The effect of climate change on forest owl species and communities

By

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California spotted owl (*Strix occidentalis occidentalis*); photo by Kate McGinn

Dissertation Abstract

Ecosystems across the globe are experiencing rapid changes due to the direct and indirect effects of climate change. The Sierra Nevada, a topographically complex landscape, is one such ecoregion undergoing unprecedented change, where rising temperatures and rapid shifts in forest structure leave the fate of the unique biotic communities in this region uncertain. While regional conditions may become unsuitable for many species as a result of these changes, local terrain and vegetation can maintain pockets of quality habitat that may act as microrefugia. The Sierra Nevada's California spotted owl (*Strix occidentalis occidentalis)* has been a cornerstone of conservation in western North America for the past several decades and faces existential threats on multiple fronts. Furthermore, the broader community of nocturnal avian predators in the Sierra Nevada may face similar challenges, yet we know little about the ecology of these species.

In Chapter 1, I demonstrate that tall forests create cooler microclimates, and that spotted owls actively exploit these refugia when temperatures are warm. In Chapter 2, I show that tall forests and shifts in behavior appear to buffer individuals from energetic consequences of exposure and likely prevent local territory extinctions where older forest characteristics are prevalent across the landscape. Together, these chapters suggest that older, taller forest stands—while functioning as microrefugia for spotted owls—may be insufficient to prevent extirpations at lower elevations near the subspecies' southern range boundary. Indeed, the status of spotted owls in southern California may reflect their future in the Sierra Nevada, where older forests face elimination from megafires and owl populations have severely declined. In Chapter 3, I use passive acoustic monitoring to demonstrate the lasting negative impacts contiguous high severity fire can have on spotted owls, though the community of forest owls in this region have diverse reposes to fire severity, spatial configuration, and temporal history. Finally, in Chapter 4, I develop novel methods to reconcile the loss of biologically relevant information often sacrificed for coverage in broad-scale acoustic surveys. Thus, this dissertation

creates an opportunity to identify compromise between conserving climate refugia for a species of concern and reducing the negative impacts of megafires for a guild of forest predators.

Dissertation Introduction

Understanding species' responses to rapidly changing environmental conditions is one of the most important prerequisites to understanding the reorganization of biological communities and the factors that contribute to loss of biodiversity (Chen et al., 2011; Maclean & Wilson, 2011; Araújo et al., 2005). Species have evolved to occur within a specific array of abiotic conditions and biological interactions, which, in conjunction with dispersal mechanisms, determine where species can occur in space (Peterson et al., 2011). Endotherms spend energy to maintain internal thermal conditions and are particularly limited by their thermal tolerance (Araújo et al., 2013). When temperatures change rapidly, organisms can be exposed to conditions outside their thermal optima, and organisms either adapt to novel environments or track suitable climatic conditions in space. Where climatic changes outpace microevolution and barriers limit dispersal capabilities, species face potential extinction (Parmesan & Yohe, 2003). Organisms are also adapted to dynamic processes that shape ecosystems, which drive and disrupt all levels of ecological organization (White & Pickett, 1985). Climate change has altered—and continues to alter—natural disturbance regimes, such that disturbance occurs at higher frequencies and with greater severity across multiple global regions (Seidle et al., 2011; Seidle et al., 2017).

While the distribution of many species is expected to shift in response to these changes and novel disturbance patterns that alter the structure of potential habitat (Beever et al., 2017; Parmesan, 2006), pockets of suitable climate space important for species' persistence may be retained as a consequence of fine-scale environmental heterogeneity despite broader changes on the landscape (De Frenne et al., 2021; Tingley et al., 2012; Riddell et al., 2021; Lenoir et al., 2017). These refugia may allow species to persist locally within regionally unsuitable climate space. Thus, key aspects of conserving biodiversity will likely involve identifying characteristics that promote the buffering capacity of habitats and understanding how these characteristics interact with disturbance regimes or are impacted by management activities.

The Sierra Nevada, the focal region of this dissertation, is an ecologically and geographically unique region that contains nearly 80 endemic animal species. Prior to Euro-American colonialization, the Sierra Nevada and the indigenous communities of the region supported a spatially complex mosaic of early seral vegetation and denser mature forest stands within a matrix of lower density forest stands (Klimaszewski-Patterson et al., 2018; Taylor et al., 2016). Wildfire was a critical disturbance process that regenerated forests and created heterogeneity across the Sierra Nevada, and frequent, mixed-severity fires created lower density stands across the landscape and maintained large, fire-resistant trees (Collins et al., 2007). Following colonization, fire suppression, logging, and grazing in national forests and private lands led to higher tree densities and more homogenized land cover (Collins et al., 2011). Furthermore, current climate models predict warming temperatures and extended periods of drought (Hoerling et al., 2013), posing concern for climate sensitive species in the region (Hulley et al., 2020; Jones et al., 2016). Climate change will likely interact with and exacerbate the effects of prolonged fire suppression, lead to an increase in the extent and intensity of stand-replacing fires, and drive the loss of critical habitat for animals that rely on closed canopy forests (Fettig et al., 2019; Westerling et al., 2019). The California spotted owl (*Strix occidentalis occidentalis*), a subspecies of spotted owl found in the Sierra Nevada, is of particular concern given its reliance on old-growth forests that are increasingly affected by forest management strategies and high severity fires (Jones et al., 2018; Stephens et al., 2016). However, old-growth forests have also demonstrated a capacity to buffer avian species from climatic extremes (Frey et al., 2016; Betts et al., 2018; Kim et al., 2022), and may function as critical refugia for spotted owls.

My first two chapters examine the role of forest microclimates in mediating the effects of anomalous thermal conditions on the behavior, physiology, and distribution of spotted owls in the Sierra Nevada (the core of their range) and in the Transverse Ranges (the southern range boundary for this subspecies; Gutierrez et al., 2017). In **Chapter 1** (McGinn et al., 2023b), I document spotted owl behavior during two exceptionally warm breeding seasons and show that taller forests create cooler microclimates, which spotted owl use as roosts during warmer days. Notably, I found that, despite access to and use of cooler microclimates, spotted owls were still exposed to temperatures outside their thermal tolerance. In **Chapter 2,** (McGinn et al., in review) I explore the buffering capacity of cooler microclimates and the individual- and population-level consequences of warm temperatures for spotted owls as mediated by their habitat selection. When temperatures are warm, an individual's use of roosts in taller forests and their movement behaviors appear to prevent elevated energetic expenditure often associated with exposure to temperatures outside thermal optima. However, where taller forests are less prevalent, local territory extinctions follow anomalously hot summers, highlighting a grim future for spotted owls in southern California—and likely for spotted owls in the Sierra Nevada—if climate change policies and forest management strategies stay the current course.

Together, these first two chapters suggest that forests with older-growth characteristics may function as potential climate refugia as temperatures continue to rise. However, in western North America, such forests face an existential challenge: larger, more frequent high severity fires (Steel et al., 2023). Spotted owls appear to abandon territories following high-severity fires, especially where loss of live canopy cover occurs contiguously across large extents (Jones et al., 2018). While existing studies suggest that spotted owls will respond negatively to an increasing prevalence of megafires, discrepancies in the literature warrant further research (Hutto et al., 2016, Lee et al., 2013). Additionally, the Sierra Nevada hosts a diverse and speciose community of forest owls, but very little is known of their local ecologies given their cryptic nature (Wood et al., 2019). One way to study this community of nocturnal carnivores under rapidly changing forest conditions is through passive acoustic monitoring (Wood et al. 2019, Borker et al., 2014, Teixeira et al., 2019). In **Chapter 3,** I examine the distribution of six forest owl species, including the spotted owl, in relation to the severity, spatial configuration, and temporal history of fire. A major finding in this chapter is that while low-moderate severity fire benefits several species, contiguous high severity fire has lasting negative impacts for older forest specialists and generally limits the distribution of the forest owl community.

In Chapter 3, I use bioacoustics data collected over a large portion of the Sierra Nevada. While this strategy enables a broad spatiotemporal examination of species' distributions, such passive acoustic surveys often sacrifice the ecological resolution necessary to extract more meaningful ecological conclusions (i.e., population vital rates). However, the automated mechanisms by which we derive detections in massive acoustic datasets, such as those I use in Chapter 3, yield detailed feature embeddings that describe characteristics of sound that are often impossible to study using the human ear alone. In **Chapter 4** (McGinn et al., 2023a), I test the utility of feature embeddings created by BirdNET, a machine learning algorithm that uses publicly available sound archives to detect species in an acoustic dataset (Kahl et al., 2021). I found that these embeddings can be used as potential markers for ecologically important, specifically to differentiate cryptic organisms by age class and identify specific behaviors within the same species.

As the climate continues to rapidly change and natural disturbance regimes break down, identifying habitat features that facilitate species persistence is increasingly important. This dissertation shows how cryptic species, including one which has been at the center of conservation and forest management decisions in western North America, respond to rapidly changing environmental conditions. Studies that seek to understand the mediating role of habitat often lack the necessary resolution to understand the biological underpinnings for patterns expressed by populations and communities. The first two chapters demonstrate responses to stressful abiotic conditions at an individual level and identify specific habitat that serves as a buffer to otherwise stressful conditions. Chapter 2 demonstrates that, while individuals appear to avoid energetic consequences of exposure, extreme environmental change may offset thermoregulatory tradeoffs and lead to local, population-level extinctions. Chapter 3 suggests that functionally similar species have markedly different associations with habitat following one of the more dynamic forces for environmental change: fire. As more research incorporates ecosystem-scale surveys to better understand biodiversity in a changing world, balancing scale and resolution will be increasingly important. Chapter 4 introduces one potential strategy to ascertain ecological detail from large acoustic datasets, which affords the possibility of studying environmental change at multiple levels of ecological organization. Nuances and potential mismatches between patterns expressed at the individual- and population-level will inform tradeoffs between conserving refugia and mitigating novel fire disturbance as our climate continues to rapidly change.

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Chapter 1: A climate-vulnerable species uses cooler forest microclimates during heat waves

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Abstract

While climate change will have significant impacts on terrestrial organisms, microclimates offer potential refugia for vulnerable species when regional conditions become unsuitable and temperatures exceed physiological limits. The efficacy of microclimates as buffers to extreme events is determined not only by their availability, but also by the behavioral flexibility of individuals to access these unique environments during stressful periods. We characterized (*i*) how forest structure and topography shaped microclimates at roost sites used by California spotted owls (*Strix occidentalis occidentalis*), a climate-vulnerable species, and (*ii*) how owls outfitted with temperature sensors used microclimates during warm temperature events. Higher elevations, taller canopies, and greater canopy cover promoted cooler maximum temperatures in stands used for roosting. Within those stands, individuals roosted in cooler sites, especially when roosts were in forest stands on warmer slopes. Tall canopies created relatively cooler microclimates when temperatures were hot, and individuals actively used roost sites that minimized increases in operative temperature, suggesting spotted owls have an adaptive capacity to use cooler microclimates. However, roosts at low elevations consistently exceeded physiological thresholds when temperatures were warm, potentially explaining vacancies in low elevation territories with more open forest. For spotted owls to persist in warming environments, conserving tall, closed-canopy forests that promote cooler microclimates for roosting is critical. While a future climate promises heat events that approach and exceed thermal extremes for a suite of canopy-dwelling species, cooler microclimates provided by forest structure and topography could constitute important refugia in a rapidly changing system.

Keywords: behavioral flexibility, climate change, climate change refugia, heat waves, microclimates, spotted owls

Introduction

Species have evolved to occur within a specific array of abiotic conditions, or climate space, and exposure to conditions that exceed or fall below their physiological tolerance can lead to stress and decreased fitness (Deutsch et al., 2008, Huey et al., 2009). Stress avoidance is a mechanism by which climate constrains the ability of organisms to occupy space, and organisms respond to deviations from suitable conditions through dispersal, physiological and behavioral plasticity, or adaptation. Warming temperatures are projected to have significant impacts on the space occupied by terrestrial organisms (Chen et al., 2011) and thus the distribution of many species has, and is expected, to shift over time as the climate warms (Beever et al., 2017, Parmesan 2006). While regional conditions may become unsuitable for climate-sensitive species (i.e., temperatures exceeding upper thermal tolerance limits), smaller areas of habitat within a landscape may retain suitable conditions where individuals can seek refuge (Keppel et al., 2012; Morelli et al., 2016).

Microclimates can be decoupled from macroclimates and emerge due to local variability in elevation, topography, and land cover (Latimer and Zuckerberg, 2017; Riddell et al., 2019; Maclean, 2020). Elevation and topography are some of the strongest drivers of microclimate variation (Frey, Hadley, Johnson, et al., 2016), yet vegetation composition and structural complexity also play a large role in determining local climatology (Dobrowski, 2011; Zellweger et al., 2019). In forested ecosystems, canopy cover provides refuge for organisms from extreme thermal events; understory air temperature extremes can be considerably less variable than macro-temperatures, especially on cooler north-facing slopes (Frey, Hadley, Johnson, et al., 2016; Suggit et al., 2011). Microclimates within forest stands are driven by the amount of solar radiation that reaches under the canopy, which is influenced by canopy cover and the height of the canopy (Chen et al., 1993; Latimer and Zuckerberg, 2017). While microclimates offer potential refugia where individuals can “wait-out” weather extremes, individuals must be able to access such sites to fully benefit from a buffering effect.

Behavioral flexibility in response to unsuitable climate conditions can be vital for climate-vulnerable species to persist. Habitat preferences change as environmental conditions like temperature and precipitation affect an individual’s energetic requirements or alter the perceived value of habitat types (Johnson, 1980). The classic example of a species that capitalizes on cool microclimates is the American pika (Ochotona princeps), a mammal sensitive to even moderate temperature increases. Pikas exhibit stronger selection for cool interstitial microclimates (e.g., rock piles, talus) when ambient temperatures exceed 20°C, allowing populations to persist even when macro-scale temperatures are outside the range of tolerance for the species (Varner and Dearing, 2014). Avian species also show preference for less extreme microclimates, and individuals actively seek out sites that more effectively buffer individuals from inclement environmental conditions (Veľký et al., 2010; Anthony et al., 2021; Shipley et al., 2020). With rising temperatures and more variable precipitation, a species’ response to changing climatic conditions will be determined by both the availability of stable microclimates and the ability of individuals to seek them out.

Older forests in western North America have demonstrated a capacity to support cool microclimates that buffer some avian populations from climatic extremes (Kim et al. 2022; Frey, Hadley, Betts, et al., 2016; Frey, Hadley, Johnson, et al. 2016; Betts et al. 2018). While microclimates can dampen population declines (Kim et al. 2022), the potential mechanisms for this relationship remain unknown. Understanding individual behavior is vital for conserving climate-sensitive species (Jirinec et al., 2021; De Frenne et al., 2021; Frey, Hadley, Betts et al., 2016), but few studies have tested the ability of organisms to access microclimates during extreme thermal events, especially in forests. The California spotted owl (*Strix occidentalis,* ssp*. occidentalis*), henceforth spotted owl, is a putatively climate-vulnerable species that occurs across a large elevational gradient and temperatures and extreme heat events are projected to increase across their range (Franklin et al., 2000; Glenn et al., 2010; Peery et al., 2012; Jones et al., 2016). With plumage as thick as boreal-zone species, like northern hawk owls (*Surnia ulula*) and boreal owls (*Aegolius funereus*), spotted owls have a limited ability to dissipate heat (Barrows et al., 1981), thus prolonged exposure to conditions that approach or exceed their upper critical temperature compromises their ability to maintain thermoneutrality and likely explains the species' use of cool microclimates for roosting during their summer breeding season (Barrows et al., 1981; Weathers et al., 2001). Roosting is an essential behavior where owls rest in trees during the day, and roost selection is likely a behavioral adaptation to compensate for their cold-adapted physiology (Barrows, 1981). The distribution and availability of roosting habitats, and an individual's ability to access such habitat, may reduce exposure to unsuitable temperatures. Many forests in western North America are managed for timber production and increasingly exposed to wildfires (Steele et al. 2022) and drought-related tree mortality (Park Williams et al. 2013), and as such, managing the landscape to conserve older forest could be an important, if not necessary, climate adaptation tool.

The southern range boundary of California spotted owls has recently experienced historic maximum temperatures during the breeding season (Hulley et al., 2020), offering an opportunity to measure individual responses to novel thermal conditions. Here, we sought to examine individual access to buffering microclimates and test whether individuals can behaviorally seek out cooler locations in a complex forest given variable access to such habitat across the landscape. We hypothesized that spotted owls have access to and seek out cooler microclimates during heat waves. Specifically, we predicted that: 1) known roost sites are relatively cooler than available sites within forest stands, 2) these differences in roost temperatures are greatest under warmer conditions and facilitated by taller, denser forest canopies, and 3) owls selectively seek out cooler microclimates in roost stands during hotter days. The capacity of spotted owls to actively seek out cooler roosts could indicate a behavioral flexibility to respond to novel environmental conditions that could ameliorate the negative consequences of anthropogenic climate change – and suggestive of similar capacity in other older-forest species like martens (*Martes americana*) and Pacific fishers (*Martes pennanti*) and canopy-dwelling species like northern goshawks (*Accipiter gentilis*), northern flying squirrels (*Glaucomys sabrinus*), and pileated woodpeckers (*Dryocopus pileatus*).

Methods

Study area

In the summers of 2020 and 2021, we took advantage of record high temperatures in the southern Sierra Nevada (Sierra National Forest, SNF) and the San Bernardino Mountains (San Bernardino National Forest, SBNF) in California (USA) to study the factors underlying roosting microclimates and organismal responses to hot temperatures (Fig. 1.1). The SBNF represents part of the warmest and southernmost portion of the subspecies' range (Tempel et al., 2022). We tracked individual spotted owls between June-August during the warmest time of year, where regional temperatures exceeded estimated thermal tolerance limits for the species (30-

35.6 °C; Weathers et al., 2001). Both the SNF and SBNF have substantial elevational gradients, where spotted owls occur in territories between ~800-3000 m and use a variety of forested habitats, leading to high variation in potential roosting microclimates. In both study areas, spotted owls occur in dense forest of mixed conifer stands and occupy hardwood forests at lower elevations, where suitable roosting habitat is generally restricted to drainages and smaller forest patches (Steger et al., 2002; Smith et al., 1999). The ecology of the SBNF is similar to the ecology of the SNF but with more rugged terrain that drives a large variety of forest structures that potentially support cool microclimates.

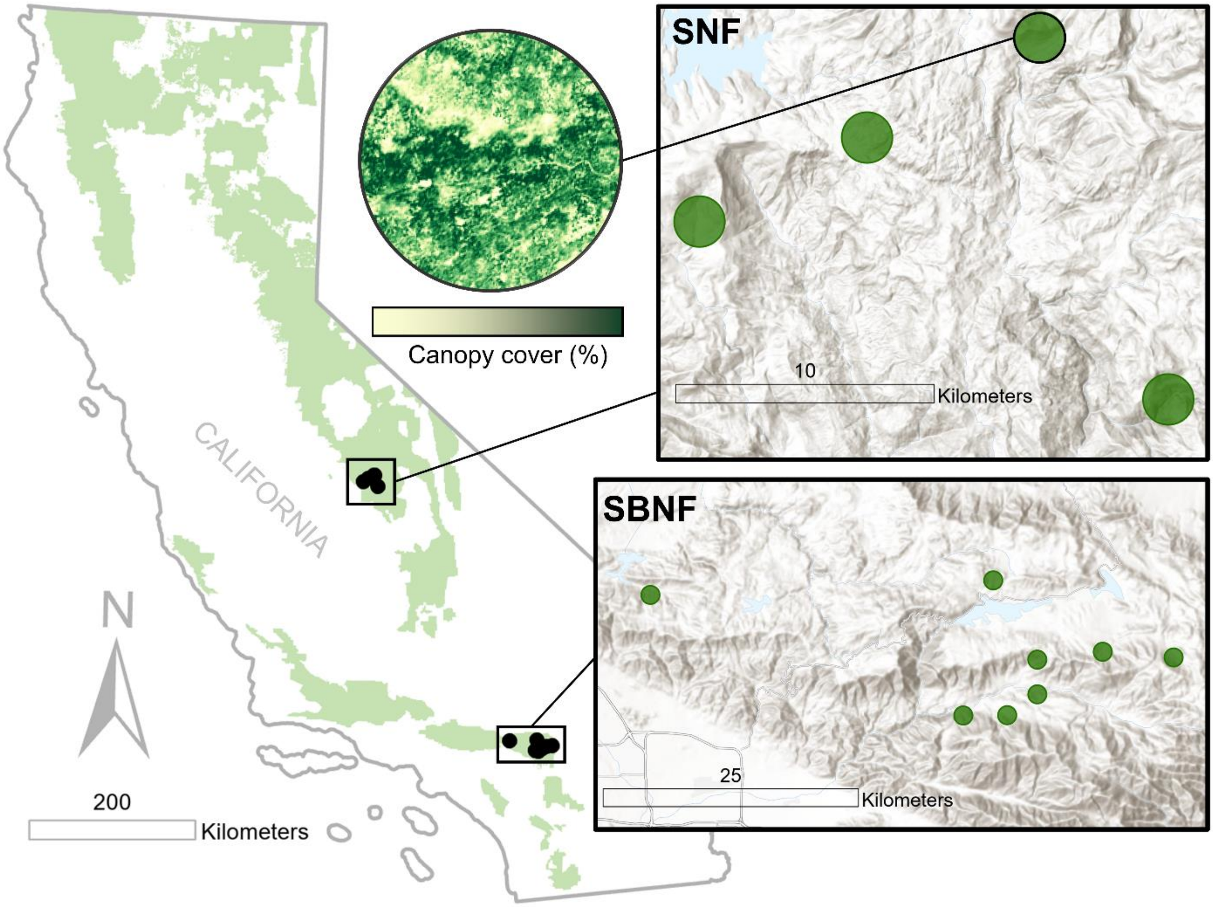

Fig. 1.1. Map showing study area and territories included in analyses. National Forests in California are indicated by light green and territories are denoted by dark green circles.

Capture and tracker attachment

We targeted our search for owls near locations where individuals had been identified within the past five years. We located individuals by making vocalizations, tracking vocal responses and visually confirming detections. For our study, we targeted breeding pairs because they were more reliable to recapture and more sensitive to stressful conditions as they were already under energetic constraints from rearing young. Individuals were captured using a hand-grab technique that minimizes stress to further ensure recaptures and decrease confounding factors that affect behavior (Zulla et al., 2022; Wilkinson et al., 2022). GPS trackers with VHF radio transmission (~6.2g, ~1% BW, Pinpoint-120, Lotek Wireless, Ontario, Canada) were attached to the two middle rectrices with non-toxic adhesive and secured with two small zip ties. Using the Pinpoint Host (v2.14.0.3), GPS trackers were programmed to record locations every hour during daytime roosting activity (6:00 - 20:00) (Lotek Wireless). Each fix recorded by GPS trackers additionally recorded operative temperature (T_O), which corresponds to a combination of radiant and ambient air temperatures and more accurately reflects the thermal conditions organisms experience (Helmuth et al., 2010). Preliminary testing showed that the pinpoints attached via tail-mount to rehabilitation barred owls (Dane County Humane Society) did not record temperatures that were significantly different than iButtons placed in enclosures (paired t-test, $t = 1.55$, $df = 28$, $p = 0.16$). More information of the precision of temperature measurements from GPS trackers is in Supplemental Table 1.4. We did not shield GPS units from solar radiation because we wanted to limit the weight of tail-mount attachments and, thus, potential damage to rectrices. The canopies of conifers and other large trees in spotted owl roosts partially filtered some solar radiation (Lundquist and Huggett 2008). Units lasted three to seven days, and we removed trackers upon recapture. Second captures were performed using the hand-grab technique, a snare-pole, or a pan trap, and tags were removed by breaking the adhesive seal on the tail mount. We aimed to minimize handling time, and birds were released in the same location as their capture. All handling of animals in this study were done by trained individuals under the proper permitting (IACUC A005367-R02-A01).

Site-level temperature sampling

We identified roost sites (n = 43) using radiotelemetry, tracking the location of tagged birds (n = 19) during daylight hours (Verner et al., 1992). Tags were programmed to transmit radio signals between 4:00-5:00, 11:00-13:00, and 18:00-20:00. Two researchers returned to capture locations and used a handheld Yagi antenna attached to a VHF receiver (R-1000 made by Communications Specialists, Orange, CA) to visually identify individuals on roost while tagged. For up to four consecutive days, we identified roost sites used by owls in each territory. Each individual or pair used 3-4 roosts in a singular stand (n=12), which we will define below, during the sampling periods.

Because we wanted to sample from habitat that was forested and potentially suitable for spotted owls, we delineated forest stands according to typical spotted owl roosting habitat for each study area using NAIP aerial photography (National Agriculture Imagery Program, USGS, 2020) and a Gradient Nearest Neighbor Forest structure dataset for our study area (LEMMA Lab, Oregon State University, Corvallis, OR, 2016). Stands were defined as groups of trees reasonably uniform in species composition, dominant-tree age class, and canopy cover. In the Sierras, we limited sample locations to conifer/mixed conifer habitat with canopy cover of at least 40% (Moen and Gutiérrez, 1997) and large trees typical of older forests (Bias and Gutiérrez, 1992) with at least 50-cm QMD (Quadratic Mean Diameter) of dominant and codominant trees, which are the two tallest crown classes and form the forest canopy. In SBNF, we limited sample locations to hardwood, conifer, or mixed stands with QMD of dominant trees of at least 20 cm in diameter and >40% canopy cover, which included at least 70% of historical roost/nest locations in the SNBF (Supplemental Table 1.1).

To obtain estimates of temperatures in a roost stand, we also sampled at “available” sites (n=43) within delineated stands. Using ArcMap (v10.7.1), we established a random “available” site for every known roost site.

At each known roost and random “available” site, we used a tree climbing sling shot to deploy a line of two iButtons into the canopy to span the range of heights spotted owls roost (~3 and ~20 m). We deployed loggers in known roosts while owls were not actively roosting in those locations. After deployment, we let iButtons collect temperature every 30 minutes for at least 20 days to increase the probability of capturing anomalous temperatures. The iButtons were secured in combined cone/tube solar shields made from insulated, reflective foil with passive ventilation that prevented UV degradation and minimized radiation from direct sunlight (Tarara and Hoheisel 2007).

Spatial covariates

At each location (both known roosts and random “available” sites within stands) where temperature sensors were distributed, we obtained both field and remotely sensed measurements for habitat covariates that prior research has shown to be important for driving microclimates (Supplemental Table 1.2). We measured diameter at breast height (DBH) of the tree in which sensors were deployed and the height at which sensors were deployed (TH) using a clinometer. We measured the orientation of sensors, which we categorized into eight groups describing cardinal direction (N, NE, E, etc.). We obtained remotely sensed habitat data from California Forest Observatory (CFO: https://forestobservatory.com) for canopy cover and canopy height. These fine-scale estimates (10 m) are created by imputing airborne lidar estimates of forest structure across the landscape using deep learning models that recognize forest structure patterns in satellite imagery (California Forest Observatory, 2020). We obtained estimates for elevation from a digital elevation model (3D Elevation Program, United States Geological Survey). To classify microtopography, we used a remotely sensed dataset with delineations for six topography groups: ridges, drainages, >30% NE-facing slopes, <30% NE-facing slopes, >30% SW-facing slopes, and <30% SW-facing slopes, in which percentage indicates slope angles (Underwood et al., 2010; North et al., 2012).

For daytime GPS locations, we considered only GPS points with HDOP (horizontal dilution of precision) of 10 or less and with at least 4 satellites, which yielded 658 locations, ~41 locations per individual, and ~10 locations per day for each individual. We established a minimum convex polygon (MCP) surrounding the remaining locations, grouped by individual and Julian day, and buffered the polygons by 50m to account for potential GPS error (Zulla et al. 2022). Within each MCP, we estimated mean canopy cover and canopy height and the most prevalent TOPO category.

Temperature processing

We estimated average daily maximum temperatures during a sampling period (~20 days) at known roost locations (T_R), averaging values between iButtons in an array. We obtained the same estimate of average daily maximum temperatures for the random “available sites” in stands (T_S). We also estimated average daily maximum operative temperature at the surface of owls (T_O). All temperature variables are denoted in Supplemental Table 1.3. We removed outliers prior to analyses using the interquartile range method (Tukey 1977), which offered an unbiased way to remove temperatures that exceeded a realistic range of thermal conditions. A point was considered an outlier if it was above the 75th or below the 25th percentile by a factor of 1.5 times the interquartile range. We estimated differences between maximum temperatures at roosts and available maximum temperatures (ΔT_{RS}, [-8.7°C, 6.1°C], M = -0.34°C) using the following equation:

$$\Delta T_{RSi,j} = T_{Ri,j} - \frac{1}{n}\sum_{i}^{n} T_{Si,j,t},$$

where *i* is unique for each site, *j* indicates Julian date, *t* indicates territories, and *n* indicates the number of available sites in selected stands. We performed the same calculations to obtain estimates for differences between maximum operative temperatures and available maximum temperatures (ΔT_{OS}, [-6.0°C, 8.5°C)], *M* = 1.55°C).

To quantify ambient temperature, which reflect regional spatiotemporal variation in temperature, we located the nearest remote automated weather station (RAWS) to each stand and obtained daily maximum ambient temperatures for each day sensors were active (T_A; Western Regional Climate Center cited 2020, 2021).

Statistical Analysis

We examined the general effect of vegetation and topography on maximum temperature using a linear mixed effects model (Bolker et al., 2009). The response variable was average daily maximum temperature at the four "available" locations in each stand (T_S), the predictors were all habitat covariates, and Julian day and site nested within stands were random effects.

To examine whether temperatures at known roost locations differed from temperatures in available habitat within stands, we fit a linear mixed effect model in which the difference in daily maximum temperatures between known roosts and available habitat (ΔT_{RS}) was the response. We treated Julian day and site nested within stand as random intercepts. The magnitude, directionality, and significance of the intercept term was indicative of differences in temperatures between roost and available sites. To examine the effects of spatial variables and ambient conditions on differences in temperature between roost sites and available sites (ΔT_{RS}), we established a series of *a priori* linear mixed effects models in which ΔT_{RS} was the response variable and spatial covariates and interactions with maximum ambient temperature (T_A) were predictors (Table 1.2). We first fit univariate models for spatial covariates that contributed to competitive models compared to the null model, and then we examined the effect of those covariates and two-way interactions with T_A on ΔT_{RS}. We added variables in order of rank until resulting models were no longer competitive. We ranked models using sample corrected Akaike Information Criteria (AIC_C) and considered competitive models as those within 2 ΔAIC_C units of the top-ranked model (Burnham and Anderson 2002). Random intercepts for all models included Julian day and site nested within stand to account for lack of independence between visual observations of an owl/pair or owls.

