

Age- and season-specific variation in local and long-distance movement behavior of golden eagles

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Abstract Animal movements can determine the population dynamics of wildlife. We used telemetry data to provide insight into the causes and consequences of local and long-distance movements of multiple age classes of conservation-reliant golden eagles (*Aquila chrysaetos*) in the foothills and mountains near Tehachapi, California. We estimated size and habitat-related correlates of 324 monthly 95 % home ranges and 317 monthly 50 % core areas for 25 birds moving locally over 2.5 years. We also calculated daily, hourly, and total distances traveled for the five of these birds that engaged in long-distance movements. Mean (\pm SD) monthly home-range size was 253.6 ± 429.4 km² and core-area size was 26.4 ± 49.7 km². Consistent with expectations, space used by pre-adults increased with age and was season-dependent but, unexpectedly, was not sex-dependent. For all ages and sexes, home ranges and core areas were dominated by both forest & woodland and shrubland & grassland habitat types. When moving long distances, eagles traveled up to 1588.4 km (1-way) in a season at highly variable speeds (63.7 ± 69.0 km/day and 5.2 ± 10.4 km/h) that were dependent on time of day.

Patterns of long-distance movements by eagles were determined by age, yet these movements had characteristics of more than one previously described movement category (migration, dispersal, etc.). Our results provide a context for differentiating among types of movement behaviors and their population-level consequences and, thus, have implications for management and conservation of golden eagle populations.

Keywords *Aquila chrysaetos* · California · Connectivity · Exploratory movements · Migration · Movement ecology

Introduction

The drivers of animal decision-making and the causes and consequences of different types of animal movements are important to modern understanding of animal behavior (Nathan et al. 2008; Singh et al. 2012; Technitis et al. 2015). The habitat requirements of wildlife change with time and, as a consequence, individuals move to more suitable areas to accommodate those needs and to maximize fitness (Barraquand and Benhamou 2008). Animal movements also can have significant effects on population dynamics and genetic structure (Gaines and McClenaghan 1980; Greenwood 1980; Nathan et al. 2008) and can have implications for connectivity of populations at a continental scale (Millsap et al. 2014). Hence, understanding key elements of movement behavior, such as daily movements and distances traveled by individuals (Soutullo et al. 2006a), dispersal by young animals (Weston et al. 2013), and year-round movements of wide-ranging species (McIntyre et al. 2008), is critical as a basis for understanding animal ecology and for developing effective conservation strategies (Singh et al. 2012).

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Evaluation of animal movements has revealed that behavioral patterns or specialized use of habitat features may differ among age classes, sexes, seasons, and breeding status (Barraquand and Benhamou 2008; Singh et al. 2012). Animals can engage in localized movements (by residents; Mueller et al. 2011; Braham et al. 2015), prospecting (by breeders or non-breeders; McCrary et al. 1992; Reed et al. 1999), sex-specific dispersal (by breeders or non-breeders; Wiens 1976; Bekoff 1977; Gaines and McClenaghan 1980; Greenwood 1980; Greenwood and Harvey 1982), partial or complete migration (that can be age- or season-specific; Newton 2008), or even nomadism (by any mature age class; Bloom et al. 2011; Singh et al. 2012). Localized movements are sometimes territorial in nature and usually refer to movements by adults or young individuals near a nest site or breeding territory (i.e., residency; Burt 1943; Mueller et al. 2011). Prospecting refers to movements by non-breeders or even experienced breeders that are designed to gather information about possible breeding opportunities within an area (Reed et al. 1999). Natal dispersal involves movements made by young individuals from a natal territory to a place where that animal eventually reproduces; breeding dispersal refers to movements by reproductive adults between successive breeding sites (Greenwood 1980; Greenwood and Harvey 1982). Migration involves long, directional movements during a specified time period after which the animals usually return to their point of origin (Gaines and McClenaghan 1980). Migration is classified as partial (only part of the population migrates) or complete (all individuals migrate) and may be undertaken by all age classes, and all individuals within a population that migrate usually do so at a similar time of year (Newton 2008). Nomadism refers to movements made by individuals who wander and may breed at multiple sites throughout their lives (Bloom et al. 2011).

In spite of the profusion of described movement types, some movements may not fit easily within any of these traditional definitions. Because many raptor species are the focus of management or conservation efforts (Morrison and Wood 2009), differentiating among and understanding these various types of movements may provide ecological or evolutionary insight. Golden eagles (*Aquila chrysaetos*), a species of high conservation concern, are long-lived raptors with a Holarctic distribution. They occur in a tremendous variety of habitats, from sea level to high mountains, including deserts and forested areas (Watson 2010). Individual eagles are capable of moving long distances, and even in their first year of life, they can travel thousands of kilometers (McIntyre et al. 2008). Eagles have among the longest-duration pre-adult stage of any bird taxa, typically not breeding before the fifth year of life (Watson 2010). During these pre-adult years, some golden eagles engage in long-distance movements away from natal areas (Soutullo et al. 2006b; Watson 2010). However, only a few studies have evaluated the drivers of movement behavior

and habitat use by young golden eagles, and the majority of them focus on the first year of life (Soutullo et al. 2006a; Soutullo et al. 2008; Soutullo et al. 2013). In contrast, resident golden eagles with established home ranges or territories have been well studied and the determinants of their habitat choices are well understood (Watson 2010; Moss et al. 2014; Sandgren et al. 2014; Braham et al. 2015). Because of the concentration of studies on adult and very young golden eagles, only a limited understanding of behavior in the “in-between” pre-adult age classes exists. Hence, we have little insight on how behavior and habitat utilization during the pre-adult period may have subsequent consequences for population biology and lifetime reproductive success of this long-lived species.

To provide insight into the causes and consequences of movement behavior across animal life cycles, we examined habitat use and movements of multiple age classes of GPS-telemetered golden eagles originally captured in southern California, USA. The overall goal of this study was to differentiate among the age-, sex-, and season-specific movement patterns by these eagles to understand their causes and effects. Our specific objectives were to (1) define environmental and topographic correlates of local movements represented by age-, sex-, and season-specific home ranges and core areas of golden eagles and (2) define environmental and topographic correlates of long-distance movements by golden eagles. We hypothesized that patterns of movement would be highly age- and sex-structured, with younger eagles and females making longer movements and ranging more widely than older eagles and males (Watson 2010). We further hypothesized that movements would differ seasonally, with adult eagles maintaining smaller home ranges during the nesting season. We also discuss how the local and long-distance movement behaviors that we measured provide insight into why these animals move as they do over their lifetimes.

Methods

Study area

We captured and telemetered golden eagles in the foothills and mountains near Tehachapi, California, located between the San Joaquin Valley and the Mojave Desert (Figs. 1 and 2). The most common vegetation communities in this area are scrub oak-savanna, sagebrush steppe, temperate forest, and Mediterranean grassland (CDFW 2013). Dense local populations of California ground squirrels (*Otospermophilus beecheyi*) likely provide an abundant food source for eagles (Carnie 1954). Elevation in the region ranges from approximately 300 to 2600 m a.s.l. The climate is Mediterranean with a mean annual precipitation of 23 mm that primarily occurs from November to April (World Climate Data 2011a).

