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NORTHERN GOSHAWK (*ACCIPITER GENTILIS*) HOME RANGES, MOVEMENTS, AND FORAYS REVEALED BY GPS-TRACKING

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Abstract.—The Northern Goshawk (*Accipiter gentilis*) is an apex predator occurring across North America and Eurasia. The species has received considerable conservation focus in late-seral conifer forests of western North America, where its habitat has been substantially reduced and altered by timber harvest and is increasingly at risk from high severity fire, drought, and forest pathogens. In the Sierra Nevada range of California, management and conservation of goshawks are hampered by a lack of knowledge of their basic space use and movement ecology. We used global positioning system (GPS) loggers to investigate space use of 20 resident, adult Northern Goshawks over 3 yr (2015–2018) in the Plumas National Forest, California. Median home range sizes of male goshawks were more than twice as large as those of females, and nonbreeding-season home ranges were three times larger than breeding-season home ranges. High resolution GPS data (location interval 1–6 min) allowed quantification of daily transit distances up to 60 km for individual goshawks and revealed long-distance forays into adjacent territories and surrounding areas. Four goshawks (three males, one female) undertook forays >8 km from their nest locations, with forays lasting up to 6 d; these forays occurred during both breeding and nonbreeding seasons for both sexes. Comparing our results to current conservation approaches, we determined that USDA Forest Service goshawk Protected Activity Centers protected <25% of both the roost locations and the area used during the daytime. Conservation efforts for Northern Goshawks in the Sierra Nevada would benefit from consideration of year-round habitat needs at larger scales than previously thought.

Key Words: *Northern Goshawk*; Accipiter gentilis; *foraging*; *forest management*; *high resolution tracking*; *late-seral forest*; *old growth forest*; *raptor*; *roost.*

ÁREA DE CAMPEO, MOVIMIENTOS E INCURSIONES DE *ACCIPITER GENTILIS* MOSTRADAS POR TELEMETRÍA GPS

Resumen.—*Accipiter gentilis* es un superdepredador que se distribuye a través de Norteamérica y Eurasia. La especie ha sido el centro de considerables esfuerzos de conservación en bosques de coníferas cuasi maduros

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del oeste de Norteamérica, donde su hábitat ha sido substancialmente reducido y alterado por aprovechamiento forestal y está cada vez más en peligro por alto riesgo de incendios, sequía y patógenos forestales. En la cordillera de la Sierra Nevada de California, el manejo y la conservación de *A. gentilis* están obstaculizados por una falta de conocimiento de su uso básico del espacio y de su ecología de movimientos. Usamos sistemas de posicionamiento global (GPS, en sus siglas en inglés) para investigar el uso del espacio en 20 individuos residentes adultos de *A. gentilis* a lo largo de 3 años (2015–2018) en el Bosque Nacional Plumas, California. La mediana del tamaño de las áreas de campeo de los machos fue más del doble que la de las hembras, y las áreas de campeo de la época no reproductiva fueron tres veces más grandes que las áreas de campeo de la época reproductiva. Los datos de GPS de alta resolución (intervalos de localización de 1–6 min) permitieron cuantificar distancias diarias de desplazamiento de hasta 60 km para un individuo y mostraron incursiones de larga distancia hacia territorios adyacentes y áreas circundantes. Cuatro individuos de *A. gentilis* (tres machos, una hembra) realizaron incursiones mayores de 8 km desde las ubicaciones de sus nidos, con incursiones de hasta 6 días de duración; estas incursiones, realizadas por ambos sexos, fueron observadas tanto en la época de cría como fuera de ésta. Comparando nuestros resultados con los enfoques actuales de conservación, determinamos que los Centros de Actividades Protegidas para *A. gentilis* del Servicio Forestal del Departamento de Agricultura de Estados Unidos protegieron menos del 25 % de los dormideros y de las áreas usadas durante el día. Los esfuerzos de conservación de *A. gentilis* en la Sierra Nevada podrían beneficiarse si se consideran las necesidades de hábitat a lo largo de todo el año y a escalas mayores que las consideradas previamente.

[Traducción del equipo editorial]

Introduction

The Northern Goshawk (*Accipiter gentilis*), an apex predator inhabiting forests throughout the Holarctic region (Squires et al. 2020), has received considerable conservation interest due to observed population declines associated with timber harvest (Reynolds et al. 2006). In North America, the Northern Goshawk ranges widely across Alaska, Canada, western United States, and Mexico, where it nests in conifer, aspen (*Populus* spp.), pinyon-juniper (*Pinus* spp. and *Juniperus* spp.), and juniper forests (Younk and Bechard 1994, Graham et al. 1999, Reich et al. 2004, Greenwald et al. 2005, Reynolds et al. 2008, Miller et al. 2013). Goshawks are vulnerable to habitat alteration in western North American forests, including both changing fire regimes and fuels-reduction efforts intended to mitigate effects of high severity fires (Ray et al. 2014, Reynolds et al. 2017, Blakey et al. 2020). Efforts to understand goshawk spatial ecology (particularly while foraging or during winter) are hampered by the species' cryptic and highly mobile nature, and its preference for dense forest where detection can be difficult.

Northern Goshawks are territorial, central-place foragers, and western North American populations may be resident, seasonally migratory, or partially migratory (Boal et al. 2003). Migratory individuals have been recorded >2500 km from capture sites (Squires et al. 2020) and whether a bird migrates in any given year may be influenced by food availability (Doyle and Smith 1994). Ecology and movements of Northern Goshawks in winter are less known than those of the breeding-season (Boal et al. 2003, Squires and Kennedy 2006). Some studies indicate the birds use winter habitat similar to breeding-season habitat (Greenwald et al. 2005), whereas others suggest use of different, potentially lower quality habitats in winter, necessitating larger home ranges (Reynolds et al. 2008). Studies that have compared space use between sexes report that females occupy smaller (Kennedy et al. 1994, Moser and Garton 2019) or similar-sized (Boal et al. 2003) home ranges compared to males. Previous investigations of Northern Goshawk movements have used either satellite tracking devices that report infrequently (Sonsthagen et al. 2006a, 2006b, Underwood et al. 2006, Moser and Garton 2019) or relied on mark-recapture or very high frequency (VHF) radio telemetry, which limits the resolution at which space use can be characterized for this far-ranging species. Insufficient knowledge of how Northern Goshawks use the landscape in western North America at finer scales may hinder conservation efforts.

