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Source: Journal of Raptor Research, 60(4) : 1-18

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/jrr2580

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Journal of Raptor Research

Advancing the science, conservation, and understanding of birds of prey

Journal of Raptor Research 60(4):jrr2580
doi: 10.3356/jrr2580
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Space Use, Habitat Selection, and Diel Activity Throughout the Annual Cycle of Great Gray Owls in the Sierra Nevada, California

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ABSTRACT.—The *yosemitensis* subspecies of Great Gray Owl (*Strix nebulosa yosemitensis*, hereafter owls) is a California endangered species with a small population centered in Yosemite National Park and adjacent Stanislaus National Forest. To support effective management and conservation efforts, we used GPS tracking and remote-sensing data to examine space use, habitat selection, and diel activity during the annual cycle of five owls. Through two breeding seasons and one nonbreeding season, we found home range size and displacement (straight-line distance between consecutive GPS locations) were smaller and lower, respectively, during the breeding seasons and larger and higher during the nonbreeding season. Owls were most active near dawn and dusk, particularly during the 2022 breeding season. Foraging owls tended to avoid areas with high canopy cover and areas that had burned at high severity, but showed mixed responses to canopy bulk density. Owls tended to select roosting sites in forested areas with multiple canopy layers and high canopy bulk density outside high-severity burned areas. Finally, owls showed inconsistent responses and mixed patterns across sexes and seasons to recreational activity intensity and proximity to roads and buildings. Our study highlights individual variation in habitat use among owls and suggests differences with other subspecies. In particular, we found *S. n. yosemitensis* owls had larger home ranges than those reported for other subspecies, primarily driven by downslope movements and home-range expansions during the nonbreeding season. Our results suggest that future management should emphasize maintaining both breeding and nonbreeding habitats, and that further investigation of the effects of fire and vehicular collisions on this population are warranted.

KEY WORDS: *Behavioral ecology*; *diel cycle*; *GPS-tracking*; *habitat selection*; *movement ecology*; *space use*; *Yosemite*.

USO DEL ESPACIO, SELECCIÓN DEL HÁBITAT, Y ACTIVIDAD DIARIA A LO LARGO DEL CICLO ANUAL DE LOS *STRIX NEBULOSA* EN LA SIERRA NEVADA, CALIFORNIA

RESUMEN.—La subespecie *Strix nebulosa yosemitensis*, catalogada en peligro de extinción en California, comprende una población muy reducida, concentrada principalmente en el Parque Nacional Yosemite y el adyacente Bosque Nacional Stanislaus. Con el fin de apoyar estrategias efectivas de manejo y conservación, investigamos el uso del espacio, la selección de hábitat y la actividad diurna durante el

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ciclo anual de cinco individuos utilizando datos GPS y percepción remota. Encontramos que durante dos temporadas de reproducción y una no reproductiva, el tamaño del rango de hogar y el desplazamiento (distancia en línea recta entre ubicaciones GPS consecutivas) fueron menores durante temporada de reproducción, y mayores durante la temporada no reproductiva. La actividad alcanzó su punto máximo cerca durante el crepúsculo, particularmente durante la temporada reproductiva de 2022. Durante la búsqueda de alimento, tendieron a evitar áreas con alta cobertura de dosel y áreas quemadas de alta severidad, aunque mostraron respuestas mixtas ante la densidad volumétrica del dosel. Asimismo, seleccionaron sitios de descanso en áreas boscosas con múltiples estratos de dosel y alta densidad del mismo, situados fuera de áreas afectadas por incendios de alta severidad. Finalmente, mostraron respuestas inconsistentes y patrones mixtos entre sexos y temporadas ante la intensidad de la actividad recreativa y la proximidad a carreteras y edificios. Nuestro estudio destaca la variación en el uso del hábitat entre individuos, y sugiere diferencias con respecto a otras subespecies. En particular, observamos que los búhos de la subespecie *S. n. yosemitensis* mostraron áreas de rango de hogar más extensas que las documentadas para otras subespecies, debido principalmente a los movimientos descendentes altitudinales y a la expansión de sus rangos de hogar durante la temporada no reproductiva. Nuestros resultados sugieren que la gestión futura debería enfocarse y priorizar las necesidades de hábitat durante la temporada reproductiva y no reproductiva, y que es necesario profundizar en la investigación de los efectos de los incendios y las colisiones con vehículos en esta población.

[Traducción de Ramiro Aragón Pérez]

INTRODUCTION

The Great Gray Owl (*Strix nebulosa*; hereafter owl) is a large raptor distributed throughout the world's Holarctic forests, with two long-recognized subspecies, *S. n. lapponica* in northern Europe and Asia, and *S. n. nebulosa* in North America from Central Alaska southward through Canada into the Rocky Mountains and the Cascade Range (Clements et al. 2024). Genetic evidence recently supported designating a third subspecies, *S. n. yosemitensis*, with a population concentrated in the central Sierra Nevada of California, USA (Hull et al. 2014). Great Gray Owls from the Sierra Nevada comprise an allopatric population endemic to California, where the population is listed as endangered by the California Department of Fish and Wildlife (2026) and occupies a range centered largely on Yosemite National Park and adjacent Stanislaus National Forest (Hull et al. 2010, 2014, Wu et al. 2016, Mendelsohn et al. 2020). Wu et al. (2016) estimated the *S. n. yosemitensis* population at approximately 160 adults, although recent discoveries of additional pairs suggested the population might be slightly larger (RAP and RBS unpubl. data).

Habitat selection, the innate and learned behavioral responses by which animals select space and resources from available environments, ultimately influences the distribution, abundance, and fitness of individuals (Block and Brennan 1993, Boyce et al. 2003, Morris 2003, Mayor et al. 2009, Matthiopoulos et al. 2023). Understanding the factors that drive habitat selection is critical for informing conservation and habitat management efforts for taxa of conservation concern (Guyot et al. 2017, Richter et al. 2020). Indeed, Schofield et al. (2023) projected a substantial redistribution of habitat for *S. n. yosemitensis* due to climate change in the coming decades. A more nuanced understanding of the subspecies' particular habitat needs and preferences could help refine these models and reduce uncertainty in the resulting projections. In turn, such refinements could yield critical information for conservation and habitat management in the context of a rapidly changing landscape where habitat and the current boundaries of protected areas may be less well aligned.

Information pertaining to space use and habitat selection for foraging and roosting by *S. n. yosemitensis* is not as well developed as for *S. n. nebulosa*, but there are reasons to suspect the two subspecies may have important ecological differences. For example, nest-site selection has been extensively investigated in *S. n. yosemitensis* (Wu et al. 2015, Polasik et al. 2016), and appears to differ markedly from nest-site selection in *S. n. nebulosa*. *S. n. yosemitensis* owls generally nest in broken-top snags or tree cavities and only rarely in abandoned stick nests built by other birds (just 1 of 42 nest observations compiled by Wu et al. 2015), whereas *S. n. nebulosa* owls more commonly use stick nests (Franklin 1988, Voous 1988, Bedrosian et al. 2015, KBG unpubl. data). This contrast suggests the possibility of other ecological, behavioral, or physiological differences between the two subspecies, and calls into question the applicability of information on habitat needs gleaned from studies of other subspecies.