Finally, we tested for the effect of ambient conditions and spatial covariates on the difference between temperature at the surface of owls (operative temperature) and temperatures in available stand locations (ΔT_{OS}) using linear mixed-effects models. Operative temperatures were shielded only by the conifers under which spotted owls roost and recorded ambient temperature as well as radiant energy. Thus, we were specifically interested in the relative rate of change, which is captured by ΔT_{OS}. As above, we fit a series of *a priori* models in which we identified habitat covariates that contributed to competitive models compared to a null model, and then we examined the effect of those covariates and two-way interactions with T_A. Again, we ranked models using Akaike Information Criteria (AIC_C) and considered competitive models as those within 2 ΔAIC_C units of the top-ranked model. Random intercepts for all models included Julian day and owl identity.

For all models, we standardized predictors using a z-transformation. We tested for multicollinearity and did not include habitat variables that were highly correlated in the same model (Pearson correlation coefficient, $|r| > 0.7$; Dormann et al., 2013). All analyses were implemented in the lme4 package (v1.1.31, Bates et al., 2015) in R 4.2.2 (R Core Team, 2022). All β estimates and 95% confidence intervals are reported in parentheses in the results section.

Results

Environmental predictors of temperatures in roost stands

Elevation, canopy height, and canopy cover explained most of the variation in daily maximum temperatures in roost stands (Supplemental Fig. 1.1). Specifically, maximum temperatures were cooler at sampling sites within roost stands at higher elevations (β_{elev} = -1.71, 95% CI [-2.03, -1.38]), with higher canopy cover (β_{CC} = -0.41, [-0.79, -0.02]), and under taller canopies (β_{CH} = -0.41, [-0.79, -0.03]). Tree size and microtopography did not have a significant influence on maximum temperatures in stands, though stands on steep NE-facing slopes tended to be warmer than stands on SW-facing slopes.

Environmental predictors of temperature differences between roosts and roost stands

Maximum daytime temperatures were cooler in roost sites compared to the surrounding forest stand (Table 1.1; β_0 = -0.46, [-0.80, -0.11]). Both microtopography and canopy structure were strong predictors for differences in temperature between known roost sites and available habitat in stands. The top two models for differences in maximum temperatures included slope characteristics (TOPO) and an interaction between maximum ambient temperature (T_A) and canopy height (CH; Table 1.2). Maximum temperatures at roost sites were cooler than available habitat on SW-facing slopes with gentle slopes (Fig. 1.2a; $\beta_{<30SW}$ = -1.79 [-2.89, -0.76]). We found that ambient temperatures alone did not affect the difference between roost and stand temperatures. However, the relationship between ambient temperature and temperature offsets depended on the height of canopies at roost sites and was negative when canopies were tall (Fig. 1.2b; β_{CH*TA} = -0.087, [-0.15, -0.024]).

Table 1.1. Intercept model for the difference in daily maximum temperatures between known roosts and available habitat in stands (ΔT_{RS}); with estimates for β_0 and σ^2 (ΔT_{RS}) and standard errors for β_0 and variance σ^2 (SE).

Model	**ΔT_{RS}**	**SE**
Intercept	**-0.46**	**0.18**
σ^2_{jdate}	0.12	0.35
$\sigma^2_{number:stand}$	0.60	0.78
σ^2_{stand}	0.16	0.40
$\sigma^2_{residual}$	0.75	0.87

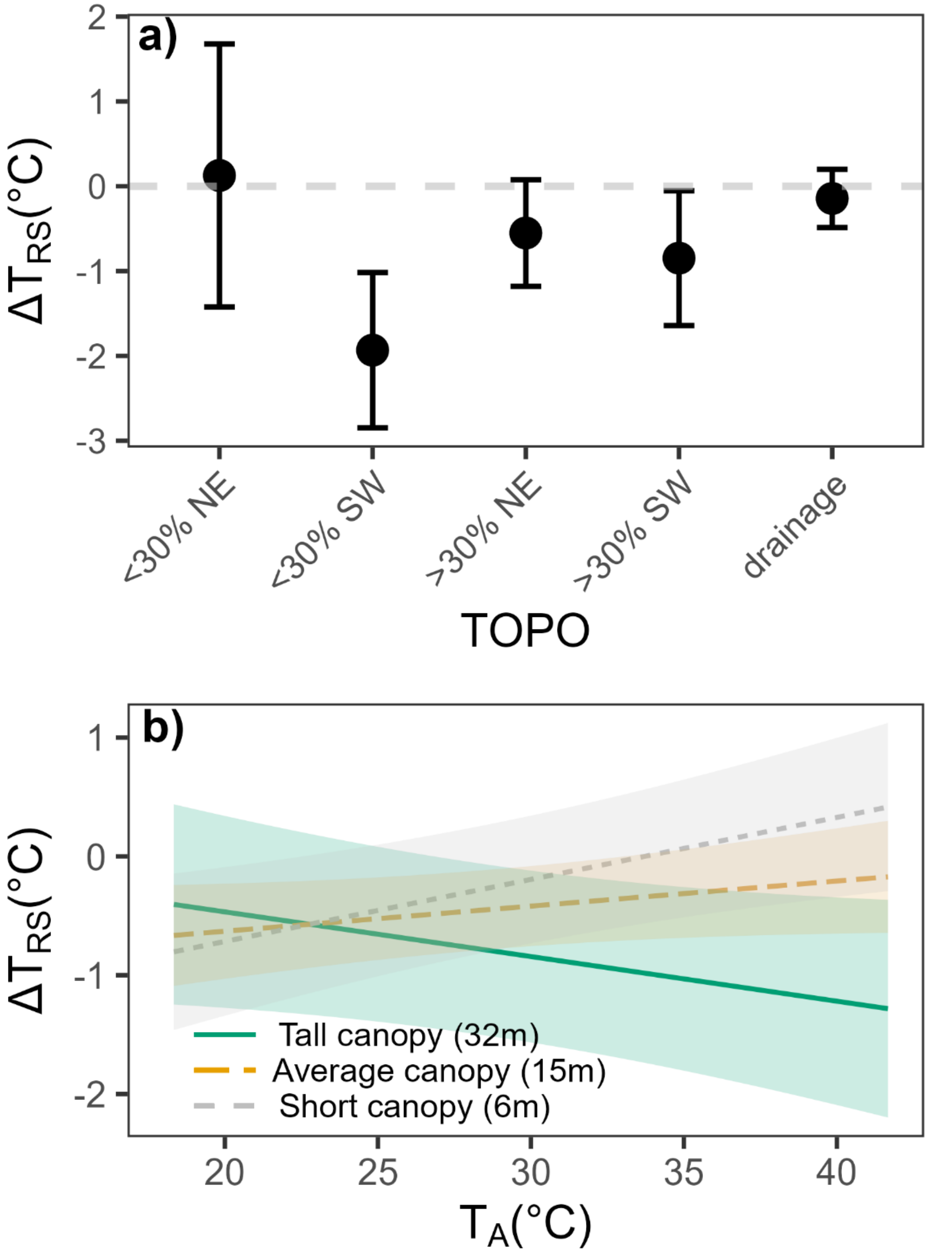

Fig. 1.2. Predicted differences between roosts and available habitat in stands. a) Differences in maximum temperatures were strongest on gentle (< 30%) SW-facing slopes. b) Roosts were cooler than stand temperatures on warmer days, but only when roosting habitat was in forests with taller canopies. Here, we show this interaction with three levels. Grey, short dash lines show the predicted relationship between ambient temperatures and ΔTRS for roosts in shorter forests; orange, long dash lines show the predicted relationship for roosts in forests with the average canopy height in this study; and emerald, solid lines show the predicted relationship in forests with tall canopies.

Predictors of temperature differences between owls and roost stands

All top models for differences in maximum temperatures on the operative temperature of owls and in available habitat included ambient temperature as a covariate, but only our top model outperformed the null model ($\Delta AIC_C > 2.00$, Table 1.2). Based on the top model, which carried 0.25 of the model weight, spotted owls were cooler relative to roost stands on warmer days (Fig. 1.3a; $\beta_{TA} = -1.17$, [-2.09, -0.25]). Temperature differences between owls and roost stands tended to decrease with canopy height (Fig. 1.3b; $\beta_{CH} = -0.77$, [-1.67, 0.13]), but models that included canopy height did not outperform the null model. Competitive model parameter estimates were similar to those reported in the top model, and the interaction between T_A and CH and CC were both uninformative.

Table 1.2. Models for the difference in daily maximum temperatures between known roosts and available habitat in stands (ΔT_{RS}) and the differences in maximums between operative temperatures and available habitat in stands (ΔT_{OS}); with number of parameters (K) Akaike Information Criterion adjusted for small sample sizes (AIC_c), Delta AIC (ΔAIC_c), model weight (ω_i), and log likelihood (LL).

Model	**K**	**AIC_c**	**ΔAIC_c**	ω_i	**LL**
Response: ΔT_{RS}					
TOPO[a] + CH[b] * T_A[c]	12	2998.87	0.00	0.40	-1487.29
TOPO	8	3000.27	1.40	0.20	-1492.07
CH * T_A	8	3000.41	1.54	0.19	-1492.14
TOPO * T_A	13	3003.74	4.88	0.04	-1488.70
null	5	3003.85	4.98	0.03	-1496.90
CC[d]	6	3004.10	5.23	0.03	-1496.01
TH[e] * T_A	8	3004.47	5.60	0.02	-1494.17
T_A	6	3004.84	5.97	0.02	-1496.38
CH	6	3004.90	6.04	0.02	-1496.41
TH	6	3005.13	6.26	0.02	-1496.53
DBH[f]	6	3005.33	6.46	0.02	-1496.63
CC * T_A	8	3006.49	7.62	0.01	-1495.18
DBH * T_A	8	3007.34	8.47	0.01	-1495.60
Orientation	6	3012.60	13.74	0.00	-1494.16
Response: ΔT_{OS}					
T_A	5	233.84	0.00	0.25	-111.19
CH + T_A	6	234.02	0.18	0.22	-109.96
CH * T_A	7	235.14	1.30	0.13	-109.13
CC + T_A	6	235.94	2.10	0.09	-110.92
null	4	235.99	2.16	0.08	-113.52
CC+ CH+T_A	7	236.69	2.85	0.06	-109.91
CH	5	236.78	2.94	0.06	-112.66
CC	5	237.53	3.69	0.04	-113.03
CC + CH * T_A	8	237.88	4.05	0.03	-109.05
CC * T_A	7	238.18	4.34	0.03	-110.65
CH + CC*T_A	8	239.27	5.44	0.02	-109.74
TOPO	9	242.41	8.57	0.00	-109.77

[a] topography

[b] canopy height

[c] ambient temperature

[d] canopy cover

[e] tree height

[f] diameter at breast height

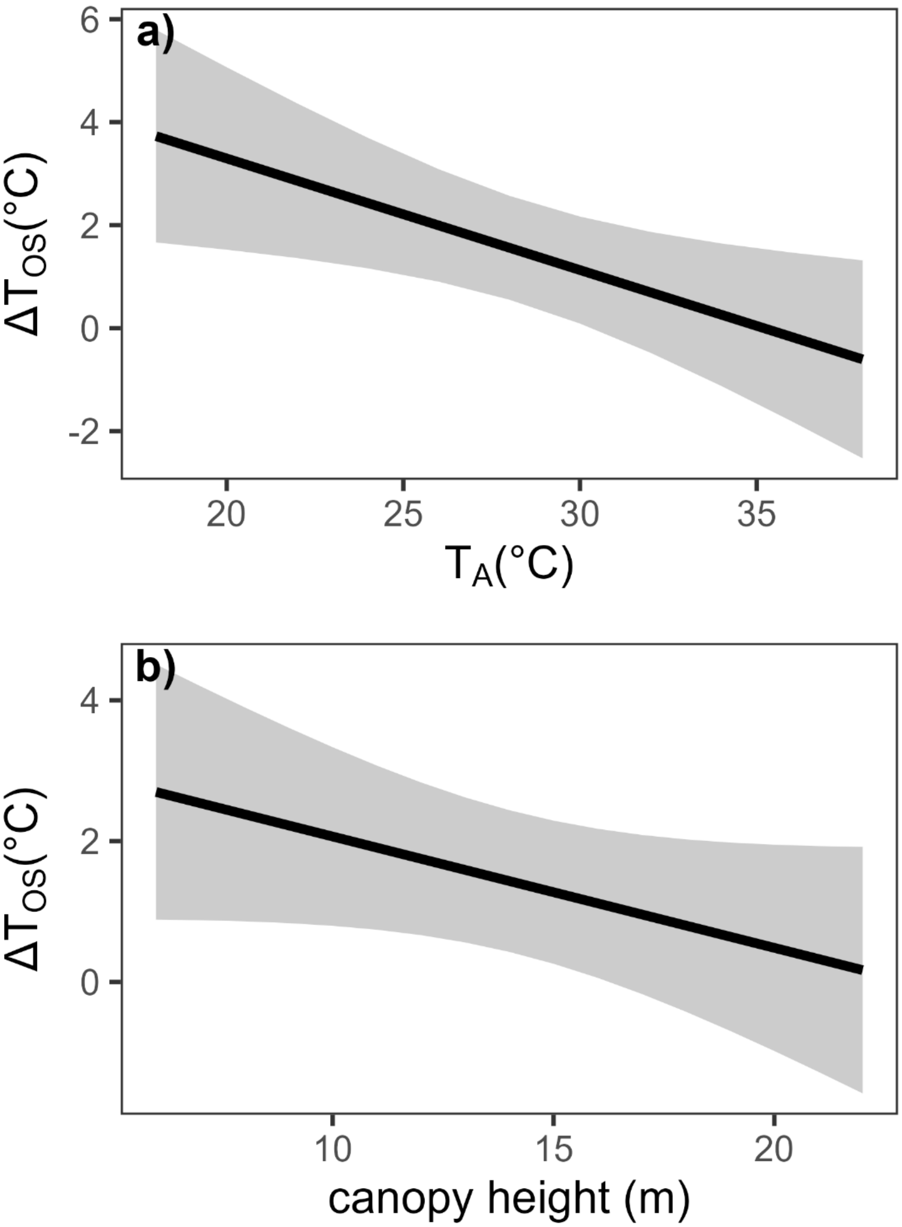

Fig. 1.3. Predicted differences between operative temperature and stand temperature. a) Differences between operative and stand temperatures decreased with ambient temperatures. b) Differences between operative and stand temperatures decreased with canopy cover

Discussion

In rapidly changing climates, organisms will face extirpation without the availability of, and capacity to use, suitable microclimates (De Frenne et al., 2021). Pockets of habitat that retain stable climate conditions, especially when conditions at broader scales become unsuitable, offer vital refugia for sensitive species (Keppel et al., 2012). Such microclimates are driven by a variety of topographic and vegetation structures, many with nuanced effects on fine-scale temperatures (Dobrowski, 2011). While understanding the extent to which species will access and use microclimates is challenging, doing so is necessary to understand species vulnerability to climate change – and mitigate the potential effects of a warming climate. Focusing on a climate-vulnerable species in western North America during a period in which individuals experienced extreme thermal conditions, we examined the features that structure forest microclimates and the subsequent ability of individuals to access such refugia. We found that high canopy cover and tall forests, elements typically selected by spotted owls for roosting habitat, supported cool microclimates. Indeed, individuals actively sought out cooler microclimates when ambient conditions were warmer, but only when they had access to tall canopies. This work emphasizes the value of conserving forest structures that create cooler microclimates, especially where temperatures consistently approach thermal extremes.

Temperature variation in microclimates

Elevation was the strongest driver of maximum temperatures in roost stands, which corroborates prior research in topographically complex regions and forests where temperatures are cooler at higher elevations (Dobrowski, 2011; Frey, Hadley, Johnson, et al., 2016). Canopy height and cover also created cool microclimates available to individuals in roost stands (Supplemental Fig. 1.1), supporting the body of work demonstrating that temperature sensitive species preferentially roost in older forests with large trees and high canopy cover (Bias and

Gutiérrez, 1992; Kramer et al., 2021). Contrary to prior research that shows SW-facing slopes sustain warmer microclimates, driven largely by more direct sunlight and xeric conditions (Frey, Hadley, Johnson, et al., 2016), roost stands on SW-facing slopes in our study were similar in maximum temperatures to roost stands in drainages and NE-facing slopes. That is, when owls roosted on SW-facing slopes, they actively sought out stands that were cooler – presumably to reduce exposure to warm temperatures.

Individual owls in our study located and used cooler daytime roost sites, which can result from fine-scale variation in forest microclimates (Chen et al., 1993; De Frenne et al., 2021; Frey et al., 2016b). Within forest stands, roost sites were indeed cooler than available habitat by as much as 5 °C, especially on SW-facing slopes. This suggests a multi-scaled strategy of habitat selection on SW-facing slopes, where individuals first identify a cooler stand and, within those cooler stands, identify roost sites that support cooler microclimates (Fig. 1.2a). Canopy height also shaped differences in maximum temperature between known roost locations and available habitat in stands when conditions were warmer. On these warmer days, roost sites under higher canopies were generally more buffered (i.e., cooler) from surrounding conditions. Higher, more complex forest structure associated with canopy height can create more stable microclimates by reducing solar radiation (Frey, Hadley, Johnson et al., 2016). However, sites with lower canopies were often warmer than surrounding habitat on hotter days. With an absence of complexity in the overstory, air temperatures heat up faster, creating relatively warmer microclimates. This suggests that roosts with higher canopies are particularly valuable when temperatures are hot.

While spotted owls managed to access cooler microclimates for roosting, the fact that some individuals roosted in warmer stands contradicts prior research that shows that spotted owls actively roost in cooler forests (Barrows, 1981). The fraction of spotted owls in this study using warmer habitat may have lacked access to forests with cooler characteristics, especially individuals limited to roost sites at low elevations. Higher orders of habitat selection confer available microclimates, and an individual’s territory may have constrained available roosting habitat to forests on warmer slopes or those with lower canopies (Johnson, 1980; Boyce et al., 2002). In the SNF and SBNF, tree mortality and recent large-scale, high-severity fire has potentially limited available habitat at the scale of stands. Additionally, individual daytime behavior is likely driven by phenology and energetic requirements of reproduction. Most of the owls in this study were active breeders, and temperature sampling occurred post-fledging. Like many avian species, adult roosts are determined in part by offspring locations, which are located near nest sites for the first few weeks post-fledge (LaHaye et al., 1997). Thus, while some individuals might have access to cool microclimates, the location of their offspring could constrain where individuals choose to roost.

Spotted owl behavior as a response to warm temperatures

Spotted owls seemed to display behavioral flexibility in response to warmer ambient temperatures. Operative temperatures were nearly ubiquitously warmer than stand temperatures, but offsets decreased as ambient temperatures increased, indicating that spotted owls successfully located microclimates that were more buffered. The loggers on the owls were unshielded and measured ambient air temperature as well as long- and short-wave radiation, wind, and humidity (Dzialowski, 2005), reflecting the thermal conditions individuals experience in nature (Bakken and Gates, 1975). Long-wave radiation is influenced by ambient temperature, and if individuals randomly used available sites within stands, then differences between operative temperatures and stand temperatures would be greater when ambient conditions were warmer. However, temperature offsets were smaller and even negative when conditions were generally warmer, reflecting daily choices made by individuals to avoid potentially stressful temperatures.

Taller canopies tended to be associated with smaller or more negative offsets between stand and operative temperatures as well (Fig. 1.3b), but top models that considered canopy height did not outperform the null model. Microclimates under tall canopies in forests are extremely variable, and even small movements to large trees may offer temporary refuge from warm conditions (De Frenne et al., 2021) or refuge from direct sunlight and short-wave radiation (Carroll et al. 2016). When tall forest is readily available, spotted owls may seek out cooler microclimates to avoid the negative consequences of heat or solar exposure. While other endotherms have been shown to actively use more stable microclimates during periods of anomalous conditions (Wolff et al., 2020; Shipley et al. 2020), we were unable to discern whether spotted owls sought relatively cooler microclimates created by tall canopies for their thermal characteristics, their shade, or both.

Microclimates, behavioral flexibility, and climate change

Our study documented important connections between microclimates and individual behavioral responses during a period of historic warming. It was also the first to characterize microclimate use for this climate-vulnerable species near its southern range boundary as well as for old forest species, like martens and pacific fishers, more broadly. When spotted owls had access to habitat with cooler microclimates and ambient conditions were warm, they actively located and used roosts that were cooler than surrounding temperatures. This finding emphasized the value of conserving large trees and forests with higher canopies and canopy cover that sustain cooler microclimates, a strategy potentially benefitting a suite of less well-studied forest associated species as the climate continues to warm.

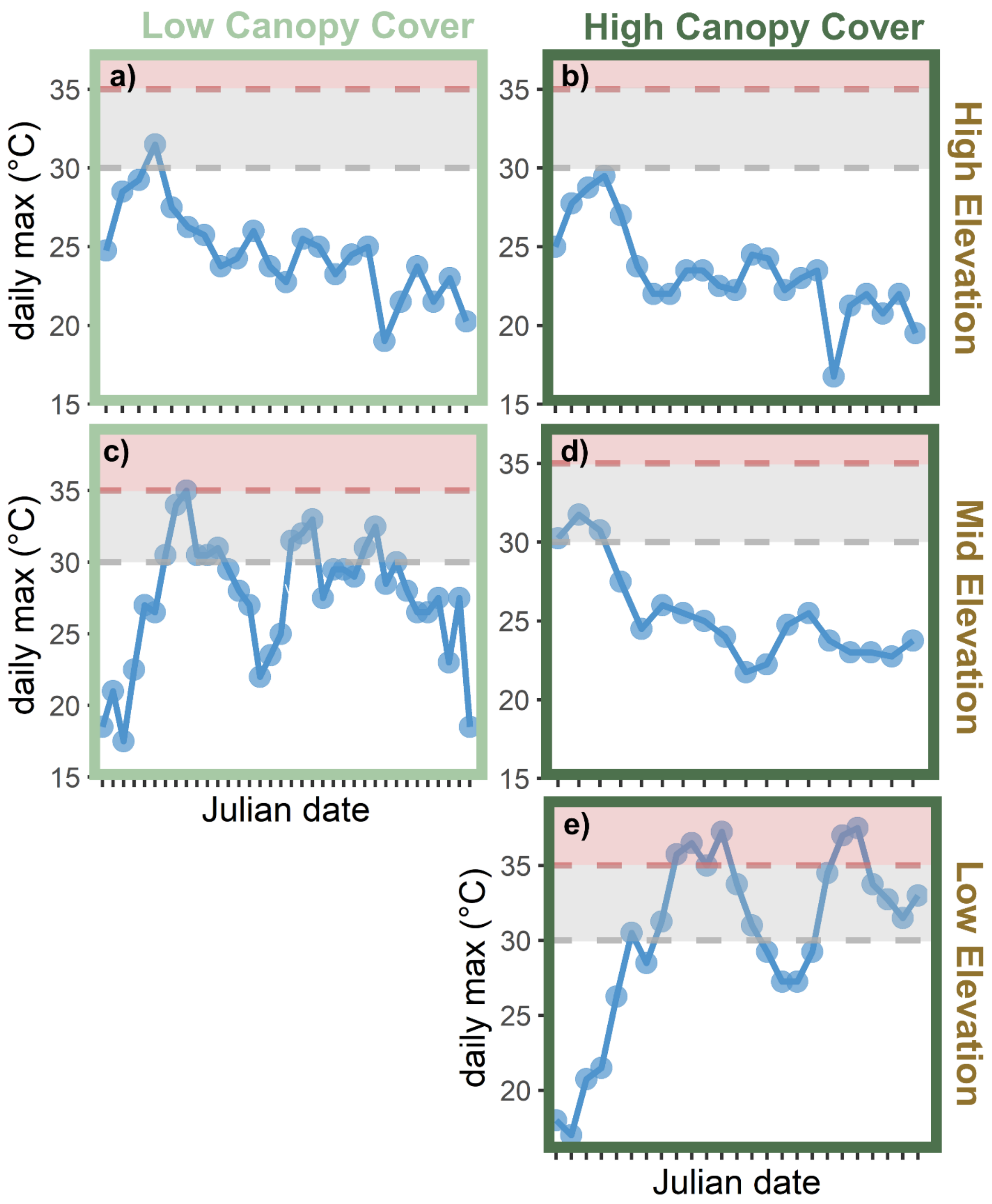

Fig. 1.4. Daily maximum temperatures at five roost sites during sampling periods (20-30 days), where thresholds (dashed lines) indicate species-specific physiological thresholds. At 30 °C, spotted owls begin to experience heat stress (grey) and 35 °C is the upper critical temperature for spotted owls (red). a) At a high elevation roost site (2500m) where canopy cover was relatively low (29%), maximum temperatures generally did not exceed thermal thresholds. b) A high elevation roost site (2500m) with high canopy cover (54%) had similar conditions. c) Low canopy cover (39%) at a mid-elevation site (1900m) yielded conditions that often exceeded the lower thermal threshold. d) A roost sites with high canopy cover (71%) at mid-elevation (2000m) experienced cooler maximum temperatures. E) At a low elevation (1200m), even high canopy cover (88%) did not buffer the site when conditions were extremely warm, where daily maximum temperatures consistently exceeded the species' thermoneutral zone and surpassed the upper critical threshold.

Despite their behavioral response to warm temperatures, spotted owls were still exposed to conditions that exceeded physiological thresholds when ambient maximums were high (Fig. 1.4). Over two-thirds of the roosts in this study reached maximum temperatures of at least 30 °C, a threshold over which individuals show signs of heat stress, and over a quarter of roosts reached maximum temperatures over 35 °C, the upper critical limit for the species (Weathers et al., 2001). Consecutive days consistently exceeded thermal thresholds, especially at lower elevations, pointing to potential cumulative exposure, which has been shown to reduce reproductive success and survival in similar species (Cruz-McDonnell and Wolf 2016). In our study, we only found roost sites at lower elevations in higher canopy cover, and even when greater canopy cover was available, temperatures still exceeded thermal thresholds (Fig. 1.4E). As documented in the SBNF, many low elevation territories, where temperatures are warmer, large trees are absent, and canopy cover is low, have gone extinct; they are also more likely to remain unoccupied and contribute to population declines (Tempel et al., 2022). Given a future climate with a higher likelihood and frequency of extreme heat events that approach and exceed thermal extremes for forest-dwelling species, some areas may be lost even with management efforts aimed at promoting cool microclimates. This may limit potential refugia to higher elevations, cementing the value of managing for cooler habitat at mid-elevations. Our results potentially explain one aspect of the rapid extirpation of spotted owls from lower elevations and a mechanistic explanation for the species shifting its distribution upslope to track its abiotic niche (Peery et al., 2012).

Forest microclimates that support climate refugia are likely important to a suite of other canopy-dwelling species in addition to spotted owls. For example, northern goshawks (*Accipiter gentilis*), great grey owls (*Strix nebulosa*), martens (*Martes americana*) and Pacific fisher (*Martes pennanti*) have been identified as potentially vulnerable species to climate change (Siegel et al., 2014), with fisher using cooler forests during daytime resting activity likely to avoid thermal stress (Zielinski et al., 2005; Purcell et al., 2009). Given current rates of forest loss due to high-severity forest fire and drought-induced tree mortality (Keyser and Westerling 2017), identifying and conserving the existing features that promote climate resiliency will be important for promoting the viability of these species. Fuel-treatments, including prescribed fire and removal of vegetation, can reduce the spread and intensity of large fires (Stephens et al., 2012), and potentially reduce the loss of important habitat (Jones et al., 2022). While such treatments may be necessary to minimize the extremity of unprecedented wildfires and habitat loss, management that also promotes large, tall trees and denser canopy cover may better sustain important microrefugia and promote climate resiliency for forest-dwelling species.

Conclusion

Climate change will alter the availability and distribution of suitable microclimates for many species and ecosystems, including the spotted owl (De Frenne et al., 2021; Jones et al., 2016). Over the next two to five decades, average temperatures in some regions may become comparable to present-day maximum temperatures (Diffenbaugh and Field, 2013; Trisos et al., 2020; Armstrong McKay et al., 2022). Large-scale, high-severity wildfire and tree mortality due to drought threaten temperate forests globally and cause the loss of canopy cover and large trees, which will exacerbate projected temperature increases (Millar and Stephenson, 2015). Increasing temperatures, canopy loss and large tree reductions comprise a deadly cocktail to further restrict the distribution of suitable microclimates and potentially lead to local and regional extirpations of climate-vulnerable species. In the context of such rapid changes in both climate and land cover, the conservation of existing refugia, and restoration and propagation of future refugia in areas that may buffer against climate-driven thermal stress, are important components of biodiversity conservation planning. Regardless of management that promotes cooler microclimates, some historic habitat will no longer be suitable for the spotted owl and other iconic forest species.

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Chapter 2: 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 labelled 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 & Yohe, 2003, Moritz & Agudo, 2014). 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 landcover 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 & Wolf, 2010). In response to changing abiotic environments, some animals alter their behavior to either 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 & 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 at., 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. 2.1). 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. 2.1a). 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. 2.1b). 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. 2.1c). 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.