Management strategies for Northern Goshawks in western North America have received limited empirical evaluation, but a need for detailed assessment has been previously identified (Beier et al. 2008, Reynolds et al. 2012, 2013). Three habitat management strategies in the southwestern US (management for prey habitat, management for late-seral forest, and promotion of characteristics of pre-

European-settlement forest structure) were either unrelated or negatively associated with goshawk productivity (Beier et al. 2008). Within United States Department of Agriculture (USDA) Forest Service lands in California, the conservation strategy for Northern Goshawk populations consists primarily of designating Protected Activity Centers (PACs), composed of 81-ha contiguous areas intended to encompass the best available habitat around tree stands surrounding known or suspected nests. Stand-altering activities are restricted within PACs, but the extent to which these areas protect roosting and foraging activities remains unknown.

Animal tracking technology that uses global positioning systems (GPS) allows collection of accurate, detailed, and extensive data on the locations and movement of marked birds (Tomkiewicz et al. 2010), and enables the evaluation of management strategies (Blakey et al. 2019). We used GPS loggers to track 20 individual Northern Goshawks over 3 yr (2015–2018) across >100,000 ha of forest in the northern Sierra Nevada, California. Our aims were (1) to characterize the use of space by Northern Goshawks during breeding season (1 April–31 August) and nonbreeding season (1 September–31 March) for both sexes, including quantifying home range sizes and distance travelled, and (2) to evaluate the extent goshawk habitat use aligned with the current PAC system intended to protect nesting and roosting habitat.

METHODS

Study Area. We studied Northern Goshawks in Plumas National Forest, within the Sierra Nevada mountain range in northern California (40°00.017′N 120°40.083′W, Fig. 1). Plumas National Forest has an elevation range of 311–2433 masl and a Mediterranean and montane climate with dry, warm summers and cool, wet winters, with mean annual precipitation of 1036 mm, and daily mean temperature ranging from 1.3 ± 2.4°C in January to 19.3 ± 1.5°C in July (1895–2017; Western Regional Climate Center 2017). Vegetation is dominated by Sierran mixed coniferous forest consisting of ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), and black oak (*Quercus kelloggii*). Upper elevations are often dominated by red fir (*Abies magnifica*; Fites-Kaufman et al. 2007).

Tracking of Northern Goshawks. During 2015–2018, we marked and tracked 20 goshawks (12 females and 8 males) from 11 territories during 33 goshawk-seasons (7 individuals were tracked during multiple seasons or years). Seasons were defined as breeding (1 April–31 August) and nonbreeding season (1 September–31 March) based on goshawk behavior and prior reports on breeding phenology (Squires et al. 2020). We used USDA Forest Service data on known nests to locate goshawks in May and June of 2015–2018. We trapped goshawks using one or two dho gaza nets with a live non-releasable Great Horned Owl (*Bubo virginianus*) as the "lure bird" (Bloom et al. 2007). We fitted three goshawks with Skua-M GPS-GSM-UHF tracking devices, and 17 other individuals with Harrier/Kite-M GPS-UHF tracking devices (Ecotone Telemetry, Sopot, Poland); both unit types were solar-powered. Each tracking unit also contained a VHF transmitter (Advanced Telemetry Systems, Isanti, MN, USA), and the entire package was attached using a backpack-style Teflon ribbon harness (total package mass = 14–18 g). Mean body masses of individuals in our study were 1015 ± 151 g (females) and 733 ± 55 g (males); therefore, packages were 1.8% and 2.5% of mean goshawk body mass, respectively. Tracking units recorded locations at defined intervals within daily duty cycles and stored locations until a connection was established with a cellular network (Skua units) to which locational data were transmitted. Stationary base stations (Kite/Harrier units; EP-BS base station, Ecotone Telemetry) were placed near nests or in areas commonly transited by goshawks to collect location data downloads as goshawks moved through the area.

We collected a mean of 791 (range = 76–3833) daytime locations and 34 (range = 12–78) nighttime roost locations per goshawk-season across >100,000 ha of forest. Daytime locations were defined as locations recorded between sunrise and sunset, and locations recorded between 2 hr after sunset and 2 hr before sunrise were considered roost locations. During the breeding season, units were programmed to collect location coordinates every hour from approximately 0600 H to 1900 H, and then every 4 hr during the remainder of the year when less light was available to charge unit batteries. We programmed loggers of thirteen individual goshawks to collect roost data (1–5 locations each night). For six of those individuals, we collected roost data in both breeding and nonbreeding seasons and for the remaining seven, only breeding-season roost locations were collected. Additionally, 10 units were set to record locations every 1-6 min for 3–5 d for higher resolution tracking (5