Prior studies of movement or space use among in *S. n. yosemitensis* (van Riper III and van Wagtendonk 2006, van Riper III et al. 2013) that used conventional

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ground-based radiotelemetry reported that home-range size and habitat use were strongly influenced by season, confirmed that owls showed a strong affinity for montane meadows, and suggested that human recreational activities might negatively impact distribution and habitat use. In contrast, *S. n. yosemitensis* space use and habitat selection for foraging and roosting had never been assessed using modern tracking methods with the potential to yield vastly more data and, consequently, a much more nuanced picture of behavior and habitat selection. Recent advances in GPS tracking technology, particularly miniaturization of tracking units and increases in data storage capacity, have enabled more precise animal tracking and automated collection and logging of high-resolution data on animal movement. When coupled with modern statistical techniques, these advances can reveal detailed patterns of habitat selection for challenging species like highly mobile, nocturnal owls (Blakey et al. 2019, Kramer et al. 2021).

Modern tracking methods have been deployed recently elsewhere in the Great Gray Owl's range (Gura 2023, Gura et al. 2025a, 2025b) and provide ample opportunities for comparison with data gathered on *S. n. yosemitensis*. It is inadvisable to assume similar habitat selection and space use compared to other subspecies, as *S. n. yosemitensis* occupies quite different habitat at substantially higher latitudes (Hull et al. 2014, Mendelsohn et al. 2020, Schofield et al. 2023). Occupying the far southern extent of the species' range, *S. n. yosemitensis* owls regularly encounter different environmental conditions than those experienced by owls farther north. Warmer summer temperatures could favor selection of cooler microhabitats or spur more upslope movements during extreme heat events. In winter, densely packed snow resulting from repeated warming and cooling cycles that characterize winter in the Sierra Nevada may become impenetrable for foraging, causing owls to seek snow-free areas downslope (van Riper III and van Wagtendonk 2006, Jepsen et al. 2011, Gura et al. 2025b).

Stewardship and habitat management for the small population of *S. n. yosemitensis*, which may be particularly vulnerable to climate change (Schofield et al. 2023), the changing fire regime in the Sierra Nevada (Siegel et al. 2019), and habitat modification or destruction for development (Wu et al. 2016), requires reliable information on habitat selection specific to *S. n. yosemitensis*.

In this study, we present an analysis of space use, resource selection, and diel activity throughout the annual cycle of *S. n. yosemitensis* within Yosemite National Park and the adjacent Stanislaus National Forest. Through two breeding seasons and one nonbreeding season, we characterized owl home-range size, evaluated habitat selection across the full annual cycle, and described activity patterns over the 24-hr daily cycle. Based on prior findings using older telemetry methods, and results from studies of other subspecies, we expected substantial variation in home-range size across the full annual cycle, including downslope movements by higher-elevation nesting birds after the breeding season (Bull et al. 1988, van Riper III and van Wagtendonk 2006, Gura et al. 2025b). We expected that breeding male owls would exhibit greater displacement (straight-line distance between consecutive GPS locations) than females and nonbreeding males during the breeding season due to their role in providing food to females and young owls (Gura et al. 2025a). In addition, we predicted greater displacement during the dusk-to-dawn period compared to diurnal hours (Gura et al. 2025a). We expected owls to select different habitats depending on time of day and season (Gura 2023). We expected that *S. n. yosemitensis* would select areas near meadows or open forests as foraging areas between dusk and dawn, but that thermoregulatory or other needs would lead to selection of closed-canopy forest with high canopy bulk density for roosting during the day (Gura et al. 2025a). We also expected that the need for shade would result in owls avoiding high-severity burned areas for roosting. Finally, because Great Gray Owls are believed to be relatively intolerant of human activity (Wildman 1992), we predicted that roosting would occur preferentially in areas away from roads, buildings, and intensive human recreational activities.

MATERIALS AND METHODS

Study Area. We studied Great Gray Owls within Yosemite National Park and the adjacent Stanislaus National Forest in the central Sierra Nevada of California, USA, from March 2022 through March 2024. We focused on known breeding territories, each roughly centered on a large meadow or meadow complex. Core meadows in the territories were distributed across the Sierran Mixed Conifer and Red Fir ecological zones at elevations ranging from 1220 to 1900 masl (Mayer and Laudenslayer 1988; Fig. 1). Owls were previously detected at 68 meadows in Yosemite National Park, although the number of distinct home ranges is likely considerably smaller (Siegel et al. 2019). We chose territory subsamples to study nonrandomly based on the feasibility of ground-based tracking and specific information needs of park managers.

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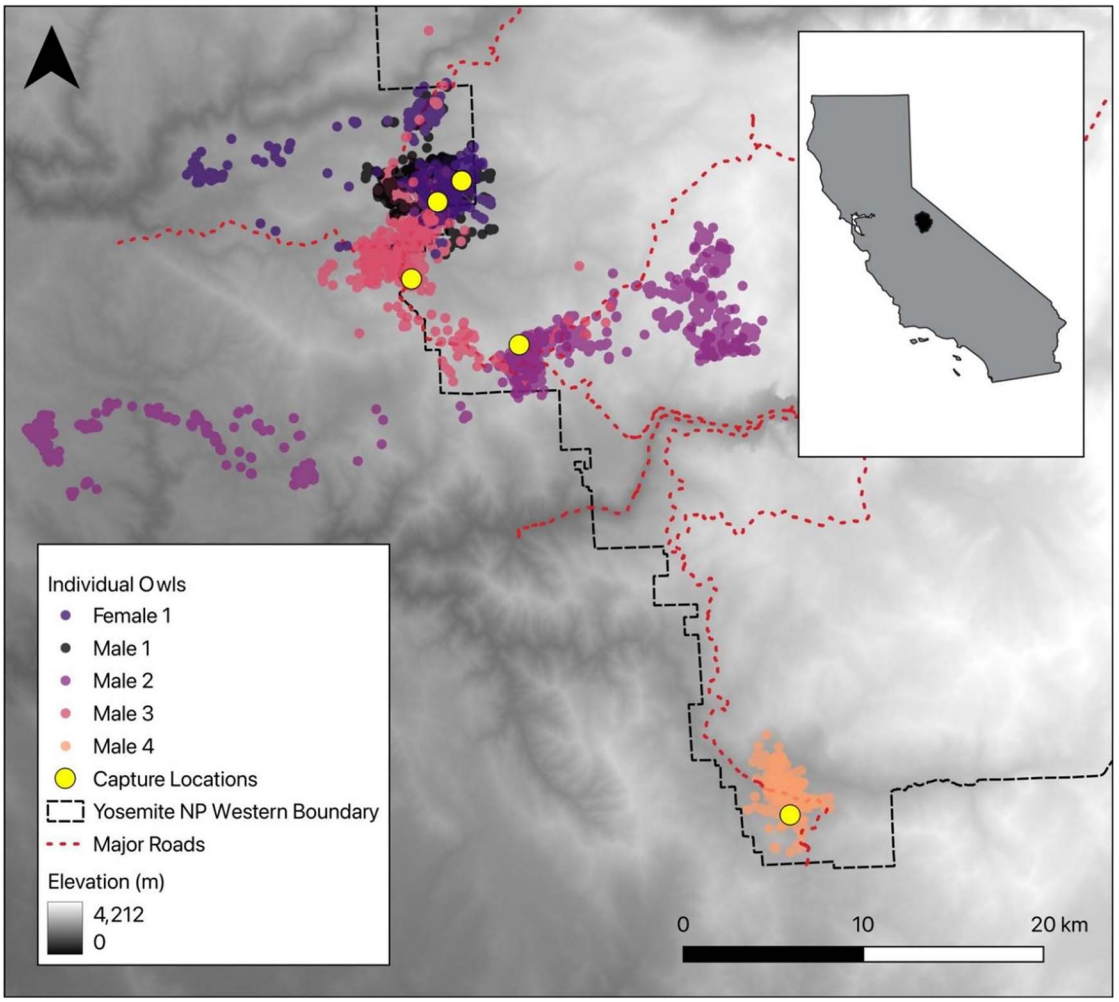

Figure 1. Study area showing boundaries of Yosemite National Park (black outline) with inset showing location of Yosemite National Park within California, USA. Great Gray Owl locations collected at a rate of 1 fix/3 hr between March 2022 and March 2024 are shown, with separate colors for each of five owls.

