{kg}^{0.71}$ ($\text{SE} = 23.1$), which was lower than a BMR estimate from a previous study (170 kJ day^{-1} , $\text{SE} = 5.80$; Weathers et al. 2001) on the species, although this study did not correct for body mass. By correcting for body mass from this study, we obtained a new estimate of about $132 \text{ kJ day}^{-1} \times \text{kg}^{0.71}$ ($\text{SE} = 4.50$; Weathers et al. 2001).

The best temperature model for residual energetic expenditure after considering movement contained T_{30} and was the only model that performed better than the null model (Online Resource 1: Table S2). The only two-way interaction model involving T_{30} and informative habitat parameters involved canopy height. Based on this model, owls that were exposed to temperatures above 30°C had lower than expected energetic expenditure [$\beta_{T_{30}} = 65.5$, (39.5, 91.5)], canopy height had a negative effect on residuals [$\beta_{\text{CH}} = -31.8$, (-53.8, -9.77)], and the interaction between canopy height and T_{30} had a positive effect on residual energetic expenditure [Fig. 3b;

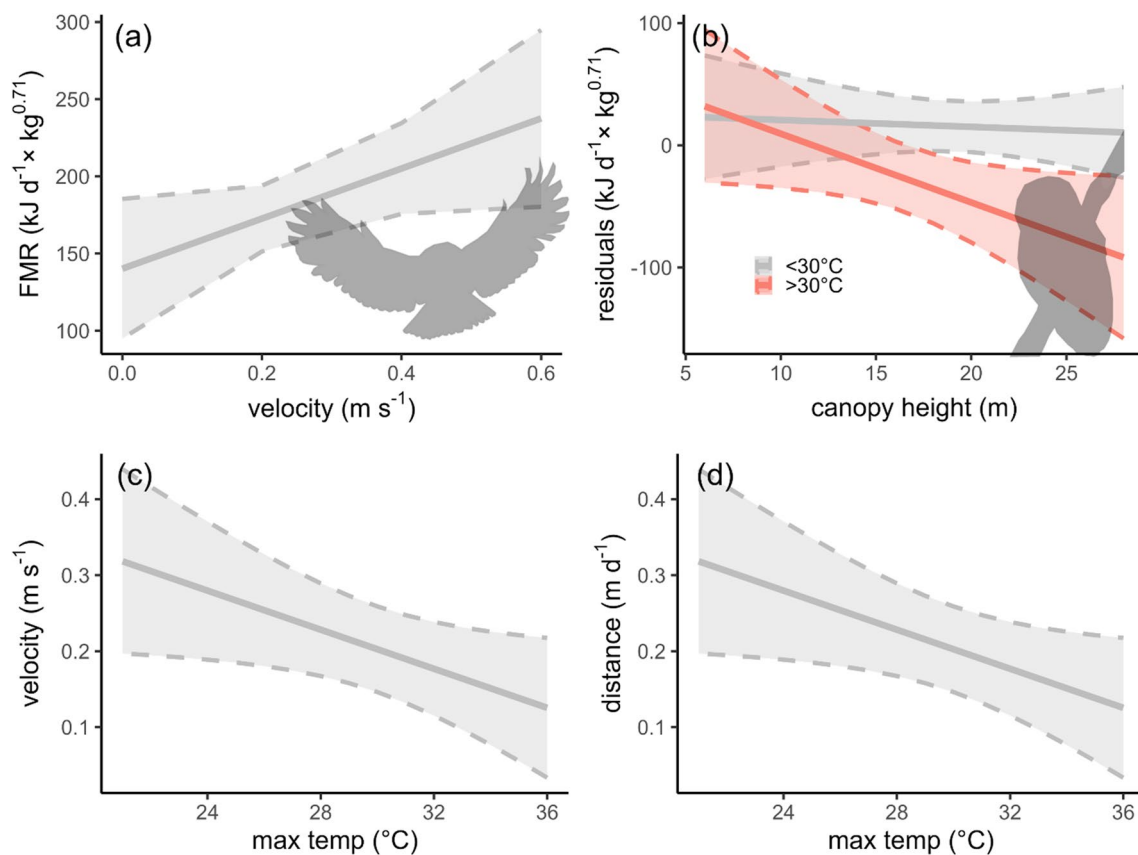


Fig. 3 Results from individual analyses. **a** The average velocity at which a bird was moving during the sampling period was a significant predictor for mass-specific energetic expenditure ($r^2 = 0.15$, $\beta_{\text{velocity}} = 162$, $p = 0.05$). **b** Residuals from that relationship, which correspond to deviations from predicted “non-moving” energetic expenditure, were partially explained by canopy height and exposure,

where higher canopies reduced residual energetic expenditure when temperatures exceeded a physiological threshold (red). **c** Average velocity and **d** average distance each tagged bird traveled decreased with the average maximum temperature during the sampling period. Colored areas represent 85% confidence intervals for predicted relationships

$\beta_{T30^{\circ}\text{CH}} = 28.6, (2.20, 55.0)$. That is, owls exposed to temperatures above 30 °C expended relatively less energy when they roosted in taller forest.