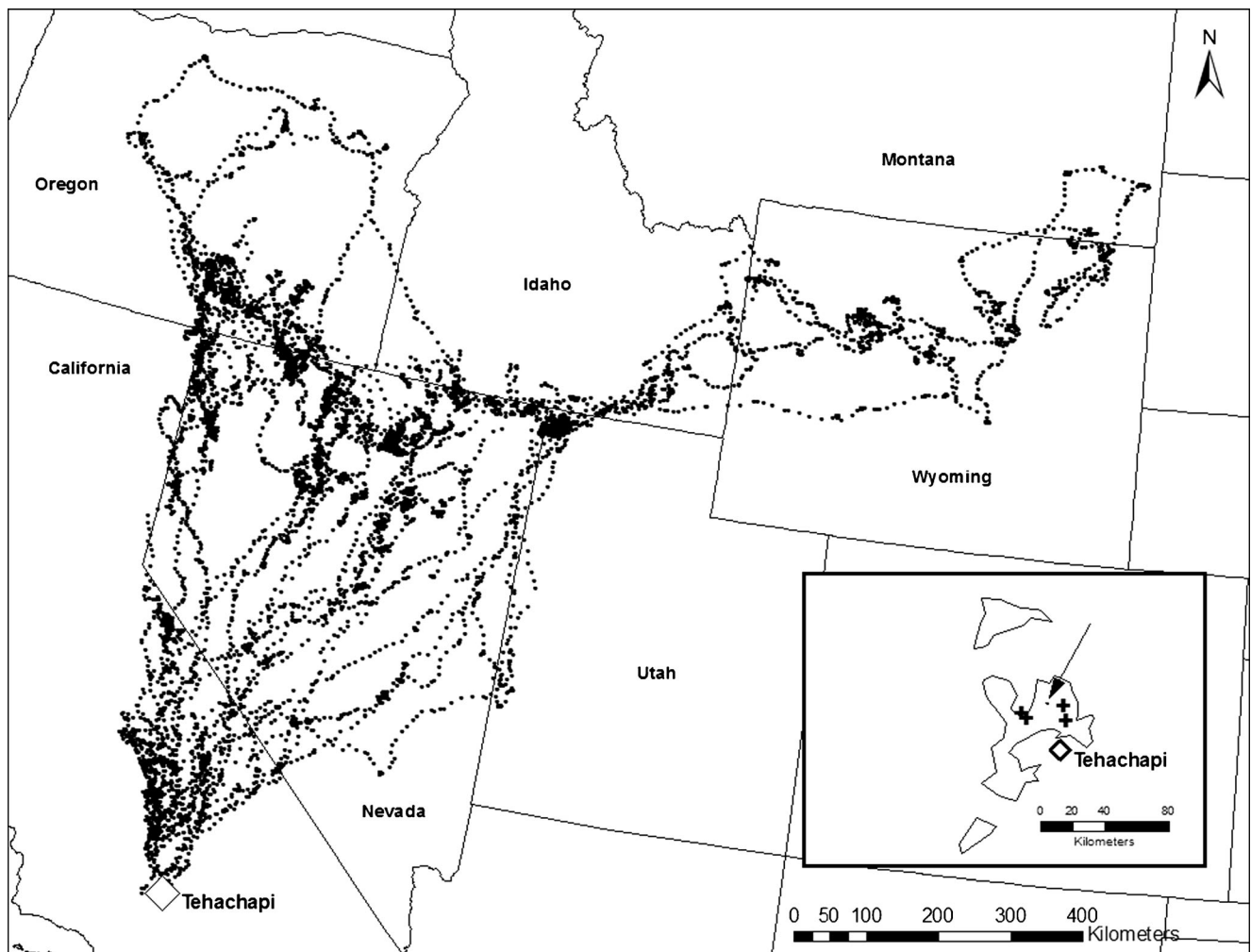


Fig. 1 Map showing the study area near Tehachapi, California with long-distance movements of five golden eagles. *Inset map* includes the four capture sites near Tehachapi, indicated by *black crosses*, and the largest

and smallest monthly home ranges observed for eagles. *Arrow* indicates the smallest home range, from an adult female eagle in February that was possibly incubating

Monthly temperatures range from a mean low of $-0.8\text{ }^{\circ}\text{C}$ in December to a mean high of $30.3\text{ }^{\circ}\text{C}$ in July (World Climate Data 2011b).

Eagle capture and telemetry

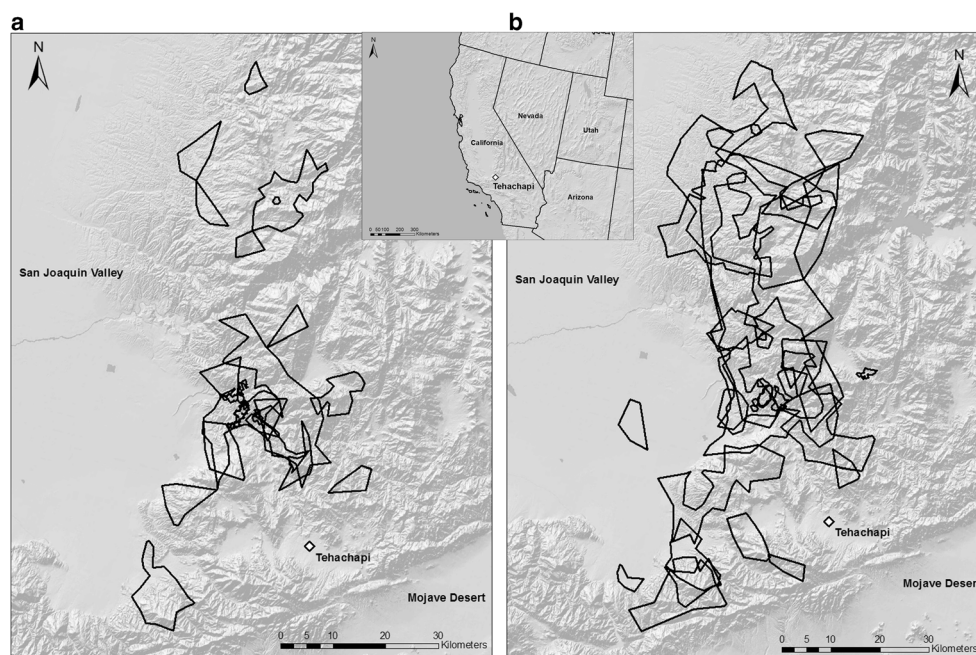
We trapped golden eagles with remote-trigger bow nets baited with fresh carrion at four sites in the study area (Fig. 1) from November 2012 to February 2013 and in March 2014. Elevation at our capture sites ranges from 698 to 1378 m. For each captured bird, we assessed age using molt patterns (Bloom and Clark 2001) and determined sex genetically (Fridolfsson and Ellegren 1999). We fitted each bird with a solar-powered Global Positioning System-Global System for Mobile Communications (GPS-GSM) telemetry unit (Cellular Tracking Technologies LLC, Rio Grande, NJ, USA) attached as a backpack with Teflon ribbon (Dunstan 1972; Kenward 1985; Walls and Kenward 2007).

Telemetry units collected GPS data between approximate sunrise and sunset at 15-min intervals for nine days and every 30 s on the tenth day. Data were sent electronically over the GSM network to data servers. We sub-sampled the 30-s data to 15-min intervals. We also removed poor-quality GPS locations (i.e., 2D fixes, locations with altitudes $>4000\text{ m}$ that appeared to be inaccurate, locations with altitudes above ground level (AGL) $<-50\text{ m}$ (Katzner et al. 2012), and locations with horizontal dilution of precision ≥ 10 (D'Eon and Delparte 2005)).

Classifying movement behavior

We classified each eagle as a resident or a non-resident based on movements from telemetry data. A resident eagle was one that remained within 100 km of the capture site throughout the study. In contrast, a non-resident eagle made long-distance movements ($>100\text{ km}$) away from the capture site during a

Fig. 2 Map showing the study area near Tehachapi, California with home ranges of 10 resident golden eagles in **a** December 2013, representing smaller home-range sizes, and **b** March 2014, representing larger home-range sizes



least 1 month of the study (Steenhof et al. 1984; Bloom et al. 2011, 2015). We analyzed jointly all movements of eagles within 100 km of the capture site (i.e., local movements), and we analyzed separately the movements of non-resident eagles that were >100 km from the capture site (i.e., long-distance movements).

Local movements—residents and non-residents

We assessed local movements by all golden eagles by calculating home ranges and core areas for each eagle separately by month. We estimated home-range and core-area size for each eagle using adaptive Local Convex Hulls (aLoCoH; Getz et al. 2007) calculated by the adehabitatHR package (Calenge 2006) in R (R Core Team 2015). We used the aLoCoH method because it is not influenced by the high degree of autocorrelation in GPS data collected at 15-min intervals. We defined a (i.e., the distance used to define nearest neighbors; Costello et al. 2014) as the maximum distance between any two locations for a given eagle-month. If the routine failed, we multiplied the a value by 1.1 and re-ran the analysis. If that again failed, we then increased the multiplier by increments of 0.1 until the routine succeeded (Costello et al. 2014). We estimated home ranges and core areas only for eagle-

months with ≥ 100 locations. We used 95 % isopleths to estimate monthly home-range sizes and 50 % isopleths to estimate monthly core-area sizes (Getz et al. 2007; Braham et al. 2015).