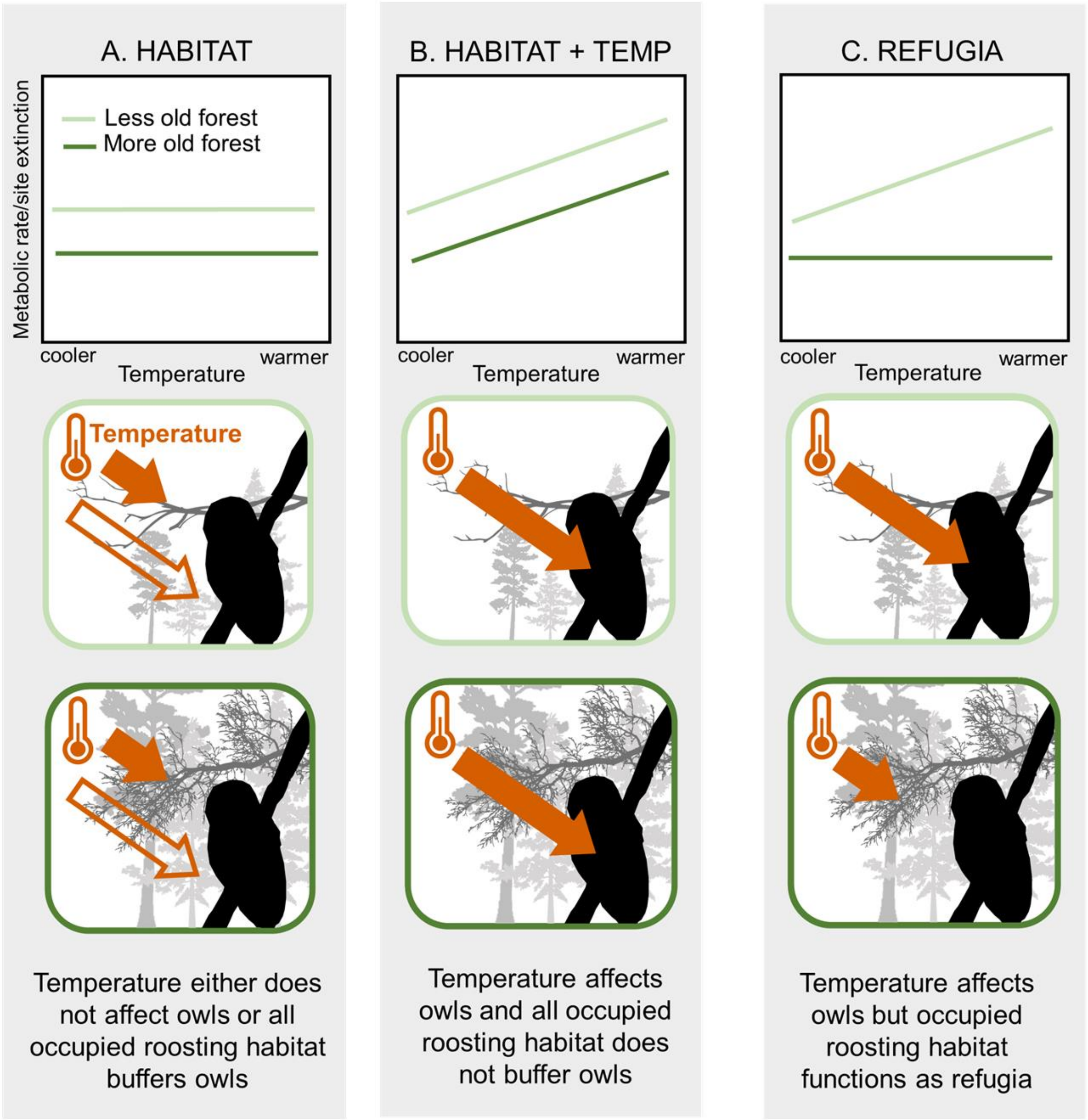

Fig 2.1. Alternative hypotheses for the role of roost/nest habitat as temperature refugia. Light green indicates characteristics associated with younger, more open forests and dark green indicates characteristics typical of older forests like closed canopies, tall trees, and vertical complexity. We show 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).

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 ~800-3000m 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% in a territory in the Sierra Nevada is 0.43 (SE = 0.03) and the average proportion of forest with canopies over 20m tall is 0.35 (SE = 0.03). In the San Bernardino Mountains, spotted owls occupy territories between 1000-2500 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 20m tall is 0.01 (SE = 0.002). Regional maximum temperatures in spotted owl territories range from 25-33 °C in the Sierra Nevada and from 21-32 °C in the San Bernardino mountains.

We captured, tagged, and obtained doubly labeled water samples from 27 California spotted owls between 2019-2021 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. 2.2a-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).

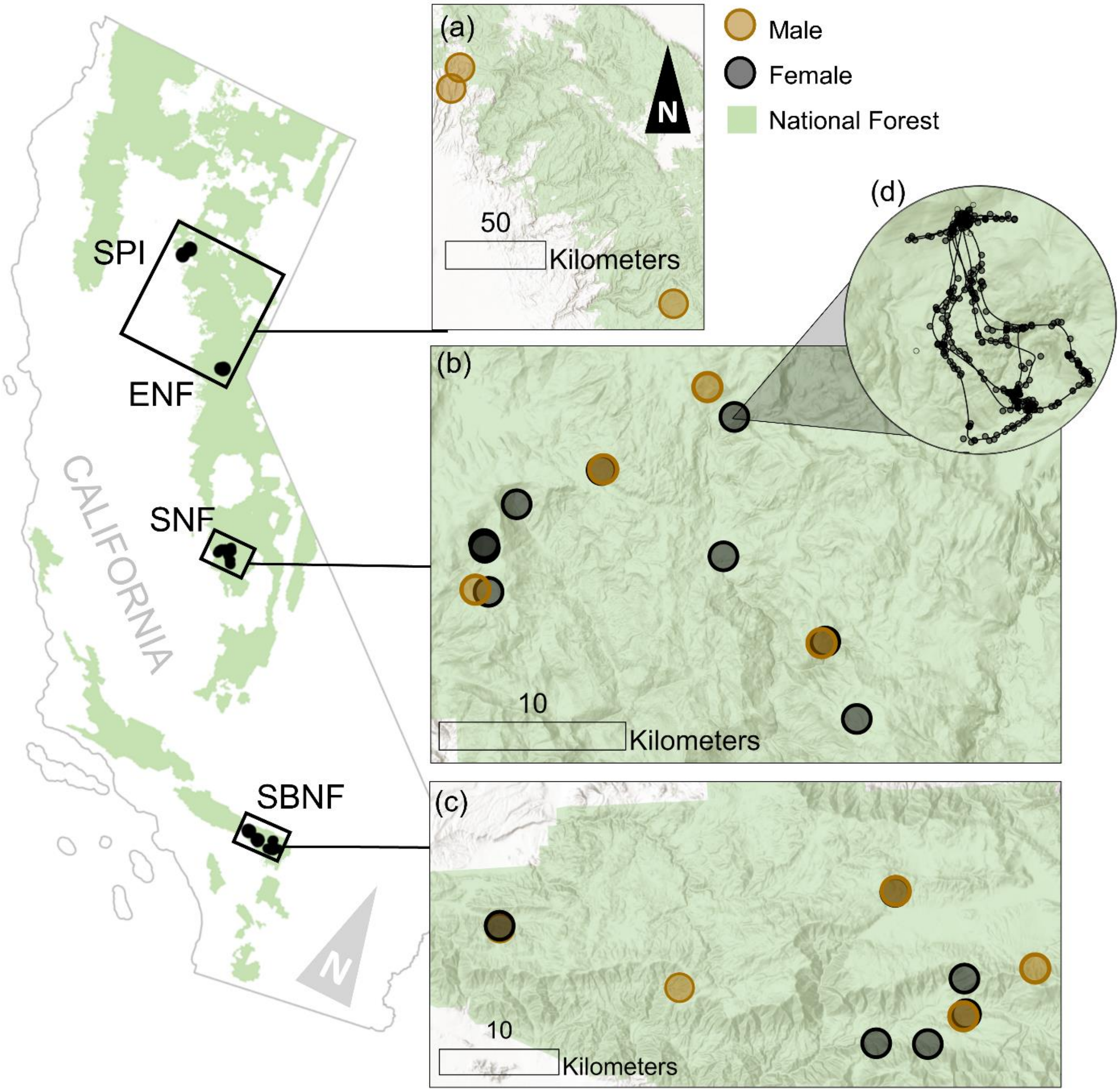

Fig 2.2. Study areas and territories where we tagged individual spotted owls. We tagged 13 males (brown) and 14 females (black) between the years 2019-2021. Field work was conducted in the a) Eldorado (ENF), b) Sierra (SNF) and c) San Bernardino (SBNF) National Forests and a) two samples for individual 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.

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 200μL blood sample was drawn from the metatarsal vein to determine background levels of ^{18}O and ^{2}H isotopes expenditure (Nagy, 1983). Using 25-gauge needles and 5mL syringes, we administered a dose of DLW into the pectoral muscle (~1.10 g ^{18}O kg^{-1} total body water, or TBW, 0.48 g ^{2}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 1mL syringes were used for all blood samples, and blood was collected in 100μL 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 ^{2}H (Nagy, 1983). We analyzed samples at the University of Wisconsin-Madison using gas source isotope ratio mass spectrometry to measure isotope ratios of ^{18}O:^{16}O and ^{2}H: ^{1}H. We ran samples collected in the field alongside standard samples for $^{2}H_2{}^{18}O$, serial dilutions, and background water, and we obtained estimates of daily energetic expenditure from isotope enrichments using the single-pool model for animals <5kg (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 & 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 & Weathers, 1989; Speakman, 1993; Schultner et al., 2010). We scaled our estimates of field metabolic rate to account for body mass (mass-specific; kJ day^{-1} x $kg^{0.71}$; 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 (~6.7g), which had relatively shorter battery life, and 5 birds with Ecotone tags (~10g), 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 minutes for 10 hours 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_{HDOP}=0.42, r_{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 Supplemental Fig. 2.1), 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. 2.2d). 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 1km grid, which are interpolated and extrapolated meteorological observations from weather stations (Daymet, Thorton et al. 2020) 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 20m 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 minutes prior to sunrise (estimated from a generic astronomy calculator) and 15 minutes after sunset (Supplemental Fig. 2.2) 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; Supplemental Fig. 2.3). We measured occupancy covariates at two different scales: a nest/roost scale with a 135m 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-August (T_S) and summer temperature anomalies (T_A; Supplemental Materials). All individual- and population-level covariates and acronyms are in Supplemental Table 2.1.

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 daytime 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 & 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 2010-2021 in ENF and 2010-2019 in SBNF to reduce the effects of forest change prior to the first year CFO-based vegetation data was 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 (Supplemental Fig. 2.3). 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 (*t*) were years and our secondary sampling periods (*j*) were two-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 three days apart to be included in separate survyes, and the total duration of the surveys with no detections needed to exceed 30 minutes in ENF and 15 minutes 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 30th 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 & Anderson, 2002). We did not include covariates that were highly correlated with one another in the same model (Pearson correlation coefficient, $|r| > 0.7$; Dormann et al., 2013). 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"; Supplemental Table 2.3). 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} (SE = 15.3) and did not vary significantly from the previous estimate for this species (249 kJ day^{-1}, 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 ($\beta_{velocity}$ = 162, 85% CI = [45, 278]; Fig. 3a). That is, for every 0.1 m s^{s} increase in average velocity over the sampling period, predicted mass specific FMR increased about 16 kJ day^{-1} x kg$^{0.71}$. We predicted that average "non-moving" metabolic expenditure was 140 kJ day^{-1} x kg$^{0.71}$(SE = 23.1), which was lower than a BMR estimate from a previous study

(170 kJ day^{-1}, 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 kJ day^{-1} x $kg^{0.71}$ (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 (Supplemental Table 2.2). 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 (β_{T30} = 65.5, [39.5, 91.5]), canopy height had a negative effect on residuals (β_{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. 2.3b; β_{T30*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} (SE = 0.023) and average nightly distance moved at night was 4073 m day^{-1} (SE = 492). Both distance and velocity varied between sexes, such that males moved faster (β_{males}= 0.09, [0.03, 0.16]) and covered more distance per night (β_{males}= 2348, [1055, 3641]) during the sampling periods. We additionally found a significant negative relationship between maximum temperature and average movement velocity (β_{Tmax}= -0.04, [-0.08, -0.01]) and maximum temperature and average daily movement distance (β_{Tmax}= -664, [-1327, -0.16]), indicating that owls experiencing warmer temperatures tended to move more slowly and shorter distances (Fig. 2.3c-d).

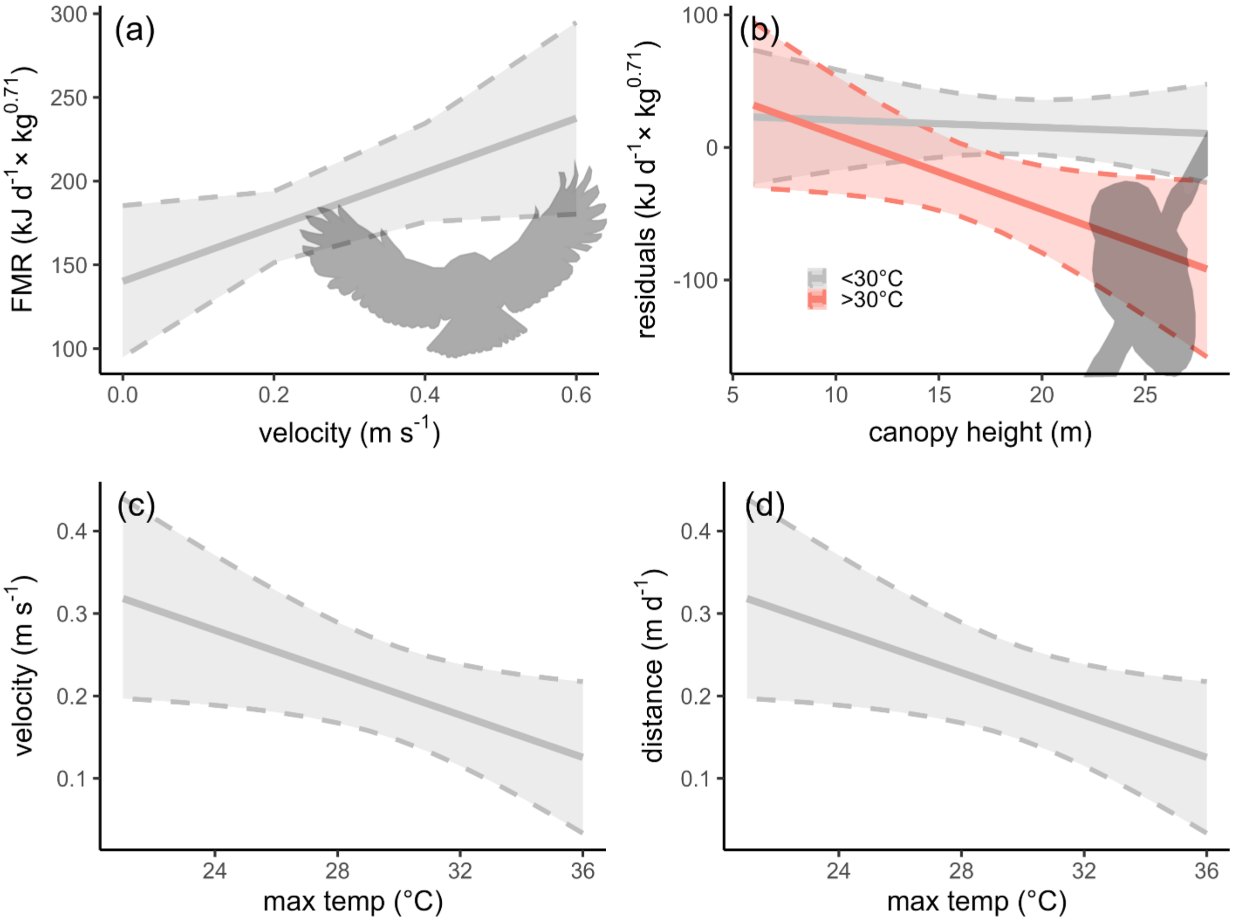

Fig 2.3. Results from individual analyses. a) The average velocity at which a bird was moving during the sampling period was a significant predictor for mass specific energetic expenditure (R^2=0.15, $\beta_{velocity}$ =162, p=0.05). b) Residuals from that relationship, which correspond to deviations 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

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 2.1). No single model in the third stage had ≥90% AIC weight from which we could make unequivocal inference (Burnham & Anderson, 2002). Habitat predictors were highly correlated (r=0.84), as were temperature predictors (r=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. 2.4):

$$\text{logit}(\gamma_t) = -1.87 - 0.40 \times T_S + 1.03 \times CH_{nest}$$

$$\text{logit}(\varepsilon_t) = -1.80 - 0.45 \times T_S$$

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 2.1). Coefficient estimates varied minimally among competing models, so we reported the top model for simplicity (Fig. 2.4):

$$\text{logit}(\gamma_t) = -2.34 + 0.31 \times CC_{nest}$$

$$\text{logit}(\varepsilon_t) = -1.87 + 0.36 \times T_S - 0.32 \times CC_{nest}$$

Table 2.1. *β*-estimates of model covariates in top-ranked models parameter estimates for colonization-γ and extinction-ε. Confidence intervals are reported (85% CI).

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
	γ	0.21	CH_{nest}	0.75	0.44, 1.05
	ε	0.27	T_S	-0.46	-0.76, -0.16
	ε	0.13	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

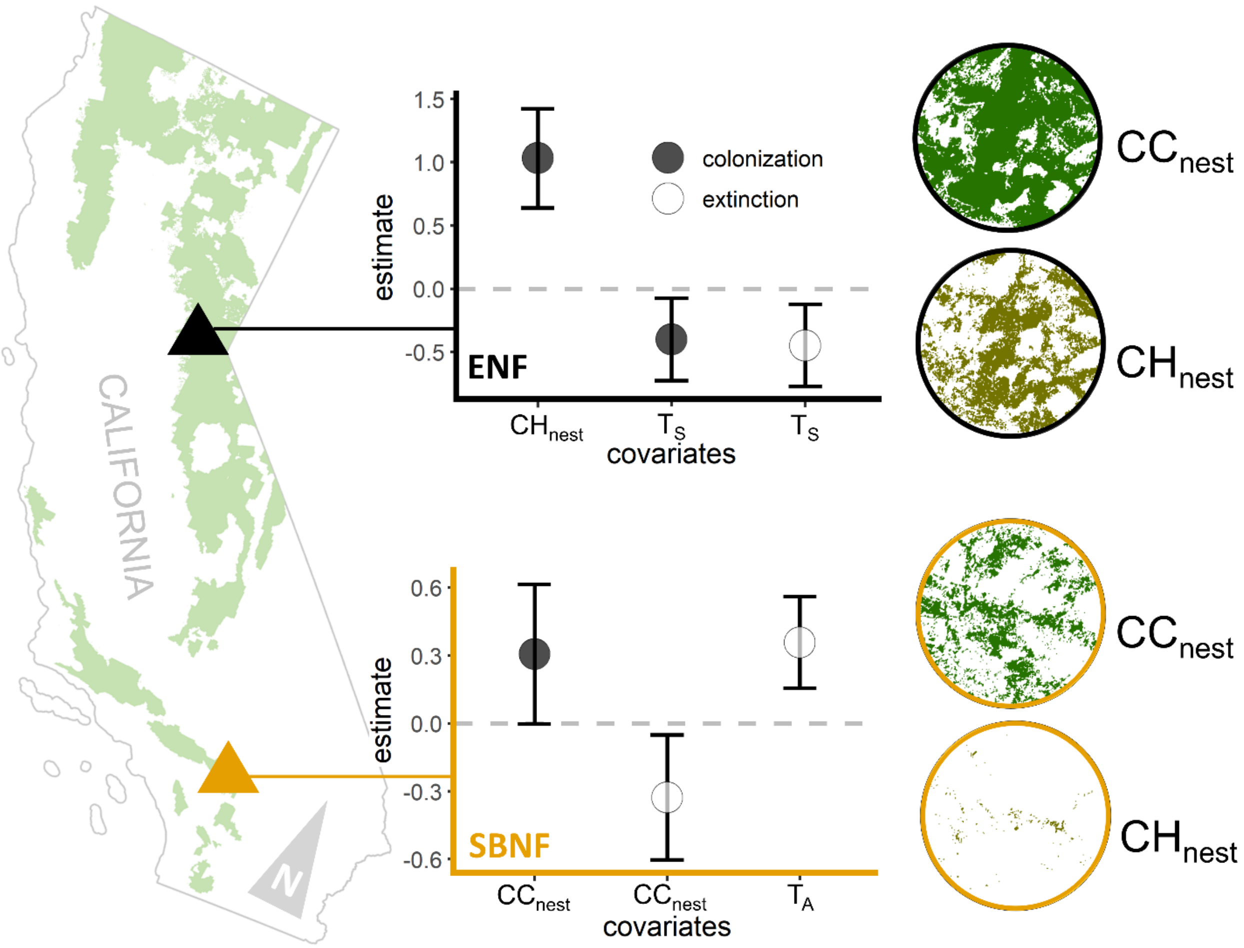

Fig 2.4. Results from population analyses. Here, we report the β-estimates for the covariates that were in the top models for each study area. The top panel is from the ENF study area and the bottom panel is from the SBNF study area. Covariates for colonization are black and covariates for extinction 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 20m (CH_{nest}) in 135 m buffers around territory centers. 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 tradeoffs 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.

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. 2.1). 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}, 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. 2.3b). 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 & King, 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 (Supplemental Fig. 2.4).

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 (Supplemental Fig 2.4). 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 (Veľký et al., 2009), which suggests support for our *refugia* hypothesis (Fig. 2.1c). Indeed, in our supplemental analysis we found that operative temperatures were lower under taller canopies (Supplemental Fig 2.4). 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. 2.3c) and shorter distances at night (Fig. 2.3d) 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., in review; 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. 2.4), 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 & 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. 2.1a). 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. 2.1b). 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. 2.4). 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 tradeoffs

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. 2.4), 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 tradeoffs 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 tradeoff 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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Chapter 3. Contiguous high severity fire limits the distribution and composition of forest owl guild

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Abstract

Fire shapes biodiversity in many forested ecosystems, but a combination of historical management practices and anthropogenic climate change has led to larger, more severe fires that threaten many animal species. As predators, owls can exert top-down control on their biological communities, and while the disruption of natural disturbance processes likely influences habitat suitability for these species, we know little of their associations with burned forest. Here, we examined the impact of fire severity, history, and configuration on six forest owl species in the Sierra Nevada, California using regional-scale passive acoustic monitoring. Low-moderate severity fire appeared to benefit flammulated owls and western screech owls, small cavity nesting species, 2-10 years after an initial disturbance. Great horned owls and northern pygmy owls were more likely to occupy sites burned at high severity, but only where high severity burns were patchier and interspersed with either low-moderate severity fire or unburned forest. California spotted owls were less likely to occupy sites burned at high severity for up to two decades following an initial disturbance. Our results suggest that while individual owl species have unique associations with burned habitat, contiguous high severity fire offered no benefits to any species and reduced habitat suitability for a mature forest species for longer than previously expected. Thus, forest owls in this, and potentially other, regions likely benefit from frequent lower severity fire resembling historical regimes, but as the climate continues to warm and fires eliminate large, contiguous areas of live canopy cover, the distribution of this socially and ecologically important guild of predators may become more constrained.

Keywords: bioacoustics, disturbance, megafire, occupancy, owls, passive acoustic monitoring, wildfire

Introduction

Disturbance can increase biodiversity by supporting species with variable sensitivities to dynamic ecological processes (Connell, 1978). Fire is a driving component of forest ecosystems (Bond & Keeley, 2005; Seavy et al., 2012; White et al., 2016), and ecosystems adapted to shorter interval, lower severity fire regimes, like seasonally dry forests, contain a dynamic mosaic of successional stages that supports high levels of biodiversity (Tingley et al., 2016, Jones & Tingley, 2022). However, climate change and forest management practices have led to novel fire dynamics that pose a potential existential threat to some forest animals and biological communities(Westerling et al., 2011; Wood & Jones, 2019; Levine et al., 2022). While this new era of large-scale, high severity megafires disrupts habitat and poses a significant conservation concern for forest specialists (Jones et al., 2021), some research has shown neutral or beneficial long-term impacts of severe fire on animals (Lee & Bond, 2015; Hutto et al., 2016). Thus, the response of species to novel fire disturbance regimes is likely complex and uncertain.

The characteristics of a fire regime—severity, return interval, configuration, size, and seasonality—can influence a species' habitat suitability (Archibald et al., 2013). These fire characteristics depend on the region's elevation, latitude, and climate (Veblen et al., 2000, McLauchlan et al. 2020). Depending on the geographic characteristics, and subsequent fire regime, of a region, many species are adapted to iterative, recurrent features of fire disturbance (Fontaine et al., 2009; White et al., 2016; Blakey et al., 2021). Low-moderate severity fire with small patches of severe fire, characteristic of lower elevations and drier climates, often reduces tree density and understory vegetation without eliminating mature forest. Shorter fire return intervals create heterogenous forest with complex forest edges and canopy openings, which can provide movement corridors and high-quality foraging habitat for a variety of animal species (Blakey et al., 2021). By contrast, high severity fire, characteristic of higher elevations and more mesic climates, eliminates most live canopy vegetation, which can take multiple decades to regenerate (Wagtendonk et al., 2018). Longer fire return intervals, often interrupted by high severity fires, promote reproductive opportunities for vegetation adapted to stand-replacing fires (Critchfield 1980) and foraging opportunities for animals (Frock & Turner, 2018). The disruption of historical fire regimes can impact forest regeneration (Frock & Turner, 2018; Rammer et al., 2021), reduce and sometimes reverse the value of fire disturbance for dependent species , and potentially induce novel community dynamics in ecosystems (Steel et al., 2022).

Predators often exhibit top-down control on biological communities and the impacts of environmental change on higher trophic levels can cascade to entire ecosystems (Pace et al., 1999). Globally, owls occupy apex positions in their resp food chains, but we lack a comprehensive understanding of how changes in natural disturbance processes affects this guild of nocturnal predators (Wood et al., 2019a). The Sierra Nevada, California hosts a diverse and speciose community of forest owls (Gutiérrez et al., 2007). Fire has been a driving ecological force in the region for over a millennium, such that fires, actively managed by Native Americans, were frequent throughout the range (Taylor et al., 2016, Klimaszewski-Patterson et al., 2018). Euro-American colonization in the 1850s significantly altered these historic regimes by excluding fire. This management strategy, in conjunction with timber harvesting and climate change, homogenized the landscape and contributed to large, stand-replacing, high-severity fires. (Skinner & Chang, 1996). Bird species in this region show extremely varied relationships with burned forest depending on their natural histories, where species abundance can peak in recently burned forests regardless of severity while other species are most abundant in unburned forests (Tingley et al., 2016; Taillie et al., 2018). However, we know very little of how owl species associate with disturbed habitat in this region given their cryptic nature (Wood et al., 2019a). Thus, the Sierra Nevada offers an ideal system to study interspecific variation in habitat associations following novel fire disturbance in an understudied guild of avian predators.

The species that comprise this owl community co-occur at the landscape scales but occupy distinct ecological niches (Wood et al., 2019a). While all forest owl species rely on trees for nesting, great horned (GHOW; *Bubo virginianus*) and western screech (WESO; *Megascops kennicottii*) owls occupy a wide variety of habitats and often forage where canopies are relatively open (Davis & Weir, 2010; Johnson, 1992). Flammulated (FLOW; *Psiloscops flammeolus*) breed in mature mixed conifer forests dominated by yellow pine and Douglas fir (Linkhart et al., 1998). California spotted owls (SPOW; *Strix occidentalis occidentalis*) rely on mature forest characteristics for roosting and nesting, while benefiting from forest heterogeneity—specifically edges between younger and more mature forest—for access to prey (Zulla et al., 2022). Northern pygmy (NOPO; *Glaucidium gnoma*) and northern saw-whet (NSWO; *Aegolius acadicus*) owls are more general in their habitat associations but often nest in mature forests (Hayward & Garton, 1988; Hinam & Clair, 2008; Groce & Morrison, 2010). Finally, western screech, flammulated, northern pygmy and norther saw-whet owls are secondary cavity nesters and often nest in cavities excavated by other species (Scott et al., 1977; Bull et al., 1997) that are more prevalent following fires (Tarbill et al., 2015). Fire disturbance influences the composition and configuration of forest successional stages, and as such, interspecific variation in habitat associations for forest owls likely induce diverse responses to burned forest.

Here, we conducted regional-scale passive acoustic surveys across the Sierra Nevada bioregion to test the hypothesis that site occupancy for six forest owl species is related to the severity, spatial configuration, and temporal history of past fire disturbance. We first examined the effect of elevation, latitude, and the proportion of closed-canopy forest to account for broad spatial variation in site occupancy and examined species' associations with mature forest characteristics. We predicted that all species would be less likely to occupy forests burned at higher severity the previous year due to a loss of live overstory, which is important for all species to varying degrees. We further predicted that species which are more general in their habitat associations and us open forest, would be more likely to occupy sites burned at higher severity after at least 5-10 years of shrub and hardwood regeneration, taking advantage of potential foraging opportunities. Mature forest species would be less likely to occupy forest burned at higher severity for extended periods of time due to the long-term loss of overstory whereas cavity nesting species would be more likely to occupy habitat burned at low-moderate severity 2-10 years post-fire due to increased nesting opportunities. Finally, we predicted that patchier high severity fire would immediately benefit species with more general habitat associations by creating edges between forest and open habitat and, after several years of regeneration, benefit mature forest species by creating edges between older and younger forest.

Methods

Acoustic monitoring in the Sierra Nevada

We conducted ecosystem-scale passive acoustic monitoring (PAM) surveys in 1648 sites across the Sierra Nevada in 2021. Our surveys spanned the western slope of the Sierra Nevada, including coverage in all seven National Forests, three of the four National Parks, and some private land (Kelly et al., in review). We divided this area into 6236 4 km^2 hexagonal grid cells, which are comparable in size to spotted owl and great horned owl territories in this region (Kelly et al., in review; Bennett & Bloom 2005) and likely encompass smaller owl territories (Peery, 2000), to obtain a total sampling area of 24,494 km^2. In 2021, we surveyed 845 non-adjacent grid cells to reduce the possibility of double-counting potential spotted owl and great horned owl territories (Wood et al., 2019b). Cells were excluded if they intersected highways, were over 50% water, or lacked road/trail access.

We deployed 1-3, but generally 2, autonomous recording units (ARUs; SwiftOne recorder, K. Lisa Yang Center for Conservation Bioacoustics) in each surveyed grid cell with a minimum spacing of 500 m. ARUs had a single omni-directional microphone with -25 dB sensitivity, 62 signal to noise ratio, and recorded 20:00 – 06:00 PDT at a sample range of 32 kHz, 16-bit resolution, and gain of + 33 dB. We began deployments in early-May, and surveys lasted through mid-July. Most locations were surveyed for approximately five weeks continuously. When possible, no ARUs in this project were closer than 500 m to one another and ARUs were placed at least 250 m from the edges of cells.

Forest owl detections

To identify forest owl vocalizations, we used the BirdNET algorithm, a deep convolutional neural network designed to identify 984 North American and European bird species by sound (Kahl et al. 2021; https://github.com/kahst/BirdNET-Analyzer). We developed a customized version of BirdNET that was overfit to the vocalizations of species of interest in this region, including the six forest owls in this study. BirdNET outputs a unitless numeric prediction score, ranging from 0-1, for each species in every 3-second interval of audio data. This prediction score indicates confidence in the identification, with larger numbers indicating greater confidence.

Acoustic validation

For all species except spotted owls, we designed species-specific probability-based thresholds in the prediction score to minimize false positives in our acoustic identifications. We aimed to set score and count thresholds for acoustic data such that an hour-long sample was marked as a true positive only if the number of BirdNET observations above a selected prediction score was above a selected number of calls per hour. For each of these species, we manually validated a random subset of at least 200 hour-long acoustic data files that each contained at least one BirdNET identification with a prediction score of at least 0.1. For each hour-long sample, we used RavenPro 2.0 (Ornell Lab or Ornithology, Ithaca, NY) to manually scan potential observations to either 1) confirm the presence of at least one true call or 2) identify false positives where no true calls were present. In each hour-long sample, we counted the number of BirdNET identifications over a series of prediction score thresholds (0.1, 0.2, …, 0.9, 0.91, …, 0.99). We then estimated the probability of a random hour of acoustic data representing a false positive as a function of the number of BirdNET observations over each prediction score. We fit logistic regressions in which the true positive/false positive status of an hour-long acoustic data file was the binary response and the number of BirdNET observations above a prediction threshold was the predictor (lme4; Bates et al., 2015). We did this for multiple prediction score thresholds for each species. We extrapolated false positive rates to the secondary sampling period (for occupancy analyses) using the following equation: $1-(1-FP)^n$, where FP is the false positive rate per hour and n is the number of hours within the secondary sampling period. For this project, our secondary sampling periods were seven days, with recording occurring for 12 hours (84 hours total).