Average nightly velocity was 0.261 m s^{-1} ($\text{SE} = 0.023$) and average nightly distance moved at night was 4073 m day^{-1} ($\text{SE} = 492$). Both distance and velocity varied between sexes, such that males moved faster [$\beta_{\text{males}} = 0.09, (0.03, 0.16)$] and covered more distance per night [$\beta_{\text{males}} = 2348, (1055, 3641)$] during the sampling periods. We additionally found a significant negative relationship between maximum temperature and average movement velocity [$\beta_{T_{\text{max}}} = -0.04, (-0.08, -0.01)$] and maximum temperature and average daily movement distance [$\beta_{T_{\text{max}}} = -664, (-1327, -0.16)$], indicating that owls experiencing warmer temperatures tended to move more slowly and shorter distances (Fig. 3c, d).

Drivers of territory colonization and extinction

Based on the most supported models for the core ENF study area, spotted owl territories were more likely to be colonized when they had a higher proportion of forest over 20 m, and warm spotted owl territories were both less likely to go extinct and less likely to be colonized (Table 1). No single model in the third stage had $\geq 90\%$ AIC weight from which we could make unequivocal inference (Burnham and Anderson 2002). Habitat predictors were highly correlated ($r^2 = 0.84$), as were temperature predictors ($r^2 = 0.98$), so we did not use model-average estimates of regression coefficients (Cade 2015). Coefficient estimates varied minimally among competing final models, so we report the top model for simplicity (Fig. 4):

$$\begin{aligned}\text{logit}(\gamma_t) &= -1.87 - 0.40 \times T_S + 1.03 \times CH_{\text{nest}}, \\ \text{logit}(\epsilon_t) &= -1.80 - 0.45 \times T_S.\end{aligned}$$

Table 1 β -estimates of model covariates in top-ranked models parameter estimates for colonization- γ and extinction- ϵ

Study area	Parameter	AIC _{wt}	Covariate	β	85% CI
ENF	γ	0.38	T_S	-0.36	-0.69, -0.04
			CH_{nest}	1.01	0.62, 1.40
	ϵ	0.27	T_S	-0.46	-0.76, -0.16
			CC_{terr}	-0.31	-0.60, -0.02
SBNF	γ	0.25	CC_{nest}	0.48	0.18, 0.78
	γ	0.11	CC_{terr}	0.38	0.08, 0.68
	ϵ	0.51	T_A	0.38	0.18, 0.58
			CC_{nest}	-0.40	-0.66, -0.14
	ϵ	0.27	T_A	-0.41	-0.67, -0.13
			CC_{terr}	-0.36	-0.63, -0.09

Confidence intervals are reported (85% CI)

