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Interpreting long-distance movements of non-migratory golden eagles: Prospecting and nomadism?

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Abstract

Movements by animals can serve different functions and occur over a variety of spatial and temporal scales. Routine movement types, such as residency (localized movements) and migration, have been well studied. However, non-routine movement types, such as dispersal, prospecting, and nomadism, are less well understood. Documenting these rarely detected events requires tracking large numbers of individuals across all age classes. We studied >500 golden eagles (*Aquila chrysaetos*) tracked by telemetry over a 10-year period in western North America, of which 160 engaged in nonroutine, long-distance (>300 km) movements. We identified spatial and temporal correlates of those movements at both small and large scales, and we quantified movement timing and direction. We further tested which age and sex classes of eagles were more likely to engage in these movements. Our analysis of 88,093 daily tracks suggested that distances traveled by eagles were responsive to the updraft potential of the spatial and temporal landscape they encountered. Tracks covered longer distances at locations and times of higher updraft potential, and older birds traveled farther than younger birds. By contrast, after decomposing daily tracks into 563 nonroutine, long-distance movements measured at a multiday scale, only the duration of travel was responsive to environmental conditions encountered by eagles. Multiday trips that were longer were those initiated in open and warm landscapes and those that ended in mountainous regions. Finally, long-distance movements were more frequently made in seasons other than winter, in north-south directions, and by young birds. We documented clear correlates of nonroutine, long-distance movements by golden eagles at small, local scales but found little evidence of such correlates at larger, regional scales. Most long-distance movements we

[†]Deceased.

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documented fit patterns associated with traditional definitions of prospecting and nomadism but not migration. Our study is the first to describe these movement types by golden eagles, and as such provides a foundation for subsequent study into the movement ecology of other species.

KEYWORDS*Aquila chrysaetos*, dispersal, migration, movement ecology, North America**INTRODUCTION**

Movement ecology is an essential component of the life history of nearly all animals (Nathan et al., 2008). Movements can serve different functions over a variety of spatial and temporal scales. For example, most animal movements that occur at relatively small spatial and temporal scales are associated with activities such as foraging, territory defense, and raising offspring (Newton, 2008). Alternatively, movements can be a consequence of larger-scale spatial and temporal processes, such as searching for a mate or territory, seeking new foraging areas, or avoiding dangerous environmental conditions.

Movements can be driven by internal (e.g., hunger) or external (e.g., photoperiod) cues and may be predictable (e.g., seasonal) or unpredictable (e.g., in response to food stress or disturbance). In conjunction with the diverse drivers of movements, a number of movement types have been identified. Definitions of some of these movement types sometimes vary by author and study (e.g., Newton, 2008; Riotte-Lambert & Matthiopoulos, 2020). The following definitions reflect our understanding of these terms and how we used them in this study. “Residency” movements are made by animals that move only short, localized distances centered within a home range or territory, whereas “migration” occurs when animals move longer, sometimes intercontinental, distances between breeding and wintering areas and on a seasonal or annual cycle (Newton, 2008). Migration can be longitudinal, latitudinal, altitudinal, or even from one habitat to another. “Natal dispersal” takes place when young animals move from a natal territory to an eventual breeding territory, and “breeding dispersal” occurs when adults move between successive breeding sites (Greenwood, 1980; Greenwood & Harvey, 1982). Natal dispersal can consist of three stages: (1) emigration from the natal site (i.e., departure from the site where the animal was born/hatched), (2) transience (i.e., a period of transition between stages 1 and 3 when the animal moves between, and may temporarily settle in, multiple sites), and (3) immigration to the breeding site (i.e., settlement at the site where the animal eventually breeds; Weston et al., 2013). “Prospecting” movements allow individuals

to gather information, for example, about habitat type, the competitive environment, or possible breeding or foraging opportunities, and may be made by animals of all ages (Boulinier et al., 2016; Murphy et al., 2017; Reed et al., 1999; Weston et al., 2013). Prospecting is not interrupted by periods of residency, but it can be short or long distances or duration, and it can occur just before or during natal dispersal, before or during breeding dispersal, or before or after migration (Reed et al., 1999). Some prospecting adult animals may also be referred to as “floaters,” who rapidly replace breeders that have died or have been displaced (Hunt, 1998). Finally, “nomadism” occurs when individuals wander from place to place with irregular timing and direction, taking up short-term residency, and sometimes even breeding, in those places (Newton, 2008; Teitelbaum & Mueller, 2019). Nomadic movements can be made by young animals (prior to reaching breeding age) or by adults (during the breeding years). These last two types of movements are not always well differentiated in the literature, and prospecting by young animals sometimes can precede nomadism by adult animals (Watson et al., 2019; Watson & Keren, 2019).