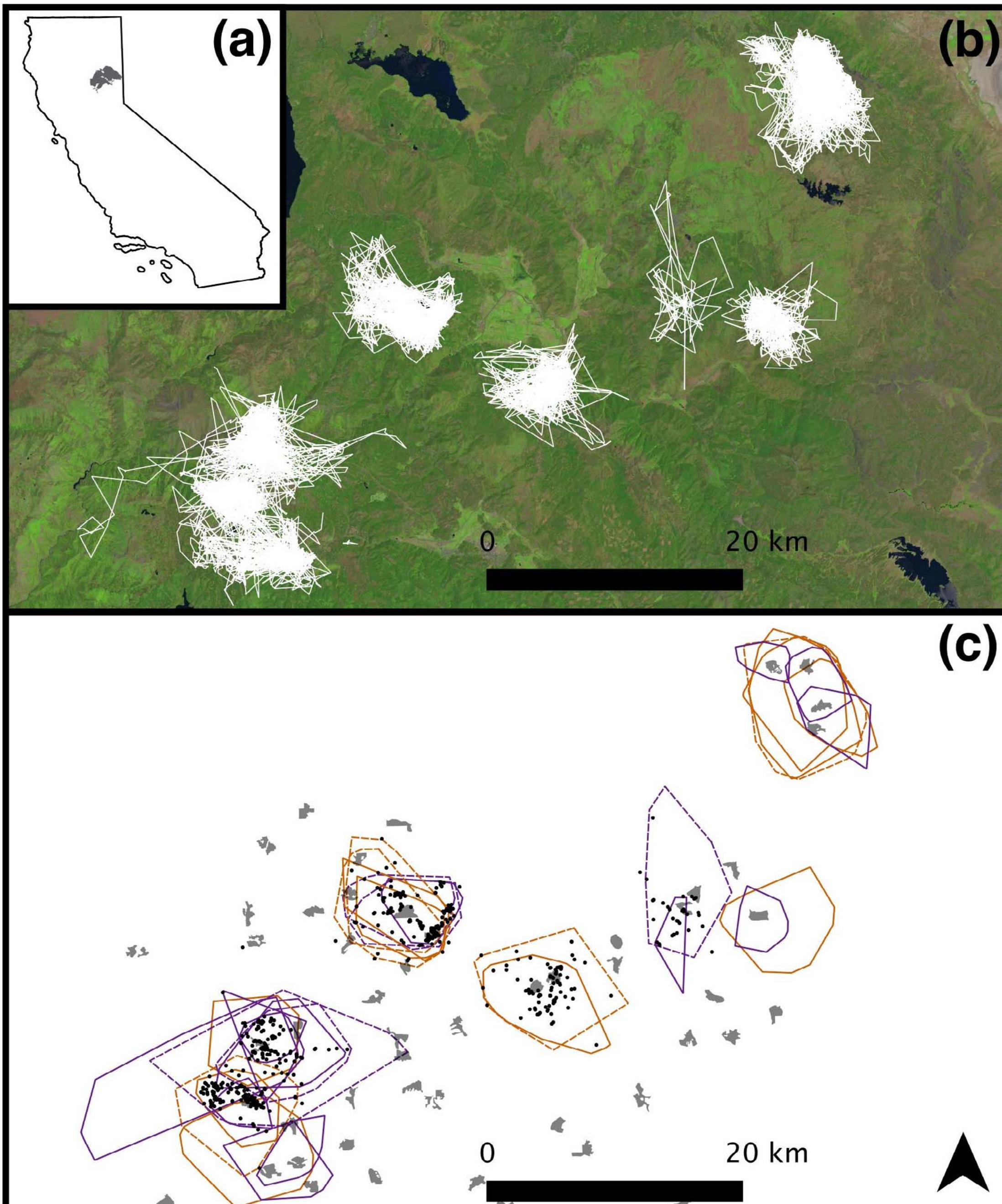

Figure 1. (a) Location of our study area in Plumas National Forest, California, USA, where we tracked 20 Northern Goshawks during the breeding season (1 April–31 August) and nonbreeding season (1 September–31 March). (b) All goshawk movement traces (white lines) overlaid on satellite imagery. (c) Goshawk home ranges (minimum convex polygons, MCPs) for each goshawk-season (purple lines = females, orange lines = males, solid lines = breeding season, dashed lines = nonbreeding season). Roost locations shown as black dots. USDA Forest Service designated Protected Activity Centers indicated by gray shaded polygons. Please refer to the online version of this article for interpretation of the references to color.

females, 5 males; 11 breeding and 1 nonbreeding goshawk-season). One male was not frequently encountered, and associated challenges reprogramming his unit resulted in collection of a mean of 49 locations per day throughout the nonbreeding season. We fitted three additional females with transmitters in the summers of 2015, 2017, and 2018 respectively, but these individuals dispersed or disappeared in <1 wk, and were excluded from the study. We did not find any dead goshawks during the study, so we do not know the fate of these individuals. Male and female goshawks that were caught at the same nest site were considered to be associated with the same territory.

We quantified movement data during the breeding (1 April–31 August) and nonbreeding season (1 September–31 March). We used a broad classification of the breeding season because our sample size was limited and timing of different phases of the breeding cycle (incubation, nestling, post-fledging) was not determined for the birds in this study. However, we estimated the dates of the different phases as 15 April–31 May (incubation), 1 June–15 July (nestling), and 1 July–31 August (post-fledging), based on the literature (Kennedy et al. 1994, Squires et al. 2020) and long-term observations by Forest Service staff. Observations confirmed that all goshawks had occupied nests (where a male and female were present in the territory and nests were refurbished) during each breeding season in which they were tracked, though nests were not monitored to determine breeding success. We tagged goshawks under authorization from the California Department of Fish and Wildlife (Scientific Collecting Permit #SC-8645) and the USFWS Bird Banding Laboratory (Permit #22423).

Statistical Analyses. *Home range size.* We estimated home range size using the 95% isopleth of the kernel density (KD) utilization distribution (Worton 1989) and the minimum convex polygon (MCP) method (Worton 1987) to make our results comparable to the majority of literature on Northern Goshawk home range (e.g., Boal et al. 2003, Hasselblad and Bechard 2007, Keane and Morrision 1994, Moser and Garton 2019). We derived KD and MCP home ranges for each goshawk-season that included > 50 locations ($n = 33$). We also derived KD and MCP home ranges for separate breeding-season phases that included ≥ 20 locations but these phases were not used in models due to insufficient sample sizes (incubation: 2 F, 2 M; nestling: 5 F, 1 M; post-fledging: 9 F, 7 M; samples sizes are goshawk-seasons). We compared home range size between sexes and seasons using generalized linear mixed effects models fitted using the Gaussian family with a log-link function, with territory as a random effect. We initially added individual bird as an additional random effect but this explained little variability in addition to territory. We also included year of study in the models to account for interannual variability, though this was not our variable of interest. We fitted year as a fixed, rather than a random, factor given the low number of levels (three; Bolker et al. 2009). We used an information-theoretic approach to model selection (Burnham and Anderson 2002). For each dataset, we compared 10 candidate models (see Table 1) using the Akaike information criterion, adjusted for small sample size (AIC_c), and retained the best approximating model with the lowest AIC_c value (Burnham and Anderson 2002). We interpreted the potential influence of variables using parameter estimates from the best approximating model. We conducted all analysis within the R environment for statistical computing (R Development Core Team 2019) using the adehabitatHR v3.3.0 package to fit KD and MCP home ranges and lme4 v1.1-12 to fit generalized linear mixed effects models.