In the SBNF study area, territories were more likely to be colonized and less likely to go extinct where they contained a higher proportion of forest with over 70% canopy cover and were more likely to go extinct the year after hot summers (Table 1). Coefficient estimates varied minimally among competing models, so we reported the top model for simplicity (Fig. 4):

$$\begin{aligned}\text{logit}(\gamma_t) &= -2.34 + 0.31 \times CC_{\text{nest}}, \\ \text{logit}(\epsilon_t) &= -1.87 + 0.36 \times T_S - 0.32 \times CC_{\text{nest}}.\end{aligned}$$

Discussion

We posed three alternative hypotheses to describe the role of older forest characteristics in buffering spotted owl individuals and populations during heat waves (Fig. 1). At the individual level, we found potential support for our *refugia* hypothesis, such that older forest characteristics (i.e., taller canopies) facilitated energetic conservation when temperatures were above thresholds associated with thermoregulatory behaviors. For the core population in the Sierras, we found support for our *habitat* hypothesis, where occupancy was not sensitive to temperature anomalies, though warmer sites were less likely to be colonized—suggesting that warmer conditions may reduce the value of territories to breeding owls. At the southern extent of the subspecies' range where older forest characteristics were less prevalent, warm temperature anomalies increased the likelihood of territories going extinct, supporting our *habitat + temperature* hypothesis. Collectively, these findings suggest that older forest characteristics serve as thermal refugia for individual spotted owls, but the population-level influence of such refugia may vary by region as a consequence of forest availability.

Older forests facilitate energetic conservation during heat waves

Our estimate of average daily energetic expenditure (269 kJ day^{-1} , $\text{SE} = 15.3$) was not significantly different than the previous estimate for this species, though the previous estimate was obtained from untagged birds captured using either extendible noose poles or mist nets (Weathers et al. 2001). Individual spotted owls expended less energy during daytime roosting, or “non-moving” activities, and during warm periods when they had access to roosting sites with higher canopies (Fig. 3b). We expected owls to spend more energy during warm periods because exposure to hot temperatures can lead to energetically costly heat dissipation behaviors (du Plessis et al. 2012; Calder and King