Capturing, Tagging, and Tracking Owls. We used a pan trap with a live mouse to trap adult owls. To minimize disturbance to nesting, we preferentially targeted males, but also tagged one female caught incidentally. Once we located a target owl, we placed the trap within sight of the owl and monitored visually until it was captured. We immediately secured and removed each trapped owl, and hooded each with a breathable hood to minimize stress. We applied a USGS aluminum leg band, took morphometric measurements, collected blood samples for future genetic analysis, and mounted a GPS data-logger with affixed VHF transmitter (GPS/PinPoint VHF large ≥200mAh data-logger, Lotek, Seattle, WA) using a backpack-style attachment with tubular Teflon ribbon. The total mass of the transmitter and harness was <5% of the mass of individual study owls. We recaptured all owls at the end of the study to remove the data-loggers and harnesses.

For data analysis, we designated inclusive dates of the breeding and nonbreeding seasons following Beck and Winter (2000), who delineated Great Gray Owl nesting phenology in the Sierra Nevada depending on latitude and elevation zone. This schema remains widely used throughout the region for setting the timing of owl occupancy or reproductive

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surveys and for establishing limited operating periods for activities that might disturb nesting. Aligning with Beck and Winter (2000) streamlines the application of our findings to future surveys and resource management decisions. Using predetermined cutoff dates for defining the breeding season also avoided subjectivity and circular reasoning in interpreting the meaning of observed movements with regard to the onset and cessation of nesting activity. For owls captured in the middle elevation zone (1219–1828 m, $n = 4$), Beck and Winter (2000) defined the breeding season as 1 April–31 August, whereas for one owl captured in the high-elevation zone (above 1828 m), the breeding season was designated as 25 April–25 September. We programmed the GPS dataloggers to collect coordinates at 1-hr intervals throughout each day of the breeding season and a 1-mo buffer at the beginning and end (1 March–30 September overall), and at 3-hr intervals during the remainder of the year (1 October to 28 February). We determined nest locations for each individual owl based on field observations.

We located tagged owls via a Yagi antenna and remotely downloaded data via a PinPoint Commander base station (Lotek) at least every 3 mo. We visually reviewed and removed obviously erroneous owl locations (e.g., where an owl would have had to fly >50 km/hr to reach the next point and then return to exactly the same location), but did not filter our locations by GPS accuracy. Because Great Gray Owls sometimes move in dense vegetation and under canopy, filtering lower accuracy GPS locations could have biased our locations to open areas only (Nielson et al. 2009).

Environmental Covariates. We represented the owls' environment through resource, risk, and range variables (Table 1). We standardized all variables prior to modeling. We evaluated lidar-derived resource variables of canopy cover, canopy bulk density, number of canopy layers, and burn severity of the most recent fire that occurred closest to 2024. We evaluated risk variables of distance to road, distance to developed area, and cumulative outdoor activity index (COI). The COI provided a direct estimate of human recreation based on frequency of humans on the landscape, instead of by measuring human presence based on structural proxies like infrastructure (Corradini et al. 2021). We obtained COI estimates from the Strava Global Heatmap (Strava 2024), a crowdsourced, global database of GPS-tracked recreational activities (e.g., hiking, running, cycling). We used the heatmap data to represent a year of human recreational activity, spanning 23 July 2023 to 24 July 2024. We used 10 yr of data (2012–2023) to estimate burn severity for all fires >10 ha within 1 km of any owl location. To estimate burn severity, we combined the annual mosaics provided by the Monitoring Trends in Burn Severity (U.S. Geological Society and U.S. Forest Service 2025) database (also see Eidenshink et al. 2007) into a raster with the maximum burn severity recorded for each pixel that was subject to fire. Because Great Gray Owls are central-place foragers, we evaluated two range variables to account for their tendency to remain close to their nest during the breeding season and range more widely during the nonbreeding season. The two range variables included log-transformed distance to nest and log-transformed distance to edge of home range (home range estimation is described below).

Statistical Analyses. *Home range.* We calculated home ranges via the autocorrelated kernel density estimator (AKDE), which uses an appropriate movement model to account for the inherent autocorrelation in high-resolution movement data (Fleming et al. 2015). Home ranges can only be calculated for individuals that show a tendency to remain in a defined region, referred to as ranging behavior or range residency (Calabrese et al. 2016). We verified semivariograms for each tracked owl to establish whether they showed range residency.

To calculate home ranges, we first used the *ctmm* package v1.3.1 within the *amt* package 0.3.1.0 wrapper in R 4.5.0 (R Core Team 2025) to automatically select the most parsimonious movement model for each individual owl by using Akaike information criterion scores corrected for small sample sizes (AICc) to compare six candidate models. The types of movement models we selected were independent identically distributed models (IID, the default for traditional kernel density estimation); the Ornstein-Uhlenbeck (OU) process, which accounts for autocorrelation of positions; and the Ornstein-Uhlenbeck foraging (OUF) process, which accounts for autocorrelation of both positions and velocities. For each of these three models, we compared anisotropic (more ellipsoidal) and isotropic (more spherical) home-range fits. We then selected from among the six candidates (automated within the *amt* package) the model with the lowest AICc as the basis for AKDE calculation. We estimated overall home ranges for each individual, as well as annual breeding and nonbreeding home ranges. Although we used data collected at a rate of 1 fix/hr to estimate breeding home ranges, we resampled the breeding-season data to a 1 fix/3 hr rate to estimate overall home-range sizes based on combining data from both the

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Table 1. Summary of environmental covariates used in analyses of Great Gray Owl foraging and roosting habitat selection.