For FLOW and GHOW, we identified a call rate and score threshold at which the false positive rate for the secondary sampling period of about 0.01 (Supplemental Fig. 3.1). For NSWO, WESO, NOPO, we used a more liberal call rate and prediction score threshold that resulted in false positive rates of over 0.40 but manually validated all resulting BirdNET identifications (Supplemental Fig. 3.1). Thus, a false positive rate of 0.01 is conservative in our final detection histories. All SPOW vocalizations above a threshold of 0.989 were validated separately from the other forest owl species as part of a separate, species-specific monitoring program (Kelly et al., in review).

To account for imperfect detection, we divided the continuous sampling in 2021 into 8 week-long secondary sampling periods starting on Julian day 130 and ending on 193. We did not consider any time between secondary sampling periods. We determined the presence of either a manually validated or threshold validated detection in each secondary sampling period. If an ARU was not recording at any point during a particular secondary sampling period, we would consider that week-long period null. For all smaller forest owls (FLOW, WESO, NSWO, NOPO), we created detections at the scale of single ARUs. These species have smaller home ranges, and their calls are quieter and propagate over shorter distances than the larger species. For the larger species (GHOW and SPOW), we created detection histories at the scale of sampling hexes because these species have larger home ranges and there is a greater chance multiple ARUs in a sampling hex are recording calls from the same individual (Reid et al. 2022).

Table 3.1. Selected count (observations per hour-long file) and prediction score thresholds and resulting number of hours and sites with detections that meet those criteria. We also report naïve occupancy (not corrected for detection).

Species	Count	Prediction score	Hours	Sites	Naïve occupancy
GHOW	34	0.90	1652	271[a,b]	0.321
WESO	60	0.90	1058	167[c]	0.101
FLOW	155	0.90	1329	159[b]	0.096
NOPO	45	0.99	379	224[c]	0.134
NSWO	10	0.90	150	62[c]	0.038
SPOW	NA	0.99	4321	343[a,c]	0.406

[a] Number of sites represents the number of hexagonal cells
[b] <0.01 false positive rate for secondary sampling period
[c] All potential detections manually vetted

Predictor variables

To account for the effects of spatial environmental variation on the probability of site occupancy for these six owl species, we calculated point estimates of elevation and latitude at each ARU location. We averaged values between ARUs in the same sampling cell for covariates to be used in occupancy models for the two larger species (GHOW and SPOW). To account for the effects of spatial characteristics on the probability of detecting each species, which have vocalizations with different acoustic characteristics and likely different propagation across the landscape, we measured terrain ruggedness and the proportion of closed canopy forest within the 250 m buffers and the hexagonal sampling cells. This buffer size was selected for the smaller species given the relative size of their territories (Linkhart et al., 1998; Giese & Forsman, 2003; Hinam & Clair, 2008; Davis & Weir, 2010). We calculated terrain ruggedness as the standard deviation of elevation in a sample buffer/cell (Duchac et al., 2021), and canopy cover was calculated as the proportion of a buffer/cell with canopy cover greater than 70% (Tempel et al., 2014; Jones et al., 2016). Canopy cover was downloaded from the California Forest Observatory Database (CFO; Salo Sciences, 2020). 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.

To examine the effects of fire severity, spatial configuration, and temporal history on each owl species, we established two classes of fire covariates: low-moderate severity fire (0-75% overstory mortality) and high severity fire (>75% overstory mortality). To estimate fire severity, we obtained fire data from the Monitoring Trend in Burn Severity (MTBS; https://www.mtbs.gov/) for fires larger than 1000 acres. We binned fire data, stacking data by most recent disturbance, into five consecutive temporal groups that increased in duration: one year following a fire disturbance, 2-4 years, 5-10 years, 11-21 years, and 21-35 years. These categories reflect early fire regeneration stages and have been shown to influence animal responses to fire disturbance (Kilgore, 1981; Russell-Smith et al., 1998; McIver et al., 2008; Nappi & Drapeau, 2009; Fontaine & Kennedy, 2012; Tempel et al, 2014; Donato et al., 2016; Tingley et al., 2018; Duchac et al., 2021; González et al., 2022; Brunk et al., 2023).

Using the *landscapemetrics* package in R (V1.5.6; Hesselbarth et al. 2019), we calculated the proportion and patch density (number of patches/area) of both fire severity classes for each temporal group. Specifically, we calculated the proportion of low-moderate and high severity burned area in 250 m buffers for small species and in hexagonal sampling cells for the two larger species. We used patch density to quantify the relative configuration of both fire classes within each 250 m buffer or 400 ha cell because it was less correlated with composition than other configuration metrics. A lower value for patch density indicates a more contiguous landscape and a higher value indicates a patchier landscape.

Fire history analysis

To examine the effects of the severity, spatial configuration, and temporal history of fire on the occupancy of forest owls across the Sierra Nevada, we used single-species, single-season occupancy models (MacKenzie et al., 2003), which enabled us to estimate the occupancy of a species of interest from our imperfect acoustic detection process. These models require repeated surveys at fixed locations, in this case ARUs, and allow spatial predictors to describe patterns in occupancy and detectability. All covariates used in analyses were standardized.

We modeled the probability of detecting each species as univariate functions of terrain ruggedness, elevation, canopy cover, a continuous covariate related to the secondary sampling period, and the number of hours ARUs recorded. These variables have previously been shown to affect the detection probability of vocalizing owl species (Duchac et al., 2021). We ranked all univariate models using Akaike Information Criteria (AIC) and considered competitive models as those within 2 ΔAIC units of the top-ranked model. We then added variables in order of rank until the resulting models were no longer within 2 AIC units of the top model. When a parameter was added to a top-ranked model but did not provide a reduction of more than 2 AIC units, we considered the parameter to be uninformative (Arnold 2010). We carried forward the top detection models that did not contain uninformative parameters.

The best detection models informed the next stage in which we modeled the probability of site occupancy. We fit three parallel sets of models in which we looked at: 1) basic covariates to account for broad spatial variation in site occupancy, 2) the composition of burned forest in sites to examine fire severity, and 3) the configuration of burned forest to examine the spatial configuration of burns at both severity classes. For the basic analysis, we examined the probability of site occupancy as univariate functions of elevation, latitude, and the proportion of a site with canopy cover over 70%. For composition, we examined the probability of site occupancy as univariate functions of the proportion of a site burned at both severity classes for all time steps. For configuration, we examined the probability of site occupancy as univariate functions of patch density of both severity classes for all time steps. As above, we ranked univariate models and added variables in order of rank until resulting models were no longer within 2 AIC units of the top model.

We combined the top basic, composition and configuration models within 2 AIC units of the top model on their respective groups that did not contain uninformative parameters. In this final stage, we ran a global model and removed covariates until the top performing model did not contain uninformative parameters (Morin et al., 2020). If any configuration and composition covariates from the same severity class and time step were in the same combined model, we additionally considered interactions between those covariates to examine if the patch density of burns mediated or mitigated the effect of the composition of burned forest on site occupancy (see predictions). In all stages of analyses, we did not include covariates that were highly collinear in the same model (Pearson correlation coefficient, $|r| > 0.7$; (Dormann et al., 2013). We standardized all covariates and ran all models in the package “unmarked” (Fiske & Chandler, 2011) in R version 4.2.1 (R Core Team).

We assessed the importance for covariates in the top-ranked models for each species using an analysis of deviance (Skalski et al., 1993; Jones et al., 2016; Tempel et al., 2016). This test estimates how much variation in occupancy was explained by the covariates in top-ranked models and compares the amount of deviance explained by covariates in a model with the amount of deviance not explained by these covariates and provides an estimate of r^2 (Skalski et al., 1993). We calculated the deviance for the top model, a saturated model with all basic and composition covariates, and a null model, each with the best detection model structure. We then used the following equation to obtain a relative measure of deviance explained: $\%D = [\mathrm{dev}_{\mathrm{top}} - \mathrm{dev}_{\mathrm{null}}]/[\mathrm{dev}_{\mathrm{saturated}} - \mathrm{dev}_{\mathrm{null}}]$.

Results

Acoustic survey efforts

We screened 555,718 hours (63.4 years) of acoustic data from early May to late July 2021 using BirdNET. We obtained usable acoustic data from surveys across 1648 sites for smaller owls and 845 sites for the two larger species across sampled locations in the Sierra Nevada. We obtained a variable number of hours and sites with detections that met our species-specific thresholds designed to eliminate the potential for false positive detections (Table 3.1). All six species were detected across the region (Fig. 3.1).

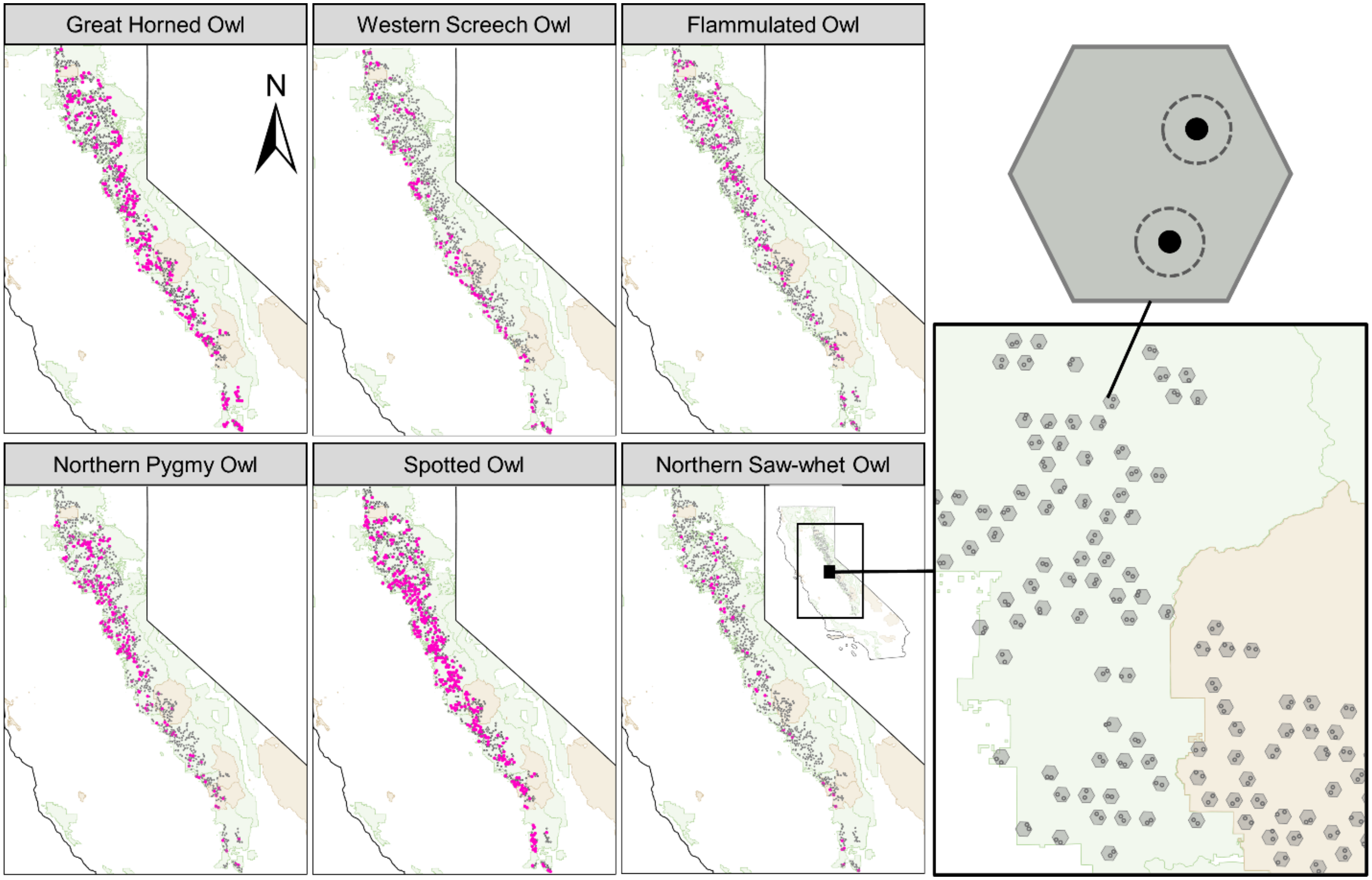

Fig. 3.1. Study area and species detections. The regional study area was divided into hexagonal sampling grids across seven national forests (green) and three national parks (brown). In 845 non-contiguous sampling hexagonal cells, we deployed 1-3 passive acoustic recording units (ARUs). We conducted analyses at the scale of the hexagonal sampling cells for the larger species and at the scale of 250m buffers around ARUs for the smaller species. Note that spotted owl detections were entirely manually vetted, while the other five species were obtained using prediction score and call rate thresholds. The distributions of those five species are likely underestimated as a consequence of eliminating false positives.

Detection probabilities

The top detection models for both great horned owls and western screech owls received 95% of the AIC weight in their respective analyses (Supplemental Table 3.2). The probability of detecting great horned owls increased with the average number of recording hours between ARUs in each cell (β_{hours} = 0.23, 85% CI = [0.10, 0.36]) and average ruggedness in cells (β_{rugged} = 0.12, [0.01, 0.22]) and decreased with the proportion of closed canopy forest (β_{CC} = -0.49, [-0.66, -0.31]), time (β_{time} = -1.29, [-1.73, -0.85]), and the average elevation between ARU units in each cell ($\beta_{elevation}$ = -0.13, [-0.23, -0.03]). The probability of detecting western screech owls increased with the number of recording hours (β_{hours} = 0.24, [0.08, 0.40]) and ruggedness (β_{rugged} = 0.24, [0.08, 0.41]), and decreased with the proportion of closed canopy forest (β_{CC} = -0.24, [-0.36, -0.12]), time (β_{time} = -0.75, [-1.30, -0.20]) and elevation ($\beta_{elevation}$ = -0.24, [-0.37, -0.10]). The top detection models for flammulated owls, northern pygmy owls, spotted owls, and northern saw-whet owls received 53%, 54%, 56%, and 61% of the AIC weight in their respective analyses (Supplemental Table 3.2). The probability of detecting any of these species decreased with time throughout the primary sampling period (in order: β_{time} = -3.40, [-4.01, -2.78]; β_{time} = -2.91, [-3.44, -2.38]; β_{time} = -0.91, [-1.29, -0.52]; β_{time} = -2.95, [-4.00, -1.90]). Flammulated owls and spotted owls were more likely to be detected in areas with more rugged terrain (in order: β_{rugged} = 0.18, [0.07, 0.28]; β_{rugged} = 0.16, [0.06, 0.26]). The probability of detecting spotted owls increased with the average number of recording hours between ARUs in each cell (β_{hours} = 0.13, [0.07, 0.18]). Northern pygmy and saw-whet owls were more likely to be detected in sites with more closed canopy forest (β_{CC} = 0.25, [0.14, 0.35]; β_{CC} = 0.65, [0.48, 0.82]), and northern pygmy owls were more likely to be detected at higher elevations ($\beta_{elevation}$ = 0.20, [0.00, 0.40]).

Effect of fire on occupancy

The top occupancy models for each species indicate that associations with fire severity, history, and composition varied among species. However, occupancy was generally lower for all species in contiguously severely burned forests. We report β-estimates and 85% confidence intervals for fire covariates with their respective severity (LM = low-moderate severity; H = high severity) followed by the time interval and/or the whether the covariate was a patch density estimate (pd).

For great horned owls, the top combined models that did not contain uninformative parameters received 26% and 22% of the AIC weight (Supplemental Table 3.1). According to these models, great horned owls were more likely to occupy sites with a lower proportion of closed canopy forest, at lower latitudes, and at lower elevations (Fig. 3.2). They were less likely to occupy sites with either higher patch density or proportion of high severity fire 2-4 years ago (Fig. 3.3a-b; $\beta_{H2\text{-}4}$ = -0.27, 85% CI = [-0.46, -0.07], $\beta_{H2\text{-}4\_pd}$ = -0.23, [-0.39, -0.07]). However, they were more likely to occupy sites with a higher patch density of high severity fire that burned 11-20 years ago (Fig. 3.3c; $\beta_{H11\text{-}20\_pd}$ = 0.14, [0.02, 0.25]) and sites with a higher proportion of low-moderate severity fire that burned 21-35 years ago (Fig. 3.3d; $\beta_{LM21\text{-}35}$ = 0.14, [0.06, 0.31]).

For western screech owls, the top combined model received 48% of the AIC weight (Supplemental Table 3.1). Similar to great horned owls, western screech owls were more likely to occupy sites with a smaller proportion of closed canopy forest, at lower latitudes, and at lower elevations (Fig. 3.2). Western screech owls were less likely to occupy sites with a higher patch density of low-moderate severity fire that burned 1 year ago (Fig. 3.3e; β_{LM1_pd} = -0.50, [-0.78, -0.22]). They were more likely to occupy sites with a higher proportion of low-moderate severity fire that burned 2-4 years ago (Fig. 3.3f; $\beta_{LM2\text{-}4}$ = 0.19, [0.09, 0.29]).

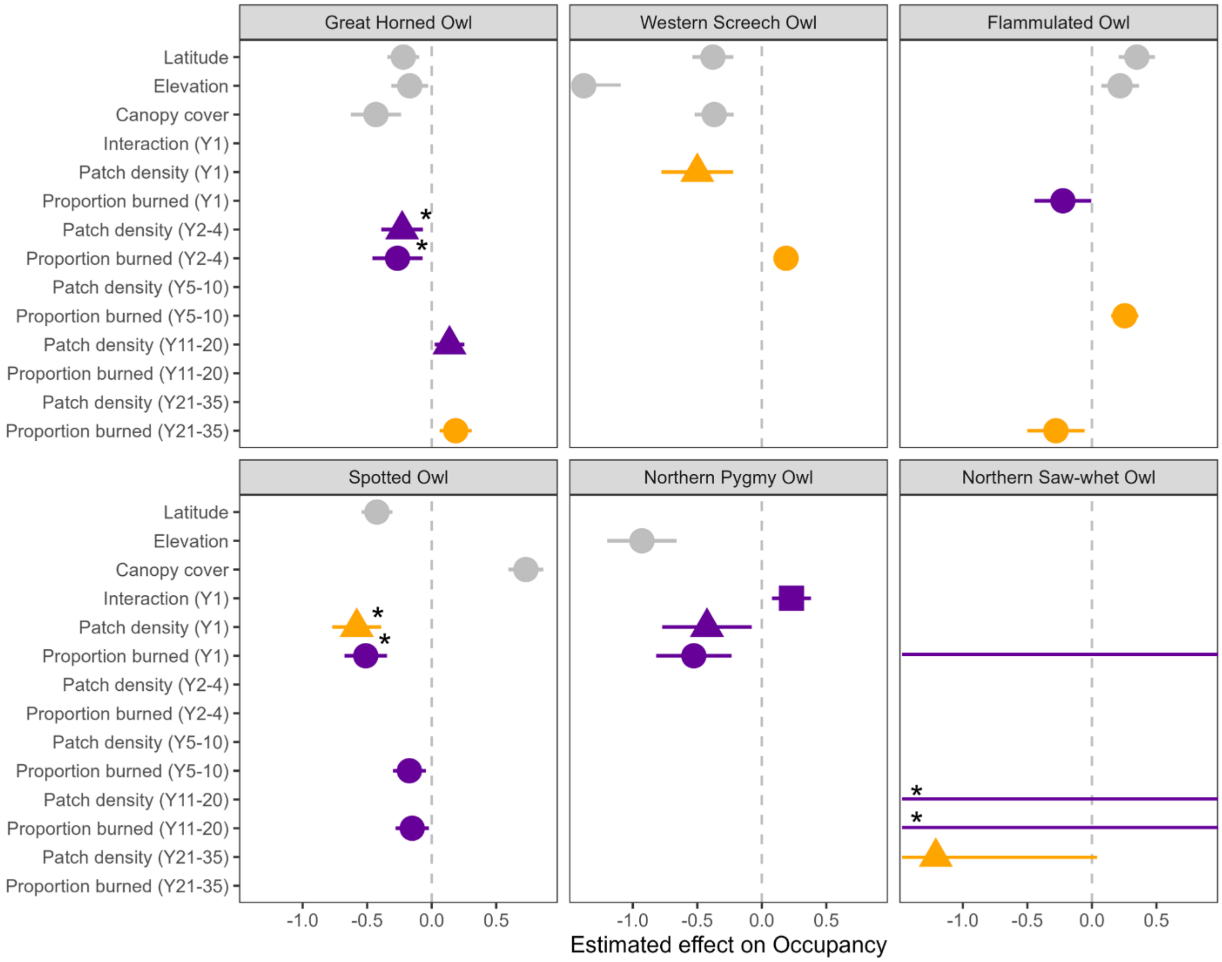

Fig. 3.2. Covariate effect sizes from top models. Grey indicates covariates that describe broad spatial associations, purple indicates a fire covariate describing high severity fire and orange indicates a fire covariate describing low-moderate severity. Triangles indicate configuration covariates and the square indicates an interaction between a composition and configuration covariate. Error bars show 85% confidence intervals. The top model describing northern saw-whet owl occupancy contained estimated effect sizes with large values and confidence intervals that overlapped zero, indicated by the horizontal error bars in the northern saw-whet panel. Parameter effects with asterisk indicate those that were unique to the first- and second-best models.

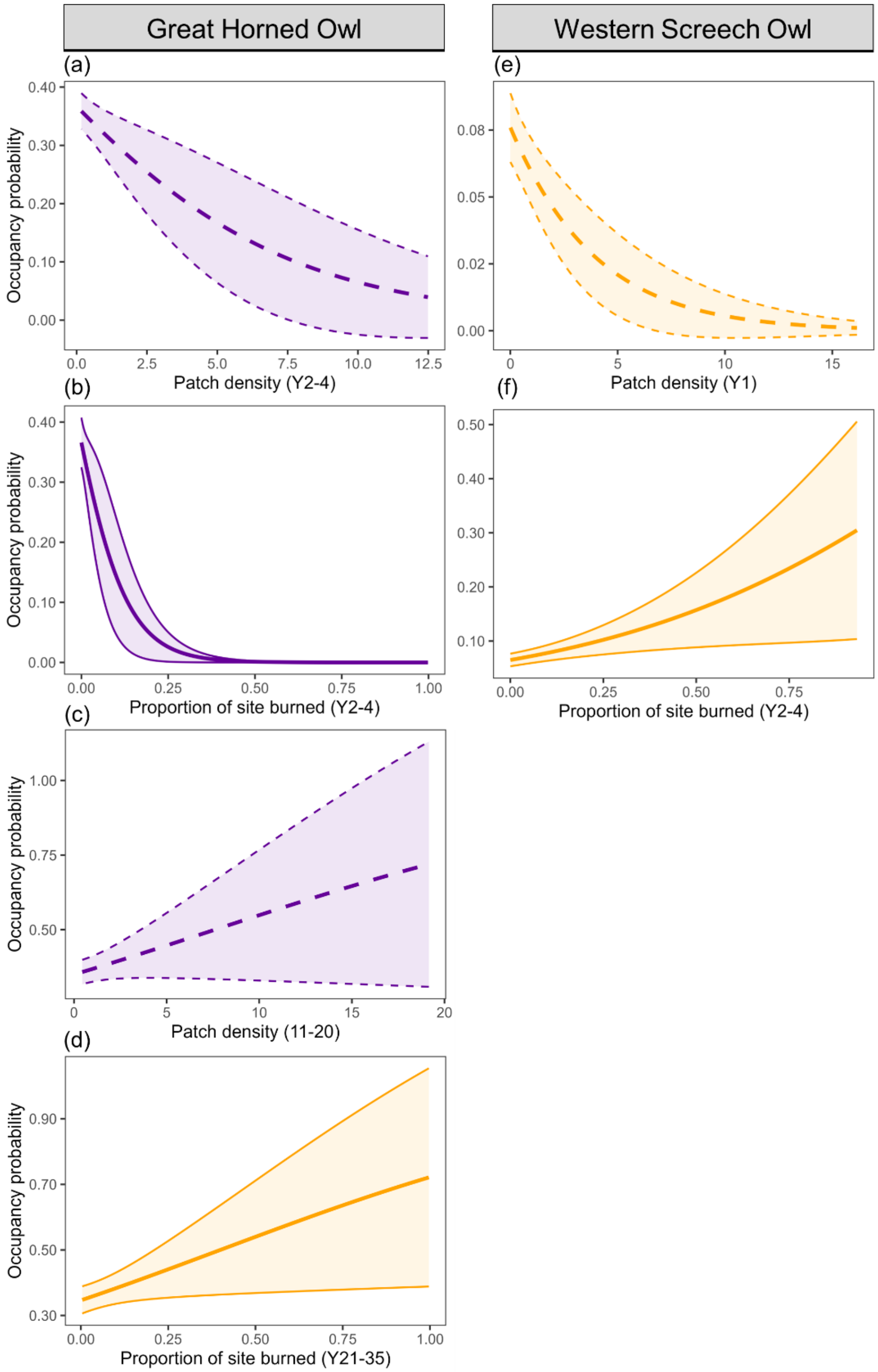

Fig. 3.3. Predicted relationships between fire covariates and the probability of site occupancy for species that are less likely to occupy closed canopied forests. Purple indicates high-severity fire covariates and orange indicates low-moderate severity fire covariates. Solid lines indicate a composition covariate and dashed lines indicate a configuration covariate. Center lines show predicted relationships and smaller lines show 95% confidence intervals for predicted relationship.

For flammulated owls, the top combined model carried 61% of the AIC weight and indicated that the probability of site occupancy increased with both elevation and latitude (Supplemental Table 3.1). Flammulated owls were less likely to occupy sites with a higher proportion of high severity fire that burned one year prior (Fig. 3.4a; β_{H1} = -0.23, [-0.44, -0.01]) and more likely to occupy sites with a higher proportion of low-moderate severity fire that burned 5-10 years ago (Fig. 3.4b; $\beta_{LM5\text{-}10}$ = 0.25, [0.15, 0.36]). Finally, flammulated owls were less likely to occupy sites with a higher proportion of low-moderate severity fire that burned 21-35 years ago (Fig. 3.4c; $\beta_{LM21\text{-}35}$ = -0.28, [-0.50, -0.06]).

For spotted owls, the top combined models that did not contain uninformative parameters received 34% and 22% of the AIC weight, respectively (Supplemental Table 3.1). The probability of site occupancy for spotted owls increased with the proportion of closed canopy forest and decreased with latitude. The top two models indicated that spotted owls were less likely to occupy sites with either a higher proportion of high severity fire or a higher patch density of low-moderate severity fire that burned one year prior (Fig. 3.4d-e; β_{H1} = -0.51, [-0.68, -0.35]; β_{LM1_pd} = -0.58, [-0.77, -0.39]). Spotted owls were also less likely to occupy sites with higher proportions of high severity fire that burned 5-10 years prior and 11-20 years prior (Fig. 3.4f-g; $\beta_{H5\text{-}10}$ = -0.17, [-0.30, -0.05]; $\beta_{H11\text{-}20}$ = -0.15, [-0.28, -0.02]).

For northern pygmy owls, the top combined model carried 55% of the AIC weight (Supplemental Table 3.1) and indicated that they were more likely to occupy sites at lower elevations. Northern pygmy owls were less likely to occupy sites with a higher proportion of high severity fire that burned one year prior (Fig. 3.4h; β_{H1} = -0.13, [-0.42, -0.17]). They were also less likely to occupy sites with a higher patch density of high severity fire that burned one year prior (Fig. 3.4i; β_{H1_pd} = -0.43, [-0.77, -0.08]). However, if a site had both a higher proportion and higher patch density of high severity fire, pygmy owls were more likely to occur (Fig. 3.4j; β_{H1*H1_pd} = 0.23, [0.08, 0.38]).

For northern saw-whet owls, the top combined models carried 36% and 34% of the AIC weight (Supplemental Table 3.1), respectively, but all high severity covariates had 85% confidence intervals that very clearly overlapped zero (Fig. 3.2). They tended to be less likely to occupy sites with higher patch density of low-moderate severity fire 21-35 years following a disturbance.

The analyses of deviance showed that covariates in all top models explained much of the possible variation in occupancy—83-84% for great horned owls, 97% for western screech owls, 78% for flammulated owls, 93-94% for spotted owls, 90% for northern pygmy owls, and 66% for saw-whet owls. These are likely overestimates of predictive power, but rather show the relative deviance explained by top models.

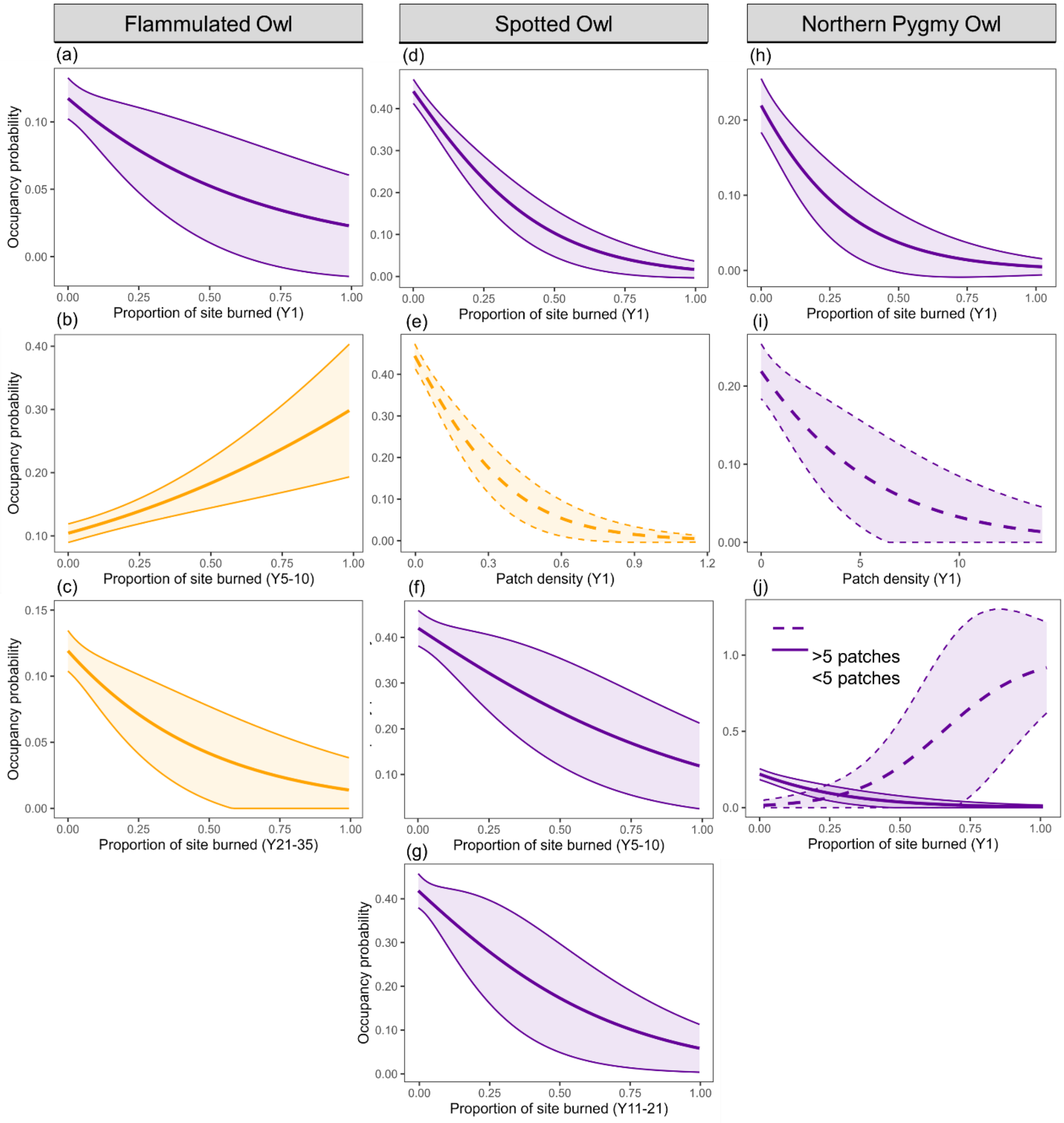

Fig. 3.4. Predicted relationships between fire covariates and the probability of site occupancy for species that are more likely to occupy closed canopy forests. Purple indicates high-severity fire covariates and orange indicates low-moderate severity fire covariates. Solid lines indicate a composition covariate and dashed lines indicate a configuration covariate. Center lines show predicted relationships and smaller lines show 95% confidence intervals for predicted relationship.