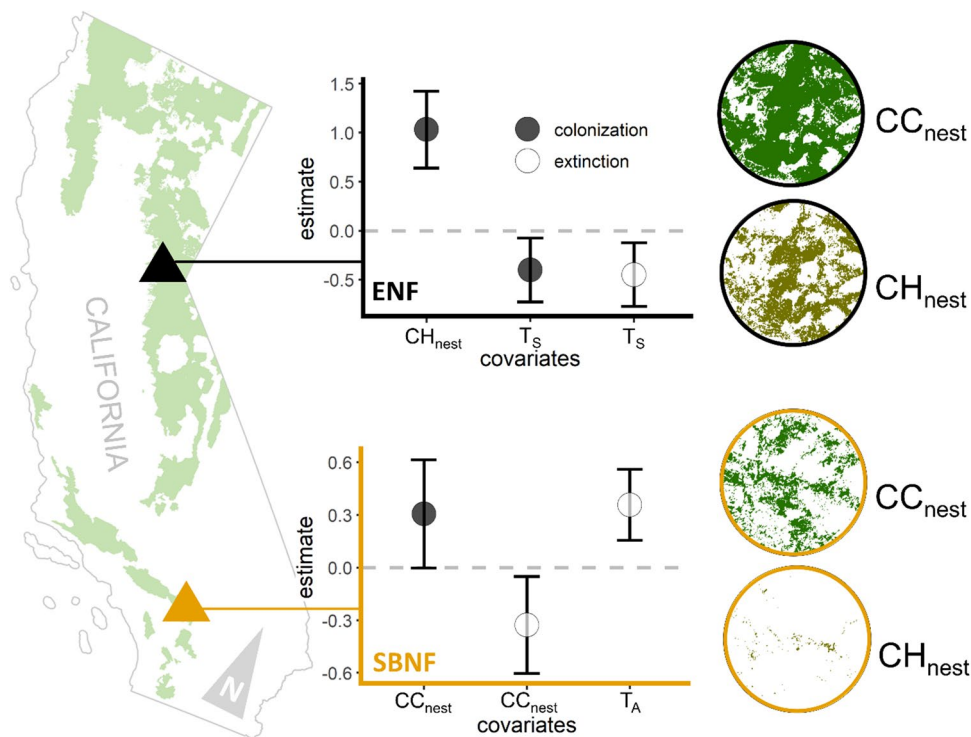


Fig. 4 Results from population analyses. Here, we report the β -estimates for the covariates that were in the top models for each study area. The top panel is from the ENF study area and the bottom panel is from the SBNF study area. Covariates for colonization are black and covariates for extinction are white. Error bars represent 85% confidence intervals. β -estimates were similar and equally significant between all top models. Circular panels show typical proportions of forest with canopy cover over 70% (CC_{nest}) and canopy height over 20 m (CH_{nest}) in 135 m buffers around territory centers.

1974), with captive spotted owls showing thermoregulatory behaviors around 30 °C and elevated energetic expenditure around 35 °C (Weathers et al. 2001). While our results may have been a consequence of scale, such that our temperature covariates did not capture the conditions individuals physically experienced (Bütikofer et al. 2020), a supplemental analysis on a subset of owls tagged with Pinpoints further suggests that “non-moving” energetic expenditure decreased with the proportion of time operative temperatures exceeded 30 °C (Online Resource 1: Fig. S4).

Animals can offset potential energetic consequences of direct exposure by selecting habitat in shaded, cooler microclimates (Street et al. 2015). Indeed, only five individuals were exposed to operative temperatures over 35 °C (Fig. S5). The daytime roosts owls used when temperatures were hot may have shielded individuals from exposure by reducing the direct radiation that reached an owl’s body, providing cool microclimates under tall canopies (Frey et al. 2016), and allowing individuals to avoid energetic costs associated with maintaining thermoneutrality (Vefký et al. 2009), which suggests support for our *refugia* hypothesis (Fig. 1c).

In the ENF (black) sites contained more prevalent older forest and temperature anomalies (T_A) did not impact changes in occupancy, though spotted owls were potentially faced with trade-offs between foraging opportunities and exposure in warmer sites with higher average maximum summer temperatures (T_s). In the SBNF (gold), sites contained less prevalent older forest and spotted owls were more likely to leave sites following summers with warm temperature anomalies.

Indeed, in our supplemental analysis, we found that operative temperatures were lower under taller canopies (Fig. S5). Individuals in our study did not appear to experience the elevated energetic expenditure associated with heat stress, but exposure to warmer conditions appeared to influence roosting behavior.

Individual spotted owls expended greater amounts of energy when they moved more quickly, consistent with a body of work showing that movement increases metabolic rate in animals (Martin et al. 2020; Shepard et al. 2013). In addition to spending less energy at rest, individuals moved more slowly (Fig. 3c) and shorter distances at night (Fig. 3d) when daytime temperatures were warmer, which may reflect (1) behaviors that conserve energy for individuals exposed to warmer conditions and (2) behaviors that facilitate access to better foraging habitat for individuals exposed to cooler conditions. Indeed, longer commuting distances do not necessarily incur lower prey delivery rates or lower reproductive success for spotted owls, but potentially indicate more overall prey biomass delivered to the nest (Zulla et al. 2023; Wilkinson et al. 2022). Accordingly, consuming more food

can contribute to higher “non-moving” expenditure associated with digesting, absorbing, and assimilated food (Cruz-Neto et al. 2001; Secor 2001), which is generally higher for animals with a larger proportion of protein in their diet (McCue et al. 2005; Secor and Faulkner 2002).