Of these movement types, those generally defined as “routine” (Newton, 2008; Riotte-Lambert et al., 2017), such as residency and migration, are the most well studied. Small-scale movements of resident animals have been studied, for example, by examination of home ranges (e.g., Bevanda et al., 2015; Rivers et al., 2014) and habitat selection (e.g., D'Eon & Serrouya, 2005; Doherty et al., 2010). Similarly, large-scale migratory movements of a variety of species are well known (e.g., Åkesson & Hedenström, 2007; Lohmann, 2018; Sergio et al., 2014). However, “nonroutine” movement types, such as dispersal, prospecting, and nomadism, are not as well understood. One reason for this poor understanding is that many of these movements are sporadic and irregular (Reed et al., 1999), and sometimes difficult to categorize. Further, technological limitations and research biases may contribute to these movements being undetected (Cooper & Marra, 2020). As a consequence, a large sample of tracked animals monitored over multiple years is required to identify and estimate the

frequency, duration, distance traveled, and environmental and demographic conditions associated with these cryptic events.

Golden eagles (*Aquila chrysaetos*) are long-lived raptors with a Holarctic distribution (Watson, 2010) that have been telemetered and tracked in large numbers (Brown et al., 2017). As such, home ranges (Braham et al., 2015; Miller et al., 2017; Watson et al., 2014), habitat selection (Domenech et al., 2015; Duerr, Braham, et al., 2019; Miller et al., 2014; Squires et al., 2020; Watson et al., 2014), and migration patterns (Bedrosian et al., 2018; Duerr et al., 2012; Eisaguirre et al., 2019; Miller et al., 2016) of golden eagles have been well studied. Because of these extensive studies, seasonal movements of golden eagles are well known and are extremely diverse. Eagles may be long-, medium-, or short-distance migrants, their migration may be northbound, southbound, or even east–west, and populations may be fully or partially migratory, or even composed of year-round residents (Katzner et al., 2020). Despite this knowledge, although a few studies have focused on movements of eagles in their first years of life (Murphy et al., 2017; Poessel et al., 2016; Soutullo et al., 2006), in general, aseasonal movements such as dispersal, prospecting, and nomadism are rarely documented. Thus, the drivers and patterns of these activities are poorly understood.

To understand potential spatial, temporal, and demographic correlates of these nonroutine, long-distance movements, we evaluated 10 years of telemetry data from >500 individual golden eagles and focused our analyses on the subset of birds that made such movements. The motivation for this study was the substantial recent focus on understanding golden eagle movements and demography in the context of rapidly emerging threats in western North America (e.g., USFWS, 2013). Past work has shown the ecological relevance of identifying distinct environmental, temporal, and demographic correlates of routine local and migratory movements of golden eagles (e.g., Braham et al., 2015; Domenech et al., 2015; Eisaguirre et al., 2019; Miller et al., 2016, 2017; Watson et al., 2014). Therefore, our specific objectives were to quantify for less-well studied and nonroutine, long-distance movements: (1) daily and (2) event-scale environmental correlates; (3) temporal and directional trends in movements; and (4) patterns in ages and sexes of eagles that made these movements. We also discuss how these movements might be related to the inconsistently defined movement types described above. Finally, we discuss the conservation and management implications of these long-distance movements for golden eagle populations in western North America.