Category	Variable	Definition	Spatial Resolution	Source
Resource	Canopy cover (%)	Horizontal cover fraction occupied by tree canopy	10 m	The California Forest Observatory (2020) develops its structural metrics from USGS 3DEP lidar and then uses deep learning to extrapolate these metrics across the landscape using satellite imagery
	Canopy layer count (count)	Number of structurally distinct canopy layers		
	Canopy bulk density (kg/m^3)	Mass of leaves and branches divided by crown volume (leaf mass index times leaf area index divided by canopy volume)		
	Burn severity (relative measure)	Differenced normalized burn ratio (dNBR) calculated for each fire that burned in study area within 10 yr prior to study	30 m	Burn Severity Mosaics, Monitoring Trends in Burn Severity, (US Geological Survey and US Forest Service 2025) and Eidenshink et al. (2007)
Risk	Distance to road (km)	Distance to nearest road, including all major roads (identified in Fig. 1)	10 m	Distance raster calculated from TIGER database (US Census Bureau 2024)
	Distance to developed area (km)	Distance to nearest buildings based on building footprints	30 m	Heris et al. 2020
	Cumulative outdoor activity index (COI; relative measure)	Index based on recreational phone app that records outdoor activities (e.g., hiking, biking) and can be used as a proxy for relative human use	~ 50 m	Corradini et al. 2021, Strava 2024
Range	Distance to nest (km)	Distance between GPS location of owl and GPS location of nest, accounting for tendency of central-place foragers to stay closer to their nest	<10 m	Nest locations were found and mapped by Yosemite National Park Staff
	Distance to edge of farthest area used (km)	Distance between GPS location of owl and closest edge of minimum convex polygon encompassing all locations, accounting for owls spending time at edge of home range to defend their territory, explore, or seek extra-pair copulations	<10 m	This study

breeding and nonbreeding seasons. We did not pool annual breeding season estimates because all tracked owls bred in 2022 but not in 2023, meaning we expected their space use to be different across those 2 yr. In contrast, we pooled data from two seasons to estimate the nonbreeding home range for one female owl (no males were tracked for two complete nonbreeding seasons).

We stress that AKDEs are the most reliable home-range estimates, because other space-use estimators (e.g., minimum convex polygon [MCP; Mohr 1947] and original kernel density estimate [KDE; Worton 1989]) assume independent and identically distributed locations and are highly sensitive to the fix rate. To facilitate comparisons to other studies, we derived additional estimators used in other published studies of Great Gray Owl home ranges: 100% MCPs and 50% and 95% KDEs. We calculated MCPs and KDEs using the *amt* package, and report least-squares, cross-validation bandwidths for KDEs.

Monthly space use and displacement. We examined monthly space use and displacement for each owl over different seasons because these measures, taken together, can indicate different behaviors. For example, males and females may both stay close to the nest during the breeding season, resulting in smaller areas of space use, but males may move around a lot while provisioning nestlings, resulting in greater displacement. To calculate monthly space use, we used the MCP approach because, during a particular month, an owl may not show ranging behavior, which is an assumption of the KDE and AKDE models. We used all available locations for each owl, regardless of fix rate. MCP estimates of space use using all of the data were highly correlated with MCP estimates of space use for the dataset thinned to a rate of 1 fix/3 hr ($r > 0.99$), so we were confident that using variable fix rates would not bias the space-use estimates. We used MCPs to estimate monthly space use for 42 owl-months during the breeding season and 42 owl-months during the nonbreeding season, totaling 84 unique months, with an average of 17 mo per individual owl. Across the 84 owl-months in the dataset, 6 did not contain full months due to missing fixes or dead batteries. One owl was missing 6 d, two owls were missing 5 d and three owls were missing 4 d. We did not expect the missing days to significantly influence the results since this small number of missing days were spread across 4 mo, four individuals, and both breeding and non-breeding seasons.

We estimated 24-hr and nightly (period from 1 hr before sunset to 1 hr after sunrise) displacement values as the sum of Euclidean distances between 3-hr location intervals for relevant periods. We also measured maximum distances from the nest for each owl and 24-hr period. During the 2023 breeding season (when none of the owls nested) and the nonbreeding seasons, we based calculations on the location of the nest during the 2022 breeding season. We then averaged the nightly displacements across each month for each individual owl and multiplied by 30 (average month length) to estimate monthly displacement. We included only nights with full sets of locations (8×1 fix/3 hr) in our displacement measurements to avoid potential biases resulting from missing locations.

Diel activity. We estimated diel activity during the two breeding seasons by calculating hourly displacements for each owl. We attributed hour of the day (continuous predictor) to each hourly displacement measurement and fit a generalized additive model for each individual owl via a cyclic penalized cubic regression spline smooth with the R package *mgcv* 1.9-1 (Wood 2004). This approach allowed for portraying continuous relationships across 24-hr cycles.

Foraging and Roosting Habitat Selection. We modeled selection of nocturnal foraging habitat for the period from 1 hr before sunset to 1 hr after sunrise by comparing each individual location to available locations (see design 4 in Thomas and Taylor 2006). Using step functions, we compared observed steps (movements connecting successive hourly locations) with random possible steps generated from distributions of turning angles and step lengths from the broader population. We used the *amt* package to fit six separate step-selection functions via conditional logistic regression. We fitted separate models for the two breeding seasons using the hourly fix data. We fitted models for the nonbreeding season (pooled across years where relevant) based resampling hourly shoulder-season data to the same 1 fix/3 hr rate used during the rest of the nonbreeding period. For the female owl, we fitted a separate step-selection function for each of the three seasons (two breeding, one pooled nonbreeding), with each stratum representing one step (including the observed step and 20 potential steps), with resource (canopy cover, canopy bulk density, canopy layers, burn severity), risk (distance to road, distance to developed area, and COI), and range variables (distance to nest, distance to edge of home range) as predictor variables. We fitted separate step-selection functions to data from the male owls, which had the same model structure but with an extra stratum (individual) to account for variability among individual males.

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We modeled diurnal roosting habitat selection by using the location collected closest to 1200 H each day. We characterized available roost locations by sampling 10 random locations for each daily roost location within the MCP quantified for each owl. We then fitted simple resource selection functions via logistic regression, with a binary response variable of 1 (roost location) or 0 (random locations), and with a random intercept for individual owls. We fitted the same six seasonal models for each sex, including the same risk, resource, and range covariates used to model foraging habitat selection (Table 1). For all habitat selection analyses, we interpreted model coefficients as representing selection if the coefficient and 95% confidence interval were greater than zero, and as avoidance if the coefficient and 95% confidence interval were less than zero.

RESULTS

We tracked all owls ($n = 5$) for a minimum of one full annual cycle, two male owls for two consecutive breeding seasons, and the one female owl for two consecutive breeding and nonbreeding seasons, Female 1 and Male 1 were confirmed to be a mated pair (Fig. 2). The all-inclusive tracking period was 17 March 2022–25 March 2024. We collected a total of 44,271 GPS locations ($\bar{x} = 8854$ locations/owl, range = 4808–12,705). All monitored owls bred during the 2022 breeding season; none were observed breeding during the 2023 breeding season.