For eagles classified as residents, each monthly home range and core area was included in our analyses because each was within 100 km of the capture site. For eagles classified as non-residents, if the centroid of the monthly 95 % home range was >100 km from the bird's capture site, we did not include the home range and core area for that month in our analyses. We did not consider these movements to be home ranges as classically defined (Worton 1989). However, we did include home ranges and core areas for non-residents in those months when the centroid of the home range was <100 km from the capture site because these represented local movements.

Environmental correlates of local movements

We examined vegetative and topographic characteristics of each home range and core area. We obtained land cover data from the National Gap Analysis Program (USGS, GAP 2011). We used ArcGIS v.10.2 (ESRI, Redlands, California, USA) to extract data for each 30-m cell within each home range and core area. We

focused on the five most common land cover types found in 95 % eagle home ranges (forest & woodland, shrubland & grassland, semi-desert, agricultural vegetation, and developed & other human use) and combined all other land cover types into an “other” category (nonvascular & sparse vascular rock vegetation, introduced & semi-natural vegetation, recently disturbed or modified, open water, polar & high montane vegetation, and aquatic vegetation). We then calculated the proportion of each home range and core area in each of the six land cover categories.

We obtained elevation data from the National Elevation Dataset (NED; Gesch et al. 2002) and used ArcGIS v.10.2 to extract the elevation value for each 30-m cell in each home range and core area. We used the standard deviation of elevation values to characterize elevational variation within each home range and core area. We also calculated surface ratios in each home range and core area using DEM Surface Tools (Jenness 2013) for ArcGIS. The tool uses an elevation dataset to calculate the 3-dimensional surface area of each cell based on the surrounding eight cells. The surface area is then divided by the planimetric, or flat, area of that cell (900 m² for a 30-m cell) to obtain the surface area ratio. This resulting ratio represents a measurement of landscape topographic roughness (Jenness 2004). We used the standard deviation of these ratios to characterize variability in roughness, or topographic variation, within each home range and core area.

Long-distance movements—non-residents only

We defined long-distance movements as movements made by non-residents that were >100 km from the capture site. We analyzed these movements only in those months for which we did not analyze home ranges and core areas. We defined the start of the long-distance movement as the start time of the flight path that continued 100 km from the capture site. Similarly, we defined the end of the long-distance movement as the end time of the flight path that resulted in the bird returning within 100 km of the capture site. We created tracks (paths flown by an eagle) for each day and hour using the Xtools Pro Extension (Data East 2015) for ArcGIS and then calculated the length of each track to estimate daily and hourly distances traveled. We calculated average daily distances traveled by month, average hourly distances traveled, and the total distances traveled by each bird. Because birds made both long-distance and local movements

when away from the capture site, we further classified each daily track as “long” (>100 km) or “short” (<100 km) based on daily distance traveled.

Environmental correlates of long-distance movements

We examined vegetative and topographic characteristics of eagle long-distance movements. We first buffered each daily track by 1 km using the Buffer tool in ArcGIS v.10.2. We then extracted land cover, elevation, and roughness data for 30-m cells within the resulting polygons. For land cover, we used the five most common land cover types found in the buffered daily tracks (forest & woodland, shrubland & grassland, semi-desert, nonvascular & sparse vascular rock vegetation, and introduced & semi-natural vegetation) and combined all other land cover types into an “other” category (agricultural vegetation, recently disturbed or modified, polar & high montane vegetation, developed & other human use, open water, and aquatic vegetation). Two of the common land cover types in daily tracks (nonvascular & sparse vascular rock vegetation and introduced & semi-natural vegetation) were not common in home ranges and core areas. We then calculated the proportion of each daily track in each of the six land cover categories. We used the standard deviation of the elevation and roughness values (calculated as for local movements) to characterize these attributes of each daily track.

Statistical analyses

To understand environmental and topographic correlates of home ranges and core areas for local eagle movements, we ran two sets of linear mixed-effects models. In each set of models, we ran two separate sub-models, one with area of 95 % home ranges as the response variable and one with area of 50 % core areas as the response variable. We log-transformed the response variables to more closely meet distributional assumptions.

In the first model set, we used the nlme package (Pinheiro et al. 2015) in R (R Core Team 2015) to test for variation in eagle monthly home-range and core-area sizes. We included month as a fixed effect and individual bird nested within year as categorical random effects. This model did not include sex, age, movement status, or habitat effects.

In the second model set, we used the lme4 package in R (Bates et al. 2015) to test for variation in home-range and core-area sizes based on multiple environmental variables,

while controlling for month and year (although nlme provides more inferential tests, lme4 allows more flexibility in the treatment of random effects; thus we used lme4 here). We first tested correlations between pairs of continuous variables and removed one of the variables in any pair that had a correlation ≥ 0.65 . After removing these correlated variables, models included sex, age (six separate age classes, with Adult as the reference), movement status, four land cover variables (all except “forest & woodland” and “other”), variability in elevation, and variability in roughness as fixed effects. For the purposes of these models, we rescaled the elevation variable by subtracting the mean and dividing by two times the standard deviation (Gelman 2008). We included individual eagle nested within year as categorical random effects and month as a separate random effect.

For each of the two models in this second model set, we first ran a global model with all fixed effects. We then used the dredge function in the MuMIn package in R (Barton 2015) to run all possible model combinations based on the global model. We used Akaike’s Information Criterion corrected for small sample size (AICc) to rank the models and select the models with the most support in the data, based on model weights ≥ 0.01 (Burnham and Anderson 2002; Anderson 2008). Cade (2015) suggested that model-averaged coefficients should not be calculated when models contain multicollinearity among the predictor variables. Because we removed the correlated variables from the models, we then averaged the models with the most support in the data and calculated variable importance factors for each fixed effect.

To understand environmental and topographic correlates of long-distance eagle movements, we ran linear mixed-effects models with daily distance as the response variable. We used a cube root transformation which most closely met the distributional assumptions of our statistical tests. We used the lme4 package in R (Bates et al. 2015) to test for variation in daily distances based on multiple environmental variables. We again tested for correlation between pairs of continuous variables. After removing correlated variables ($r \geq 0.65$), we ran a global model that included sex, age, month, four land cover variables (all except “semi-desert” and “other”), and variability in elevation as fixed effects. We again rescaled the elevation variable as above. We included individual eagle nested within year as categorical random effects.

Because of the small sample sizes in this dataset (i.e., three of five birds had only one year of data), we first ran a model containing only data from the year with the largest amount of data (2013). The results of this model were similar to the model with the full dataset, indicating that fewer observations for some birds did not substantially influence the results. Hence, we proceeded with the model from the full dataset. We again used the MuMIn package in R (Barton 2015) to run all possible model combinations based on the global model. We used AICc to rank the models and select the models

with the most support in the data (model weights ≥ 0.01). We then averaged these models and calculated variable importance factors for each fixed effect.

Results

Eagle capture and telemetry

We captured and telemetered 23 golden eagles (11 females, 12 males) in 2012/2013 and two eagles (one female, one male) in 2014 (Supplementary Table S1). For this study, we only considered GPS locations collected from November 2012 to May 2015. During this period, eagles were tracked an average of 452 ± 337 (SD) days (range = 11–922 days), and the telemetry units collected 964,293 locations. After sub-sampling the 30-s data and removing poor-quality GPS locations, we used 335,954 locations (mean = $13,438 \pm 11,962$ locations per eagle; range = 300–35,574 locations; Supplementary Table S1) for data analysis.