METHODS

Eagle capture, telemetry, and study area

Golden eagles were captured throughout the year in grassland, shrubland, and desert ecosystems of the western United States and tracked across the entire western portion of North America (Figure 1; for details of the many studies that contributed data, see Brown et al., 2017). Generally, each bird was fitted with a transmitter mounted with a custom-made backpack-style harness. Transmitters used included GPS/Argos Platform Transmitter Terminals (PTTs) and GPS/Global System for Mobile Communications (GSM) units from various manufacturers (Table 1 in Brown et al., 2017). These telemetry devices collected data at intervals ranging from 30 s to 1 h. The sex of most captured birds was identified by morphological traits, and age classes were assessed by examining molt patterns (Bloom & Clark, 2001). Because of inconsistencies in age class assignment across the large number of investigators in our study, we grouped age estimates into three categories that were consistently identified across investigators (Millsap et al., 2016): juvenile (hatch-year birds, including those captured as nestlings), subadult (second- and third-year birds), and adult (all birds after their third year).

To identify nonroutine, long-distance movements, we first filtered the telemetry data by removing locational implausibilities (such as locations over the ocean). Next, we removed any eagles from our dataset that might be considered true migrants, defined in literature on this species as those spending the summer above 55° N latitude (Katzner et al., 2020). Finally, for each of the remaining birds, we used telemetry data to determine the maximum distance traveled from the initial capture location. We created a histogram of these maximum distances with 100-km bins from 0 to 1000 km, then 500-km bins thereafter. We found that bin frequencies decreased up to 300 km, then became fairly stable (Appendix S1: Figure S1). Thus, we defined a “long-distance mover” as a non-migratory eagle that moved ≥ 300 km from its initial capture location over the time period of data collected for that bird. We defined a “local mover” as a non-migratory eagle that moved < 300 km from its initial capture location. Others have used the terms “transient” and “resident” to describe movements of such birds. However, those terms have specific meanings in the literature (e.g., Coyle et al., 2013; Newton, 2008; Watson, 2010) distinct from the research questions we asked. As such, in this study, we used the terms long-distance mover and local mover because they provide intuitive and precise definitions of exactly the types of movements we considered.