Discussion

The alteration of historical fire regimes leaves the fate of many species in disturbance-adapted ecosystems uncertain. This is the first study to examine the effect of fire on an entire predator guild across a bioregion, with a focus on understudied forest owls likely to have important top-down effects on multiple animal communities (Wood et al., 2019a). Our results suggest that these species have distinct associations with burned forests and that occupancy across this landscape depends on a combination of fire severity, patchiness, and temporal history. While responses to burned forests varied among species, contiguous high severity fire generally limited the distribution of forest owl species—particularly mature forest species—and low-moderate severity fire generally promoted the distribution of smaller cavity nesting owls.

Lasting negative impacts of high severity fire for mature forest species

Spotted owls avoided burned forests for up to two decades following high severity fire, whereas previous, shorter-term studies have only shown that historical territories remain unoccupied for up to six years following fires that burned large proportions of the sites (Jones et al., 2021). Our study shows that these short-term negative impacts of high severity fire may persist longer than previously documented for this species. Spotted owls rely on closed canopy habitat for nesting and roosting, and such habitat also supports stable microclimates when conditions exceed physiological thresholds (Jones et al., 2016; McGinn et al., 2023). High severity fire, especially when homogenous, leads to the loss of suitable nesting and roosting habitat that is unlikely to regenerate for many decades (Jones et al., 2021). While spotted owls appeared to be absent from forests burned at high severity 1 year prior and 5-20 years prior, they had neither a negative nor positive relationship with forest burned at high severity 2-4 years prior. Hexagonal sampling cells that overlapped burns from 2017-2019 had a maximum proportion of high severity burn of 0.27, while cells that overlapped burns from 2020 had a maximum proportion of 0.96. Therefore, there either was not enough variation in the dataset to determine if the proportion of high severity fire from that timestep impacted, although it appears spotted owl occupancy or spotted owls are not particularly sensitive to high severity fire if it burns less than a quarter of a site 2-4 years following a fire. Regardless, our results strongly suggest that spotted owls face long-term loss of suitable habitat as fires become larger and more contiguously severe in the Sierra Nevada.

High severity fire has differential effects on generalists

Great horned owls are widely distributed across North America and occur within a broad range of habitat types (Bennett & Bloom, 2005). Consistent with previous work, we found they were less likely to occupy sites with more closed-canopy forests. Further, great horned owls in the Sierra Nevada were less likely to associate with high severity fire 2-4 years following a disturbance but more likely to associate with patchy high severity fire 11-20 years following a disturbance. These findings corroborate previous studies in which great horned owls tend to avoid forests burned at high severity a few years prior but benefit from heterogeneity in habitat types (Grossman et al., 2008; Duchac et al., 2021). Severe fire leads to a loss of standing overstory, followed by regrowth of early succession wildflowers and forbs in the few years following a disturbance. While this ephemeral vegetation provides potential food resources for other birds like mountain quail (Brunk et al., 2023), the mammalian prey great horned owls often hunt may not recolonize severely burned sites until shrubs regenerate (Culhane et al., 2022). A decade of regeneration in high severity burns allows sufficient time for shrubs and small trees to grow, which small mammals use for foraging and cover (Torre & Díaz, 2004). A patchy configuration of such burns may afford great horned owls enough access to edge habitat to take advantage of this prey resource.

Western screech owls have previously been described as rare in the central Sierra Nevada (Groce, 2008), though our work demonstrates that they are currently distributed throughout the region (Fig. 3.1). Like great horned owls, western screech owls were also less likely to occupy sites with more closed-canopy forest. Previous research on forest owl occupancy in the Pacific Northwest showed that western screech owls were more likely to occupy sites burned at high severity two years prior (Duchac et al., 2021). However, we found that this species neither avoid nor prefer sites burned at high severity at any successional stage, but they were less likely to occupy sites with patchy low-moderate severity burns from fire the year prior. In this timestep, low-moderate severity patchiness was highly and positively correlated with the proportion of sites burned at high severity. In the Sierra Nevada, especially at mid-elevations, high severity fire facilitates shrub regeneration but often hinders tree regrowth while low-moderate severity fire (Crotteau et al., 2013; Collins & Roller, 2013). For western screech owls in this region, patchy low-moderate severity fire interspersed with more high severity fire may limit any potential benefits of either resulting vegetation structure.

Low-moderate severity fire benefits small forest owls

The smaller forest owls in this study, specifically western screech, flammulated, northern pygmy, and northern saw-whet owls, are secondary cavity nesters, which may explain occupancy patterns we observed in relation to fire history. Flammulated owls and western screech owls were more likely to occupy sites burned at low-moderate severity 2-10 years following a disturbance. Low-moderate severity fire reduces understory but leaves snags interspersed with surviving trees (Crotteau et al. 2013). northern flickers (*Colaptes auratus*), pileated woodpeckers (*Dryocopus pileatus*), sapsuckers (*Sphyrapicus*), and hairy woodpeckers (*Dryocopus villosus*) create cavities in these standing dead trees (Raphael & White, 1984; Bull & Holthausen, 1993). Standing dead trees following fires are a source for woodpecker nesting habitat, but older burned areas can lose their value for woodpeckers over time (Nappi & Drapeau, 2009; Tingley et al., 2018). Secondary cavity nesters may take advantage of potential nesting habitat created by woodpeckers immediately following fire, but then subsequently abandoned (Duchac et al., 2021). Our results suggest that these owls may take advantage of nesting habitat created after low-moderate severity burns, indicating successional recolonization of different species following disturbance events like fire.

Low-moderate severity fire may also create foraging habitat by opening the understory for these small predators to access prey. Both western screech and flammulated owls prey upon insects and other arthropods, which can recover quickly following fires (Choi 2018). These two species often forage by either catching insects in the air or gleaning insects from the needles of large conifer trees, and a more open understory following a disturbance may facilitate these behaviors (Reynolds & Linkhart, 1987; Hayward & Garton, 1988). Flammulated owls did not have any association with closed canopy forest, which corroborates prior research on the species in other mid-elevation, dry forest ecosystems where they prefer large trees with more open understories (Linkhart et al., 1998; Yanco & Linkhart, 2018). Western screech owls often hunt small mammals, which can increase in abundance after fires (Culhane et al., 2022). Forest regeneration 2-4 years following low-moderate severity fire may create forest structures where there is simultaneously enough understory regeneration for prey species to benefit from protection and food resources and enough standing overstory for western screech owls to access their prey from trees (Reid et al., 2006).

Tradeoffs between heterogeneity and habitat loss

Lower-severity fire is considered to be relatively benign, if not beneficial, for spotted owls (Lee et al., 2012; Jones et al., 2018) potentially by promoting foraging habitat (Zulla et al., 2022; Wilkinson et al., 2022), and therefore we expected that this species would be more likely to occur in areas burned at low-moderate severity. Contrary to our expectations, low-moderate severity patchiness appeared to reduce the suitability of sites immediately following a disturbance. We believe this was because the proportion of high severity fire and patchiness of low-moderate severity patchiness were correlated (r = 0.75), such that the loss of habitat to contiguous high-severity fire outweighed the potential benefits of heterogeneity created by patchy low-moderate severity fire (Fig. 3.5).

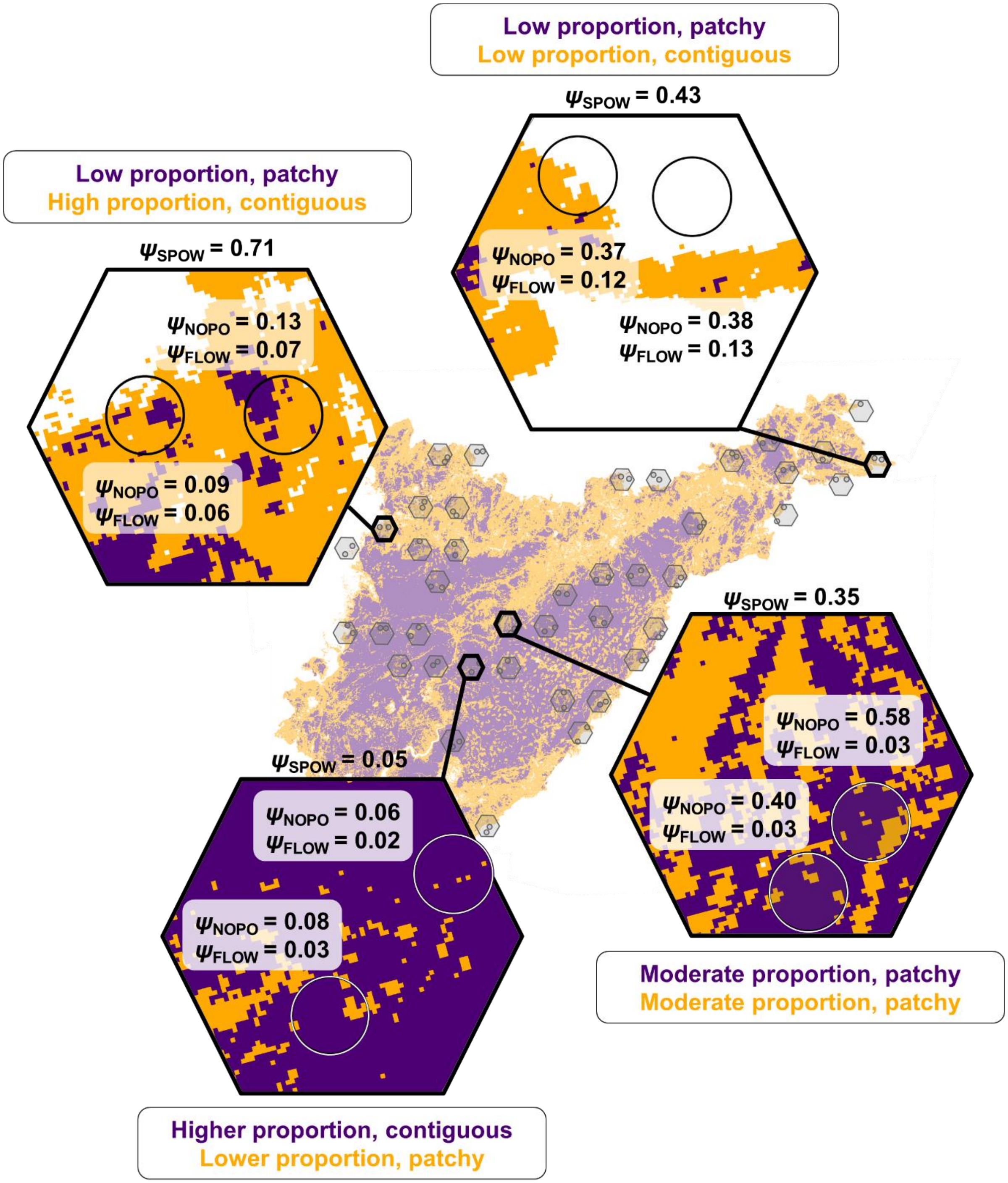

Fig. 3.5. Occupancy estimates for spotted owls (SPOW), norther pygmy owls (NOPO), and flammulated owls (FLOW) one year post disturbance. Orange indicates low-moderate severity fire, and purple indicates high severity fire. Occupancy estimates for spotted owls are model averaged between the top two models.

In contrast, patchiness appeared to benefit northern pygmy owls, which were more likely to occupy sites with both a higher proportion and patchiness of high severity fire one year after a disturbance. Specifically, the loss of overstory caused by high severity fire appears to reduce habitat suitability for pygmy owls where it is contiguous but benefit them where it is patchier (Fig. 3.5). While northern pygmy owls nest in structurally diverse and often late successional coniferous forest, they are diurnal predators that prey mostly upon small passerines—which can increase in diversity following heterogenous fire disturbance—and often foraging at the edges between open areas and forest (Giese & Forsman, 2003; Tingley et al., 2016; Robinson et al., 2016). A moderate amount of high severity fire interspersed with low-moderate or unburned habitat may thus facilitate potential foraging opportunities for this species, offsetting the negative impacts of the loss of live canopy cover.

Potential tradeoffs between heterogeneity and habitat loss occur across taxa, and while heterogeneity in burned forests can benefit many species, there is no unequivocal evidence that variation in post-fire landscape characteristics, or pyrodiversity, inherently increases biodiversity (Turner et al., 2013; Jones & Tingley, 2022). Often, potential benefits of heterogeneity following fire disturbance depend on broader ecological contexts. For example, spotted owls prefer pyrodiverse areas where the surrounding landscape is homogenous but avoid pyrodiverse areas where the surrounding landscape has more heterogeneity in forest structure (Jones et al., 2020; Kramer et al., 2021). Thus, there appears to be some critical threshold for heterogeneity that can either be facilitated by patchy fire or hindered where fire contributes to the loss of critical habitat. Such tradeoffs are likely dictated by scale. While spotted owls may benefit from structural heterogeneity following a combination of low-moderate and high severity fire, such habitat may lose value for northern pygmy owls, which use space at a much smaller scale than their larger relatives (Fig. 3.5). We examined only the proportion and patchiness of two burn classes, and while patchier landscapes can often be considered as more pyrodiverse (Menges

& Quintana-Ascencio, 2004; Lawes et al., 2015; McGranahan et al., 2018), our study was not adequately comprehensive to directly examine pyrodiversity *per se*. Future work that seeks to quantify the effect of pyrodiversity on this community of predators could consider tradeoffs between heterogeneity and habitat loss, which are likely influenced by species-specific ecologies, the scale at which animals move across the landscape, the temporal dynamics of forest regeneration, and interspecific variation in recolonization following forest fires.

Lessons learned in acoustic surveys

Our acoustic survey program deploying 1648 autonomous recording units across 25,800 km^2 is one of the largest acoustic monitoring programs in North America and the first to quantity the distribution of a community of forest owls across an entire bioregion. We were successfully able to obtain enough detections for five of six forest owl species to examine the effects of fire on site occupancy for a cryptic guild of predators using a combined effort of manual validation and automated, machine-learning based detections. However, we were unable to successfully examine potential drivers for northern saw-whet owls, for which we obtained fewer detections than all other species. Based on our field observations, northern saw-whet owls appeared to cease territory vocalizations earlier than the other small forest owl species and our acoustic surveys may only overlap the tail-end of their vocalization behaviors. Additionally, while occupancy estimates for spotted owls were derived from comprehensive and manually validated detection histories—and likely reflect a reasonable estimate for the true proportion of sites in the Sierra Nevada occupied by spotted owls (Kelly et al., in review)—the five other species occupancy estimates likely underestimate their occupancy given our strategy to minimize false positives at the expense of potential true positives. Future research may consider lowering the initial prediction score thresholds and performing a comprehensive manual validation of all potential detections for species of interest.

The breakdown of historical fire regimes

The forest owls in the Sierra Nevada have unique associations with burned habitat and that spatiotemporal diversity in fire severity across the landscape likely benefits this community of avian predators. Other species in this region also show variable associations with burned habitat, and understanding interspecific variation in response to fire is necessary to conserve biodiversity in a rapidly changing environmental context (Taillie et al., 2018; Jones & Tingley 2022; Brunk et al., 2023). Management following Euro-American colonization led to a buildup of fuels, which can negatively impact species that rely on pulse disturbance processes. In our study, long intervals between disturbances may have led to a higher density of understory vegetation and reduced habitat suitability for flammulated owls, which rely on open understories for foraging (Linkhart et al., 1998). A combination of rising temperatures, more variable precipitation events, and fire suppression has created a perfect storm for massive fires that burn the majority of live overstory (Westerling, 2016; Steel et al., 2023). For older forest species like spotted owls, the negative impacts of large, contiguous fires are apparent and long-lasting. For other species that tend to be more general in their habitat associations, the negative impacts of large, contiguous high severity fires may be less obvious but nevertheless limit distribution and reduce abundance.

We did not examine the effect of post-fire management on the occupancy of forest owl species because data across this bioregion are not yet available. However, post-fire management like salvage logging potentially exacerbates and prolongs the negative impacts of fire on the distribution of this community by disrupting forest regeneration (Lee et al., 2013; Jones et al., 2021). Future work will examine the impact of pre- and post-fire management on this community of forest owls across the Sierra Nevada, as well as the impacts of management on the severity and configuration of fire in and of itself. When fire mitigation practices reduce habitat suitability for some species, more nuanced and spatially explicit approaches to forest restoration may be necessary to preserve biodiversity (Jones et al., 2021). Management that seeks to conserve biodiversity in the context of degrading disturbance processes should consider interspecific variation in associations with burned habitat and variable temporal scales over which fire impacts habitat suitability for animal species.

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Chapter 4. Feature embeddings from the BirdNET algorithm provide insights into avian ecology

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Abstract

Bioacoustics has become widely used in the study of acoustically active animals, and machine learning algorithms have emerged as efficient and effective strategies to identify species vocalizations. Current applications of machine learning in bioacoustics often identify acoustic events to the species-level but fail to capture the complex acoustic repertoires animals use to communicate, which can inform habitat associations, demography, behavior, and the life history of cryptic species. The penultimate layer of most machine learning algorithms results in a vector of numbers describing the input, called feature embeddings. Here, we demonstrate that the feature embeddings generated by the BirdNET algorithm can enable within-species classifications of acoustic events. First, we successfully differentiated adult and juvenile Great Gray Owls; second, we identified three unique sounds associated with Great Spotted

Woodpeckers (series call, alarm call, and drumming). These applications of BirdNET feature embeddings suggest that researchers can classify vocalizations into groups when group membership is unknown, and that within-species grouping is possible even when target signals are extremely rare. These applications of a relatively “black-box” aspect of machine learning algorithms can be used to derive ecologically informative acoustic classifications, which can inform the conservation of cryptic and otherwise difficult to study species.

Introduction

Bioacoustics has become a widely utilized tool in conservation ecology (Sugai et al., 2020) and is especially valuable when species of interest are rare, secretive, or otherwise difficult to study (Wood et al., 2019a; Sueur & Farina, 2015). Passive acoustic monitoring (PAM) is often used to identify where and when species occur (Teixeira et al., 2019; Borker et al., 2014; Stevenson et al., 2015) and how their populations are changing over time (e.g., Hofstadter et al., 2022). Passive acoustic survey efforts often rely on a single stereotyped, high-amplitude vocalization as an indicator of a species’ presence. However, many species have diverse acoustic repertoires, with different acoustic signals used – and acoustic cues produced – in different contexts.

Animals communicate via a wide variety of acoustic signals, which enable individuals to find conspecifics, signify risk or danger, coordinate behaviors in a group, or elicit food resources (Stegmann, 2013; McCracken & Sheldon, 1997). The songs, calls, and other sounds birds use to communicate serve vital biological purposes and can be highly variable among regions, populations and individuals (Marler et al., 2006). Similarly, acoustically active mammals, such as wolves, elephants, and many primates, communicate via a wide range of vocalizations and sounds (Manly, 2005). Identifying where and when those various acoustic events are occurring has the potential to provide much more nuance and ecological insight than single-vocalization studies, which could be important for understanding the habitat associations, demography, behavior, and the life history of cryptic species. For example, event- or life stage-specific acoustic signals could reveal the distribution of predation pressure or breeding activity, respectively, across the landscape. Rapid advances in machine learning may enable both among- and within-species classification of acoustic events.

Machine learning algorithms have been transformative detection and classification tools in bioacoustics, enabling rapid assessments of species richness in massive datasets (Bermant et al., 2019; Stowell et. al., 2019; Bianco et al., 2019; Kahl et al., 2021). Training data is a critical component of supervised approaches and any machine learning tool. In the context of avian species classification, many algorithms have relied on publicly available archives such as the Macaulay Library (macaulaylibrary.org) and xeno-canto (xeno-canto.org; Kahl et al., 2022). For many species, multiple types of vocalizations have been uploaded, such as examples of a call or song. The presence of multiple diagnostic acoustic events in a machine learning algorithm's training data raises the possibility that it is already classifying a species based on more than just one component in its repertoire. However, the "black box" nature of such tools can make harnessing such classification capabilities difficult. Moreover, even if a machine learning tool can identify a species based on multiple acoustic events, researchers still need to sort species-level detections into event types, which can be different types of acoustic communication or vocalizations specific to intraspecific groups.

Scalable, repeatable grouping of acoustic events requires quantitative multivariate summaries of acoustic events. Manual classification of acoustic events is possible based on visual inspection of spectrograms or auditory assessment of audio files (e.g., Wood et al., 2022), but quickly becomes prohibitively time-consuming. Current techniques for unsupervised clustering can be highly accurate, but most require a manually annotated dataset for calibration (Clink & Klinck, 2021). Here, we present an advance in unsupervised acoustic event clustering for ecology that is a simple extension of the species classification process: using the feature embeddings generated in the penultimate layer of a machine learning algorithm, the deep convolutional neural network BirdNET (Kahl et al., 2021), as a form of unsupervised, pre-trained acoustic event annotation.

Feature embeddings are high-dimensional vectors of floating-point values that summarize the algorithm's internal representation of a given segment of audio. In practice, they are multivariate descriptions of segments of audio, or, most simply, strings of numbers. Feature embeddings have been applied to identify rare acoustic events, classify sounds, and identify individuals (Arora et al., 2019; Zhang et al, 2022; Thomas et al., 2022; Sainburg et al., 2020), but, to our knowledge, applications of this technique in ecology are limited. We present two case studies in which acoustic events were successfully identified to species using the standard implementation of BirdNET, followed by a secondary classification phase wherein feature embeddings were successfully used to group distinctive, ecologically informative acoustic events. In the first example, we used passively recorded audio from a landscape-scale monitoring project in western North America to differentiate adult and juvenile owls; in the second example, we used audio collected by citizen scientists to identify two call types and the drumming of a European woodpecker. The disparate audio datasets, species, and acoustic events in our examples suggest that the feature embeddings produced by BirdNET may be a robust and broadly applicable means of implementing within-species acoustic event classification. The ability to efficiently distinguish multiple acoustic events that are species-specific but ecologically distinct has broad implications for the ecology and conservation of acoustically active species.

Two examples of within-species acoustic event classification

Differentiating adult and juvenile Great Gray Owls

We conducted passive acoustic surveys across the entire mixed conifer zone of the Sierra Nevada, USA in 2021, with almost 2,000 Swift recording units distributed across ~18,000 km^2 (for general study design information, see Wood et al., 2019b), and applied the BirdNET algorithm to that audio data to assess the distribution of Great Gray Owls (*Strix nebulosa*), among other species. The Great Gray Owl is an extremely cryptic and rare species that is at the southern limit of its range in the Sierra Nevada and has high individual variation in song (Rognan et al., 2010). During the manual validation of randomly selected putative Great Gray Owl detections, we identified 263 juvenile vocalizations and 27 adult vocalizations. Juvenile vocalizations are raspy, food-solicitation calls; adult vocalizations are low-frequency hoots used for long-range communication and territorial defense (Fig 4.1). We used Raven Pro 1.6 (K. Lisa Yang Center for Conservation Bioacoustics) to export 263 juvenile and 27 adult vocalizations for analysis with the BirdNET “embeddings.py” script from the publicly available BirdNET-Analyzer repository (https://github.com/kahst/BirdNET-Analyzer, Model version 2.1).

We used R programming language (v4.0.4; R Core Team 2022) to match vectors of feature embeddings with their manual classification (juvenile or adult) and then calculated the Euclidean distance between all pairs of audio clips. We used Euclidean distance because we had no prior knowledge of the relationships between embeddings, and, thus, wanted to quantify multivariate distance using a simple, non-weighted method. We randomly selected 60% of the adult and juvenile vocalizations to serve as a training dataset, with the remaining 40% reserved as a validation dataset (the 60-40 split was applied to each vocalization type, not the whole dataset). We did not perform formal stratification when splitting the training and validation data, but all units from which samples were drawn were present in both datasets (Roch et al., 2015). In our case, our sample size of owl territories was quite small (n = 5) which precluded the creation of training and validation datasets partitioned by individual. Splitting data by individual, territory, or some other biologically meaningful partition could improve the independence of the validation dataset.

In the test dataset, the average distance between: adult:adult pairs ($\bar{d}_{A:A}$) was 7.43 ± 1.24 SD, juvenile:juvenile pairs ($\bar{d}_{J:J}$) was 7.85 ± 1.02, and adult:juvenile ($\bar{d}_{A:J}$) pairs was 11.4 ±

1.19. We fit an analysis of variance (ANOVA; Girden, 1992) model to the training data to test whether vocalizations of the same type were closer in the multivariate space generated by the feature embeddings than vocalizations of different types. The one-way ANOVA revealed a statistically significant difference in Euclidean distance between embeddings for different types than between those of the same type (Fig. 4.1, F = 26,976, $p < 0.001$). Tukey's HSD Test (Lane, 2010) for multiple comparisons found the mean distance between vocalization types in the test dataset was significantly different between all comparison groups ($p < 0.001$).

We then used the validation dataset to test whether we could distinguish age-class-specific vocalizations using feature embeddings and Euclidean distance. We calculated the Euclidean distance between each "unknown" vocalization in the validation dataset and all j known adult vocalizations and all k known juvenile vocalizations (i.e., those in the training dataset). We then classified each unknown vocalization (U_i) as either an adult ($\hat{A}$) or juvenile ($\hat{J}$) by comparing the resulting distances to means calculated with the test dataset. We categorized an unknown vocalization as "adult" if the median distance between that vocalization and all known adult vocalizations ($\tilde{d}_{U_i:A_{1:j}}$) was less than the mean distance between all known adults ($\bar{d}_{A:A}$) plus one standard deviation ($SD_{d_{A:A}}$), and, additionally, if the median distance between the unknown vocalization and all known juvenile vocalizations was greater than the mean distance between all known juveniles plus one standard deviation.

$$\tilde{d}_{U_i:A_{1:j}} < \bar{d}_{A:A} + SD_{d_{A:A}} \wedge$$

$$\tilde{d}_{U_i:J_k} > \bar{d}_{J:J} + SD_{d_{J:J}}$$

$$\Rightarrow U_i = \hat{A}$$

We used the opposite criteria to classify unknowns as juveniles.

$$\tilde{d}_{U_i:A_{1:j}} > \bar{d}_{A:A} + SD_{d_{A:A}} \wedge$$

$$\tilde{d}_{U_i:J_k} < \bar{d}_{J:J} + SD_{d_{J:J}}$$

$$\Rightarrow U_i = \hat{J}$$

We then compared our unsupervised, feature embedding distance-based classifications of the “unknowns” to the manual classifications of age-classes (i.e., adult or juvenile) and found that 78% all vocalizations were successfully classified, about 22% were not classified, and none were mis-classified.

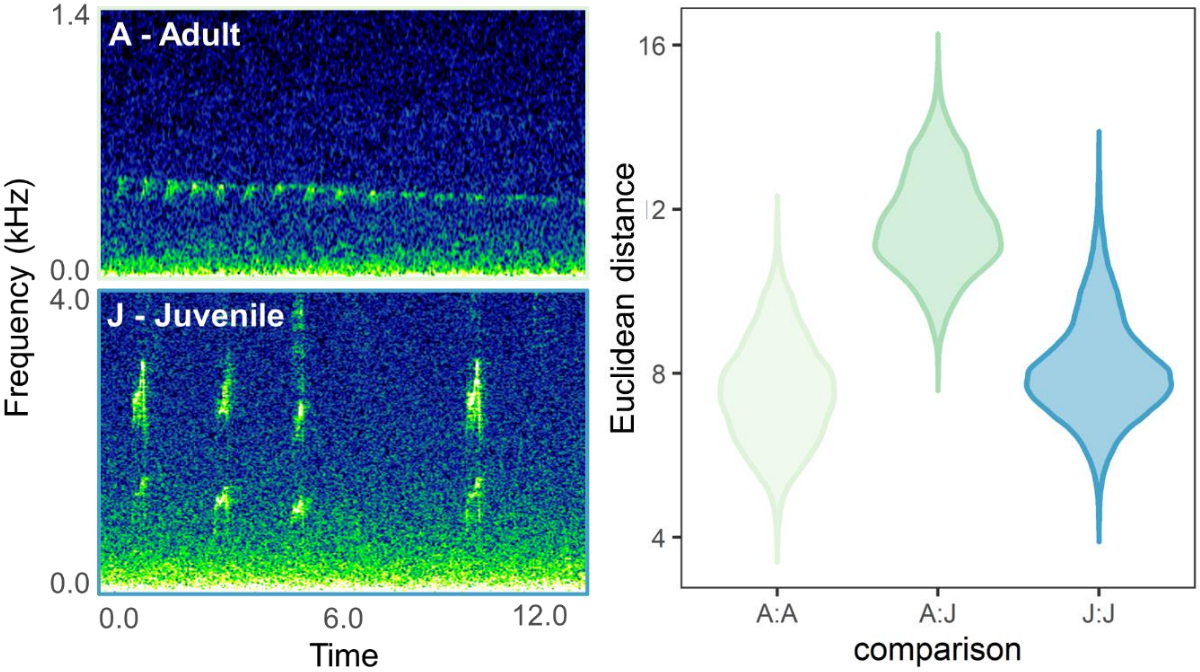

Fig. 4.1. Great Gray Owl vocalizations from adults (A) and juveniles (J) recorded as part of a passive acoustic monitoring program in the Sierra Nevada, USA. The left panels show spectrograms of an adult and juvenile vocalization. The right panel shows Euclidean distance between embeddings of adult and juvenile. Initial detections were generated by the BirdNET algorithm, which identified all call types simply to species. Distances were calculated between all detections; we then grouped these distances into three comparison groups: distances between adult vocalizations (A:A), between juvenile vocalizations (J:J), and distances between adult and juvenile vocalizations (A:J).