Transit and travel distance. We calculated daily distance transited (sum of all daily movements) using high resolution data (1–6 min position interval) for days when >6 hr of data were collected ($n = 10$ individuals, 64 d total). For comparison, we thinned these high resolution data to one record per hour to assess differences in estimated daily distance transited using hourly and high resolution data. We also calculated maximum distance travelled from the nest (straight-line distance) for each individual and each day (2322 d total). During the nonbreeding season, we defined nest site as the nest location of the prior breeding season. As for the home range analysis, we also calculated daily distance transited and distance from nest for the three separate phases of the breeding season (incubation, nestling, post-fledging), though these phases were not used in models. Transit distances were not calculated for females in the incubation phase or for either sex during the nonbreeding season due to a lack of data (no data for females and data from a single male). Just as with the home-range size analysis, we used the same generalized linear mixed effects models (Gaussian distribution with log-link) to compare distance travelled from the nest between sexes and between seasons (breeding and nonbreeding),

Table 1. Results of model selection and model summaries for mixed effects models analyzing Northern Goshawk home range size (using the kernel density method) and goshawk distance from nest including number of estimated parameters (K), AIC_c, ΔAIC_c, and Akaike weight (ω_i). Similarities between paired birds sharing the same territory were accounted for as a random factor (1|territory). When males and females were caught at a nest we associated them with the same territory because all adult goshawks were captured at nest sites.

Model	K	AIC_c	ΔAIC_c	ω_i
Home range area ~ sex * season + year + (1|territory)	9	721.7	0	0.95
Home range area ~ sex * season + (1|territory)	6	727.7	6.0	0.05
Home range area ~ sex + season + year + (1|territory)	8	732.0	10.3	0.01
Home range area ~ sex + season + (1|territory)	5	737.5	15.8	<0.01
Home range area ~ season + year + (1|territory)	7	742.1	20.4	<0.01
Home range area ~ season + (1|territory)	4	742.4	20.7	<0.01
Home range area ~ 1 + (1|territory)	3	779.7	58.0	<0.01
Home range area ~ sex + (1|territory)	4	780.0	58.3	<0.01
Home range area ~ year + (1|territory)	6	782.7	61.0	<0.01
Home range area ~ sex + year + (1|territory)	7	783.2	61.5	<0.01
Distance from nest ~ sex * season + year + (1|territory)	9	9262.3	0	1
Distance from nest ~ sex * season + (1|territory)	6	9286.6	24.3	<0.01
Distance from nest ~ sex + season + year + (1|territory)	8	9327.8	65.5	<0.01
Distance from nest ~ sex + season + (1|territory)	5	9367.7	105.4	<0.01
Distance from nest ~ sex + year + (1|territory)	7	9423.7	161.4	<0.01
Distance from nest ~ sex + (1|territory)	4	9507.7	245.4	<0.01
Distance from nest ~ season + year + (1|territory)	7	9541.7	279.4	<0.01
Distance from nest ~ season + (1|territory)	4	9558.5	296.2	<0.01
Distance from nest ~ year + (1|territory)	6	9660.5	398.2	<0.01
Distance from nest ~ 1 + (1|territory)	3	9710.7	448.4	<0.01

except that distance traveled was the response variable and individual goshawk was included as a random effect. We conducted all analysis within the R environment for statistical computing (R Development Core Team 2019). We used the adehabitatHR v3.3.0 (Calenge 2015a) package to fit MCPs and KD utilization distributions and lme4 v1.1-12 (Bates et al. 2015) to fit generalized linear mixed effects models.

Forays. We recorded birds travelling relatively long distances from their nests, a phenomenon we defined as foray behavior. The mean distance between known neighboring nests in our study was 5 km, so we defined forays as movements >5 km from the nest and temporally extending for > 1 hr and ≥ 10 locations, and ending when the goshawk returned to within 5 km of the nest (Blakey et al. 2020). We included both high and low resolution data in classifying foray behavior.

Protected Activity Center analysis. We analyzed overlap between PACs and goshawk habitat use using roost locations and daytime space use (intensity of use during the daytime) based on methods described by Blakey et al. (2019). To quantify daytime space use, we derived the Brownian bridge utilization distribution (UD) for each goshawk-season, with a spatial accuracy of 30 m (corresponding to conservative estimated accuracy of our GPS units) and a grid cell size of 50 m (Horne et al. 2007). We chose to use Brownian bridge UDs to quantify daytime use rather than our home ranges as calculated above (KD and MCP), because the Brownian bridge UD gives an estimate of intensity of use by calculating the probability density for the fraction of time spent in different areas (Horne et al. 2007). When calculating UDs, we excluded time lags >4 hr, and thinned our data to one location per hour (higher resolution data addressed below), using the adehabitatLT v3.3.0 package (Calenge 2015b). All PACs (designated to consist of the best available 81 ha of goshawk habitat surrounding known and suspected nest stands) were delineated in previous years by Forest Service biologists. For each goshawk-season we identified the "nest PAC" as the PAC that contained the nest, or the previous season's nest for birds during the nonbreeding season, and "all PACs," as PACs or sections of PACs, overlapped by the MCP home range. We assessed overlap with all PACs (in addition to nest PACs) because this area represents the total amount of land managed for goshawk conservation within our study area. We acknowledge that the number of PACs designated in an area is likely to vary across management units on National Forest land. We then calculated the percentage of daytime space use (summed intensity of use within UD) that overlapped with PACs (UD intensity of use within PACs) within each goshawk's MCP home range for all goshawks (33 goshawk-seasons). Although PACs are intended only to protect breeding habitat, we chose to assess their overlap with all aspects of goshawk habitat use (roosting and daytime use), because they are the only formal conservation measure for this species within the National Forest system. To assess the overlap of PACs with roost locations, we intersected PACs with roost locations for 12 of the 33 goshawk-seasons for which there were >20 roost locations and calculated the frequency at which locations fell within PACs.

RESULTS

Home Range Size. Northern Goshawk 95% KD home range size (mean = 3606 ha, SE = 433 ha, median = 3218 ha) differed by sex, season, and their interaction (Table 1, Fig. 2). Median home range size for males (3926 ha) was 2.4 times that of females (1619 ha) for the KD method. Median nonbreeding-season home range size (6085 ha; females: 6670 ha; males: 5500 ha) was three times larger than median breeding-season home range size (1967 ha; females: 1198 ha; males: 3343 ha). Median home range of females was smaller than that of males in the breeding season, but greater than males in the nonbreeding season (sex*season interaction, Table 1, Fig. 2). Within-season home range size increased as the breeding season progressed from incubation to the nestling phase to the post-fledging phase for female goshawks, but remained similar across phases for males (Fig. 2).