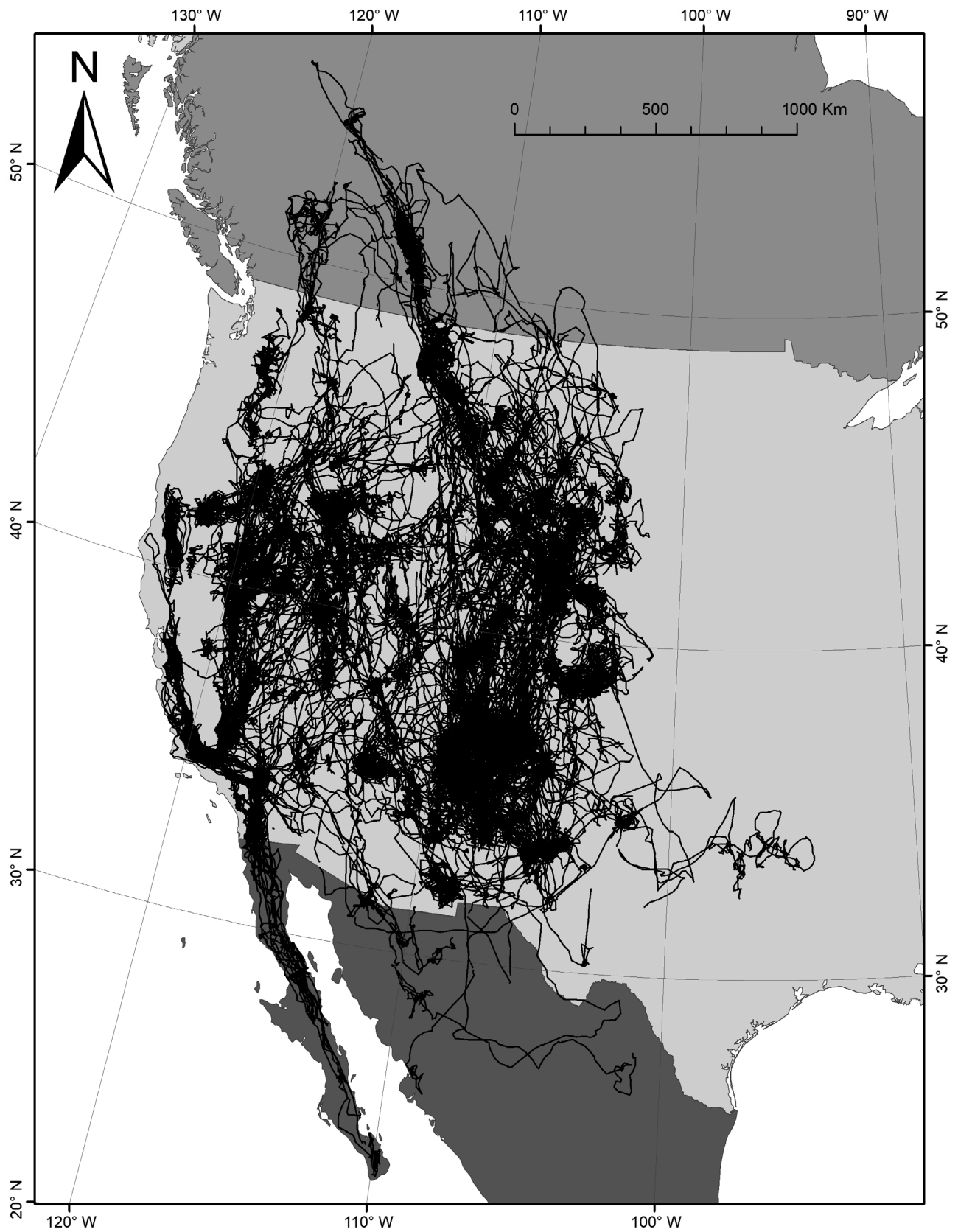


FIGURE 1 Map of western North America and composite of 88,093 daily tracks flown by 160 golden eagles tracked by telemetry devices, 2007–2017

For each long-distance mover, we removed nighttime locations, defined as the time period between 30 min after sunset and 30 min before sunrise, when the birds were presumed to be roosting (Craig & Craig, 1984). We also subsampled the telemetry data to intervals no more frequent than 1 h.

Data organization

We organized our data from long-distance movers in two ways. First, for each day that we monitored these birds, we created “daily tracks” of paths flown by eagles, using the Xtools Pro Extension (Data East, 2017) for ArcGIS v.10.6 (Esri, Redlands, CA) to link successive telemetry locations in each day. Second, we created “long-distance events,” defined as continuous, usually multiday, unidirectional movements of ≥ 300 km from the initial location. We used the daily track as the base unit of each long-distance event. Thus, a long-distance event consisted of a series of consecutive daily tracks, including both tracks with directional movements and tracks when the bird was at a stopover location.

We used the following criteria in our definition of a long-distance event. If a long-distance event had a directional change of $>90^\circ$ and the bird continued moving in the new direction, then the daily track before the track containing the point where the turn occurred was the last track of the long-distance event. However, if the daily track containing the point where the turn occurred began in the same direction as the long-distance event movement, but changed direction more than halfway through the day, then that track was still included and was the last track of the long-distance event. If a long-distance event had a directional change of $>90^\circ$, but the bird, within 8 days, turned to resume the original direction, then those tracks occurring after the directional change were still included in the long-distance event. If a long-distance event had a directional change of $>90^\circ$, but this change was due to a stopover of ≤ 7 days, after which the bird resumed travel in the original direction, then those stopover tracks were still included in the long-distance event. Finally, if a long-distance event had a gap in the telemetry data, or if the bird entered a stopover, lasting >7 days, then the daily track before the gap or stopover was the last track of the long-distance event.

Daily tracks

After compiling daily tracks, we removed any day represented by only one location record. We then calculated the length of each track to estimate daily distance

traveled. For each bird, we also calculated the cumulative distance traveled across all days and the overall displacement distance (calculated as the greatest straight-line distance between any two points from that bird).