Identifying two call types and drumming of the Great Spotted Woodpecker

We collected more than 100 million observations of more than 1,500 bird species generated by citizen scientists using the BirdNET App between 2018 and 2022 (Wood et al., 2022). Briefly, the BirdNET App is freely available and allows users to actively record animals on a smartphone and submit snippets of audio for identification. The audio and fully anonymized metadata are stored on the BirdNET server, enabling researchers to study continental-scale spatiotemporal variation in species presence and vocal structure, among other things. We randomly selected 100,000 high-scoring observations for avian species made in Europe in 2021 along with their audio data for this study. As before, we then applied the BirdNET script “embeddings.py” to all audio snippets to generate feature embeddings.

We then manually selected three observations representing unique acoustic events diagnostic of the Great Spotted Woodpecker (*Dendrocopos major*): the series call, single call, and drumming (Fig. 4.2, top row). The series call may be used for territorial defense and as an alarm call, both of which have important implications for woodpecker ecology. The single call is likely used for intrapair communication and thus could be valuable for population estimation (Wood et al., 2020; Węgrzyn et al., 2021). Drumming can be used to identify individuals (Budka et al., 2018), so rapidly identifying these acoustic events from a large dataset could facilitate detailed population estimates. Using a query-by-distance approach that is commonly employed in machine learning, we calculated the pairwise Euclidean distance between each of our three query samples and all other observations in our dataset (n = 999,997). The resulting similarity score was used to rank audio snippets by distance to each of the queries to retrieve the most similar observations from the collection.

We were able to match sounds from the same species to given queries based on feature embeddings despite the fact that classification initially was only done on species level. Visually investigating ranked results for each query revealed that top-ranked results show high similarity with the target call and match the species identification (Fig. 4.2, bottom four rows). Interestingly, high-ranked results for the drumming query did not contain the drumming of other woodpeckers; as distance to the query increased, Great Spotted Woodpecker vocalizations began to appear, rather than other drumming events. The absence of a general, multispecies “woodpecker drumming” group reveals that visual similarity of spectrograms is only one aspect of the ranking process. Feature embeddings appear to implicitly encode species identity, which helps with ranking sounds based on target queries.

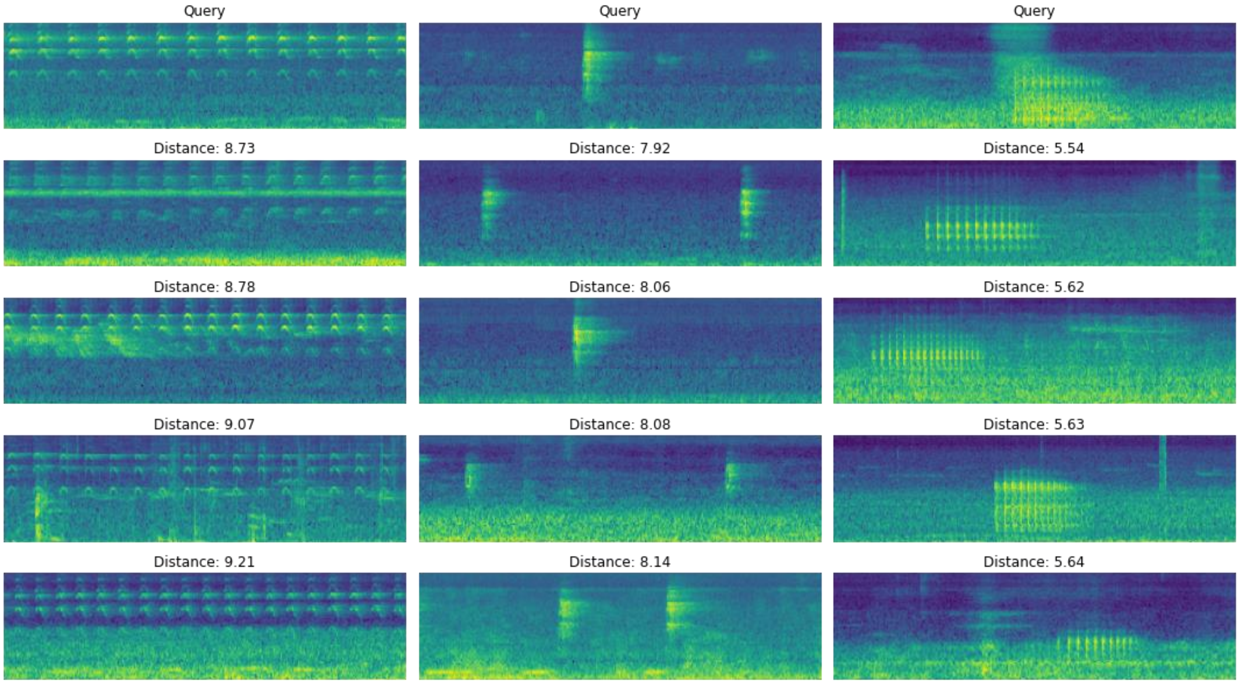

Fig. 4.2. Great Spotted Woodpecker vocalizations ranked by similarity (Euclidean distance) to three given query calls. Each column represents a call type (right to left: series call, single call, and drumming), the top row visualizes queries, rows 2-5 show the four most similar audio snippets for each query retrieved from 100,000 randomly selected BirdNET App observations. Results show that different call types can be recovered and matched to a query by utilizing feature embeddings.

Discussion

Machine learning algorithms have proven highly capable of identifying species based on sound; we have shown that the feature embeddings generated by one such algorithm, BirdNET (Kahl et al., 2021), can be an effective means of differentiating acoustic events within species. The success of within-species acoustic event identification is predicated on the availability of sufficient data, but, if it can be applied, secondary classification based on unsupervised clustering has substantial promise as a means of improving basic and applied ecological research on acoustically active species.

There are two basic data requirements for within-species grouping of acoustic events such as multiple elements of a species repertoire. First, if species-level identification of all target sounds is desired, as in the Great Gray Owl example, examples of the target sounds, such as various songs, calls, drumming, or other activities, must be included in the training data of the detection/classification algorithm. For users of pre-made and publicly available tools like BirdNET (https://github.com/kahst/BirdNET-Analyzer), reviewing the public archives that were used for training data can provide some insight as to whether a desired sound of interest may be identifiable for a given species – though analyzing an annotated dataset containing the sounds of interest is, of course, a more direct test. In our case, we knew that BirdNET could recognize a variety of *Strix* vocalizations, and we knew that the training data for most common woodpeckers in North America and Europe contained vocalizations and drumming. The authors' personal use of the BirdNET App had provided further examples of the BirdNET algorithm's ability to reliably make species identifications based on multiple call types (e.g., three call types of the Red-winged Blackbird [*Agelaius phoeniceus*], the song and call of the Black-capped Chickadee [*Poecile atricapillus*], song and call of the Northern Cardinal [*Cardinalis cardinalis*]).

If researchers know that an algorithm can correctly identify multiple species-specific acoustic events, the next data challenge is the sample size of target signals. In practice, this is likely to be an unknown quantity, as locating (and enumerating) those signals is a fundamental objective of the methods we have outlined. The Great Gray Owl example illustrates an approach when sample sizes are likely to be high, enabling accurate classification of the vocalizations in our validation dataset. To extend that example, embeddings for all Great Gray Owl detections above a user-defined prediction score could be calculated and their pairwise distances compared to the distances observed in the training dataset to rapidly assess vocalization type (adult or juvenile). As we demonstrated with the validation dataset, very simple unsupervised grouping criteria yielded high accuracy and no false positives; of course, specific criteria and acceptable error rates will be application-specific. The Great Spotted Woodpecker example illustrates a possible approach when target signals are known or suspected to be rare. Rather than employing formal significance tests, whose performance generally improves with sample size, querying all embeddings based on distance to a given example may enable researchers to identify acoustic signals of interest. Open-ended query-based inquiries could also enable researchers to develop a set of labelled target signals, thus allowing for the cluster analyses used in the preceding example.

Feature embeddings can enable at least three broad classes of distance-based multivariate grouping. First, the woodpecker example used manual examining of query results based on decreasing similarity to the query (i.e., increasing Euclidean distance between two sets of embeddings). Second, the owl example allowed for multivariate grouping where the number of groups was known *a priori* (adult and juvenile) but group membership of the samples in the validation dataset were treated as unknown. Another strategy that would allow for such grouping could use discriminant function analysis (Manly 2005). Cluster analyses (e.g., k-means clustering) represent a third, more challenging approach. In these cases, both the number of groups and samples' group membership may either be known or unknown (Manly, 2005). Cluster analyses may be a desirable third tier of classification: species, call type, and then individual. Both Great Gray Owls and Great Spotted Woodpeckers have been identified to individual (Rognan et al., 2009; Budka et al., 2018) based on acoustic event types that we successfully isolated using feature embeddings.

In both of our examples, the feature embeddings functioned well as tool for unsupervised acoustic feature extraction, enabling us to rapidly and accurately group species' acoustic event types. However, it is important to reiterate that feature embeddings are not solely, or explicitly, extracting acoustic features. As noted above, the absence of a generalized "woodpecker drumming" cluster in the BirdNET App citizen science data revealed that additional information beyond acoustic structure is encoded in the feature embeddings. The "black box" nature of some elements of machine learning tools can make additional information difficult to extract and results might not be easily interpretable. Open-ended queries of vast quantities of feature embeddings, as we did in the woodpecker example, are where this issue is most relevant. Limiting the application of feature embeddings to clustering acoustic events within a set of species-specific detections, as we did in the owl example, may mitigate the influence of non-acoustic information encoded in feature embeddings.

From a basic ecological perspective, identifying where and when a species produces different sounds can enable a wide variety of research into phenology, behavior, communication, and evolution (Stegmann, 2013). Bioacoustics has been utilized to study migration phenology, where peaks in vocal activity indicated arrival on breeding grounds (Oliver et al., 2018). Unique vocalizations and sounds can indicate behaviors necessary for reproduction (e.g., mate attraction), defense of resources (e.g., antagonistic alarm calls), and group dynamics (e.g., communication for group foraging), which are often difficult to study across taxa (Teixeira et al., 2019). Evolution, which is a difficult process to study in larger organisms, can be tracked by examining acoustic signals and associated morphology in sound-producing animals (Odom et al., 2021).

From an applied ecological perspective, the ability to differentiate adults and juveniles is particularly exciting. Bioacoustics data are often used in occupancy models (e.g., Wood et al. 2020, Hofstadter et al. 2022), but the ecological significance of a species vocalizing at a given location can be ambiguous in passive acoustic surveys (Wood & Peery, 2022). If certain vocalization types are better indicators of residency, such as vocalizations used for short-range, intra-pair communication, identifying sites at which those vocalizations were recorded could be a valuable means of defining a “detection” in an occupancy analysis. Classifying sites as occupied by adults only or adults and juveniles would enable the implementation of multi-state occupancy models, which partition the probability of occupancy into discrete states (Nichols et al., 2007). Already, multi-state models parameterized with acoustic data (sites were occupied by a single male bird or by male and female birds) offered promising improvements upon the inferences attainable from single-state models (Wood et al., 2020). Yet there are often mismatches between occupancy and important demographic metrics like survival and reproduction (McGinn & Atuo et al., 2022). Understanding population processes is a prerequisite to establishing effective conservation strategies, and analyses that simultaneously quantify both occupancy and demographic success paint a much more informative picture of population dynamics than occupancy models alone (Fandos et al., 2021). Explicitly identifying sites at which juvenile birds fledged, as opposed to merely observing the possibility of reproduction by virtue of a pair of birds, would be a significant improvement and could compliment demographic studies on elusive species. Knowledge about where juveniles vocalize during a breeding season is informative for ongoing demographic studies on organisms that are difficult track, as vocalizations from juveniles can help optimize on-the-ground survey effort in the short term and, in the long term, indicate the location of productive territories of conservation concern.

Passive acoustic monitoring has been presented as an alternative to mark-recapture monitoring in which researchers sacrifice detail (e.g., reproductive output) in order to obtain landscape-scale survey coverage (Wood et al., 2019b). Yet our success in identifying multiple acoustic event types, including demographically critical information such as the presence of juveniles, suggests that perhaps researchers can have the best of both worlds: landscape-scale survey coverage with rich biological detail. Although our two case studies featured birds, we expect these methods to be applicable to the study of many acoustically active animals. Many mammals, notably non-human primates, have diverse acoustic repertoires suggesting that intra-specific grouping of acoustic events could have extensive value well beyond ornithology. Further explorations of the capabilities of feature embeddings as a tool for within-species acoustic event classification are warranted.

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Supplemental Materials

Supplemental Table 1.1. Vegetation conditions at historical roost locations (n=99) from spotted owl surveys in the SBNF from 1991-2019 (Gutiérrez et al. 2017, California Natural Diversity Database 1991-2019). These conditions informed the thresholds at which we delineated roosting stands.

Vegetation conditions	Number	Percent	Source
CANCOV[a] > 40%	112	75.2	GNN[d]
CANCOV > 70%	34	22.8	GNN
QMD_DOM[b] > 15cm	121	81.2	GNN
QMD_DOM > 20cm	105	72.5	GNN
QMD_DOM > 25cm	92	61.7	GNN
QMD_DOM > 50cm	19	12.8	GNN
BAH_PROP[c] > 20%	104	69.8	GNN
BAH_PROP > 65%	53	35.6	GNN
CANCOV > 40%	115	77.2	CFO[e]
CANCOV > 70%	26	17.5	CFO
HEIGHT > 10m	71	47.7	CFO

[a] Canopy cover
[b] Quadratic mean diameter of dominant and codominant trees
[c] Proportion of hardwood basal area to total basal area
[d] LEMMA Lab, Oregon State University, Corvallis, OR
[e] California Forest Observatory, Salo Sciences

Supplemental Table 1.2. Spatial covariates for linear mixed effects models. We examined both site- and stand level characteristics and tested interactions with ambient temperatures. These covariates were used in linear mixed effects models.

Variable	Abbreviation	Prediction	Mean ± SD
Tree height[a]	TH	Roost cooler than available habitat higher in canopy	10 m ± 4.3m
Orientation[a]		Roost cooler than available habitat on NE side of trees	Categorical
Canopy cover[b]	CC	Roost cooler than available habitat under denser canopy	61% ± 17%
Tree size[a]	DBH	Roost cooler than available habitat in larger trees	71 cm ± 41cm
Canopy height[b]	CH	Roost cooler than available habitat under higher canopies	16 m ± 6.7 m
Microtopography[c]	TOPO	Roost cooler than available habitat under on NE-facing slopes and higher on SW-facing slopes	Categorical

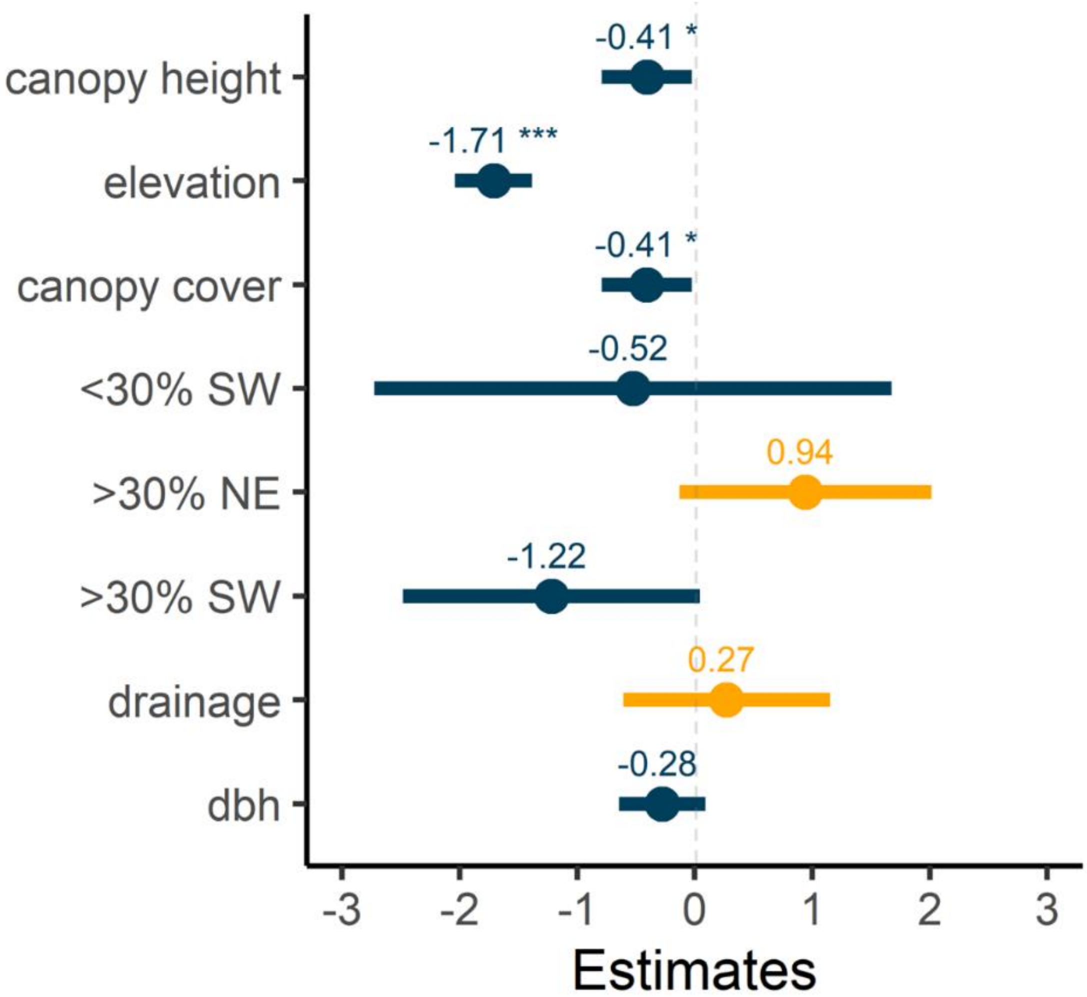
[a] Field measurements
[b] California Field Observatory (Salo Sciences)
[c] Landscape management unit tool (North et al. 2021)

Supplemental Table 1.3. Temperature variables used in linear mixed effects models. Daily maximum temperatures at roosts (T_R), in available habitat in stands (T_S), and operative temperatures (T_O) were used to derive ΔT_{RS} and ΔT_{OS}. Ambient daily maximum temperature (T_A) was used as a covariate in linear mixed effects models for ΔT_{RS} and ΔT_{OS}.

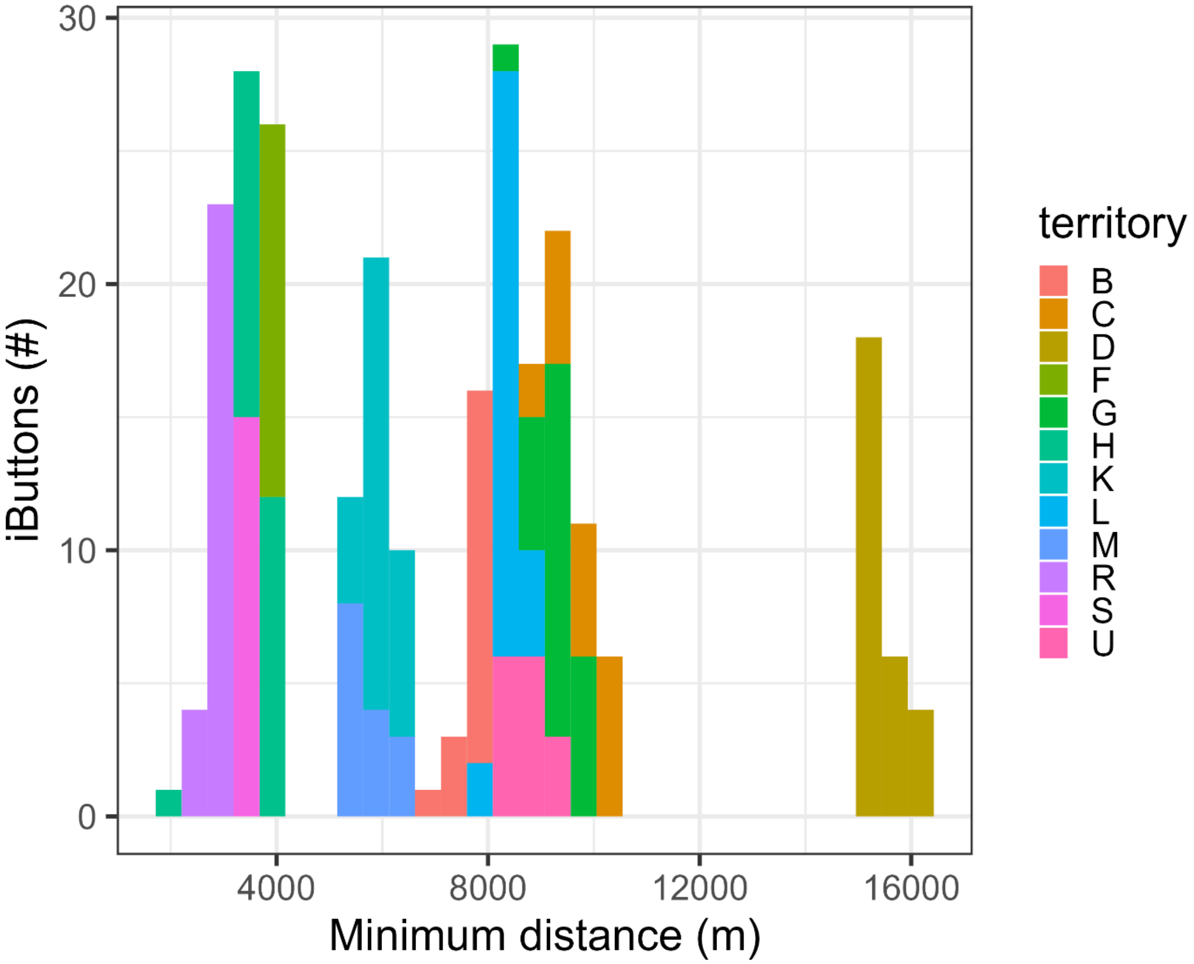
Variable	Description
T_R	Daily maximum temperature recorded by ibutton at roost locations
T_S	Daily maximum temperature recorded by ibutton at stand locations
T_O	Daily maximum temperature recorded by GPS tracker on owl
ΔT_{RS}	Daily temperature offset between maximums at roosts and average maximums for each stand
ΔT_{OS}	Daily temperature offset between maximums on the surface of owls and average maximums for each stand
T_A	Daily maximum temperature recorded by nearest RAWS weather station

Supplemental Table 1.4. Precision check for four Lotek pinpoint units placed ~15m from the ground under a closed canopy outside of our field station in 2021. Temperatures were taken every two minutes. Here, we report average deviation of the measurements from the mean pinpoint temperature at each time.

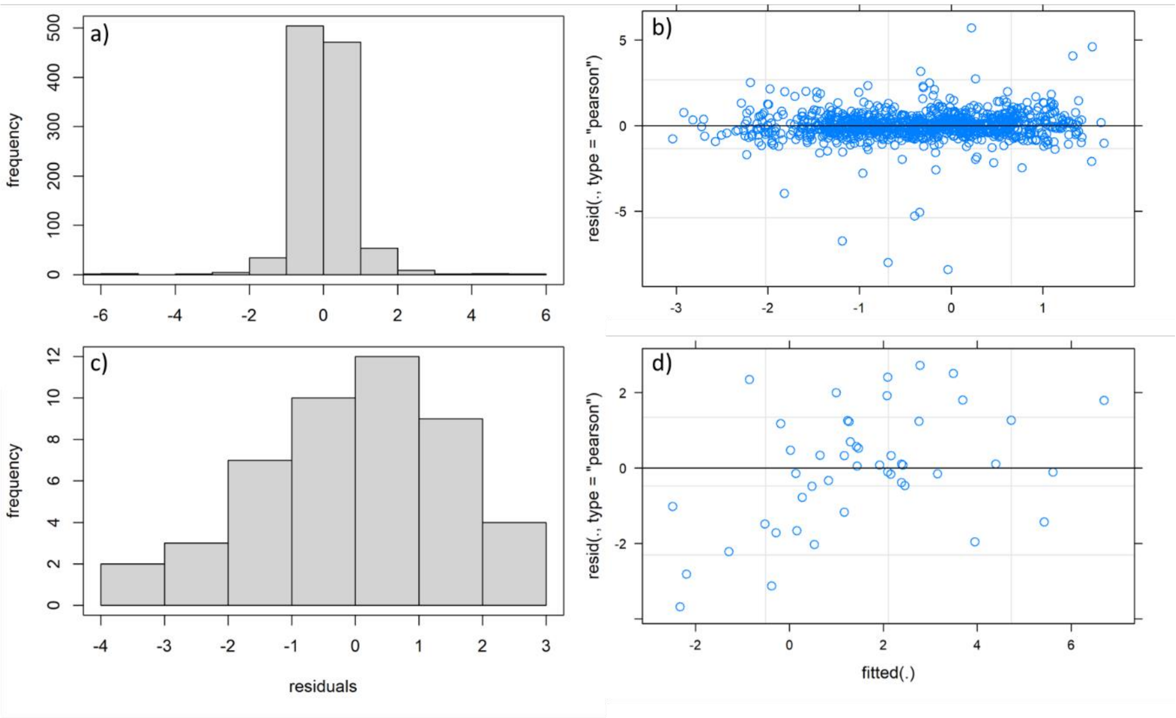
Device	**Average deviation +/- SD**
Pinpoint1	-0.05 +/- 0.31
Pinpoint2	-0.46 +/- 0.33
Pinpoint3	0.26 +/- 0.37
Pinpoint4	0.19 +/- 0.38
Pinpoint5	0.13 +/- 0.56
Pinpoint6	-0.08 +/- 0.34



Supplemental Fig. 1.1. Temperature in roost stands. Roost stand temperatures were largely driven by canopy height, elevation, and canopy cover. Effect sizes are indicated by points, and 95% confidence intervals are indicated by lines extending from points. Negative (cooler) effects are dark blue and positive (warmer) effects are yellow. Stars indicate statistical significance, where the "*" is equivalent to $p < 0.05$, "**" is equivalent to $p < 0.01$, and "***" is equivalent to $p < 0$.



Supplemental Fig. 2. Minimum distances between iButtons and RAWS. Individual territories are color coded. Nearly all iButtons were within 10km of a weather station. Territory “D” was further from weather stations than the other territories. However, we opted to use the same weather station for territories “F”, “G”, and “D” because alternative weather stations were too low in elevation.



Supplemental Fig. 1.3. Diagnostic plots for our top models. Our linear mixed effects models assume a Gaussian distribution of residuals. Here, we show the a) frequency distribution and b) residual plots for the top roost-level model. There are several outliers in the model, which we attempted to limit using the IQR methods described in the main manuscript. We also show the c) frequency distribution and d) residual plot for the top owl-level model.

Calculating Temperature Anomalies (T_A)

To calculate the anomaly of a given year *j* in relation to the study period, we first calculated an average July-August temperature value for each year across sites,

$$\overline{T}_{Si}=\frac{\sum_{i=1}^{m} T_{Si,j}}{m}$$

where $T_{Si,j}$ is the average daily maximum temperature for territory *i* during July-August in year *j* and *m* is total the number of territories. We then calculated a mean “regional” climate across years for each study area,

$$\overline{R}_S=\frac{\sum_{j=1}^{t} \overline{T}_{Sj}}{t}$$

where R_S is the regional climate during July-August and *t* is the duration of the study. We then calculated the difference between yearly conditions and the regional climate to calculate the yearly anomaly:

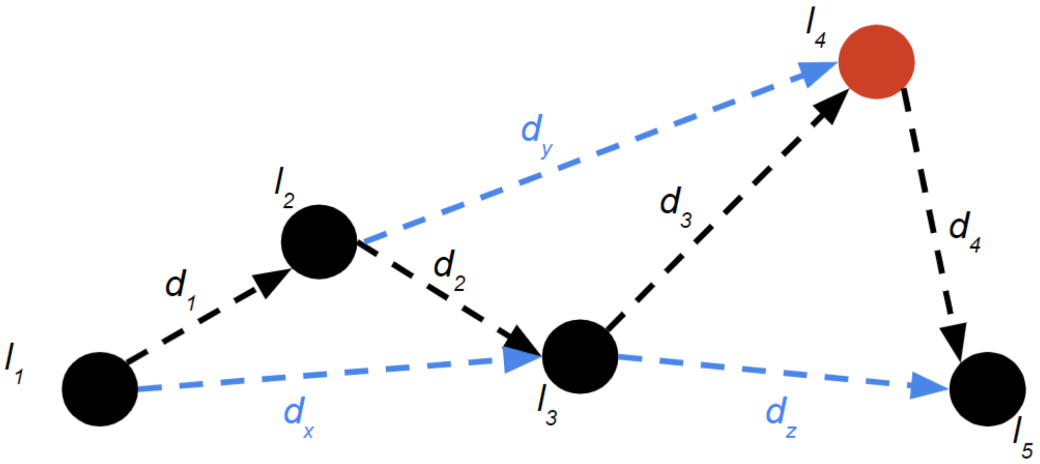
$$T_A=\overline{T}_{Sj}-\overline{R}_S$$

We transformed all habitat and temperature covariates using a z-transformation to scale and center them. All covariate acronyms are in Table 1.