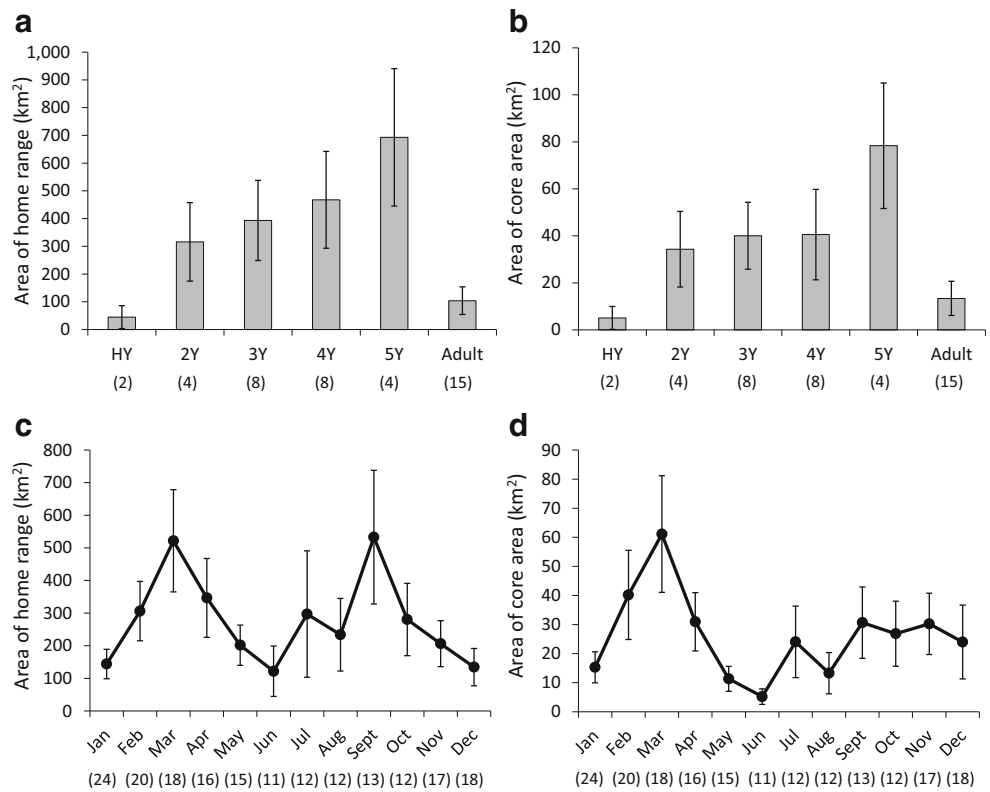
We identified 20 eagles (9 females, 11 males) as residents and five eagles (three females, two males) as non-residents. At time of capture, two birds were hatch-year (HY), two were second-year (2Y), four were third-year (3Y), three were fourth-year (4Y), one was fifth-year (5Y), and 13 were adult. For analysis purposes, we made two assumptions about bird age. First, we associated the current age of the bird with each location (i.e., for birds with >1 year of data, we increased the age of the bird each year on 1 January). Second, based on previous work on other raptor species indicating that birds in adult plumage only sometimes exhibit adult breeding behavior (Bloom et al. 2015), we categorized our 5Y birds as pre-adults (their behavior was consistent with this classification; see Results and Fig. 3).

Local movements—residents and non-residents

We estimated 359 monthly home ranges and 352 core areas; the aLoCoH program could not estimate seven monthly core areas distributed among six eagles. We excluded 35 home ranges and 35 core areas for non-residents because the centroid of their home range was >100 km from the capture site (range = 2–16 home ranges/core areas per each of the five non-resident eagles). Hence, we included 324 home ranges and 317 core areas in our analyses of local movements (Supplementary Table S2).

Local home ranges and core areas were larger for non-residents than for residents, but, contrary to expectations, they were similar for males and females (Table 1). Home ranges for resident birds frequently overlapped (Fig. 2). Consistent with the expectations of our hypotheses, home ranges and core areas were larger for pre-adult eagles (other than HY birds) than for adults (Fig. 3a, b). Home-range sizes ($F_{11,255} = 5.36$;

Fig. 3 Mean (\pm SE) monthly **a** home-range size and **b** core-area size by age class and **c** home-range size and **d** core-area size for each month of 25 golden eagles captured near Tehachapi, California, 2012–2015. Numbers of eagles are shown in parentheses below each age class and month



$P < 0.001$) and core-area sizes ($F_{11,248} = 5.65$; $P < 0.001$) differed among months. Mean (\pm SE) home-range sizes were largest in March (521.9 ± 156.8 km²; range = 2.5–2323.2 km²) and September (533.1 ± 204.9 km²; range = 4.1–2025.3 km²) and smallest during the spring (May–June; 167.9 ± 48.0 km²; range = 0.7–833.0 km²) and

late fall/early winter (November–January; 159.0 ± 32.1 km²; range = 0.7–1091.3 km²) months (Fig. 3c). Likewise, mean core-area sizes were largest in March (61.1 ± 20.0 km²; range = 0.1–312.2 km²) and smallest in May (11.3 ± 4.3 km²; range = 0.1–54.8 km²) and June (5.2 ± 2.7 km²; range = 0.02–24.6 km²; Fig. 3d).

Table 1 Home-range and core-area sizes (in km²) for the 25 golden eagles captured near Tehachapi, California, 2012–2015

	Mean	SD	Range	n ^a
Home ranges:				
All eagles	253.6	429.4	0.3–2649.1	324
Residents	146.7	259.1	0.3–1445.7	262
Non-residents ^b	705.3	657.8	6.2–2649.1	62
Males	259.0	492.0	1.3–2649.1	146
Females	249.2	371.6	0.3–1699.7	178
Core areas:				
All eagles	26.4	49.7	0.01–328.5	317
Residents	16.0	35.3	0.01–271.7	256
Non-residents ^b	70.4	72.5	0.45–328.5	61
Males	26.4	55.8	0.03–328.5	144
Females	26.5	44.0	0.01–226.5	173

^a Sample size (*n*) represents the number of eagle-months
^b Home ranges and core areas were included for non-residents only in those months when the centroid of their home range was <100 km from the capture site

Environmental correlates of local movements

The predominant land cover types within areas golden eagles used were forest & woodland (49 ± 27 % (SD) in home ranges and 53 ± 31 % in core areas) and shrubland & grassland (46 ± 29 % in home ranges and 45 ± 33 % in core areas; Supplementary Table S2). This pattern was consistent across all months (Fig. 4). Variability in elevation within home ranges coincided with variation in home-range size and was highest in March (mean \pm SD elevation = 305.3 ± 177.8 m; $n = 35$ eagle-months) and April (304.8 ± 191.2 m; $n = 30$ eagle-months) and lowest in June (213.6 ± 152.6 m; $n = 19$ eagle-months), July (222.1 ± 176.9 m; $n = 19$ eagle-months), and November (224.7 ± 97.2 m; $n = 27$ eagle-months). Variability in elevation within core areas was highest when core areas were large in March (272.4 ± 211.9 m; $n = 33$ eagle-months) and lowest when core areas were smaller in August (142.6 ± 142.3 m; $n = 18$ eagle-months). Variability in topographic roughness was similar across all months within both home ranges (0.070 ± 0.013) and core areas (0.064 ± 0.018).

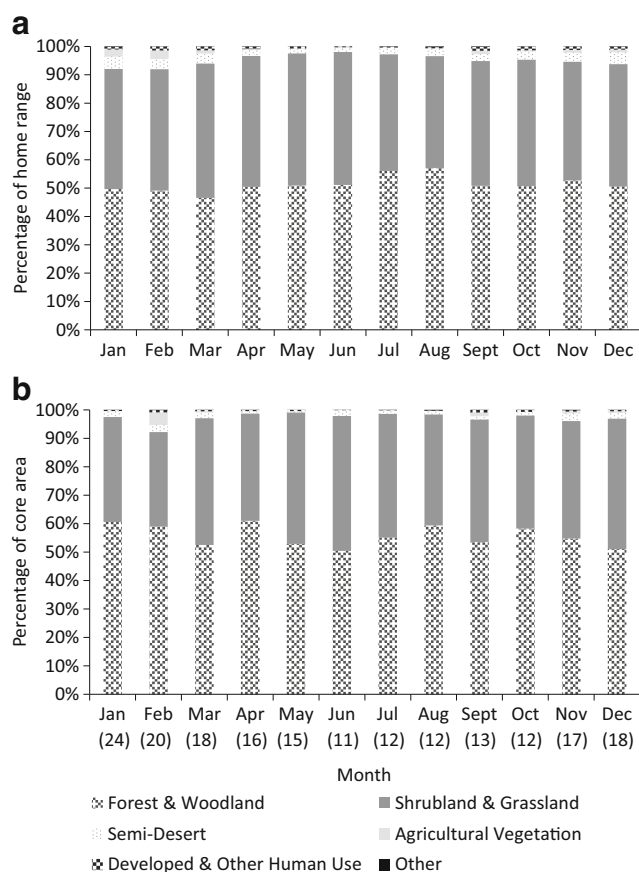


Fig. 4 Mean percentage of six land cover types by month within **a** home ranges and **b** core areas of 25 golden eagles captured near Tehachapi, California, 2012–2015. The “other” category includes nonvascular & sparse vascular rock vegetation, introduced & semi-natural vegetation, recently disturbed or modified, open water, polar & high montane vegetation, and aquatic vegetation. *Numbers* of eagles are shown in *parentheses* below each month