Environmental correlates of daily tracks

We linked daily tracks to landscape, topographic, and meteorological characteristics. To identify landscape characteristics associated with eagle movements, we obtained 250-m resolution land cover data for North America from the North American Land Change Monitoring System (NALCMS, 2013) and reclassified the data into 10 classes (Appendix S1: Table S1). We buffered each location in the daily tracks by 500 m and then combined those buffers within a track. We then resampled the land cover dataset to 50-m cells and extracted the land cover class for each cell within the combined buffers. Finally, we calculated the proportion of each combined buffer in each land cover class, and we then assigned the most common land cover class to the daily track. Less than 0.5% of daily tracks were assigned to each of the low vegetation, water/wetland, urban, and snow/ice land cover classes, so we combined these four classes into an “other” category.

To identify topographic characteristics associated with eagle movements, we linked each daily track location to a measurement of a Terrain Ruggedness Index (TRI; Riley et al., 1999) in the 30-m cell directly below each location. Terrain Ruggedness Index, estimated with Geomorphometry and Gradient Metrics Tools (Evans et al., 2014), reflects landscape roughness and is calculated as the square root of the sum of the squared differences between the elevation in a cell and the elevation of its neighboring cells (Riley et al., 1999). We then calculated the mean and SD of TRI values for all locations within a daily track.

Finally, to identify meteorological characteristics associated with eagle movements, we linked each location to five weather variables obtained from the Environmental-Data Automated Track Annotation System (Dodge et al., 2013) in Movebank (Wikelski et al., 2020; see Appendix S1: Table S2 for definitions of the weather variables). We focused on weather variables that could influence eagle flight behavior. Total precipitation at the earth’s surface (precipitation) can affect a bird’s decision to fly (Duerr et al., 2015; Studds & Marra, 2011). Downward shortwave radiation flux (DSR), surface temperature (temperature), and wind speed and direction are known to influence development of updrafts and can affect flight speeds and distances traveled by soaring birds (Chevallier et al., 2010; Duerr et al., 2015; Miller

et al., 2016; Poessel, Brandt, Miller, & Katzner, 2018; Shamoun-Baranes et al., 2007). We derived wind speed and wind direction from u-wind and v-wind values at 10-m aboveground, downloaded from Movebank (see Poessel, Brandt, Miller, & Katzner, 2018 for these calculations). We then averaged the values of each weather variable for all locations within a daily track. Lastly, we categorized the average wind direction for a track into one of four classes, north ($>315^\circ$ and $\leq 45^\circ$), east ($>45^\circ$ and $\leq 135^\circ$), south ($>135^\circ$ and $\leq 225^\circ$), or west ($>225^\circ$ and $\leq 315^\circ$).

Long-distance events

We calculated both the cumulative and displacement distances of each long-distance event. The cumulative distance was the sum of the daily track distances and distances between tracks from consecutive days. The displacement distance was the distance between the first and last locations of the long-distance event. We also calculated the number of days in each long-distance event, speed traveled (in kilometers per day), and direction of movement. To obtain direction, we used the Linear Directional Mean tool in ArcGIS v.10.6 to calculate the compass angle (aspect) of each long-distance event. We then converted this value to one of eight categories, north ($>337.5^\circ$ and $\leq 22.5^\circ$), northeast ($>22.5^\circ$ and $\leq 67.5^\circ$), east ($>67.5^\circ$ and $\leq 112.5^\circ$), southeast ($>112.5^\circ$ and $\leq 157.5^\circ$), south ($>157.5^\circ$ and $\leq 202.5^\circ$), southwest ($>202.5^\circ$ and $\leq 247.5^\circ$), west ($>247.5^\circ$ and $\leq 292.5^\circ$), or northwest ($>292.5^\circ$ and $\leq 337.5^\circ$).

Environmental correlates of long-distance events

Similar to daily tracks, we examined landscape, topographic, and meteorological characteristics of each long-distance event. However, because of the coarse spatial resolution of eagle long-distance events, we focused on environmental data that were broader in scale than those associated with the daily tracks. To identify landscape characteristics associated with eagle movements, we obtained ecological region (ecoregion) data for North America from the Commission for Environmental Cooperation (CEC, 2018). Ecoregions denote areas of similarity in ecosystems and environmental resources. We condensed the 14 Level II ecoregions in our study area to 6 categories (Appendix S1: Table S3). To determine whether ecoregion type at the starting and ending points of a long-distance event influenced the length of that event, we linked the first and last GPS

locations of each long-distance event to their corresponding ecoregion.