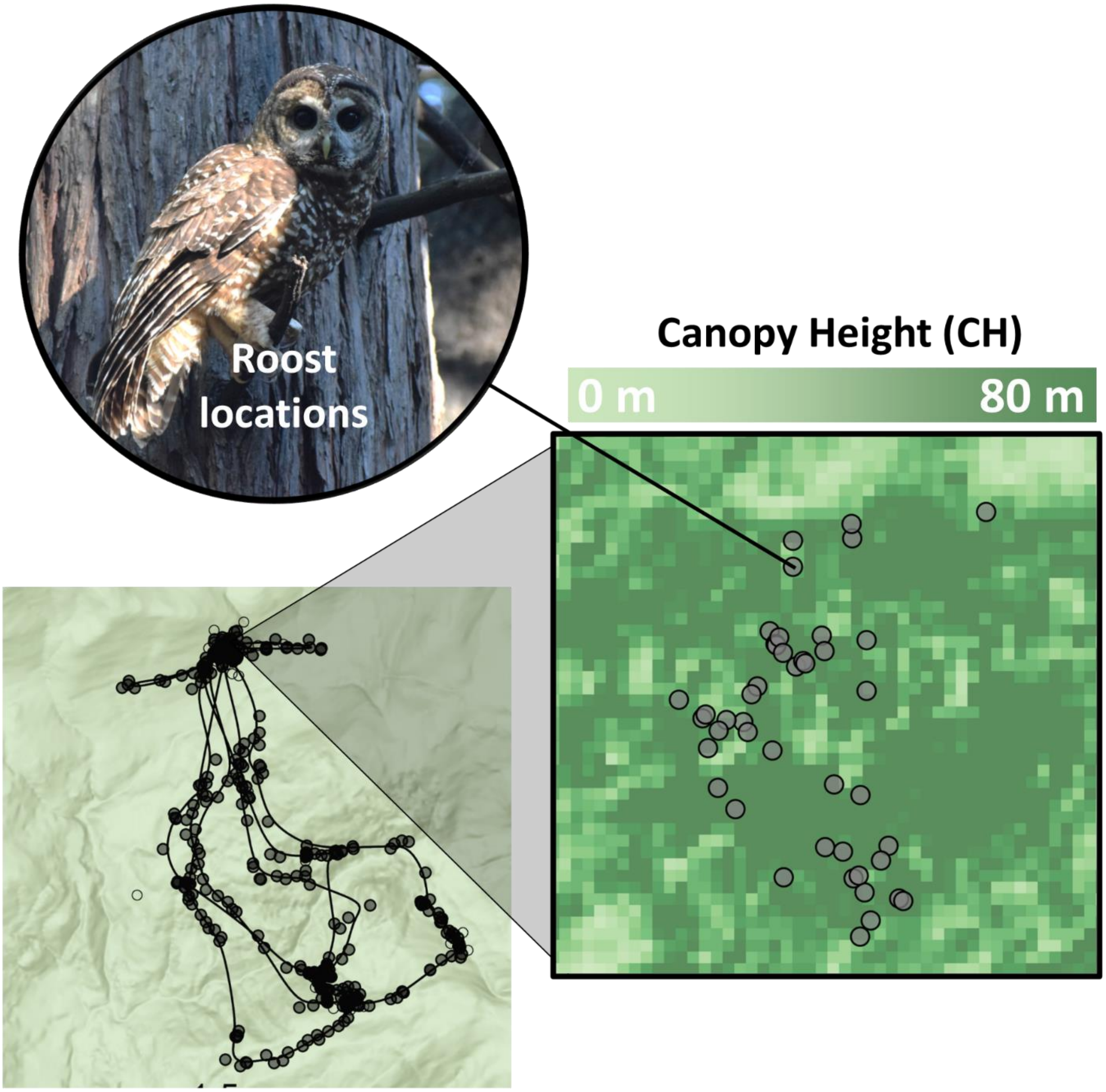
Subsample Analysis

Only Pinpoint tags recorded operative temperature, a combination of air temperature and radiative heat, every hour during the day. Here, we examined the potential effect of the time spent above physiological thresholds on “non-moving” energetic expenditure and the effect of canopy height on operative temperatures. For all birds that were tagged with Pinpoints, we calculated daily average operative temperature, the proportion of tagged time above 30 °C (p_{30}), and the proportion of tagged time above 35 °C (p_{35}). We performed the following analyses using a subset of the final dataset in which all birds were tagged with Pinpoints ($n = 20$). We fit a linear regression where residual energetic expenditure from the original relationship between FMR and velocity was the response and p_{30} and p_{35} were the fixed effects. We also fit a linear regression where daily average operative temperature was the response and daily average temperature (Daymet, Thorton et al. 2020) and canopy height (California Forest Observatory, 2020) were the fixed effects. We included average temperature as an additional covariate to account for the inherent variation in temperature based on latitude and elevation, which are accounted for in the Daymet interpolation/extrapolation process.

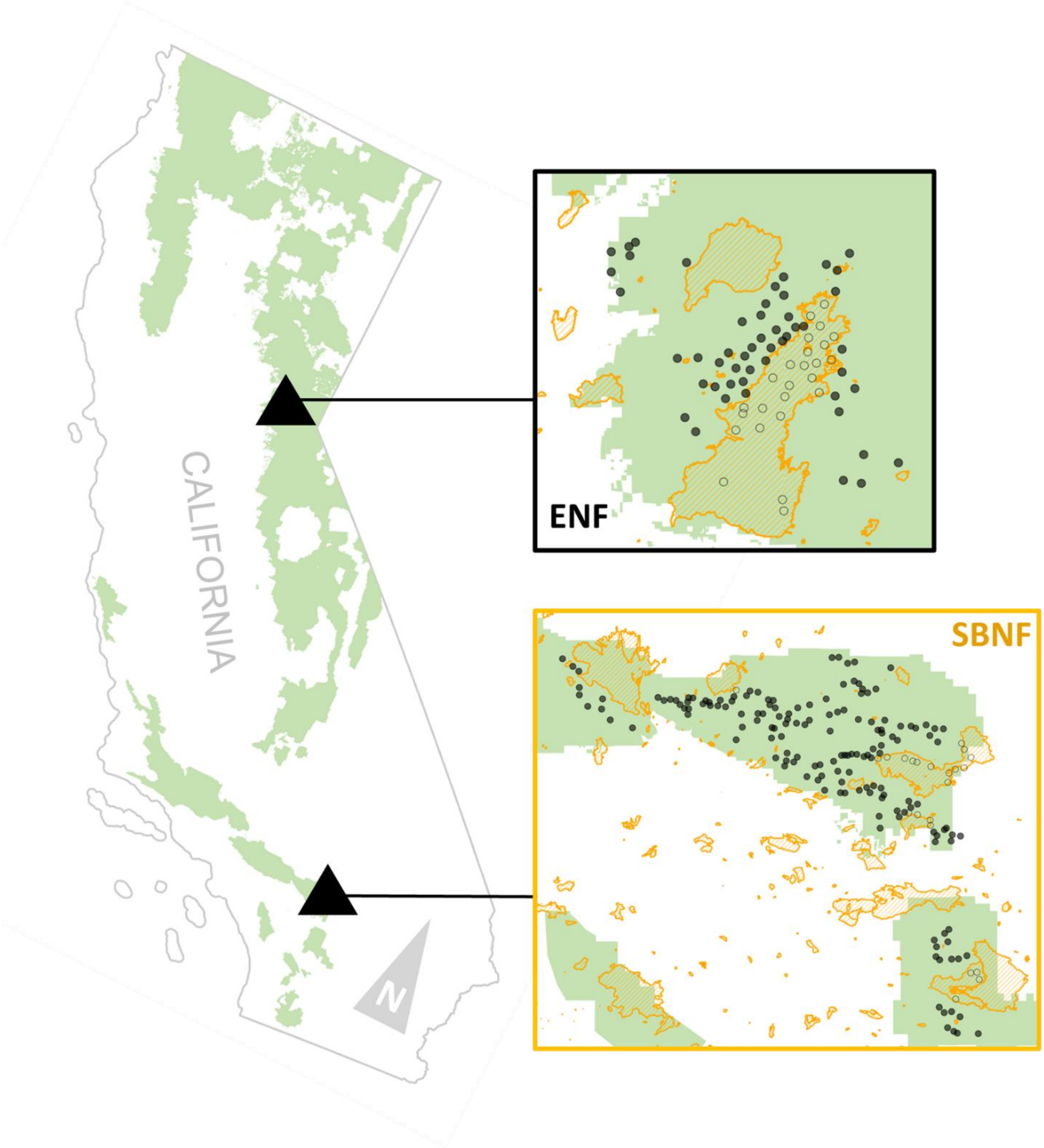
Five individuals in this study experienced operative temperatures over 35 °C (Supplemental Figure 5a), and 16 individuals experienced operative temperatures over 30 °C (Supplemental Figure 5b). “Non-moving” energetic expenditure decreased with the proportion of time owls were exposed to operative temperatures above 30 °C (Supplemental Figure 5d; $\beta_{p30} = -76.4$, [-148, -3.85]) and had no relationship with the proportion of time owls were exposed to temperatures above 35 °C (Supplemental Figure 5c). “Non-moving” energetic expenditure of owls exposed to temperatures above 35 °C tended to be higher than owls that were not exposed to 35 °C (-6.93± 21.29 kJ/day x $kg^{0.71}$; $t = -1.02$, $df = 8.20$, $p = 0.34$). Daily operative temperatures decreased with canopy height (Supplemental Figure 5e; $\beta_{CH} = -0.38$, [-0.67, -0.09]) and increased with daily average temperatures (Supplemental Figure 5f; $\beta_{Tmean} = 3.37$, [3.08, 3.67]).



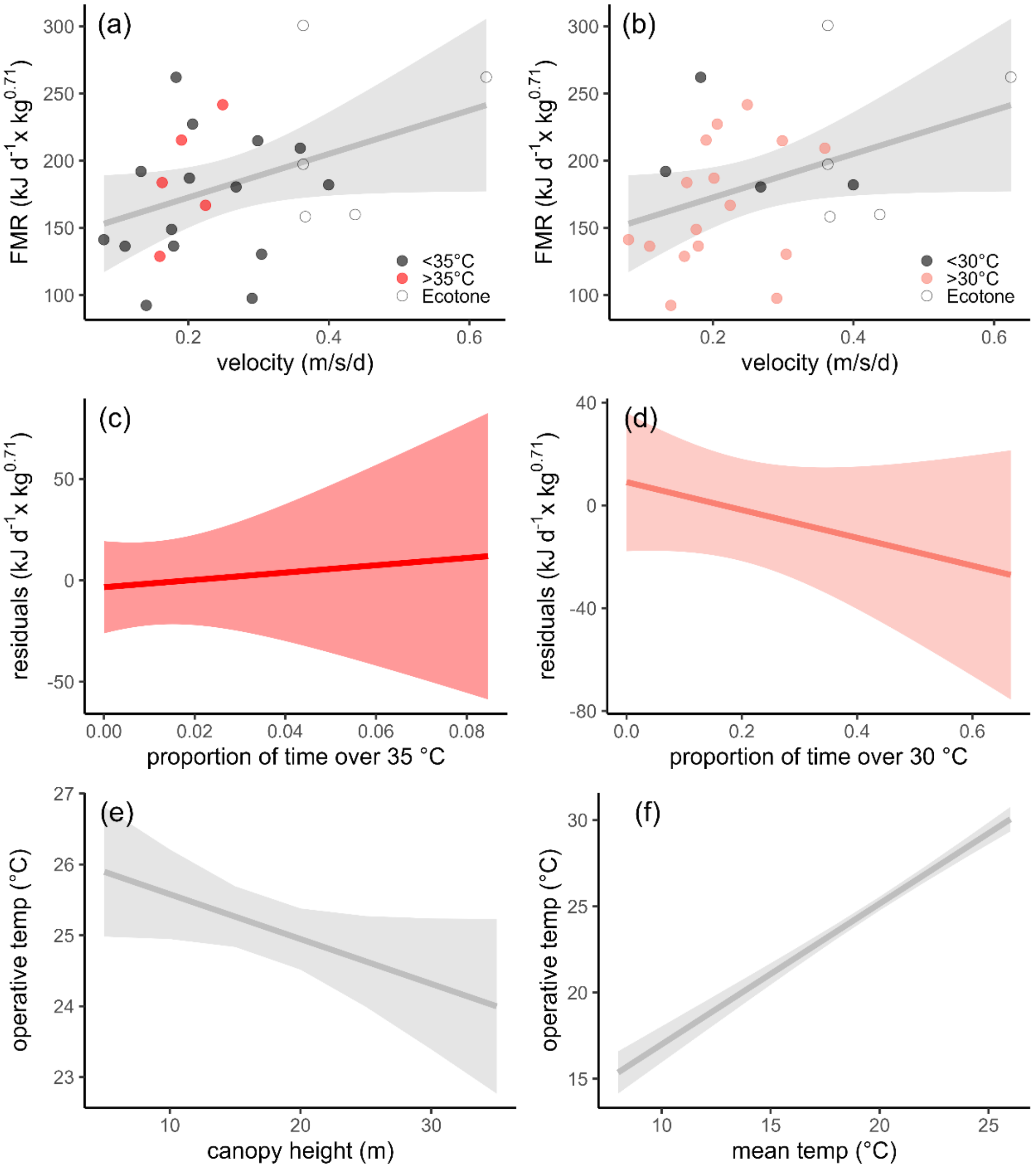
Supplemental Fig. 2.1. GPS location filtering. We filtered data to measure distance traveled by eliminating locations that were further from the subsequent and prior locations than the distance between the subsequent and prior locations. In this example, d_3 and d_4 are both longer than d_z, so the location l_4 was eliminated.



Supplemental Fig. 2.2. Movement path and roost locations for one individual. We extracted habitat covariates (eg. CH) from locations collected from GPS units between 15 minutes prior to sunrise and 15 minutes after sunset.



Supplemental Fig. 2.3. Territory centers for occupancy analyses. The top panel shows territories in the ENF and the bottom panel show territories in the SBNF (and surrounding areas). Hollow circles indicate territories we did not include in analyses because they overlapped with fires that occurred between 2010-2021 (2010-2019 for SBNF), indicated by orange. We eliminated 25 territories in the ENF and 20 territories in the SBNF.



Supplemental Fig. 2.4. Results from supplemental subsample analysis. a) Three out of five individuals exposed to temperatures above 35 °C (red) expended more energy than predicted by the relationship between average velocity and mass specific energetic expenditure. Birds tagged by Ecotones, which did not record operative temperatures, are depicted in grey. b) Nine out of 16 individuals exposed to temperatures above 30 °C (light red) expended less energy than predicted by the relationship between average velocity and mass specific energetic expenditure. c) There was no relationship between the residuals, or “non-moving” energetic expenditure and the proportion of time operative temperatures exceeded 35 °C. d) “Non-moving energetic expenditure did decrease with the proportion of time operative temperatures exceeded 30 °C. e) Daily average operative temperature decreased with canopy height at roost sties and f) increased with daily average temperature.

Supplemental Table 2.1. All vegetation and temperature covariates for individual and occupancy analyses.

Covariate	Units	Analysis	Description
T_{max}	°C	Individual	Average daily maximum temperature at each individuals' daytime/dusk/dawn locations
T_{mean}	°C	Individual	Average daily temperature at each individuals' daytime/dusk/dawn locations
T_{30}		Individual	Binary covariate for an individual's exposure to temperature over 30 °C
CH	m	Individual	Canopy height (m) averaged between an individuals' daytime/dusk/dawn locations
CC	%	Individual	Canopy cover (%) averaged between an individuals' daytime/dusk/dawn locations
VC	layers	Individual	Number of vertical layers averaged between an individuals' daytime/dusk/dawn locations
T_S	°C	Occupancy	Average maximum temperature between July-August
T_A	°C	Occupancy	Temporal temperature anomaly: a regional average all territories averaged per year subtracted from a regional average
CH_{nest}	%	Occupancy	The proportion of nest/roosting area with canopy height > 20m
CH_{terr}	%	Occupancy	The proportion of territory with canopy height > 20m
CC_{nest}	%	Occupancy	The proportion of nest/roosting area with canopy cover > 70%
CC_{terr}	%	Occupancy	The proportion of territory with canopy cover > 70%

Supplemental Table 2.2. Ranked temperature models for residual energetic expenditure. We report Akaike's information criterion (AIC_c), the relative difference in AIC_c (ΔAIC_c), the weighted AIC_c (AIC_{wt}), the model liklehood (ModelLik), the number of parameters in the model (noPar) and the Log-liklihood (LogLik).

Covariates	AIC_c	ΔAIC_c	AIC_{wt}	ModelLik	noPar	LogLik
T_{30}	265.07	0.00	0.63	1.00	2	-128.96
null	267.89	2.82	0.15	0.24	1	-131.67
T_{max}	268.41	3.34	0.12	0.19	2	-130.63
T_{mean}	268.77	3.70	0.10	0.16	2	-130.72

Supplemental Table 2.3. Ranked sub-models and combined models. We report Akaike's information criterion (AIC), the relative difference in AIC (ΔAIC), the weighted AIC (AIC_{wt}), the model liklehood (ModelLik), the number of parameters in the model (noPar) and -2(log-likelihood; -2*LogLik). If 85% confidence intervals overlapped zero, we defined a covariate as uninformative (Arnold 2010).

Ranked colonization (γ) sub-models for ENF study area.

Covariates	AIC	ΔAIC	AIC_{wt}	ModelLik	noPar	-2*LogLik
$T_S + CH_{nest}$	1351.20	0.00	0.28	1.00	28	1295.20
CH_{nest}	1351.79	0.59	0.21	0.74	27	1299.41
$T_A^* + CH_{nest}$	1352.11	0.91	0.18	0.63	28	1296.11
$T_S + CH_{terr}$	1352.30	1.10	0.16	0.58	28	1297.30
CH_{terr}	1353.41	2.21	0.09	0.33	27	1305.30
$T_A + CH_{terr}$	1353.74	2.54	0.08	0.28	28	1297.74
CC_{nest}	1359.30	8.10	0.00	0.02	27	1307.38
CC_{terr}	1361.38	10.18	0.00	0.01	26	1312.72
T_A	1364.85	13.65	0.00	0.00	27	1310.85
null	1364.72	13.52	0.00	0.00	36	1297.05
T_S	1366.01	14.81	0.00	0.00	27	1312.01
year	1369.05	17.85	0.00	0.00	28	1294.10
T_S	1360.70	0.00	0.24	1.00	27	1306.70
CC_{terr}	1362.15	1.45	0.12	0.48	27	1308.15
$T_S + CC_{terr}^*$	1362.44	1.74	0.10	0.42	28	1306.44
$T_S + CC_{nest}^*$	1362.46	1.76	0.10	0.41	28	1306.46
CC_{nest}^*	1362.34	1.64	0.11	0.44	27	1308.34
null	1362.61	1.91	0.09	0.38	26	1310.61
$T_A + CC_{terr}$	1363.55	2.85	0.06	0.24	27	1307.55
CH_{nest}	1363.72	3.02	0.05	0.22	27	1309.72
$T_A + CC_{nest}$	1363.75	3.05	0.05	0.22	28	1307.75
CH_{terr}	1363.88	3.18	0.05	0.20	27	1309.88
T_A	1364.50	3.80	0.04	0.15	27	1310.50
year	1369.05	8.35	0.00	0.02	36	1297.05

Ranked extinction (ε) sub-models for the ENF study area.

Covariates	AIC	ΔAIC	AIC_{wt}	ModelLik	noPar	-2*LogLik
T_S	1360.70	0.00	0.24	1.00	27	1306.70
CC_{terr}	1362.15	1.45	0.12	0.48	27	1308.15
$T_S + CC_{terr}^*$	1362.44	1.74	0.10	0.42	28	1306.44
$T_S + CC_{nest}^*$	1362.46	1.76	0.10	0.41	28	1306.46
CC_{nest}^*	1362.34	1.64	0.11	0.44	27	1308.34
null	1362.61	1.91	0.09	0.38	26	1310.61
$T_A + CC_{terr}$	1363.55	2.85	0.06	0.24	27	1307.55
CH_{nest}	1363.72	3.02	0.05	0.22	27	1309.72
$T_A + CC_{nest}$	1363.75	3.05	0.05	0.22	28	1307.75

CH_{terr}	1363.88	3.18	0.05	0.20	27	1309.88
T_A	1364.50	3.80	0.04	0.15	27	1310.50
year	1369.05	8.35	0.00	0.02	36	1297.05

Ranked combined models for the ELD study area.

γ	ε	AIC	ΔAIC	AIC_{wt}	ModelLik	noPar	-2*LogLik
$T_S + CH_{nest}$	T_S	1342.54	0.00	0.38	1.00	19	1305.54
CH_{nest}	T_S	1343.41	0.87	0.25	0.65	18	1307.41
$T_S + CH_{terr}$	T_S	1344.01	1.47	0.18	0.48	18	1306.01
$T_S + CH_{nest}$	null	1345.34	2.80	0.09	0.25	18	1309.34
CH_{nest}	null	1346.24	3.70	0.06	0.16	17	1312.24
$T_S + CH_{terr}$	null	1347.33	4.79	0.03	0.09	18	1311.33

Ranked colonization (γ) sub-models for SBNF study area.

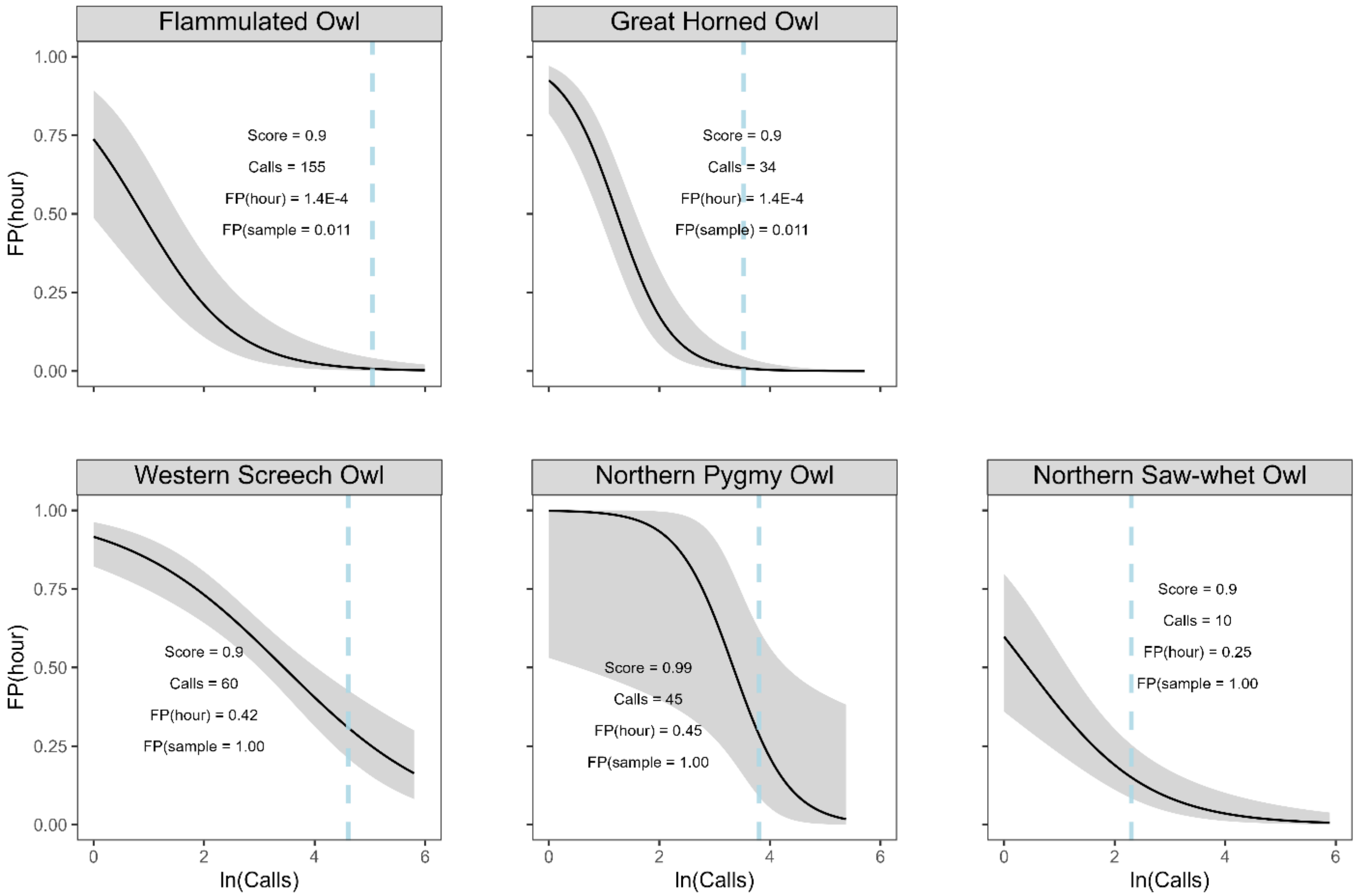
Covariates	AIC	ΔAIC	AIC_{wt}	ModelLik	noPar	-2*LogLik
CC_{nest}	1609.98	0.00	0.25	1.00	23	1563.98
$T_S^* + CC_{nest}$	1610.93	0.95	0.16	0.62	24	1562.93
CC_{terr}^*	1611.57	1.59	0.11	0.45	23	1565.57
$T_A + CC_{nest}$	1611.98	2.01	0.09	0.37	24	1563.98
null	1612.39	2.41	0.08	0.30	22	1568.39
$Ta + T_S + CC_{nest}$	1612.93	2.95	0.06	0.23	25	1562.93
$T_S + CC_{terr}$	1612.97	2.99	0.06	0.22	24	1564.97
$Ta + CC_{terr}$	1613.57	3.59	0.04	0.17	24	1565.57
year	1613.59	3.61	0.04	0.16	30	1553.59
CH_{terr}	1614.05	4.07	0.03	0.13	23	1568.05
CH_{nest}	1614.34	4.36	0.03	0.11	23	1568.34
T_A	1614.38	4.40	0.03	0.11	23	1568.38
T_S	1614.39	4.41	0.03	0.11	23	1568.39

Ranked extinction (ε) sub-models for the SBNF study area.

Covariates	AIC	ΔAIC	AIC_{wt}	ModelLik	noPar	-2*LogLik
$T_A + CC_{nest}$	1603.61	0.00	0.49	1.00	24	1555.61
$T_A + CC_{terr}$	1604.86	1.25	0.26	0.54	24	1556.86
T_A	1606.94	3.33	0.09	0.19	23	1560.94
CC_{nest}	1607.91	4.30	0.06	0.12	23	1561.91
CC_{terr}	1609.06	5.45	0.03	0.07	23	1563.06
$T_S + CC_{nest}$	1609.62	6.01	0.02	0.05	24	1561.62
$T_S + CC_{terr}$	1610.95	7.34	0.01	0.03	24	1562.95
T_S	1612.34	8.73	0.01	0.01	23	1566.34
null	1612.38	8.77	0.01	0.01	23	1566.38
CH_{nest}	1613.00	9.39	0.00	0.01	23	1567.00
CH_{terr}	1613.59	9.98	0.00	0.01	30	1553.59
year	1613.86	10.25	0.00	0.01	31	1551.86

Ranked combined models for the SBNF study area.

γ	ε	AIC	ΔAIC	AIC_{wt}	ModelLik	noPar	-2*LogLik
CC_{nest}	$T_A + CC_{nest}$	1604.67	0.00	0.25	1.00	18	1570.67
CC_{terr}	$T_A + CC_{nest}$	1605.54	0.87	0.16	0.65	17	1571.54
CC_{nest}	$T_A * CC_{nest}^*$	1605.57	0.90	0.16	0.64	18	1569.57
CC_{nest}	$T_A + CC_{terr}$	1605.87	1.20	0.13	0.55	18	1571.87
CC_{terr}	$T_A * CC_{nest}^*$	1606.48	1.81	0.10	0.40	18	1570.48
CC_{terr}	$T_A + CC_{terr}$	1606.88	2.21	0.08	0.33	17	1572.88
CC_{nest}	$T_A * CC_{terr}^*$	1607.00	2.33	0.08	0.31	18	1570.00
CC_{terr}	$T_A * CC_{terr}^*$	1608.04	3.37	0.05	0.19	18	1572.04



Supplemental Fig. 3.1. Species-specific call and prediction score thresholds. We report the probability of a false positive in any random hour in our validation dataset and our extrapolated probability of a false positive in an hour during a secondary sampling period. BirdNET produced more accurate identifications of GHOW and FLOW, such that no further validation was necessary following our primary validation of the 200 random potential observations. BirdNET was less successful in accurately identifying NOPO, WESO, and NWSO. For these species, we identified count and score thresholds that yielded less than a 0.5 false positive rate for random hours in the dataset and manually validated potential observations in the remaining cells.

Supplemental Table 3.1. Final ranked combined models for all species. We report the number of parameters in each model (nPar), Akaike's information criterion (AIC), the relative difference in AIC (ΔAIC), and the weighted AIC (AICwt).