Movement. *Home range.* We estimated the female's overall (full annual cycle) home range to be 46 km^2. Inspection of a semi-variogram plot of movement data revealed that one male's (Male 2) home range was not estimable because he did not exhibit ranging behavior (Calabrese et al. 2016) sufficient to satisfy assumptions required to calculate AKDE/KDEs. Estimated overall home ranges for the remaining three males were 7, 25, and 42 km^2(Table S1). The female's breeding season home range was smaller during the 2022 breeding season when she bred (4 km^2; Table S2) than during the 2023 breeding season when she did not (7 km^2; Table S3). Males showed a similar pattern; except for the high-elevation individual (Male 2), their home ranges varied from 7 to 14 km^2 during the 2022 breeding season when they bred, and from 19 to 20 km^2 during the 2023 breeding season when they did not breed. During the nonbreeding season, two of three males with estimable home ranges exhibited enlarged home ranges (28 and 31 km^2) compared to the breeding seasons, whereas the third exhibited a smaller home range

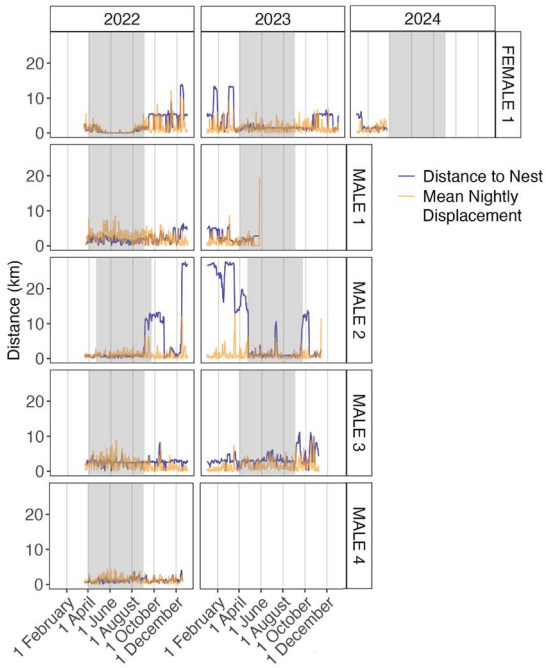

Figure 2. Daily maximum travel distances from nest and 24-hr displacements (sum of straight-line distances between consecutive locations sampled at 1 fix/3 hr) by Great Gray Owls in the Sierra Nevada of California from March 2022 through March 2024. Periods defined as breeding seasons (gray shading) varied by elevation (Male 2 nested higher than the other owls). The five owls were distinct individuals; Female 1 and Male 1 were mates.

(7 km^2; Table S4). The female's nonbreeding season home range (151 km^2) was much larger (Table S4). The high-elevation male (Male 2) covered more area than the other owls, ranging across 49 km^2 during the 2022 breeding season (Table S2), 29 km^2 during the 2023 breeding season (Table S3), and 270 km^2 during the non-breeding season (Table S4).

Space use and displacement. For the female owl, displacement and space use were both lowest during the 2022 breeding season, highest during the nonbreeding season, and intermediate during the 2023 breeding season (Fig. 3, Table S5). The same space-use pattern was evident for males; however, males showed the greatest displacement distances during the 2022 breeding season and the lowest during the 2023 breeding season (Fig. 3, Table S5).

The female owl traveled a maximum of 3.2 km from her nest in a 24-hr period during the breeding season (2022: 2.5 km, 2023: 3.2 km), and 14.0 km during the nonbreeding season (2022–2023), in comparison, males traveled a maximum of 19.9 km

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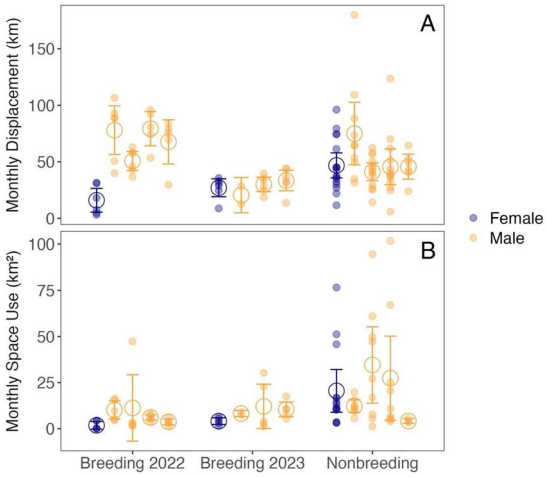

Figure 3. A) Mean monthly displacement (km) and B) mean space use (km^2) (with 95% confidence intervals) for five Great Gray Owls in the Sierra Nevada of California. All tracked owls bred during the 2022 breeding season, but none bred during the 2023 breeding season.

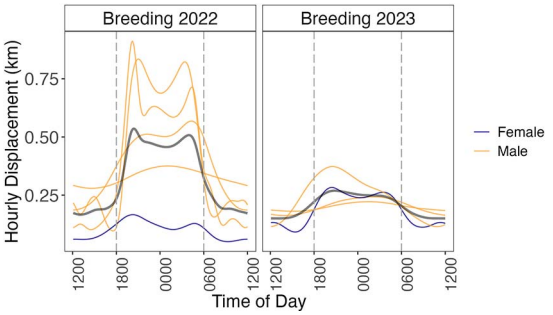

Figure 4. Diel activity patterns for five Great Gray Owls in the Sierra Nevada of California across two breeding seasons, shown as hourly displacement (km) by female (blue line), male (yellow line), and mean (thick gray line).

from the nest during the breeding season (2022: 5.3, 2023: 19.9) and 27.7 km during the nonbreeding season (Fig. 2). The high-elevation male (Male 2) traveled the farthest from the nest (Fig. 2).

Diel activity. During the 2022 breeding season, four of the five owls showed two distinct peaks in daily activity (Fig. 4), one from 2010–2215 H (predicted hourly displacement $\bar{x} = 0.6$ km, range 0.5–0.9 km) and one from 0325–0445 H ($\bar{x} = 0.6$ km, range 0.1–0.8 km). During the 2023 breeding season when hourly displacement levels were lower overall, only the female individual showed peaks in activity at both dawn and dusk.

Foraging and Roosting Habitat Selection. For nocturnal foraging, male and female owls tended to avoid areas with greater canopy cover but showed mixed responses to canopy bulk density and presence of multiple canopy layers (Fig. 5). Both sexes also tended to avoid foraging in areas that had burned at high severity. When nesting in 2022, the female owl also avoided foraging near roads, whereas in all other cases, owls either foraged closer to roads or used them in proportion to their availability. In relation to human recreational activity and proximity to buildings, owls generally showed no discernable responses or inconsistent patterns across sexes and seasons (Fig. 5).

We modeled roosting habitat selection based on a sample of 27,852 locations that included 2532 roost observations. For diurnal roosting, both sexes tended to select late seral forest that included multiple canopy layers, high canopy bulk density, and substantial canopy cover (Fig. 5 and 6). Other aspects of roosting habitat selection were similar to foraging habitat selection. Owls avoided areas burned at high severity during the nonbreeding season and either avoided or used these areas in proportion to availability during breeding seasons (Fig. 5). Except for the nesting female in 2022 who avoided roosting near roads, owls either roosted closer to roads or used them in proportion to their availability, and did not show consistent roosting patterns across sex or season in relation to human recreational activity or proximity to buildings (Fig. 5).