Home ranges calculated using the MCP method (mean = 4395 ha, SE = 453 ha, median = 3869 ha) were larger than for the KD method, but differences in median home ranges between sexes were similar (e.g., MCP home range size for males was twice as large as that for females; estimated home range sizes calculated using both methods are shown in Supplemental Materials Table S1). However, the difference between seasons was weaker when we used the MCP method; nonbreeding season home ranges were 1.9 times larger than breeding home ranges, compared to 3.1 times using the KD method. Although results for the different home range size measures were similar, the best approximating model for the MCP method included sex and season, but not their interaction. The best approximating models of home range size also included year, indicating variability in home range size across years, after accounting for sex and season (breeding and nonbreeding; Table 1).

Transit and travel distance. Female daily transit distances (sum of all movements) during the breeding season ranged from 6.9 to 38.2 km (median = 13.5 km, SE = 2.2 km), whereas males transited twice that far daily (median = 30.8 km, SE = 1.7 km, 8.6–61.0 km; Fig. 2). As expected, estimates based on lower resolution data (collected every hour) yielded shorter transit distances compared to high resolution data (collected every 1–6 min; Fig. 3a). Transit distance underestimation was particularly severe for goshawks transiting farther, as low-resolution estimates of transit distances were half those estimated with high resolution data (Fig. 3a).

Goshawks in our study did not migrate; tracked individuals remained in the same area year-round, generally within a few kilometers of their nest location from the previous breeding season (Fig. 4). Home ranges of individual goshawks in different seasons (Fig. 5a, 5b) and sometimes within the same season (Fig. 5c) overlapped substantially. Only one goshawk exhibited breeding dispersal: a male that moved 3.5 km to an adjacent territory between 2016 and 2017 and paired with a new female (Fig. 5c). We consider the two areas to be different territories because they were simultaneously occupied by distinct individuals in previous years.

Maximum daily distances travelled from the nest (straight-line distance, not transit distance) by goshawks differed between sexes and by season, with sex and season interacting significantly (Table 1, Fig. 2). Males travelled farther (median = 3.2 km) each day than females (median = 2.0 km), and both sexes travelled farther daily during the nonbreeding season (median = 3.2 km) than during the breeding season (median = 2.2 km). However, one female travelled the farthest of all goshawks, flying >15 km from the nest in the post-fledging phase and remaining >10 km from the nest for 4 d (Fig. 4a). Males travelled similar distances from the nest in breeding and nonbreeding seasons, whereas females travelled twice as far during the nonbreeding season (median = 3.3 km) than during the breeding season (median = 1.5 km; Figs. 2, 4). Within the breeding season, female goshawks transited farther and

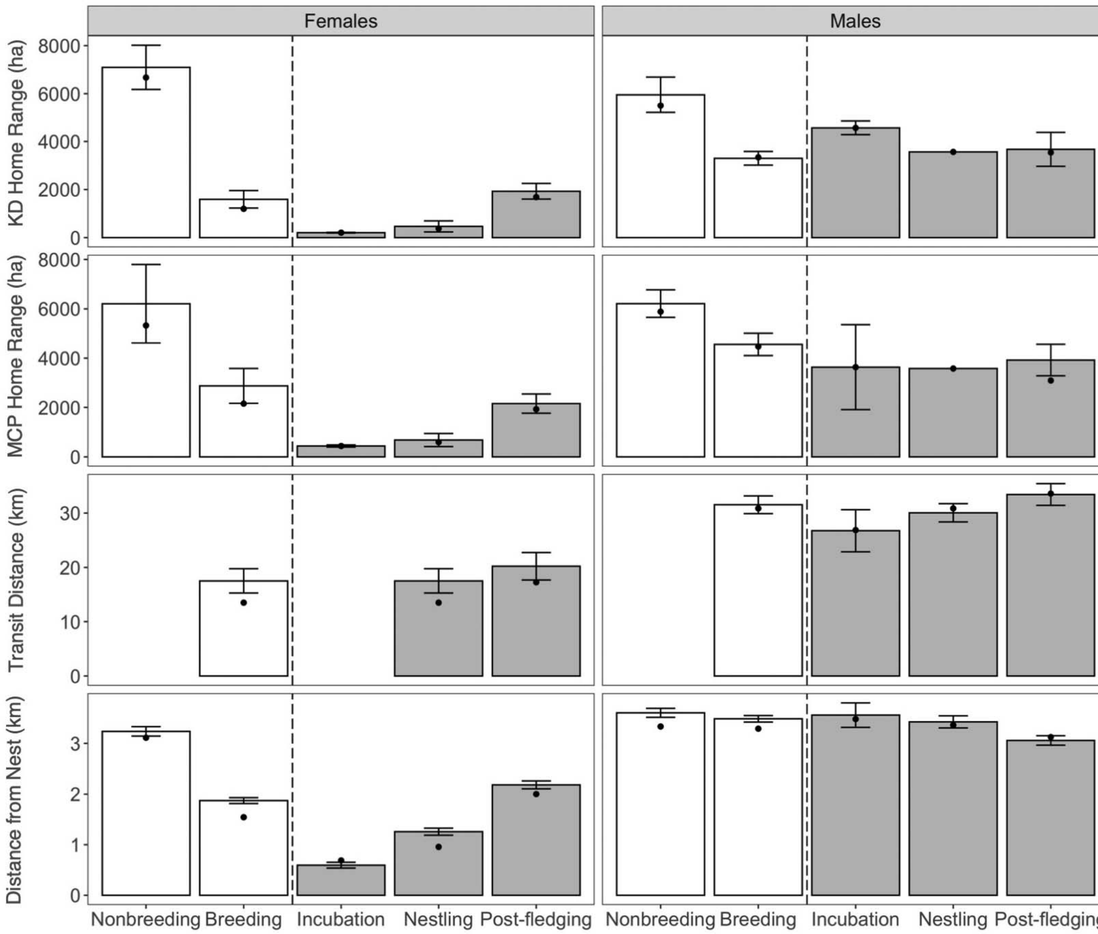

Figure 2. Summary of space use by Northern Goshawks, by sex, including measurements of KD and MCP home range size (ha), transit distance (km), and daily distance travelled from the nest (km). Females are shown on the left panel and males on the right. Bars show means, error bars indicate standard errors, and black circle markers indicate medians. Metrics calculated across full seasons (white bars: nonbreeding, breeding) and also phases within the breeding season (gray bars: incubation, nestling, post-fledging). Note that there were insufficient high resolution data to calculate transit distances during the nonbreeding season and for females during the incubation phase of the breeding season.

travelled farther from nests as the season progressed (Fig. 2), but males did not.