In the home-range analysis, we ran 512 models, 24 of which showed support in the data (model weights ≥ 0.01 ; Table 2). These 24 models contained 95 % of the weights of all models. Age, developed & other human use, and variability in elevation were included in all 24 supported models (i.e., their variable importance factors were 1.0; Table 2). Variability in roughness was included in all but one supported model. Semi-desert was included in 15 of the supported models, and agricultural vegetation was included in 13 of the supported models. The best model contained all variables except sex, movement status, and shrubland & grassland. These three factors also had the lowest variable importance and were not included in all supported models. Variability in elevation, semi-desert, agricultural vegetation, and developed & other human use were positively associated with home-range size, whereas variability in topographic roughness and shrubland & grassland were negatively associated with home-range size (Table 2). Pre-adult birds had larger home-ranges than adult birds (Table 2).

In the core-area analysis, we ran 512 models, 16 of which showed support in the data (Table 2). These 16 models again contained 95 % of the weights of all models. Age, agricultural vegetation, developed & other human use, variability in elevation, and variability in roughness were included in all 16 supported models (i.e., their variable importance factors were 1.0; Table 2). Semi-desert was not included in all supported models but had variable importance of 0.6 (Table 2). The best model contained all variables except sex, movement status, and shrubland & grassland. These three factors also had the lowest variable importance and were not included in all supported models. Shrubland & grassland, semi-desert, agricultural vegetation, developed & other human use, variability in elevation, and variability in roughness were positively associated with core-area size (Table 2). Pre-adult birds had larger core areas than adult birds (Table 2).

Long-distance movements—non-residents only

Five pre-adult eagles made long-distance movements; as expected, no adults made these types of movements. These included two females and one male for which we only had 1 year of data (2013: female and male; 2014: female), one male for which we had 2 years of data (2013, 2014), and one female for which we had 3 years of data (2013, 2014, 2015; Table 3; Supplementary Figs. S1–S5). For the latter bird, the telemetry unit only transmitted data for one long-distance movement month in 2015 (February).

Eagles generally traveled north from the southern California capture sites, and they returned each year to within 100 km of the capture sites. We identified 816 daily tracks and 9863 hourly tracks from these five birds (Table 3; Supplementary Table S3). Even during these travels, the majority (77 %) of daily tracks were short-distance movements (<100 km/day). The farthest an eagle we monitored traveled was 1588.4 km (1-way and measured as a straight-line distance), from southern California to southern Montana by a male in 2014 (Table 3; Fig. 1; Supplementary Figure S4).

Each bird began long-distance movements during different months. Start dates were from February to June, and end dates were between June and October. The mean distance eagles traveled in the course of a single day was 63.7 ± 69.0 km (SD; range = 0.002–397.4 km; Table 3). When eagles traveled <100 km/day, the average daily distance traveled was 32.0 ± 27.9 km. When eagles traveled >100 km/day, the average daily distance traveled was 168.9 ± 59.8 km. The longest average daily distances traveled occurred in February (124.2 km; $n = 1$ eagle) and March (102.8 km; $n = 1$ eagle) and the shortest mean (\pm SE) distances occurred in June (61.8 ± 13.2 km; range = 24.9–93.4 km; $n = 5$ eagles), July (62.7 ± 16.1 km; range = 36.0–108.0 km; $n = 4$ eagles), and August (59.3 ± 8.2 km; range = 35.8–71.8 km; $n = 4$ eagles; Fig. 5a).

Table 2 Model-averaged coefficients and variable importance factors from best-performing linear mixed-effects models explaining variable influences on sizes of 95 % home ranges and 50 % core areas, based on model weights ≥ 0.01 , for the 25 golden eagles captured near Tehachapi, California, 2012–2015

Home range/core area modeled	Variable	Averaged coefficient	Adjusted SE	Importance
95 % ^a	Intercept	3.351	0.477	
	Sex—male	−0.004	0.083	0.137 ^b
	Movement status—resident	0.001	0.153	0.203 ^b
	Age HY	1.048	0.734	1.000 ^b
	Age 2Y	1.716	0.438	
	Age 3Y	1.650	0.356	
	Age 4Y	1.124	0.381	
	Age 5Y	2.006	0.428	
	Shrubland & grassland	−0.002	0.167	0.215
	Semi-desert	1.184	1.070	0.762
	Agricultural vegetation	0.709	1.607	0.653
	Developed & other human use	36.302	5.769	1.000
	Elevation variability	2.596	0.167	1.000
	Roughness variability	−11.482	5.761	0.993
50 % ^c	Intercept	−0.347	0.653	
	Sex—male	0.119	0.260	0.329 ^b
	Movement status—resident	−0.356	0.511	0.511 ^b
	Age HY	0.352	1.102	1.000 ^b
	Age 2Y	1.755	0.719	
	Age 3Y	1.873	0.582	
	Age 4Y	1.749	0.615	
	Age 5Y	3.054	0.673	
	Shrubland & grassland	0.003	0.172	0.228
	Semi-desert	0.475	1.110	0.574
	Agricultural vegetation	5.999	1.561	1.000
	Developed & other human use	14.671	7.361	1.000
	Elevation variability	1.544	0.179	1.000
	Roughness variability	9.135	4.156	1.000

^a Model-averaged coefficients for 95 % home ranges include the 24 best-performing models

^b Variable importance factors for categorical variables (sex, movement status, and age) were calculated on the variable as a whole

^c Model-averaged coefficients for 50 % core areas include the 16 best-performing models

The mean (\pm SD) hourly distance traveled was 5.2 ± 10.4 km (range = 0.0004–82.8 km; Table 3). Eagles traveled the longest distances during the middle of the day, between 11:00 and 14:00 h PST, with the longest average (\pm SE) distance during 12:00 h (11.4 ± 0.9 km; range = 9.0–14.5 km; $n = 5$ eagles; Fig. 5b). The shortest hourly distances occurred in early morning (between 03:00 and 08:00 h) and late afternoon (between 17:00 and 19:00 h; Fig. 5b). Over 90 % of hourly distances were <20 km and 77 % were <5 km.

Environmental correlates of long-distance movements

The predominant land cover type non-resident eagles flew over was semi-desert (60 ± 28 % (SD)); forest & woodland was the second most frequently used land cover class (25

± 24 %; Supplementary Table S3). Buffered daily tracks consisted of 5 % or less of each of the other land cover types. Use of semi-desert was highest during short-distance daily movements (61 ± 3 % (SE)), and use of forest & woodland was highest during long-distance daily movements (28 ± 3 %; Fig. 6). Use of semi-desert was highest in May (73 ± 8 %) and when average daily distances were short in July (67 ± 4 %; Fig. 7). Use of forest & woodland was highest in October (55 ± 5 %) and when average daily distances were longest in February (41 %; Fig. 7).