DISCUSSION

Most studies of habitat selection by vertebrates have focused on a single period of the annual cycle, typically the breeding season (Marra et al. 2015). Fully understanding a species' habitat needs requires information from all components of the annual cycle, however, including nonbreeding, dispersal, and migration periods. We evaluated habitat selection, space use, and diel activity through the annual cycle for *S. n. yosemitensis,* a subspecies with a small, geographically restricted population. As is often the case with studies of rare or sparsely distributed wildlife (Bissonette 1999), our sample size was small ($n = 5$ owls) but we were able to collect large amounts of data for each owl. Further, the only female owl was mated to one of the male subjects, precluding formal testing of predictions related to effects of sex or breeding status. Nevertheless, our tracking efforts yielded some notable patterns that may aid conservation of this small population, facilitate comparison with other subspecies, and perhaps

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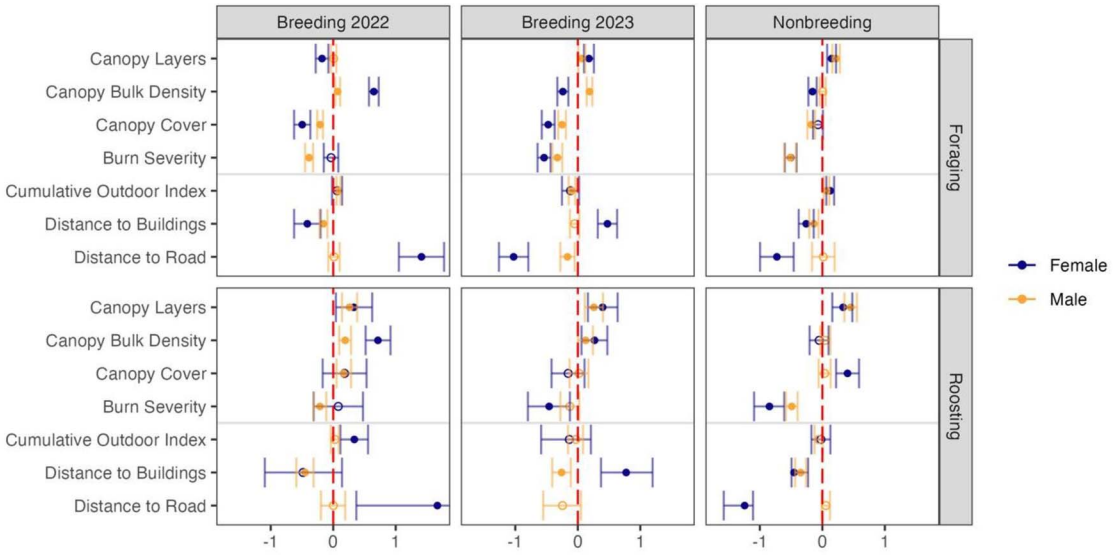

Figure 5. Nocturnal foraging and diurnal roosting habitat selection for one female and four male Great Gray Owls during the 2022 and 2023 breeding and nonbreeding seasons (two nonbreeding yr combined for female) in the Sierra Nevada of California. Plots show the coefficients and 95% confidence intervals from the models used to infer selection or avoidance of different habitats by owls based on resource selection functions (roost) and step–selection functions (foraging). Coefficients with confidence intervals that do not overlap zero (filled circles) indicate a statistically significant selection for or against the indicated variable. Positive distance variables indicate habitat use farther from the indicated features and negative values indicate habitat use closer to the features. The roosting coefficient for the distance-to-roads variable for the female owl during the 2023 breeding season is not graphed due to a scale mismatch, but was strongly negative (coefficient = -4 ± 1 CI).

further contribute to formal testing of predictions if more data can be obtained in the future.

Home Range. As expected, we found substantial variation in home-range size across the annual cycle. Pooling data across all individuals, nonbreeding home ranges averaged about three times larger than breeding home ranges, and overall year-round home ranges averaged approximately three to five times larger than home ranges during the breeding season. One male, which bred at a higher elevation than the other owls we tracked, exhibited a relatively large nonbreeding home range, reflecting extensive elevational movements following the breeding season that were consistent with previous reports on *S. n. yosemitensis* (Winter 1986). Great Gray Owls tend to avoid higher snow accumulation and severe snow crust (Gura et al. 2025b), suggesting that these movements may have been facultative in response to high snow accumulation at higher elevations within the breeding range. The 2022–2023 winter, in particular, featured near-record snowfall throughout the region (Cunha 2023).

Previous studies of Great Gray Owls yielded highly variable results for home-range size, which might be attributed to factors such as sampling variation resulting from small-sample studies, differences in the seasonal extent of tracking, and variability in the tracking technology and quantitative methods used for estimating home ranges (Table 2). For instance, Bull et al. (1988) reported a year-round home range size, whereas other researchers (van Riper III and van Wagtendonk 2006, Gura 2023, Gura et al. 2025a) presented home-range sizes disaggregated by breeding and nonbreeding seasons, breeding status, and sex. Earlier home-range estimates reported for *S. n. yosemitensis* (Winter 1986, van Riper III and van Wagtendonk 2006) exclusively used conventional radiotelemetry, whereas we used GPS technology to provide more intensive and accurate location data. Notably, from all published studies on the three subspecies, only one home-range estimate (for a nonbreeding male in Yosemite National Park; van Riper III and van Wagtendonk 2006) was larger than the home-range means we obtained (Table 2). Some of our estimates were, however, influenced by the large home range of one high-elevation male. This outcome might have reflected

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Figure 6. Example of Great Gray Owl roosting habitat in an area burned by mixed-severity fire on National Forest land just outside Yosemite National Park in the Sierra Nevada of California (Photo: Connor Ragland).

stochastic variation or that high-elevation breeders generally exhibit more extensive movements in the nonbreeding season, which aligns with our expectation of downslope winter movements among owls nesting at higher elevations.

Designated start and end dates to the breeding season may substantially affect the estimated size of seasonal home ranges. Great Gray Owls in the Sierra Nevada and elsewhere (Winter 1986, van Riper III and van Wagtendonk 2006, Gura et al. 2025b) undertake relatively long facultative movements after the breeding season, as was the case for multiple individuals in our study. The misclassification of such movements as part of the breeding season could inflate breeding home-range estimates and diminish nonbreeding estimates. We lacked sufficient behavioral observations of focal birds needed to pinpoint the start and stop dates of breeding activities for individual owls. Therefore, we chose to standardize our seasonal assessments by adhering to the guidelines in Beck and Winter (2000). A final caveat is that some prior studies assessed home-range sizes over multiple years with reproduction, whereas our study encompassed two breeding seasons but only one active breeding season, which corresponded to a year with near-record snowpack.

Despite these caveats and our limited sample size, we were able to draw tentative inferences about *S. n. yosemitensis* home-range size relative to other subspecies. Our breeding home-range estimates were similar to those obtained for *S. n. nebulosa*; e.g., our mean AKDE estimate for males of 12.3 km^2 was comparable to Gura et al.'s (2025a) estimate of 11.8 km^2 (both entries marked vi in Table 2). However, our *S. n. yosemitensis* home-range estimates generally diverged from corresponding *S. n. nebulosa* estimates when we compared nonbreeding home ranges. For example, pooling estimates from both sexes, we estimated a mean ADKE of 36.9 km^2 for the nonbreeding season, which was more than twice as large as Gura 2023 mean estimate of 13.4 km^2 (see entries marked as ix in Table 2). This pattern of *S. n. yosemitensis* exhibiting similar breeding home-range sizes as *S. n. nebulosa*, but much larger nonbreeding home ranges, suggested that *S. n. yosemitensis*

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Table 2. Published estimates of home-range sizes of Great Gray Owls.