Forays. We recorded 34 forays ranging from 5 to 15 km by three males and one female over three nonbreeding and four breeding seasons, with a median foray duration of 40 hr (range = 1 hr to 6 d), and 14 forays (41%) exceeding 24 hr (shown as peaks in Fig. 4). During the 2017 breeding season, one paired male visited an adjacent territory occupied by a different goshawk pair and also forayed into a second, apparently unoccupied, area in which he had bred with a different female the previous season (Fig. 5c). The three males conducted forays throughout the year and the female forayed only between early July and late September.

Protected Activity Center analysis. The 81-ha PAC that contained the nest (or previous season's nest) of each tracked bird encompassed a mean of 22.4% (range: 2.7–60.8%, SE = 3.3%) of the home range (goshawk-season UDs). When all PACs were considered, they accounted for a mean of 24.9% (range = 4.9–65.2%, SE = 3.2%) of the home range (goshawk-season UDs). Goshawks visited a mean of two PACs

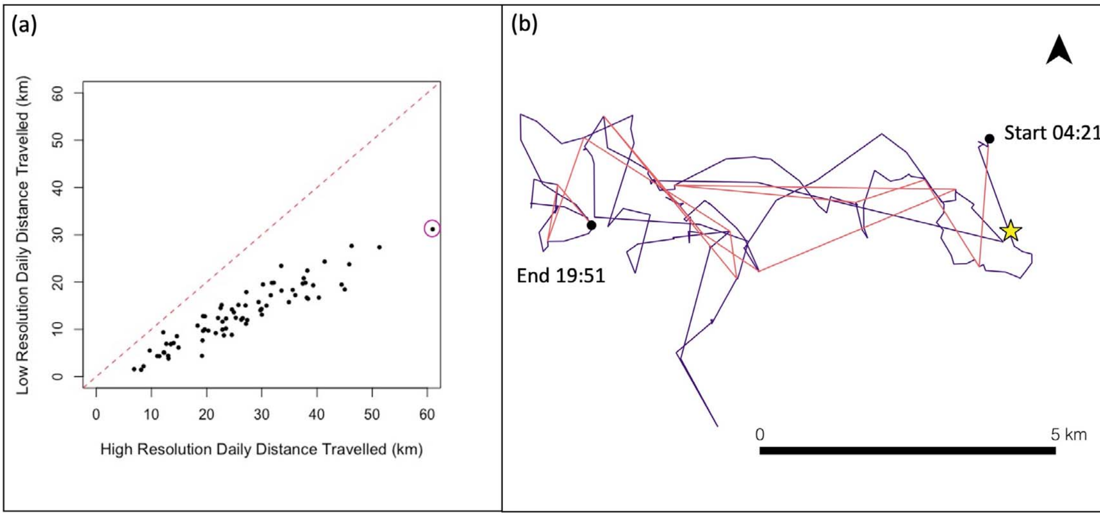

Figure 3. Comparison of high resolution (locations collected every 1–6 min) and low resolution (locations collected every hour) data used to estimate daily transit distance of individual Northern Goshawks. (a) Correlation between transit distances estimated using each data resolution. The largest transit distance (60 km) is circled, and shown in panel (b), where the dark (purple) line is a plot of high resolution data and the light (orange) line is the low resolution data over the course of a day (from 0421 H to 1951 H PST). The yellow star indicates the last known nest location for the tracked bird. Movements were made by a male goshawk on 18 July 2018. Please refer to the online version of this article for interpretation of the references to color.

per goshawk-season (range = 1–6). The PACs containing nests from current or past years protected a mean of 23.1% (range = 1.4–76.9%, SE = 6.4%) of roosts, and when all PACs were considered, they contained a mean of 24.3% (range = 5.6–76.9%, SE = 6.3%) of roosts (see Supplemental Materials Table S1 for all PAC overlap values).

DISCUSSION

We recorded resident Northern Goshawks in the Sierra Nevada range of California using large home ranges, transiting up to 60 km per day, with both sexes exhibiting foraying behavior (Figs. 1, 2, 4, 5). Our study highlights the importance of temporal resolution when gathering locational data, and its effect on our perception of how animals move through and use space. Home-range sizes using KD estimates were smaller than those reported using similar methods in Idaho (Moser and Garton 2019). Our MCP-estimated home ranges were larger than those derived from radiotelemetry data in Idaho, Nevada, Arizona, Washington, and Oregon (Hasselblad and Bechard 2007), but comparable to estimates from the adjacent Lake Tahoe region of California, and other estimates from Minnesota (Keane and Morrision 1994, Boal et al. 2003). Further research will be needed to determine whether regional differences in goshawk home ranges are related to resource availability, home-range estimation methodology, territory density, or other factors. As reported previously, we found male and nonbreeding-season home ranges were larger than female and breeding-season home ranges, respectively (Boal et al. 2003, Reynolds et al. 2006). However, one female travelled farther from the nest than any other individual (>15 km) and there was evidence that female home ranges were larger than male home ranges in the nonbreeding season. We found no evidence for migration during the nonbreeding season and the four individuals that were tracked through an entire nonbreeding season all returned to within 1 km of the nest regularly (Fig. 3). Goshawk populations in western North America may be resident or exhibit seasonal or partial migration (in which an individual's decision to migrate in any given year is influenced by food availability; Doyle and Smith 1994, Boal et al. 2003). Goshawks were also year-round residents in the adjacent Lassen National Forest (Rickman et al. 2005), indicating birds in the northern Sierra Nevada were able to obtain sufficient food to remain on territories throughout the annual cycle. However,