Our individual analyses were conducted using temperature data derived from regional conditions, so findings suggest relationships between movement and relative thermal conditions rather than the temperature organisms actually experience (Bütikofer et al. 2020). Many avian and mammalian species slow or cease activity and seek shade when exposed to hot temperatures as strategies to maintain thermoneutrality, opting to spend less time foraging or defending territories and spend more time stationary and resting (Cunningham et al. 2021). Large-bodied birds in arid climates, for example, are less active during typical foraging periods and seek out shaded microclimates when temperatures exceed thermal optima (Pattinson et al. 2020). During extreme heat waves, koalas (*Phascolarctos cinereus*) seek out cool microclimates near tree trunks and display thermoregulatory tree-hugging behaviors (Briscoe 2015). Our finding suggests a two-pronged strategy in which spotted owls use cooler microclimates for roosting during periods of warm temperatures and spend less time and energy moving even when temperatures cool off at night. As a result, spotted owls appeared to avoid elevated energetic expenditure through habitat selection and behavioral adaptation.

Prevalent older forests buffer populations from heat waves

In our core population (ENF), sites with higher proportions of tall-canopied forest were more likely to be colonized (Fig. 4), a finding consistent with previous studies (North et al. 2017). Spotted owls strongly select older forests for nesting and roosting, which are taller and more structurally complex than younger forests and support cool microclimates that serve as potential buffers against hot temperatures (Moen and Gutiérrez 1997; Betts et al. 2018). However, we did not detect an interaction between habitat and temperature, which supports our *habitat* hypothesis, implying that either all forested habitat is sufficient to buffer high temperatures, or that individuals in our study were not exposed to temperatures that exceeded thermal thresholds for long enough to impact their physiology (Fig. 1a). However, extinction and colonization dynamics, which were both negatively related to maximum summer temperature, suggest the story may be more nuanced. At lower elevations where temperatures are warmer, spotted owl diets contain a higher proportion of woodrats—which are more calorically efficient prey for spotted owls—than sites at higher elevations (Hobart et al. 2019; Zulla et al. 2022). Access to such resources may offset potential consequences of heat exposure on territory extinction but

colonizing an unoccupied warm site may not be energetically worthwhile if an individual is naïve to the area, regardless of the foraging opportunities the site provides. Thus, the effects of habitat—temperature interactions on spotted owl occupancy are likely complex and appear mediated by both direct physiological effects and prey availability that varies across elevational gradients. Indeed, Jones et al. (2016) found that cooler (high elevation) territories were more likely to go extinct after warm summers where there was less closed-canopy forest, which was attributed to potential negative effects of temperatures on the dominant prey in spotted owl diets at higher elevations—flying squirrels (Hobart et al. 2019).

In our southern periphery population (SBNF), habitat and temperature did not have synergistic effects on colonization and extinction, supporting our *habitat + temperature* hypothesis in which high temperatures affect owls but habitats do not serve as efficient buffers (Fig. 1b). Owls were more likely to colonize and less likely to abandon sites with more high canopy cover forest, which is less prevalent in southern California than in the Sierra Nevada (Fig. 4). Large trees with higher canopy cover likely promote foraging opportunities and nesting habitat (Tempel et al. 2022; Wilkinson et al. 2022). While habitat did not appear to influence the effect of temperature on either extinction or colonization in our peripheral population, the probability of a site becoming unoccupied increased following summers with warm temperature anomalies, which is a novel finding. Prior research on northern spotted owls showed warm temperatures and dry conditions benefit spotted owl reproduction (Franklin et al. 2000; Glenn et al. 2010). However, high temperatures can also reduce avian foraging efficiency, survival, and reproduction and lead to population declines, range shifts, and range contractions in climate-sensitive species (Cunningham et al. 2015; Stewart et al. 2015). Historical spotted owl sites in the SBNF at lower elevations have gone extinct, likely due to unsuitable warm conditions, though large trees appear to buffer this effect (Tempel et al. 2022). In our study, we found no interaction between temperature and habitat, suggesting that the distribution of tall forests in the SBNF, which function as thermal refugia for individuals, may not be sufficient to buffer spotted owl populations from local site extinctions caused by warm temperature anomalies. Forests with canopies shorter than those historically associated with nesting and roosting, which we did not explore in this study, may potentially buffer spotted owls from negative effects of hot temperature anomalies and explain the importance of large trees for spotted owls at low elevations (Tempel et al. 2022).