Species	Occupancy model structure	nPars	AIC	ΔAIC	AICWt
GHOW[a]	$\Psi_{\text{latitude + CC + elevation + LM21-35+ H2-4 + H11-20\_pd}}$	13	2866.71	0.00	0.26
	$\Psi_{\text{latitude + CC + elevation + LM21-35 + H5-10 + H2-4 + H11-20\_pd}}$	14	2867.03	0.32	0.22
	$\Psi_{\text{latitude + CC + elevation + LM21-35 + H2-4\_pd + H11-20\_pd}}$	13	2867.15	0.44	0.21
	$\Psi_{\text{latitude + CC + elevation + LM21-35 + H5-10 + H2-4\_pd + H11-20\_pd}}$	14	2867.52	0.81	0.17
	$\Psi_{\text{latitude + CC + elevation + LM21-35 + H5-10 + H21-35\_pd + H11-20\_pd + H2-4}}$	15	2869.02	2.31	0.08
	$\Psi_{\text{latitude + CC + elevation + LM21-35 + H5-10 + H21-35\_pd + H11-20\_pd + H2-4\_pd}}$	15	2869.49	2.78	0.06
	$\Psi_{\text{latitude + CC + elevation}}$	10	2873.87	7.16	0.01
	$\Psi_{\text{LM\_21-35 + H5-10 + H2-4}}$	10	2879.96	13.26	0.00
	$\Psi_{\text{H21-35\_pd + H11-20\_pd + H2-4\_pd}}$	10	2880.52	13.81	0.00
WESO[b]	$\Psi_{\text{elevation + latitude + CC + LM2-4 + LM1\_pd}}$	12	1970.12	0.00	0.48
	$\Psi_{\text{elevation + latitude + CC + LM2-4 + H2-4\_pd + LM1\_pd}}$	13	1971.73	1.61	0.21
	$\Psi_{\text{elevation + latitude + CC + LM2-4 + H2-4 + LM1\_pd}}$	13	1972.11	2.00	0.18
	$\Psi_{\text{elevation + latitude + CC + LM2-4 + H2-4 + H2-4\_pd + LM1\_pd}}$	14	1973.49	3.38	0.09
	$\Psi_{\text{elevation + latitude + CC + LM2-4 + H2-4*H2-4\_pd + LM1\_pd}}$	15	1974.88	4.76	0.01
	$\Psi_{\text{latitude + CC + elevation}}$	8	1991.52	21.41	0.00
	$\Psi_{\text{LM1\_pd + H2-4\_pd}}$	7	2134.95	164.83	0.00
	$\Psi_{\text{LM2-4 + H2-4}}$	7	2146.45	176.33	0.00
FLOW[c]	$\Psi_{\text{latitude + elevation + LM5-10 + LM21-35 + H1}}$	9	1985.99	0.00	0.59
	$\Psi_{\text{latitude + elevation + LM5-10 + LM21-35 + H1 + LM5-10\_pd}}$	10	1987.22	1.45	0.28
	$\Psi_{\text{latitude + elevation + LM5-10+H1 + LM5-10\_pd + H21-35\_pd}}$	10	1990.56	3.05	0.13
	$\Psi_{\text{latitude + elevation}}$	7	1996.78	11.33	0.00
	$\Psi_{\text{LM5-10 + LM21-35 + H1}}$	6	1998.56	11.83	0.00
	$\Psi_{\text{LM5-10\_pd + H1\_pd}}$	6	2006.98	13.19	0.00
SPOW[d]	$\Psi_{\text{CC + latitude + H5-10 + H11-20 + LM1\_pd}}$	10	3494.69	0.00	0.34
	$\Psi_{\text{CC + latitude+ H1 + H5-10 + H11-20}}$	10	3495.50	0.81	0.22
	$\Psi_{\text{CC + latitude + H5-10+ H11-20 + LM1\_pd + H5-10\_pd}}$	11	3496.65	1.96	0.13
	$\Psi_{\text{CC + latitude + H5-10\_pd + H11-20 + LM1\_pd}}$	10	3497.43	2.75	0.09
	$\Psi_{\text{CC + latitude+ H1 + H5-10 + H11-20 + H5-10\_pd}}$	11	3497.47	2.78	0.08
	$\Psi_{\text{CC + latitude + H1 + H5-10\_pd + H11-20}}$	10	3497.98	3.29	0.07
	$\Psi_{\text{CC + latitude + H5-10*H5-10\_pd + H\_0110+LM\_20\_pd}}$	12	3498.62	3.93	0.05
	$\Psi_{\text{CC + latitude+ H\_20 + H\_1116*H\_1116\_pd + H\_0110}}$	12	3499.41	4.72	0.03
	$\Psi_{\text{CC + latitude}}$	7	3525.66	30.97	0.00
	$\Psi_{\text{H1 + H5-10 + H11-20}}$	8	3572.85	78.17	0.00
	$\Psi_{\text{LM1\_pd+ H5-10\_pd}}$	7	3574.06	79.38	0.00

NOPO[e]	$\psi_{\text{elevation + H1*H1\_pd}}$	9	2394.64	0.00	0.55
	$\psi_{\text{elevation + H1}}$	7	2396.11	1.47	0.26
	$\psi_{\text{elevation + H1 + H1\_pd}}$	8	2397.45	2.81	0.13
	$\psi_{\text{elevation + H1\_pd}}$	7	2399.60	4.96	0.05
	$\psi_{\text{elevation}}$	6	2403.22	8.59	0.00
	ψ_{H1}	6	2415.34	20.70	0.00
	$\psi_{\text{H1 + H1\_pd}}$	7	2416.24	21.60	0.00
	$\psi_{\text{H1\_pd}}$	6	2416.35	21.72	0.00
NSWO[f]	$\psi_{\text{H1 + H11-20\_pd + LM21-35\_pd}}$	7	750.10	0.00	0.35
	$\psi_{\text{H1 + H11-20 + LM21-35\_pd}}$	7	750.16	0.07	0.34
	$\psi_{\text{H1 + H11-20 + H11-20\_pd + LM\_1-35\_pd}}$	8	752.10	2.00	0.13
	$\psi_{\text{H1+H\_0110}}$	6	754.07	3.98	0.05
	$\psi_{\text{H1 + H11-20*H11-20\_pd + LM\_8600\_pd}}$	9	754.10	4.00	0.05
	$\psi_{\text{H1 + LM21-35\_pd}}$	6	754.56	4.47	0.04
	$\psi_{\text{H11-20\_pd + LM21-35\_pd}}$	6	756.78	6.68	0.01
	$\psi_{\text{H11-20 + LM21-35\_pd}}$	6	756.81	6.72	0.01
	$\psi_{.}$	4	766.09	15.99	0.00

Footnotes indicate variables used to model detection, obtained from model selection reported in Supplemental Table 2.

[a] $p_{\text{CC +time + hours + rugged + elevation}}$

[b] $p_{\text{elevation + rugged + time + CC + hours}}$

[c] $p_{\text{time + rugged}}$

[d] $p_{\text{time + rugged + hours}}$

[e] $p_{\text{time + elevation + CC}}$

[f] $p_{\text{CC + time}}$

Supplemental Table 3.2. Ranked detection models for all species. We report the number of parameters in each model (nPar), Akaike's information criterion (AIC), the relative difference in AIC (ΔAIC), and the weighted AIC (AICwt).

Species	Occupancy model structure	nPars	AIC	ΔAIC	AICWt
GHOW	$p_{\text{CC + time + hours + rugged + elevation}}$	7	2889.03	0.00	0.95
	$p_{\text{CC + time +hours + rugged}}$	6	2895.01	5.98	0.05
	$p_{\text{CC + time + hours}}$	5	2899.29	10.26	0.00
	$p_{\text{CC + hours}}$	4	2914.23	25.20	0.00
	p_{CC}	3	2920.19	31.16	0.00
	p_{hours}	3	2951.51	62.48	0.00
	p_{time}	3	2952.30	63.27	0.00
	p_{rugged}	3	2957.56	63.53	0.00
	$p_{.}$	2	2963.52	74.49	0.00
	$p_{\text{elevation}}$	3	2964.56	75.53	0.00
WESO	$p_{\text{elevation + rugged+ time +CC + hours}}$	7	2145.41	0.00	0.95
	$p_{\text{elevation + hours + rugged + time}}$	6	2152.50	7.09	0.03
	$p_{\text{elevation + hours + rugged}}$	5	2152.73	7.33	0.02
	$p_{\text{elevation + hours}}$	4	2158.28	12.87	0.00
	$p_{\text{elevation}}$	3	2161.08	15.68	0.00
	p_{hours}	3	2214.06	68.65	0.00
	p_{rugged}	3	2218.93	73.52	0.00
	P_{time}	3	2223.47	78.07	0.00
	$p_{.}$	2	2226.65	81.24	0.00
	p_{CC}	3	2227.87	82.47	0.00
FLOW	$p_{\text{time + rugged}}$	4	2009.89	0.00	0.54
	$p_{\text{time + rugged + CC}}$	5	2011.79	1.90	0.21
	p_{time}	3	2012.93	3.04	0.12
	$p_{\text{time +rugged + CC + elevation}}$	6	2013.74	3.85	0.08
	$p_{\text{time + rugged+ CC + elevation + hours}}$	7	2014.58	4.68	0.05
	p_{rugged}	3	2074.82	64.93	0.00
	$p_{.}$	2	2075.07	65.18	0.00
	p_{CC}	3	2075.69	65.79	0.00
	$p_{\text{elevation}}$	3	2076.48	66.59	0.00
	p_{hours}	3	2077.01	67.12	0.00
SPOW	$p_{\text{time + rugged + hours}}$	5	3596.18	0.00	0.53
	$p_{\text{time + rugged + hours + elevation}}$	6	3597.70	1.51	0.25
	$p_{\text{time + rugged}}$	4	3599.10	2.92	0.12
	$p_{\text{time + rugged + hours + elevation + CC}}$	7	3599.52	3.33	0.10
	p_{time}	3	3607.25	11.06	0.00
	p_{rugged}	3	3610.91	14.72	0.00

	p_{hours}	3	3610.97	14.78	0.00
	$p_{.}$	2	3617.84	21.66	0.00
	$p_{elevation}$	3	3619.48	23.29	0.00
	p_{CC}	3	3619.83	23.64	0.00
NOPO	$p_{time + elevation + CC}$	5	2419.65	0.00	0.56
	$p_{time + elevation + CC + hours}$	6	2421.37	1.71	0.24
	$p_{time + elevation}$	4	2422.83	3.17	0.11
	$p_{time + elevation + CC + hours + rugged}$	7	2423.35	3.70	0.09
	p_{time}	3	2478.06	58.40	0.00
	$p_{elevation}$	3	2493.67	74.02	0.00
	p_{CC}	3	2514.13	94.48	0.00
	$p_{.}$	2	2562.28	142.63	0.00
	p_{hours}	3	2563.37	143.71	0.00
	p_{rugged}	3	2563.49	143/84	0.00
NSWO	$p_{CC + time}$	4	766.09	0.00	0.61
	$p_{CC + time + elev}$	5	767.95	1.86	0.24
	$p_{CC + linear + elevation + rugged}$	6	768.88	2.79	0.15
	p_{CC}	3	782.12	16.03	0.00
	p_{time}	3	792.63	26.54	0.00
	$p_{elevation}$	3	805.03	38.94	0.00
	p_{rugged}	3	818.52	52.43	0.00
	$p_{.}$	2	819.12	53.03	0.00
	p_{hours}	3	820.91	54.82	0.00

Supplemental Table 3.3. Ranked sub-models for great horned owls (GHOW). We report the model set (Set), the number of parameters in each model (nPar), Akaike's information criterion (AIC), the relative difference in AIC (ΔAIC), and the weighted AIC (AICwt). All potential detection variables were used to model detection in all models.

Set	Model structure	nPars	AIC	ΔAIC	AICWt
Basic	$\psi_{\text{latitude + CC + elevatopm}}$	10	2873.87	0.00	0.73
	$\psi_{\text{latitde + CC}}$	9	2876.26	2.38	0.22
	ψ_{latitude}	8	2879.98	6.11	0.03
	ψ_{CC}	8	2881.62	7.75	0.02
	$\psi_{.}$	7	2889.03	15.16	0.00
	$\psi_{\text{elevation}}$	8	2890.88	17.01	0.00
Composition	$\psi_{\text{LM21-35 + H5-10 + H2-4 + H11-20}}$	11	2878.08	0.00	0.35
	$\psi_{\text{LM21-35 + H5-10 + H2-4 + H11-20 + LM1}}$	12	2878.36	0.28	0.31
	$\psi_{\text{LM\_8600+H\_1116+H\_1719}}$	10	2879.96	1.89	0.14
	$\psi_{\text{LM21-35 + H5-10 + H2-4 + H11-20 + LM1 + LM5-10}}$	13	2880.24	2.16	0.12
	$\psi_{\text{LM21-35 + H5-10}}$	9	2882.58	4.51	0.04
	$\psi_{\text{LM21-35}}$	8	2884.28	6.21	0.03
	$\psi_{\text{H5-10}}$	8	2886.61	8.53	0.01
	$\psi_{\text{H2-4}}$	8	2887.36	9.28	0.00
	$\psi_{\text{H11-20}}$	8	2887.98	9.90	0.00
	ψ_{LM1}	8	2888.77	10.70	0.00
	$\psi_{\text{LM5-10}}$	8	2888.95	10.87	0.00
	$\psi_{\text{H21-35}}$	8	2889.02	10.95	0.00
	$\psi_{.}$	7	2889.03	10.95	0.00
	ψ_{H1}	8	2889.23	11.15	0.00
	$\psi_{\text{LM2-4}}$	8	2890.07	12.00	0.00
	$\psi_{\text{LM11-20}}$	8	2890.39	12.31	0.00
Configuration	$\psi_{\text{H21-35\_pd + H11-20\_pd + H2-4\_pd}}$	10	2880.52	0.00	0.27
	$\psi_{\text{H21-35\_pd + H11-20\_pd + H2-4\_pd + H5-10\_pd}}$	11	2880.85	0.33	0.23
	$\psi_{\text{H21-35\_pd + H11-20\_pd + LM21-35\_pd + H2-4\_pd}}$	11	2881.69	1.17	0.15
	$\psi_{\text{H21-35\_pd + H11-20\_pd + LM21-35\_pd + H2-4\_pd + H5-10\_pd}}$	12	2882.11	1.59	0.12
	$\psi_{\text{H21-35\_pd + H11-20\_pd}}$	9	2883.07	2.55	0.08
	$\psi_{\text{H21-35\_pd + H11-20\_pd + LM21-35\_pd + H2-4\_pd + H5-10\_pd + LM5-10\_pd}}$	13	2884.07	3.56	0.05
	$\psi_{\text{H21-35\_pd + H11-20\_pd + LM21-35\_pd}}$	10	2884.40	3.89	0.04
	$\psi_{\text{H21-35\_pd}}$	8	2885.28	4.77	0.02
	$\psi_{\text{H11-20\_pd}}$	8	2886.98	6.46	0.01
	$\psi_{\text{LM21-35\_pd}}$	8	2887.29	6.78	0.01
	$\psi_{\text{H2-4\_pd}}$	8	2887.56	7.04	0.01
	$\psi_{\text{H2-4\_pd}}$	8	2888.52	8.01	0.00
	$\psi_{.}$	7	2889.03	8.51	0.00
	$\psi_{\text{LM5-10\_pd}}$	8	2889.46	8.94	0.00
	$\psi_{\text{LM2-4\_pd}}$	8	2890.16	9.64	0.00
	$\psi_{\text{LM1\_pd}}$	8	2890.34	9.82	0.00
	$\psi_{\text{H1\_pd}}$	8	2890.57	10.06	0.00
	$\psi_{\text{LM11-20\_pd}}$	8	2890.94	10.43	0.00

Supplemental Table 3.4. Ranked sub-models for flammulated owls (FLOW). We report the model set (Set), the number of parameters in each model (nPar), Akaike's information criterion (AIC), the relative difference in AIC (ΔAIC), and the weighted AIC (AICwt). All potential detection variables were used to model detection in all models.

Set	Model structure	nPars	AIC	ΔAIC	AICWt
Basic	$\psi_{\text{elevation + latitude + CC}}$	10	1986.32	0.00	0.99
	$\psi_{\text{elevation + latitude}}$	9	1995.78	9.47	0.01
	$\psi_{\text{elevation}}$	8	2014.46	28.14	0.00
	ψ_{latitude}	8	2126.41	140.10	0.00
	ψ_{CC}	7	2145.41	159.09	0.00
	$\psi_{.}$	8	2146.89	160.57	0.00
Composition	$\psi_{\text{LM2-4}}$	8	2134.35	0.00	0.60
	$\psi_{\text{LM2-4 + H2-4}}$	9	2136.28	1.94	0.23
	$\psi_{\text{LM2-4 + H2-4 + LM1}}$	10	2137.62	3.28	0.12
	$\psi_{\text{H2-4}}$	8	2140.96	6.61	0.02
	ψ_{LM1}	8	2143.14	8.79	0.01
	ψ_{H1}	8	2143.62	9.28	0.00
	$\psi_{\text{H\_11-20}}$	8	2144.88	10.54	0.00
	$\psi_{.}$	7	2145.41	11.06	0.00
	$\psi_{\text{LM21-35}}$	8	2146.70	12.35	0.00
	$\psi_{\text{H21-35}}$	8	2146.93	12.59	0.00
	$\psi_{\text{LM5-10}}$	8	2147.03	12.68	0.00
	$\psi_{\text{LM11-20}}$	8	2147.33	12.98	0.00
	$\psi_{\text{H5-10}}$	8	2147.36	13.02	0.00
Configuration	$\psi_{\text{LM1\_pd + H2-4\_pd}}$	9	2128.95	0.00	0.63
	$\psi_{\text{LM1\_pd + H2-4\_pd + H1\_pd}}$	10	2130.81	1.86	0.25
	$\psi_{\text{LM1\_pd + H2-4\_pd + H1\_pd + LM2-4\_pd}}$	11	2132.72	3.77	0.10
	$\psi_{\text{H2-4\_pd}}$	8	2136.58	7.63	0.01
	$\psi_{\text{LM1\_pd}}$	8	2137.65	8.69	0.01
	$\psi_{\text{H1\_pd}}$	8	2144.60	15.65	0.00
	$\psi_{\text{LM2-4\_pd}}$	8	2145.10	16.14	0.00
	$\psi_{\text{LM11-20\_pd}}$	8	2145.24	16.29	0.00
	$\psi_{.}$	7	2145.41	16.46	0.00
	$\psi_{\text{H11-20\_pd}}$	8	2145.73	16.78	0.00
	$\psi_{\text{H5-10\_pd}}$	8	2146.43	17.48	0.00
	$\psi_{\text{H21-35\_pd}}$	8	2146.52	17.57	0.00
	$\psi_{\text{LM5-10\_pd}}$	8	2147.05	18.09	0.00
	$\psi_{\text{LM21-35\_pd}}$	8	2147.19	18.24	0.00

Supplemental Table 3.5. Ranked sub-models for flammulated owls (FLOW). We report the model set (Set), the number of parameters in each model (nPar), Akaike's information criterion (AIC), the relative difference in AIC (ΔAIC), and the weighted AIC (AICwt). Time and ruggedness were the variables used to model detection in all models.

Set	Model structure	nPars	AIC	ΔAIC	AICWt
Basic	$\psi_{\text{latitude + elevation}}$	6	1998.56	0.00	0.59
	$\psi_{\text{latitude + elevation + CC}}$	7	1998.56	1.45	0.28
	ψ_{latitude}	5	2001.61	3.05	0.13
	$\psi_{.}$	4	2009.89	11.33	0.00
	$\psi_{\text{elevation}}$	5	2010.39	11.83	0.00
	ψ_{CC}	5	2011.75	13.19	0.00
Composition	$\psi_{\text{LM5-10 + LM21-35 + H1}}$	7	1996.78	0.00	0.50
	$\psi_{\text{LM5-10+LM21-35 + H1 + LM1}}$	8	1998.61	1.83	0.20
	$\psi_{\text{LM5-10 + LM21-35}}$	6	1998.69	1.91	0.19
	$\psi_{\text{LM5-10 + LM21-35 + H1 + LM1 + LM11-20}}$	9	2000.22	3.44	0.09
	$\psi_{\text{LM5-10}}$	5	2003.88	7.10	0.01
	$\psi_{\text{LM21-35}}$	5	2006.34	9.56	0.00
	ψ_{H1}	5	2007.50	10.71	0.00
	$\psi_{.}$	4	2009.89	13.11	0.00
	ψ_{LM1}	5	2010.82	14.04	0.00
	$\psi_{\text{LM11-20}}$	5	2011.46	14.68	0.00
	$\psi_{\text{H21-35}}$	5	2011.71	14.93	0.00
	$\psi_{\text{H11-20}}$	5	2011.79	15.01	0.00
	$\psi_{\text{H5-10}}$	5	2011.83	15.05	0.00
	$\psi_{\text{L2-4}}$	5	2011.88	15.10	0.00
	$\psi_{\text{H2-4}}$	5	2011.89	15.11	0.00
Configuration	$\psi_{\text{LM5-10\_pd + H21-35\_pd + LM1\_pd}}$	7	2006.67	0.00	0.23
	$\psi_{\text{LM5-10\_pd + H21-35\_pd}}$	6	2006.98	0.31	0.20
	$\psi_{\text{LM5-10\_pd}}$	5	2008.47	1.80	0.10
	$\psi_{\text{LM5-10\_pd + H21-35\_pd + LM1\_pd + H1\_pd}}$	8	2008.55	1.88	0.09
	$\psi_{\text{H21-35\_pd}}$	5	2009.04	2.37	0.07
	$\psi_{\text{LM1\_pd}}$	5	2009.39	2.72	0.06
	$\psi_{.}$	4	2009.89	3.22	0.05
	$\psi_{\text{H1\_pd}}$	5	2009.89	3.63	0.04
	$\psi_{\text{LM5-10\_pd + H21-35\_pd + LM1\_pd + H1\_pd + H5-10\_pd}}$	9	2010.30	3.87	0.03
	$\psi_{\text{H5-10\_pd}}$	5	2010.54	4.63	0.02
	$\psi_{\text{LM\_21-35\_pd}}$	5	2011.29	4.64	0.02
	$\psi_{\text{H2-4\_pd}}$	5	2011.48	4.82	0.02
	$\psi_{\text{LM11-20\_pd}}$	5	2011.49	4.83	0.02
	$\psi_{\text{LM2-4\_pd}}$	5	2011.78	5.11	0.02
	$\psi_{\text{H11-20\_pd}}$	5	2011.89	5.22	0.02

Supplemental Table 3.6. Ranked sub-models for spotted owls (SPOW). We report the model set (Set), the number of parameters in each model (nPar), Akaike's information criterion (AIC), the relative difference in AIC (ΔAIC), and the weighted AIC (AICwt). Time, ruggedness, and recording hours were the variables used to model detection in all models.

Set	Model structure	nPars	AIC	ΔAIC	AICWt
Basic	$\psi_{\text{CC + latitude}}$	7	3525.66	0.00	0.56
	$\psi_{\text{CC + latitude + elevation}}$	8	3526.18	0.52	0.44
	ψ_{CC}	6	3548.32	22.66	0.00
	ψ_{latitude}	6	3592.32	66.66	0.00
	$\psi_{\text{elevation}}$	6	3592.69	67.03	0.00
	$\psi_{.}$	5	3596.18	70.52	0.00
Composition	$\psi_{\text{H1 + H5-10 + H11-20}}$	8	3572.85	0.00	0.44
	$\psi_{\text{H1 + H5-10 + LM1 + H11-20}}$	9	3574.00	1.14	0.25
	$\psi_{\text{H1 + H5-10 + LM1 + H11-20 + LM11-20}}$	10	3575.41	2.56	0.12
	$\psi_{\text{H1 + H5-10}}$	7	3575.45	2.59	0.12
	$\psi_{\text{H1 + H5-10 + LM1}}$	8	3576.72	3.87.	0.06
	ψ_{H1}	6	3583.46	10.61	0.00
	$\psi_{\text{H5-10}}$	6	3589.53	16.68	0.00
	ψ_{LM1}	6	3591.90	19.05	0.00
	$\psi_{\text{LM5-10}}$	6	3592.69	19.84	0.00
	$\psi_{\text{H11-20}}$	6	3594.33	21.48	0.00
	$\psi_{\text{LM11-20}}$	6	3595.08	22.22	0.00
	$\psi_{.}$	5	3596.18	23.33	0.00
	$\psi_{\text{H21-35}}$	6	3596.25	23.39	0.00
	$\psi_{\text{LM2-4}}$	6	3596.96	24.11	0.00
	$\psi_{\text{H2-4}}$	6	3598.02	25.16	0.00
	$\psi_{\text{LM21-35}}$	6	3598.06	25.20	0.00
Configuration	$\psi_{\text{LM1\_pd + H5-10\_pd + H11-20\_pd}}$	8	3573.24	0.00	0.37
	$\psi_{\text{LM1\_pd + H5-10\_pd}}$	7	3574.06	0.82	0.24
	$\psi_{\text{LM1\_pd + H1\_pd + H5-10\_pd + H11-20\_pd}}$	9	3575.00	1.76	0.15
	$\psi_{\text{LM1\_pd + H1\_pd + H5-10\_pd}}$	8	3575.88	2.63	0.10
	$\psi_{\text{LM1\_pd + H1\_pd + H5-10\_pd + LM5-10\_pd + H11-20\_pd}}$	10	3576.65	3.41	0.07
	$\psi_{\text{LM1\_pd + H1\_pd + H5-10\_pd + LM5-10\_pd}}$	9	3577.56	4.31	0.04
	$\psi_{\text{LM1\_pd}}$	6	3579.06	5.81	0.02
	$\psi_{\text{LM1\_pd + H1\_pd}}$	7	3580.80	7.56	0.01
	$\psi_{\text{H1\_pd}}$	6	3589.96	16.71	0.00
	$\psi_{\text{H5-10\_pd}}$	6	3592.35	19.10	0.00
	$\psi_{\text{LM5-10\_pd}}$	6	3595.45	22.21	0.00
	$\psi_{\text{H11-20\_pd}}$	6	3595.45	22.21	0.00
	$\psi_{.}$	5	3596.18	22.94	0.00
	$\psi_{\text{LM11-20\_pd}}$	6	3596.58	23.34	0.00
	$\psi_{\text{H2-4\_pd}}$	6	3597.08	23.83	0.00
	$\psi_{\text{LM21-35\_pd}}$	6	3597.64	24.40	0.00
	$\psi_{\text{H21-35\_pd}}$	6	3598.15	24.90	0.00
	$\psi_{\text{LM2-4\_pd}}$	6	3598.16	24.91	0.00

Supplemental Table 3.7. Ranked sub-models for northern pygmy owls (NOPO). We report the model set (Set), the number of parameters in each model (nPar), Akaike's information criterion (AIC), the relative difference in AIC (ΔAIC), and the weighted AIC (AICwt). Time, elevation, and canopy cover were the variables used to model detection in all models.

Set	Model structure	nPars	AIC	ΔAIC	AICWt
Basic	$\psi_{\text{elevation}}$	6	2403.22	0.00	0.60
	$\psi_{\text{elevation + CC}}$	7	2404.90	1.67	0.26
	$\psi_{\text{elevation + CC + latitude}}$	8	2406.45	3.23	0.12
	ψ_{CC}	6	2409.80	6.58	0.02
	ψ_{latitude}	6	2418.73	15.50	0.00
	$\psi_{.}$	5	2419.65	16.43	0.00
Composition	$\psi_{\text{H1 + H21-35}}$	7	2414.83	0.00	0.33
	ψ_{H1}	6	2415.34	0.50	0.26
	$\psi_{\text{H1 + H21-35 + LM21-35}}$	8	2416.79	1.96	0.13
	$\psi_{\text{H1 + H21-35 + LM21-35+ LM1}}$	9	2417.86	3.03	0.07
	$\psi_{\text{H21-35}}$	6	2419.36	4.53	0.04
	$\psi_{.}$	5	2419.65	4.82	0.03
	$\psi_{\text{LM21-35}}$	6	2419.78	4.95	0.03
	ψ_{LM1}	6	2420.02	5.19	0.03
	$\psi_{\text{H2-4}}$	6	2420.18	5.35	0.02
	$\psi_{\text{LM2-4}}$	6	2420.52	5.68	0.02
	$\psi_{\text{LM5-10}}$	6	2421.39	6.55	0.01
	$\psi_{\text{H5-10}}$	6	2421.42	6.59	0.01
	$\psi_{\text{LM11-20}}$	6	2421.60	6.76	0.01
	$\psi_{\text{H11-20}}$	6	2421.61	6.77	0.01
Configuration	$\psi_{\text{H1\_pd + LM11-20\_pd + H21-35\_pd}}$	8	2415.63	0.00	0.24
	$\psi_{\text{H1\_pd + LM11-20\_pd}}$	7	2415.76	0.14	0.23
	$\psi_{\text{H1\_pd}}$	6	2416.35	1.73	0.17
	$\psi_{\text{H1\_pd + LM11-20\_pd + H21-25\_pd + LM1\_pd}}$	9	2417.61	1.98	0.09
	$\psi_{\text{LM11-20\_pd}}$	6	2419.11	3.49	0.04
	$\psi_{\text{H21-25\_pd}}$	6	2419.27	3.64	0.04
	$\psi_{\text{LM1\_pd}}$	6	2419.34	3.72	0.04
	$\psi_{\text{H1\_pd + LM11-20\_pd + H21-25\_pd + LM1\_pd + LM21-35\_pd}}$	10	2419.54	3.92	0.03
	$\psi_{.}$	5	2419.65	4.03	0.03
	$\psi_{\text{LM21-35\_pd}}$	6	2420.53	4.91	0.02
	$\psi_{\text{LM2-4\_pd}}$	6	2420.88	5.25	0.02
	$\psi_{\text{LM5-10\_pd}}$	6	2421.35	5.73	0.01
	$\psi_{\text{H2-4\_pd}}$	6	2421.48	5.86	0.01
	$\psi_{\text{H5-10\_pd}}$	6	2421.57	5.95	0.01
	$\psi_{\text{H11-20\_pd}}$	6	2421.65	6.03	0.01

Supplemental Table 3.8. Ranked sub-models for northern saw-whet owls (NSWO). We report the model set (Set), the number of parameters in each model (nPar), Akaike's information criterion (AIC), the relative difference in AIC (ΔAIC), and the weighted AIC (AICwt). Canopy cover and time were the variables used to model detection in all models.

Set	Model structure	nPars	AIC	ΔAIC	AICWt
Basic	ψ_{latitude}	5	764.78	0.00	0.34
	$\psi_{\text{latitude + CC}}$	6	765.38	0.60	0.25
	$\psi_{.}$	4	766.09	1.31	0.18
	ψ_{CC}	5	766.53	1.75	0.15
	$\psi_{\text{elevation}}$	5	768.05	3.27	0.07
Composition	$\psi_{\text{H1 + H11-20}}$	6	754.07	0.00	0.45
	$\psi_{\text{H1 + H11-20 + LM11-20 + H5-10}}$	8	755.39	1.32	0.23
	$\psi_{\text{H1 + H11-20 + LM11-20}}$	7	756.13	2.06	0.16
	$\psi_{\text{H1 + H11-20 + LM11-20 + H5-10 + LM1}}$	9	757.30	3.22	0.09
	ψ_{H1}	5	758.39	4.31	0.05
	$\psi_{\text{H11-20}}$	5	760.99	6.91	0.01
	$\psi_{\text{LM11-20}}$	5	764.66	10.59	0.00
	$\psi_{\text{H5-10}}$	5	765.58	11.51	0.00
	ψ_{LM1}	5	765.65	11.58	0.00
	$\psi_{\text{LM5-10}}$	5	765.73	11.66	0.00
	$\psi_{.}$	4	766.09	12.02	0.00
	$\psi_{\text{H2-4}}$	5	766.70	12.62	0.00
	$\psi_{\text{LM21-35}}$	5	766.81	12.73	0.00
	$\psi_{\text{H21-35}}$	5	767.71	13.63	0.00
	$\psi_{\text{LM2-4}}$	5	768.02	13.95	0.00
Configuration	$\psi_{\text{H11-20\_pd+LM21-35\_pd+H1\_pd}}$	7	754.79	0.00	0.31
	$\psi_{\text{H11-20\_pd+LM21-35\_pd+H1\_pd+LM1\_pd+H5-10\_pd}}$	9	755.02	0.24	0.28
	$\psi_{\text{H11-20\_pd+LM21-35\_pd+H1\_pd+LM1\_pd}}$	8	756.29	1.51	0.15
	$\psi_{\text{H11-20\_pd+LM21-35\_pd}}$	6	756.78	1.99	0.12
	$\psi_{\text{H11-20\_pd+LM21-35\_pd+H1\_pd+LM1\_pd+H5-10\_pd+LM5-10\_pd}}$	10	756.96	2.17	0.11
	$\psi_{\text{H11-20\_pd}}$	5	760.95	6.16	0.01
	$\psi_{\text{LM21-35\_pd}}$	5	762.12	7.34	0.00
	$\psi_{\text{H1\_pd}}$	5	763.10	8.32	0.00
	$\psi_{\text{LM1\_pd}}$	5	763.93	9.14	0.00
	$\psi_{\text{H5-10\_pd}}$	5	764.50	9.71	0.00
	$\psi_{\text{LM5-10\_pd}}$	5	765.09	10.31	0.00
	$\psi_{.}$	4	766.09	11.31	0.00
	$\psi_{\text{H2-4\_pd}}$	5	766.70	11.91	0.00
	$\psi_{\text{LM5-10\_pd}}$	5	766.95	12.16	0.00
	$\psi_{\text{H21-35\_pd}}$	5	767.60	12.81	0.00
	$\psi_{\text{LM2-4\_pd}}$	5	779.20	24.42	0.00