Variability in elevation was higher during long-distance daily movements (334.4 ± 184.0 (SD) m; $n = 189$ daily tracks) than short-distance daily movements (182.7 ± 120.0 m; $n = 627$ daily tracks). Variability in elevation coincided with variation in average daily distances and was highest in

Table 3 Detailed data (travel times and distances traveled in km) for five golden eagles captured near Tehachapi, California, 2013–2015, that made long-distance movements away from the capture site

Eagle ID	Sex	Age	Year	Start date	End date	% of year away from capture site	Daily tracks				Hourly tracks				Longest distance north
							# tracks	Mean distance	Maximum distance	Minimum distance	# tracks	Mean distance	Maximum distance	Minimum distance	
6846	F	4Y	2013	8 June	17 Aug	19.2 %	64	60.30	333.26	0.026	767	4.97	56.95	0.001	788.77
6994	M	3Y	2013	21 May	30 June	11.0 %	40	70.12	303.00	0.702	514	5.36	82.82	0.002	733.28
7224	F	3Y	2014 ^a	16 June	4 Sept	21.9 %	81	64.58	297.51	0.876	1162	4.41	63.96	0.001	1189.81
7364	M	3Y	2014	10 Sept	20 Oct	11.0 %	41	68.40	261.51	0.903	479	5.82	70.65	0.002	874.97
		2Y	2013 ^a	12 June	14 June	0.6 %	3	184.06	272.86	33.938	29	19.04	77.57	0.025	233.19
		2Y	2013	28 June	23 July	6.8 %	26	170.14	391.71	10.296	378	11.67	74.44	0.002	1134.17
		2Y	2013	21 Oct	27 Oct	1.6 %	7	98.09	124.72	62.532	63	10.85	38.59	0.002	155.24
7463	F	3Y	2014 ^a	15 May	16 Sept	34.0 %	125	69.32	397.38	0.878	1725	4.94	68.14	0.0004	1588.42
		3Y	2014	19 Sept	7 Oct	4.9 %	19	106.47	281.91	1.763	197	10.24	61.81	0.002	770.44
		3Y	2014	17 Oct	21 Oct	1.1 %	5	63.85	113.82	32.051	47	6.77	27.47	0.003	82.00
		3Y	2014	24 Oct	30 Oct	1.6 %	7	66.66	110.53	32.621	61	7.17	35.42	0.003	138.34
Totals		4Y	2015 ^b	15 Feb	21 Feb	Unknown	7	124.17	185.78	78.817	69	12.60	43.50	0.007	760.56
							7	49.67	264.12	0.065	2552	4.14	55.96	0.001	941.13
							816	63.70 ^c			9863	5.15 ^d			

^a Eagle made multiple long-distance movements (i.e., > 100 km from the capture site) during the same year

^b The telemetry unit for eagle 7463 only collected data in 2015 for seven days, resulting in an incomplete record of her movements that year

^c Mean daily distance calculated as the sum of distances of daily tracks traveled by all five birds (51,978.50) divided by the sum of the number of daily tracks (816)

^d Mean hourly distance calculated as the sum of distances of hourly tracks traveled by all five birds (50,805.58) divided by the sum of the number of hourly tracks (9863)

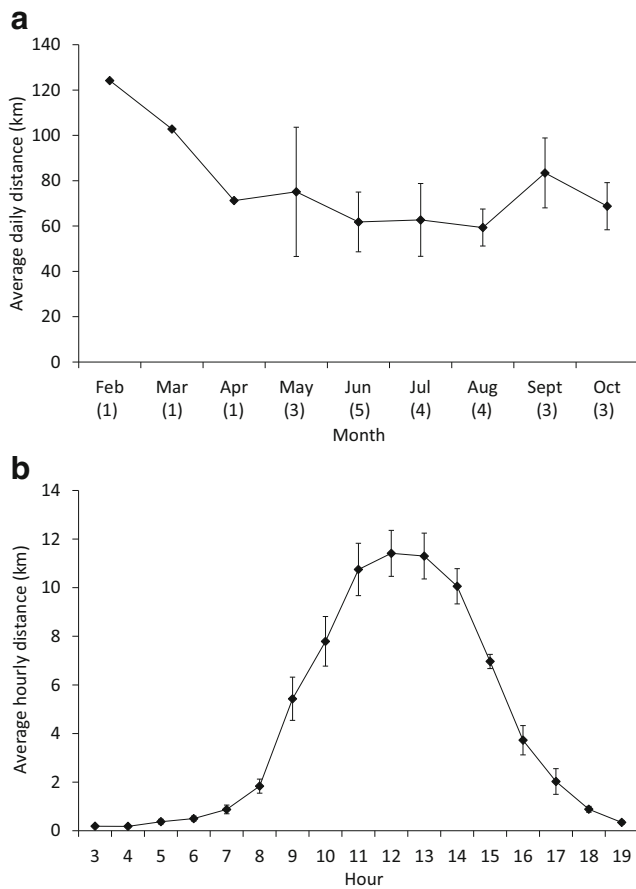
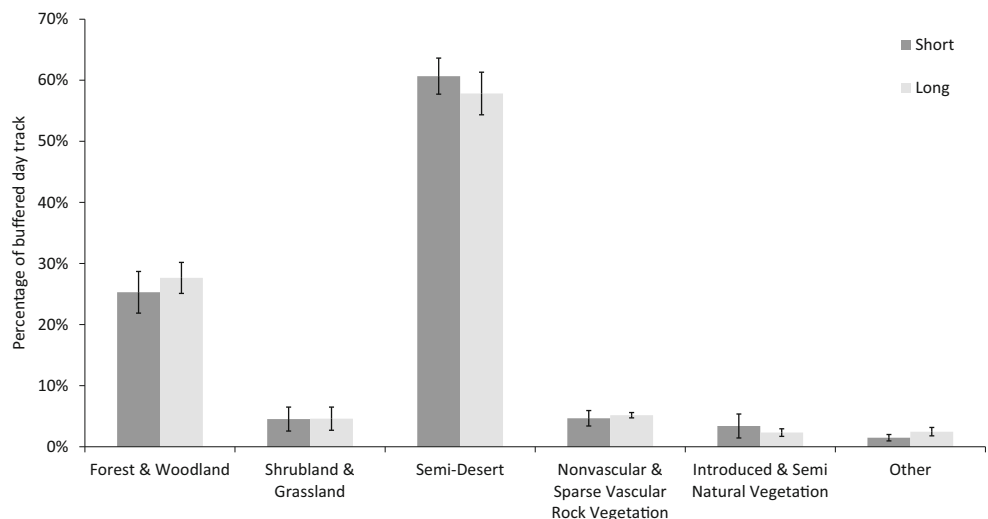


Fig. 5 Mean (\pm SE) **a** daily distances traveled by month and **b** hourly distances traveled by five golden eagles captured near Tehachapi, California, 2013–2015. Long-distance movements occurred between February and October. Telemetry units collected data between 03:00 and 19:00 h PST (birds were sometimes in other time zones, hence the early PST start times). Numbers of eagles in **a** are shown in parentheses below each month. In **b**, $n=5$ eagles for each hour except 03:00, when $n=1$

Fig. 6 Mean (\pm SE) percentage of six land cover types within daily paths, buffered by 1 km, traveled by five golden eagles captured near Tehachapi, California, 2013–2015, during short-distance (<100 km) and long-distance (>100 km) flights. The “other” category includes agricultural vegetation, recently disturbed or modified, polar & high montane vegetation, developed & other human use, open water, and aquatic vegetation



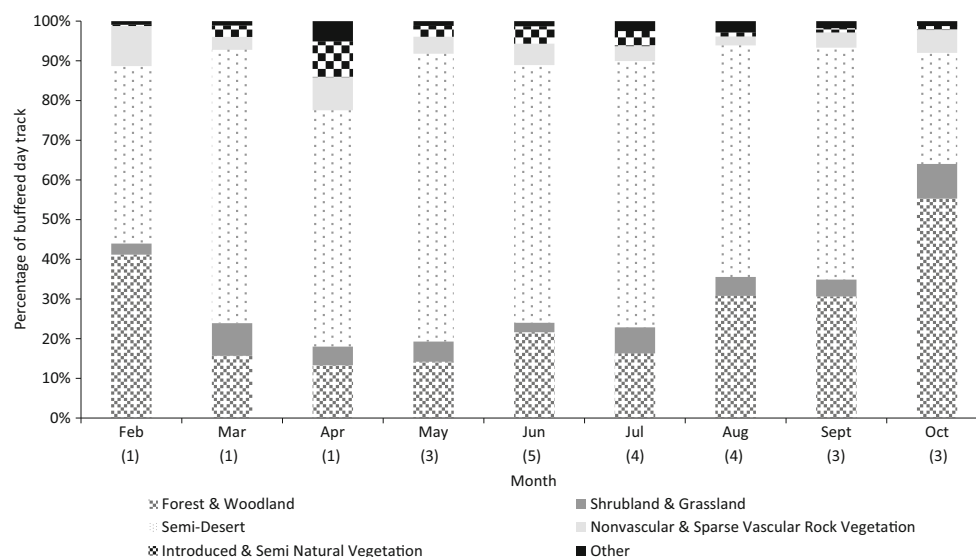
February (409.3 ± 148.1 m; $n=7$ daily tracks) and October (321.8 ± 201.3 m; $n=91$ daily tracks) and was smallest in May (187.0 ± 161.1 m; $n=86$ daily tracks) and July (168.7 ± 118.2 m; $n=168$ daily tracks). Variability in topographic roughness was higher during long-distance daily movements (0.069 ± 0.032 ; $n=189$ daily tracks) than short-distance daily movements (0.055 ± 0.028 ; $n=627$ daily tracks). Variability in roughness coincided with variation in average daily distances and was highest in February (0.092 ± 0.039 ; $n=7$ daily tracks) and October (0.078 ± 0.031 ; $n=91$ daily tracks) and was smallest in May (0.048 ± 0.018 ; $n=86$ daily tracks) and July (0.047 ± 0.028 ; $n=168$ daily tracks).