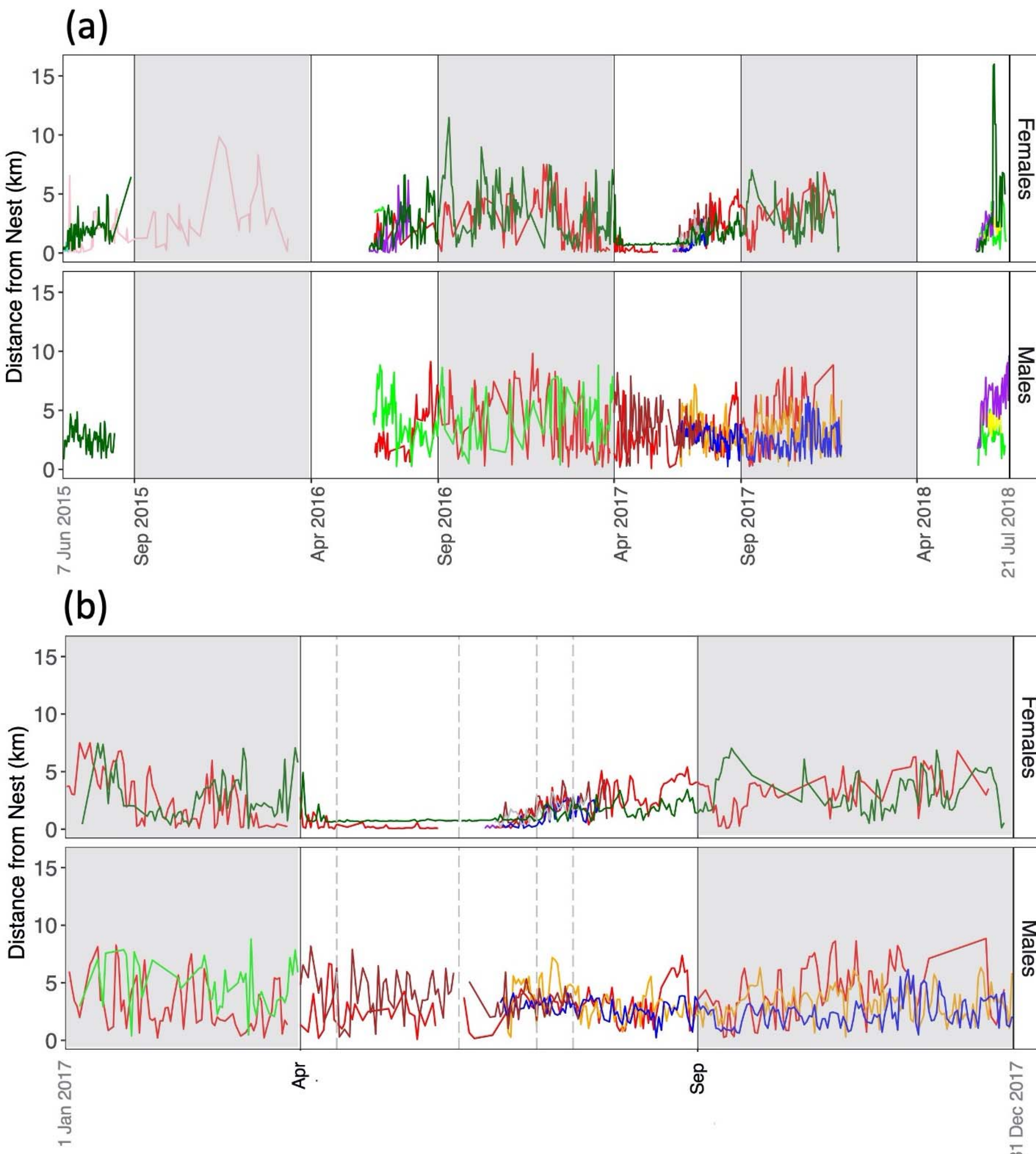

Figure 4. (a) Distance travelled from the nest (or nest site of prior breeding season for nonbreeding birds) by 20 Northern Goshawks (top = 11 females; bottom = 8 males over the study (2015–2018). (b) Detail of panel (a) showing only the year 2017 (top = 5 females; bottom = 5 males). Areas with white backgrounds indicate breeding seasons (1 April–31 August) and areas with gray backgrounds indicate nonbreeding seasons (1 September–31 March). Dashed gray lines in (b) indicate the beginning and ends of the phases within the breeding season: incubation (April 15–May 31), nestling phase (June 1–July 15), and post-fledging phase (July 1–August 31). Distances are calculated as maximum daily straight-line distance from the nest. Line colors indicate territories; male and female from the same territory have the same line color (n = 10). Please refer to the online version of this article for interpretation of the references to color.