Subspecies/Study[a]	Home-range Size (km^2)						Method[b]	Location[c]	Season[d]	Sex	Tracking Technique[e]
	Mean	SE	SD	Minimum	Maximum	*n*					
Strix nebulosa yosemitensis											
i Winter 1986	1.60			0.96	2.41	3	MCP	CA	AC	Male	RT
ii van Riper III and van Wagtendonk 2006	0.61			0.49	0.75	3	AKDE	CA	B	Female	RT
iii van Riper III and van Wagtendonk 2006	24.57			8.54	55.39	3	AKDE	CA	NB	Female	RT
iv van Riper III and van Wagtendonk 2006	0.19					1	AKDE	CA	B	Male	RT
v van Riper III and van Wagtendonk 2006	21.12					1	AKDE	CA	NB	Male	RT
i Present Study	95.71			8.87	284.18	4	MCP	CA	AC	Male	GPS
ii Present Study	4.17					1	KDE	CA	B	Female	GPS
iii Present Study	90.18					1	KDE	CA	NB	Female	GPS
iv Present Study	10.34			7.04	14.97	3	KDE	CA	B	Male	GPS
v Present Study	19.11			8.13	27.63	3	KDE	CA	NB	Male	GPS
vi Present Study	12.29			7.04	17.98	4[f]	KDE	CA	B	Male	GPS
vii Present Study	19.88			7.71	48.89	4[g]	MCP	CA	B	Male	GPS
viii Present Study	33.43					1	KDE	CA	AC	Female	GPS
ix Present Study	36.88			8.13	90.18	4	KDE	CA	NB	Both	GPS
x Present Study	85.62			8.87	284.18	5	MCP	CA	AC	Both	GPS
Strix nebulosa nebulosa											
x Bull et al. 1988	67.3			4	312	8	MCP	OR	AC	Both	RT
vi Gura et al. 2019	6.25		0.82			15	KDE	ID-WY	B	Male	GPS
vii Gura et al. 2019	9.97		2.38			15	MCP	ID-WY	B	Male	GPS
ix Gura 2023	13.37		0.84			42	KDE	ID-WY	NB	Both	GPS
vi Gura et al. 2025a	11.8	2.14				19	KDE	ID-WY	B	Male	GPS
Strix nebulosa lapponica											
viii Mirski et al. 2021	19.43					1	KDE	CB	AC	Female	GPS

[a] Roman numerals indicate studies that used the same estimation method and focused on owls of the same sex (or both sexes).
[b] Minimum convex polygon (MCP), adaptive kernel density estimate (AKDE), kernel density estimate (KDE). All values are at the 95th percentile, except that values from Winter (1986) and Bull et al. (1988) were unspecified.
[c] Oregon (OR), California (CA), Idaho-Wyoming (ID-WY), Central Belarus (CB).
[d] Annual cycle (AC), breeding (B), nonbreeding (NB).
[e] Radiotelemetry (RT), GPS data loggers (GPS).
[f] The mean, min, and max were calculated by pooling five estimates from three individuals across two breeding seasons.
[g] The mean, min, and max were calculated by pooling seven estimates from four individuals across two breeding seasons.

required greater winter space use. This result could reflect the particular challenges to foraging posed by densely packed Sierra Nevada snows that results from frequent warming and cooling cycles, or other ecological or environmental differences between owls in the Idaho-Wyoming study area (tracked by Gura 2023) and the central Sierra Nevada.

Monthly Displacement and Space Use. As we predicted, males exhibited the greatest monthly displacement during the 2022 breeding season when they nested, contrasting with the lowest monthly displacement exhibited during the 2023 breeding season when they did not nest. Breeding males play a crucial role in providing prey to their mates and offspring through the breeding season, including the incubation, nestling, and post-fledging periods (Gura et al. 2025a). The increased need to hunt to feed nestlings likely explains the relatively high displacement for males during the 2022 breeding season. In contrast, the tracked female's displacement and space use were lowest during the 2022 breeding season, which likely reflects the distinct roles females assume in incubation, brooding, and tending nestlings. The female exhibited her greatest displacement and space use during the nonbreeding season, however, whereas the males' displacement during the nonbreeding season did not increase compared to during the 2022 breeding season. Notably, however, the males' monthly space use was larger during the nonbreeding season, which might indicate that breeding males travel more frequently to specific, high-productive hunting areas (Greene 1995), whereas during the nonbreeding season they exhibit more opportunistic and ranging foraging behavior. Also, Great Gray Owls tend to make facultative movements to lower elevations during the winter where snow depth is shallower (Bull et al. 1988, Beck and Winter 2000, van Riper III and van Wagtendonk 2006, Gura et al. 2025b), which may increase nonbreeding season displacement and space used relative to the breeding season. The high-elevation male illustrated this trend, traveling farther than the rest of the owls to lower elevations away from his nesting site after the breeding season.

Diel Activity and Hourly Displacement. Great Gray Owls are considered less strictly nocturnal than other *Strix* species (Nero 1980). Nevertheless, although the Great Gray Owls we tracked exhibited variability in diel activity, hourly displacement and movement patterns suggested they primarily foraged during twilight and nocturnal hours, and roosted during daylight (Fig. 4), which is consistent with recent findings from a *nebulosa* study (Gura et al. 2025a). The female we tracked exhibited lower hourly displacement than all four males during the 2022 breeding season, contrasting with the 2023 breeding season and the nonbreeding season, when hourly displacement of males and the female was similar. Males exhibited their highest hourly displacement during the 2022 breeding season, contrasting with the lowest displacement observed in the 2023 breeding season, suggesting differences in displacement related to sex and breeding status. As with sex-specific differences in home range, the relatively low hourly displacement values for the female while nesting likely reflected more time spent tending the nest and less travel for nest provisioning relative to the males.

Variability in hourly displacement among individuals, particularly during the 2022 breeding season, might also have reflected variability in brood size (which we did not assess) or prey availability within the home ranges. Voles (*Microtus* spp.) and pocket gophers *(Thomomys* spp.), the main prey of Great Gray Owls in the central Sierra Nevada (Winter 1986), have highly cyclic populations (Fitzgerald 1977, Pinter 1986). Although it was outside the scope of our work to study prey density, cyclical changes in prey abundance could drive Great Gray Owls' hourly displacement, especially during the breeding season when males need to provide prey to females and juveniles. Furthermore, our results show variability in foraging behavior among individuals within and between seasons. For instance, during the 2022 breeding season three males exhibited crepuscular and nocturnal foraging habits, while the fourth male foraged extensively during both nocturnal and diurnal hours, exhibiting the lowest displacement among the males (Fig. 4). This may indicate that highly productive hunting areas were closer to the nest and or roosting areas, allowing the owls to passively or actively hunt at any time (Winter 1986). Notably, hunting behavior of all the males shifted from mainly nocturnal in the 2022 breeding season to crepuscular-nocturnal during the nonbreeding season, and back to nocturnal again during the 2023 breeding season. Wildman (1992) reported a similar, but even more strongly contrasting shift from diurnal to strictly nocturnal hunting, and then back to diurnal hunting within 9 wk of nest abandonment.