We ran 256 models describing behavior of eagles that moved long distances, 10 of which showed support in the data (Table 4). These 10 models contained 99 % of the weights of all models. Month, forest & woodland, non-vascular & sparse vascular rock vegetation, and variability in elevation were included in all 10 supported models (i.e., their variable importance factors were 1.0; Table 4). Sex, age, shrubland & grassland, and introduced & semi-natural vegetation were not included in all supported models and, thus, had lower variable importance (Table 4). The best model was the global model containing all variables. Shrubland & grassland, introduced & semi-natural vegetation, and variability in elevation were positively associated with daily distance traveled, whereas forest & woodland and nonvascular & sparse vascular rock vegetation were negatively associated with daily distance traveled (Table 4).

Discussion

Our analysis of habitat and age-, sex-, and season-specific movement behavior of golden eagles provides insight into

Fig. 7 Mean percentage of six land cover types by month within daily paths, buffered by 1 km, traveled by five golden eagles captured near Tehachapi, California, 2013–2015. The “other” category includes agricultural vegetation, recently disturbed or modified, polar & high montane vegetation, developed & other human use, open water, and aquatic vegetation. *Numbers* of eagles are shown in *parentheses below each month*



the drivers of animal movement and how those forces may change as an animal ages. The eagles in our study exhibited two distinct types of movement. All eagles of all age classes engaged in local movements that were fairly consistent regardless of age. In contrast, certain pre-adult eagles were the only ones to engage in long-distance movements. These movements were not easily categorized and had many characteristics associated with migration but others associated with prospecting, dispersal, and nomadism. The majority of previously published studies of golden eagles have focused only on one age class (i.e., adults or HY birds) whose

behaviors are relatively easily categorized. In contrast, our study spans all ages of eagles. The diversity of movements that we observed was, on the one hand, atypical for studies of movement of long-lived raptors, but on the other hand, not surprising given the stratification of age classes we monitored.

Local movements—residents and non-residents

All eagles made localized movements and established home ranges or territories near the capture site. These were the only types of movements recorded for 20 of the 25 individuals that

Table 4 Model-averaged coefficients and variable importance factors from the 10 best-performing linear mixed-effects models (based on model weights ≥ 0.01) explaining variable influences on daily distance traveled by the five golden eagles captured near Tehachapi, California, 2013–2015, that made long-distance movements

Variable	Averaged coefficient	Adjusted SE	Importance
Intercept	47.079	4.769	
Sex—male	4.039	2.124	0.934 ^a
Age 2Y	3.274	3.138	0.945 ^a
Age 3Y	0.295	2.900	
Month 3	−3.585	6.024	1.000 ^a
Month 4	−5.350	5.633	
Month 5	−14.702	5.485	
Month 6	−12.495	5.367	
Month 7	−7.630	5.352	
Month 8	−7.783	5.350	
Month 9	−5.609	5.418	
Month 10	−8.361	5.425	
Forest & woodland	−16.643	2.122	1.000
Shrubland & grassland	2.016	3.695	0.811
Nonvascular & sparse vascular rock vegetation	−37.077	6.090	1.000
Introduced & semi-natural vegetation	0.749	5.559	0.845
Elevation variability	20.416	0.962	1.000

^a Variable importance factors for categorical variables (sex, age, and month) were calculated on the variable as a whole

we monitored. Home-range sizes were among the largest reported for this species; the biggest monthly home range we measured of a resident eagle was more than twice the size of the largest previously reported for the species (605 km², calculated as a 95 % minimum convex polygon over the entire breeding season; Moss et al. 2014). We identified two distinctions between our study and previous work that may explain differences between studies. First, many of our resident eagles appeared not to produce chicks during the study period, likely contributing to larger home ranges. Second, we evaluated many different age classes of eagles. In our study, all pre-adults (except HY birds) maintained larger home ranges and core areas than did adults (Fig. 3). These observations are consistent with predicted distinct differences in movement patterns between younger and older eagles, in which younger eagles move more widely in search of productive or vacant nesting territories (Watson 2010). However, the lack of a sex effect is inconsistent with established models of raptor movements, in which females are generally the dispersive sex (Newton 2003) and thus, on average, move farther.

Five of our 25 birds made long-distance movements in addition to local movements. The tendency to make long-distance movements seems to be accompanied by a general pattern of increased wandering. Thus, even when making local movements, the average home-range sizes of these eagles were more than twice the size of those of the pre-adult birds that did not make long-distance movements and 12 times the size of those of adult eagles. This considerable difference likely reflects the drifting nature of young birds that, even when moving <100 km, still range more than older animals and other young birds that do not make long-distance movements.

Consistent with our hypotheses and as has been observed elsewhere (Braham et al. 2015), sizes of home ranges of eagles in our study area varied seasonally and in response to breeding status. Although nesting adult eagles maintain small home ranges during the winter pre-breeding and spring breeding seasons (or until nest failure), approximately half of our study animals were not territorial adults. Home-range sizes of all birds increased in March and October, the periods during which some of our eagles made long-distance movements. This pattern suggests that eagles, even those that do not leave their primary home ranges, increase their wandering activity when not nesting. Thus, the high degree of individual variation in movement that we observed likely was a consequence of the nesting outcomes and multiple age classes of the birds we monitored.

We also observed almost equal use of forested and grassland habitat types during all months of the year, regardless of the size of the home range (Fig. 4). This result contrasts to at least two previous studies that have linked an increase in home-range size with an increase in forested landscapes (Moss et al. 2014; Braham et al. 2015). Eagles generally are thought to prefer open areas that may be more suitable for

hunting than are forested cover types (Watson 2010). However, the forested habitat in the Moss et al. (2014) study was very dense and impenetrable, unlike the open oak savannah habitat in our study area. Further, our results likely were influenced by our focus on local movements within 100 km of the capture site, thus only including areas that were fairly homogeneous in habitat.

Although the Mojave Desert is located within 100 km of the study area, our eagles did not increase their use of semi-desert when expanding their home ranges. This behavior contrasts directly with the activities of Mojave breeding eagles that make repeated trips from the desert to the mountains (Braham et al. 2015). It also suggests that desert eagles may benefit from the presumed high resource availability in the mountains, whereas mountain eagles have less to gain by making trips to the desert.

When golden eagles traveled away from their nest sites, they flew over terrain of varying elevations. Eagles likely fly over a mixture of topographic features when traveling longer distances, in contrast to the relative homogeneous features of short, foraging trips near their nesting or roosting sites. Variation in use of topographic roughness was similar in all months, reflecting the uniform year-round use of this habitat feature and the consistent use of land cover types.

Interestingly, we found a strong, positive relationship between human development and sizes of home ranges and core areas (Table 2), suggesting that eagles may expand the size of their home ranges in conjunction with increasing development. This finding is similar to the results of studies conducted on urban wildlife species in which habitat fragmentation resulting from urbanization may cause animals to increase their home ranges to meet their daily needs (e.g., Riley et al. 2003; Gehrt et al. 2009). Regions with human development are highly disturbed, likely have scarce food resources for eagles, and may increase sensitivity of eagles to urbanization, all forcing eagles to use more space.