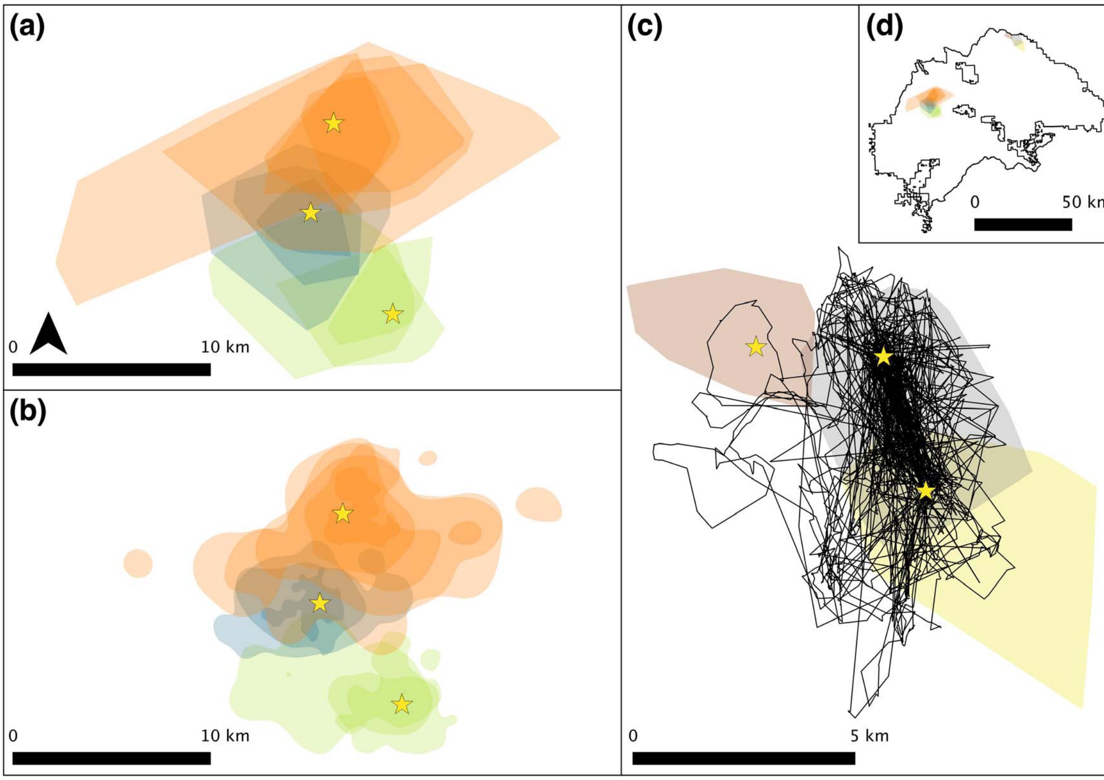

Figure 5. Illustration of overlap among Northern Goshawk home ranges in Plumas National Forest. Yellow stars show nest locations for each territory in panels (a), (b), and (c). Panels (a) and (b) illustrate the same three adjacent territories in the western part of the study area, showing overlap of home ranges [calculated by two methods: (a) MCP; (b) KD] for all individuals in those territories from 2015–2018: one male and two females (separate seasons) for the northernmost (orange) territory, one pair in the center (blue) territory, and one pair in the southernmost (green) territory. (c) Movement traces (black lines) of a male within the eastern part of the study area during one season (breeding 2017). In 2017, this male nested (yellow star) with the female whose 2017 breeding-season home range is shown by the gray polygon in the center. In the same season, the movement traces show the male passing through the home range of another female nesting in the adjacent territory in 2017 (brown polygon to the west, yellow star denotes nest). In the prior breeding season (2016), the focal male had nested with a different female in the southern territory, approximately 3.5 km south (nest shown by southern yellow star). As the female he nested with had insufficient data points to calculate a home range for this territory, we show the breeding-season home range of a separate female occupying the same territory with a different male in 2018 with the yellow polygon to the south. The nests (yellow stars) in the north (within brown and grey polygons) were occupied during the 2017 breeding season, while the southern nest (within the yellow polygon), was not known to be occupied in the 2017 season. (d) Locations of home ranges within the Plumas National Forest. Please refer to the online version of this article for interpretation of the references to color.

we note that we only tracked adult goshawks and therefore we do not know whether goshawks of other age-classes migrated away from our study area.

Goshawks making forays may have been conducting habitat reconnaissance (prospecting for alternative territories), seeking extra-pair copulations, or exploiting ephemeral or alternative foraging opportunities. Reconnaissance has been described in >100 species of birds (Reed et al., 1999 and references therein) and foray behavior was observed among nonbreeding female California Spotted Owls (*Strix occidentalis*) in the same study area as our study (Blakey et al. 2019). Foray behavior may be a precursor to dispersal, as mature forest is relatively rare and fragmented on the landscape, and individuals that are able to use knowledge of alternative resource availability would likely experience fitness benefits (Reed and Oring 1992). Breeding dispersal by goshawks in Northern California was undertaken by 18% of females and 23% of males over a 9-yr period, with somewhat larger mean dispersal distances for females (9.8 km) compared to males (6.5 km; Woodbridge and Detrich 1994). One male in our study moved 3.5 km into an adjacent territory between 2017 and 2018, and nested there with a new female, while continuing to use both the new and old territories. Extra-pair copulations were unlikely to be a primary motivator of foray behavior as goshawk extra-pair copulations are rare (Gavin et al. 1998), and we recorded foray behavior throughout the annual cycle; however, one male in our study area flew within 300 m of the nest of an adjacent pair in late May. As suggested by Blakey et al. (2020), some foraying goshawks may have been exploiting foraging opportunities created by low intensity fire (i.e., open understory and intact canopy; Squires and Kennedy 2006), given that two individuals forayed into areas that had burned during the 20 yr prior. Use of burned landscapes for foraging also has been observed by other late-seral forest predators (Spotted Owls, Bond et al. 2009; Pacific fishers [*Pekania pennant*], Hanson 2015). Understanding such fine-scale habitat use decisions will likely be improved by the use of high resolution GPS-tracking data (e.g., 1–6 min intervals) as coarser data (e.g., hourly intervals) can underestimate distances travelled by half (Fig. 3).

We found that <25% of space used during daytime and nighttime roost sites are protected via PACs in our study area; conservation threats may arise if habitat alteration or disturbances occur outside PACs but within goshawk roosting and foraging areas. Forestry activities surrounding goshawk PACs have the potential to negatively affect the species, although the effects of timber harvest on goshawks are still unclear. Several studies indicated negative effects of timber harvest (Crocker-Bedford 1990, 1995, Reynolds et al. 1992), whereas others reported no effects of timber harvest on nesting success (Moser and Garton 2009) or positive effects (more frequent breeding) in thinned areas (Reynolds et al. 2017). A global meta-analysis indicated that goshawk nest sites or territories characterized by less timber harvest and larger trees were more likely to be occupied, but productivity was not associated with timber harvest activities or tree size (Rodriguez et al. 2016). In a study within the Sierra Nevada (Lassen National Forest, adjacent to our study area) that identified specific night roost locations, no goshawk roosts were within areas where timber harvest had occurred during the past 20 yr (Rickman et al. 2005). Conversely, fuels-reduction management (forest thinning) designed to mimic wildfire-maintained historical vegetation patterns may increase resistance and resilience to high severity fire (Stephens et al. 2012). Goshawks avoid areas where high severity fires burned (Blakey et al. 2020), and may ultimately abandon severely burned territories (Reynolds et al. 2017), leading to projected population declines (Ray et al. 2014). Overall, our findings suggest conservation efforts for Northern Goshawks in the Sierra Nevada may benefit from consideration of year-round habitat needs at larger scales than previously thought.

Supplemental Materials (available online). Table S1: Summaries of Northern Goshawk data collection, home ranges, and percentage of goshawk space use area and roost sites overlapping with Protected Activity Centers (PACs).

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