Absence of older forest leads to behavioral trade-offs

Tall canopies facilitated energetic conservation for spotted owls, which appeared to ubiquitously buffer potential

consequences on occupancy in the Sierra Nevada, where we did not find an effect of temperature anomalies on either extinction or colonization. Older forest characteristics are more prevalent in the ENF (Fig. 4), and owls have more access to buffering microclimates than in the southern study area. During warm temperature anomalies, any behavioral changes associated with exposure may not require trade-offs between conserving energy and resource acquisition where old forest is more readily available. Greater prairie chickens (*Tympanachus cupido*) display similar behaviors in response to warm temperatures, selecting cooler microclimates within food-rich patches to avoid trade-offs between thermoregulation and foraging (Londe et al. 2021).

In the SBNF, where older forest characteristics are generally less prevalent, strategies to conserve energy, such as spending more time at rest and less time obtaining resources, may limit an individual's ability to acquire sufficient energy required for reproductive efforts. Even small changes in activity can lead to consequences for reproduction and survival (Sinervo et al. 2010; Visser 2008). Indeed, southern yellow-billed hornbills and southern pied babblers (*Tockus leucomelas* and *Turdoisses bicolor*) exposed to extreme temperatures exhibit lower foraging success while engaging in heat dissipating behaviors and avoiding exposure, leading to reductions in body condition (van de Ven et al. 2019; du Plessis et al. 2012). Without sufficient access to prevalent refugia or refugia in sufficient proximity to food-rich patches, owls are required to move more and spend more time obtaining the resources for survival and reproduction. Exposure to heat may lead to unbalanced trade-offs between thermoregulation and foraging and reduce available energy for survival and reproduction. During hot weather in non-buffered sites, this unbalanced trade-off may lead to site extinctions the year following extreme heat events. Even in buffered sites, extreme regional temperatures can overwhelm the capacity of these sites to support biologically viable microclimates (Wolf et al. 2021).

Conclusions

Older forest characteristics, and their buffering microclimates, are under threat in western North America due to historical land use, drought-related tree mortality, and an era of unprecedented megafires (Davis et al. 2019; Jones et al. 2022; Steel et al. 2022). Forest-dwelling species rely on these habitats for many behaviors and life history events, including refuge from increasingly common and extreme heat events (Frey et al. 2016). Our study demonstrates that forest refugia can facilitate individual behaviors with population-level consequences. In the SBNF, sites at lower elevations have become unoccupied, and while the presence of large trees mitigates site extinctions

(Tempel et al. 2022), temperatures exceed physiological thresholds regardless of the prevalence of high canopies. Conserving larger, taller trees offers one strategy to mitigate the consequences of rising temperatures. As temperatures continue to rise and heat events become more frequent and extreme, the role of forest refugia will become increasingly important where such habitat is prevalent and accessible. To promote temperature refugia for climate-sensitive forest species, managers may explore a combination of strategies that 1) directly promote older forest characteristics on the landscape by conserving and recruiting mature forests, and 2) indirectly conserve older forest characteristics by reducing fuel loads to reduce the severity and extent of disturbance.

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Availability of data and materials The datasets used during the current study are available from the corresponding author on request.

Code availability Codes used for statistics and occupancy models are available from the corresponding author on request.

Declarations

Conflict of interest Not applicable.

Ethics approval All handling of animals in this study were done by trained individuals under the proper permitting (IACUC A005367-R02-A01). All institutional and national guidelines for the care of animals were followed.

Consent to participate/consent for publication This article does not contain any studies with human participants.

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