Long-distance movements—non-residents only

Five of the 25 golden eagles in our study made long-distance movements >100 km from the capture site (Table 3; Supplementary Figs. S1-S5). The longest distance traveled by an eagle we monitored was 1588 km (measured as 1-way). However, this trip to southeastern Montana was still shorter than the long-distance migratory movements of northern-latitude breeders (McIntyre et al. 2008; Miller et al. 2016).

The maximum daily distance traveled by an eagle was 397 km and the maximum hourly distance was 83 km. These distances were longer than the maximum daily distance (53 km) and hourly distance (~30 km) documented by Soutullo et al. (2006a) for HY birds. Eagles concentrated these movements during the middle of the day, with peak distances traveled occurring between 11:00 and 14:00 h PST (Fig. 5).

Golden eagles generally intensify their movements during midday when updrafts favoring soaring or gliding flight are more likely to occur (Soutullo et al. 2006a; Watson 2010; Katzner et al. 2015). Additionally, eagle activity may increase during this time because some of their preferred prey become more active during the day, which may increase their foraging success (Soutullo et al. 2006a).

Although these five eagles made extreme long-distance movements, the majority of their daily movements were still short-distance (i.e., <100 km). Previous work distinguished between two scales of movements and found that young eagles make random movements at biweekly “exploratory” scales but display non-random movements at daily “foraging” scales (Soutullo et al. 2013). That study suggested that larger-scale movements were used to gather information about vacant territories or available mates, and smaller-scale movements were driven by an active search for food. However, the scale of our large-scale movements appears to be much greater than in that study, and our eagles may have been engaged in different behaviors during these long-distance directional trips (i.e., >100 km/day). Although we also evaluated short-distance movements at a larger scale than that study, our birds likely were actively foraging or evaluating local resource availability during these movements.

The two scales of movement we observed are also relevant to our habitat selection analyses. The semi-desert habitat type eagles used during short-distance movements should be well suited for foraging, due to its openness. In contrast, the forest habitat type that eagles sometimes flew over during longer-distance movements might be better suited to traveling or exploring over long distances, as well as providing perching or resting sites. Variability in both elevation and topographic roughness varied positively with distance traveled by eagles. These findings indicate that golden eagles will fly over diverse topographic features with variable terrain, which can be beneficial to soaring flight when making long-distance movements.

Each of the five eagles in our study that moved long distances north away from the capture site in southern California each spring or summer also returned to the capture area in late summer or fall, remained in this area during winter, and then traveled long distances again the following spring or summer. Young non-migratory Spanish imperial eagles (*Aquila adalberti*) display similar behavior (but not always traveling north), departing from the natal population, making exploratory movements, using temporary settlement areas, and returning frequently to the natal area (Ferrer 1993). The golden eagles in our study also used temporary settlement areas in which they would make localized movements for several weeks at a time before moving long distances to another area. This strategy may be a response to resident adults defending their territories, motivating young eagles to move from place to place (Watson 2010). The eagles in our study did not,

however, return as frequently to the origin (capture site) as did the Spanish imperial eagles in Ferrer’s (1993) study.

Interpreting non-resident eagle movement

Several potential lines of evidence may explain the long-distance movements we observed. Home ranges of resident eagles in the study area consistently overlapped each other (Fig. 2), with insufficient room available for additional birds. Thus, at times when resources were scarce, these five non-resident eagles may have made long-distance movements to avoid competitive interactions. Similarly, California ground squirrel abundance near Tehachapi may vary throughout the year. As these animals are primary eagle prey, changes in their availability also may influence the decision by eagles to leave the local area. These competitive and resource-related mechanisms provide one plausible set of reasons why some eagles may choose to depart the capture site.

The movements we observed do not meet, in the strict sense, the traditional definitions of typical avian movement behavior (Newton 2008). For example, “migration” typically is defined by long, directional movements during a specified season, after which the animals usually return to their point of origin. Migration also is usually in fixed directions and a response to seasonal changes in food availability (Gaines and McClenaghan 1980; Newton 2008). Previous research conducted on eagles has referred to nearly all long-distance, non-dispersive movements as migration (e.g., McIntyre et al. 2008; Bohrer et al. 2012).

Our five eagles made long-distance movements, they returned to the point of origin each year, and their movements can plausibly be tied to variation in food availability, all behaviors consistent with traditionally-defined migration. However, their movements were interrupted and irregular, and they did not settle in one place for more than a few weeks at a time. Instead, they continued making intermittent long-distance exploratory movements throughout their time away from the capture site. Although optimal migration theory suggests that birds will balance costs of time and energy by including stopovers in their travels (Alerstam 2011; Miller et al. 2016), these movements seemed more random in nature and were not contained within one specific area. Further, individuals behaved very differently from each other. In fact, two of the five birds spent only ~10 % of the year away from the capture site (Table 3), making these movements hardly seem “seasonal” in nature. Thus, although many elements of this behavior do appear migratory in nature, other patterns are atypical of migration as it has been classically defined (Newton 2008).

The movements of these five birds also do not appear to be “dispersive.” “Natal dispersal” is generally defined as movements made by young individuals from a natal territory to a new place where that animal eventually reproduces, and “breeding dispersal” refers to movements by reproductive

adults between successive breeding sites (Greenwood 1980; Greenwood and Harvey 1982). These behaviors are obviously not breeding dispersal because these eagles were not of breeding age (however, if an eagle eventually settled north to breed, then we might change our interpretation of this behavior; see discussion of “prospecting” below). Because the eagles in our study returned to the capture site every year, their behavior also does not appear to be natal dispersal. Further, because the birds we studied were not captured as nestlings, we are uncertain of their natal origin.

Finally, these long-distance movements also cannot usefully be described as either prospecting or nomadism. “Prospecting” is the process of gathering information about possible breeding sites (Reed et al. 1999). Although unlikely, these five eagles may have been searching for vacant breeding territories during their long-distance journeys. However, because they returned to the capture site each year and because we do not have information on their ultimate breeding sites, we cannot, with our current knowledge, refer to these movements as prospecting. Likewise, “nomadism” is defined as movements made by individuals who wander and breed at multiple sites throughout their lives (Bloom et al. 2011). Although these birds did display characteristics of wandering, especially after they had traveled long distances away from the capture site, they returned annually to southern California and we observed no evidence of breeding behavior.

Hence, because the movements of these five eagles are not precisely described by existing terminology, we are unclear about how best to categorize these behaviors. Ultimately, knowing the locations of the natal area and the eventual breeding sites is essential to classifying these movements. Additional long-term study of the movements of pre-adult golden eagles, from the nestling stage to the breeding stage, would enhance our knowledge and understanding of, and better characterize, the movement behavior of this species.

Conclusions

We observed two distinct movement types by golden eagles that demonstrate consistent patterns associated with age- and season-, but not sex-, specific movement behavior within this eagle population. Although the behavior of the birds that remained near the capture site and made only local movements is, largely, what might be expected from eagles, the long-distance movements we observed, although similar to movements of other southern California raptors, are not as easily explained. Thus, the drivers of local movements within this population are largely consistent with established movement theory. In contrast, the drivers of the long-distance movements we observed are less clear, largely because sample size considerations and lack of knowledge of natal and

ultimate breeding sites constrain insight into the decision-making underpinning these movements.

Our analysis has implications for connectivity, and thus management, of golden eagle populations on a continental scale. The frequent long-distance movements we observed demonstrate that pre-adult eagles from this area could, upon maturity, breed in other locations. Such movements would promote gene flow and genetic variability within North American golden eagle populations (Gaines and McClenaghan 1980; Greenwood 1980). Recent work has shown the high likelihood of distinct genetic population structure within golden eagle populations in North America (J. Doyle, personal communication). Because the implication of this finding is that gene flow between populations is limited, those data are not congruent with the movements we documented. Thus, studies that link natal and ultimate breeding sites of eagles would be important to understand the determinants of movements and connectivity of golden eagle populations across North America.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Animal handling was approved by the West Virginia University Animal Care and Use Committee protocol #14-0303.

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