Habitat Selection and Effects of Fire and Human Activity. Our study suggests that several factors influenced Great Gray Owl habitat use, including time of day and season. Although our sample size was too small for rigorous hypothesis testing, our results were also at least consistent with sex and breeding status affecting habitat selection. As we

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expected, Great Gray Owls generally avoided forest with high canopy cover for foraging at night. This aligns with studies on all three subspecies, which consistently select open forest, montane wet meadows, and edge of meadows as preferred foraging habitats (Mikkola 1983, Winter 1986, Franklin 1988, Bull and Henjum 1990, van Riper III and van Wagtendonk 2006, Wu et al. 2015, Gura et al. 2025a). We also found that, during the 2022 breeding season, roosting owls selected forests with high canopy bulk density; however, the female selected lower canopy bulk density during the nonbreeding season and during the 2023 breeding season when she did not nest, suggesting that breeding status may help to explain habitat selection in females (Fig. 5). Our results are consistent with prior research that identified owls' preference for diurnal roosting in forest stands generally associated with greater canopy cover and density, and the presence of multiple canopy layers, likely to reduce heat stress during summer (Winter 1986, Blakey et al. 2019, Gura 2023, McGinn et al. 2025, Gura et al. 2025a) and perhaps cold stress during winter.

Given the preference for roosting in stands with attributes of older forests, we expected owls to avoid high-severity burned areas for foraging and roosting throughout the annual cycle. However, although female and male owls consistently avoided high-severity burned areas for roosting and foraging during the nonbreeding season, they either avoided or used high-severity areas in proportion to their availability during the breeding season. This suggests a level of resilience to high-severity fires as suggested by Siegel et al. (2019), who found that the 2013 Rim Fire did not reduce occupancy rates of Great Gray Owl territories within its boundaries during the first 3 yr after the fire, much of which was considered high severity (Lydersen et al. 2014). Indeed, some authors have hypothesized that high-severity forest fires might increase the abundance of pocket gophers or their availability to Spotted Owls (*Strix occidentalis*; Franklin et al. 2000, Bond et al. 2013). A similar dynamic could be occurring for Great Gray Owls foraging in meadow-adjacent forest stands; however, due to the generally negative response of Great Gray Owls to high-severity burned areas during the nonbreeding season, and the increasing incidence of such fires in the region, these relationships warrant further investigation.

Yosemite National Park receives millions of recreational visitors each year (National Park Service 2025), yielding substantial potential for owl-human conflicts. Previous studies in the Sierra Nevada and Wyoming suggested that developed areas and human recreational activities adversely affected Great Gray Owl habitat use (Reid 1988, Wildman 1992, Jepsen et al. 2011, van Riper III et al. 2013, Gura 2023, Gura et al. 2025a). Studies in Yosemite have yielded contrasting outcomes, however. Past work in Yosemite suggested the presence of humans in montane meadows, including recreational birders observing Great Gray Owls, could cause owls to abandon hunting efforts if they were flushed from perches and leave the area for up to 45 min (Reid 1988, Wildman 1992). Other research suggested birders or researchers likely had little to no impact on the owls' overall hunting efforts (Winter 1986). Furthermore, Great Gray Owls in Europe tended to visit developed areas and farmhouses, particularly during winter, when they could appear notably fearless of humans (Mikkola 1983). We found evidence that males during the 2022 breeding season and nonbreeding season selected areas with more human recreational activity and closer proximity to buildings for foraging and roosting. The drivers behind the selection of these areas are unclear, however. It is possible that this apparent preference might not be due to owls being attracted to human encroachment, but rather simply reflect that humans and owls have chosen to concentrate in the same areas, and for these owls the resources these areas provide may outweigh any aversion to human activity and buildings (Gura et al. 2025a). More research assessing Great Gray Owl tolerance of human activity and encroachment throughout the annual and diel cycles is needed to better understand the response of owls to anthropogenic disturbance.

Except for the female nesting during the 2022 breeding season, owls either selected areas closer to roads or used them in proportion to their availability, suggesting that Great Gray Owls either do not perceive the roads as a risk or the drive to feed their offspring is strong enough to outweigh the perceived risks associated with roads. This is concerning because vehicle collisions are a frequent cause of mortality of Great Gray Owls in Yosemite and adjacent areas (Jepsen et al. 2011, Wu et al. 2016). In Wyoming, Gura et al. (2025a) found that Great Gray Owls preferentially foraged near roads, particularly when roads were juxtaposed with key foraging habitat. They suggested the owls might have been attracted to prey congregated near roads or to the artificial hunting corridors created by roadways. Roads may also serve as travel corridors between nesting areas and foraging areas with high prey. In either scenario, the attraction to roads might outweigh the perceived disturbance from vehicle traffic

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(Grilo et al. 2014). Relatively frequent owl-vehicle collisions in Yosemite, combined with our ambiguous results pertaining to effects of road proximity on habitat selection, suggest a need for additional investigation of factors that govern owl use of roads and roadside habitat in the park. Such factors include road juxtaposition with preferred foraging habitat, roadside vegetation structure, prey availability, and intensity of vehicle traffic through the annual and diel cycles. A better understanding of these factors could inform management approaches for reducing owl mortality from vehicle collisions.

Conclusions. Understanding habitat needs is critical for conserving range-restricted, small populations like those of *S. n. yosemitensis*, and technical advances in tracking technology allowed us to collect far more information on space use and habitat selection by the subspecies than has been achieved previously using conventional radiotracking methods. Our findings reveal many similarities in foraging and roosting habitat use with the much more broadly distributed *S. n. nebulosa*, but also suggest some possible differences that may be important for future conservation efforts. In particular, our results suggest that *S. n. yosemitensis* may have substantially larger home ranges than *S. n. nebulosa*, primarily driven by downslope movements and substantial expansions of home ranges during the nonbreeding season. We caution that although these results are based on tens of thousands of GPS fixes, they comprise data from only five individual owls. Nevertheless, if representative of the subspecies, they suggest that threats such as high-severity fires, owl-vehicle collisions, and habitat loss due to development and timber harvest in nonbreeding habitat may be at least as critical for owl conservation as breeding habitat constraints. This aligns with recent findings about the importance of nonbreeding habitat for *S. n. nebulosa* (Gura et al. 2025b) and corroborates the suggestion by Jepsen et al. (2011) that *S. n. yosemitensis* conservation efforts may need to encompass winter habitat requirements at lower elevations outside Yosemite National Park.

SUPPLEMENTAL MATERIAL (available online). Table S1: Estimated overall home-range sizes for Great Gray Owls across full annual cycles between March 2022 and March 2024 in the Sierra Nevada, with all GPS telemetry locations resampled at a rate of 1 fix/3 hr. Table S2: Estimated home-range sizes for Great Gray Owls during the 2022 breeding season in the Sierra Nevada of California when all study owls nested. Table S3: Estimated home-range sizes for Great Gray Owls in the Sierra Nevada of California during the 2023 breeding season when no study owls nested. Table S4: Estimated home-range sizes (km_2) for Great Gray Owls in the Sierra Nevada of California during the 2022/2023 and 2023/2024 nonbreeding seasons. Table S5: Mean monthly space use and displacement for Great Gray Owls in the Sierra Nevada of California during the breeding season (when they bred in 2022, and when they did not breed in 2023) and nonbreeding season (also see Figure 3).

ACKNOWLEDGMENTS

We thank Yosemite Conservancy, Sierra Foothills Audubon Society, and San Fernando Valley Audubon Society for funding this project. Esther Burkett and Neil Clipperton at California Department of Fish and Wildlife provided invaluable help with permitting and Ryan Kalinowski provided information and logistical assistance for working on Stanislaus National Forest. This is Contribution Number 840 of The Institute for Bird Populations. We thank three anonymous reviewers for comments that improved the manuscript.

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Received 1 October 2025; accepted 6 June 2026
Associate Editor: Marion A. Clément

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