To identify topographic characteristics associated with eagle movements, we obtained landform data for North America from AdaptWest (<https://adaptwest.databasin.org/pages/adaptwest-landfacets>; Michalak et al., 2018). We used 100-m resolution data comprising nine landform categories, which were classified by using a combination of Topographic Position Index (TPI; i.e., the difference between the elevation of a cell and the mean elevation of surrounding cells) and slope (Jenness, 2006). Based on natural breaks in the nine categories (Michalak et al., 2018), we collapsed these into four landform classes, valleys (≤ -30 TPI), ridges (>30 TPI), flat (>-30 and ≤ 30 TPI; slope $\leq 2^\circ$), and slopes (>-30 and ≤ 30 TPI; slope $>2^\circ$). To determine whether the terrain over which a bird flew influenced the length of a long-distance event, we extracted the landform class for each GPS location in each long-distance event, then calculated the percentage of locations in each class for each long-distance event.

Finally, to identify meteorological characteristics that may result in the initiation of eagle movements (e.g., birds may move long distances in response to drought; McCrary et al., 2019), we linked the beginning of each long-distance event to precipitation and temperature data obtained from Daymet (Thornton et al., 2016). For each of the 30 days before the first location of each long-distance event, we extracted daily total precipitation (in millimeters) and daily maximum and minimum 2-m air temperature (in degrees Celsius). We then summed the precipitation data and averaged the temperature data over this 30-day period. We used this time period because a bird's decision to begin a long-distance movement can be affected by weather in the prior month (Studds & Marra, 2011).

Statistical analyses

Correlates of daily tracks

To evaluate environmental correlates of daily tracks by long-distance movers, we analyzed multivariate relationships within the data by using linear mixed-effects models ("lme4" package; Bates et al., 2015) in R (R Core Team, 2018). Our response variable was daily distance traveled, to which we applied a square root transformation to meet Gaussian distributional assumptions.

We tested correlations between pairs of continuous variables and removed one of the variables in any pair that had a correlation ≥ 0.50 , choosing the variable that has previously been shown to strongly predict eagle flight

behavior. After removing such variables, the model included as fixed effects the age category of the bird, month in which the track began, land cover class, the SD of TRI, mean DSR, mean precipitation, and an interaction between wind speed and direction. We included the individual eagle ID as a random effect to account for repeated measurements of individuals. We also included the number of locations in a daily track as a random effect to account for variability in movement behavior influenced by the number of locations collected each day. For modeling purposes, we associated the current age of the bird with each location by increasing the age of the bird each year on 1 January. To allow for easier and more direct comparison of model coefficients, we rescaled the continuous predictor variables (topography and weather variables) by subtracting the mean and dividing by two times the SD (Gelman, 2008).

Correlates of long-distance events

To understand environmental correlates of the long-distance events, we again evaluated multivariate relationships within the data by using linear mixed-effects models (“lme4” R package; Bates et al., 2015). We ran three sets of models, in which response variables were as follows: (1) cumulative distances, (2) displacement distances, and (3) number of days of the long-distance event. We log-transformed cumulative distances and used a Johnson transformation (Fernandez, 2014) on displacement distances to meet Gaussian distributional assumptions. Because number of days is a count variable, and to correct for overdispersion, we specified a negative binomial distribution of the response variable in this model.

We tested correlations between pairs of continuous variables and removed one of the variables in any pair that had a correlation ≥ 0.50 . After removing such variables, the three models included a random effect for the individual eagle and fixed effects for age category, month, ecoregion at the start of the long-distance event, ecoregion at the end of the long-distance event, percentage of locations in flat and slopes landform classes, and precipitation and maximum temperature at the start of the long-distance event. For modeling purposes, we rescaled the topography and weather variables as previously described (Gelman, 2008).

Model selection and averaging

For each of the four model sets (one for the daily tracks and three for the long-distance events), we ran a global model with all variables, then used the dredge function

in the “MuMIn” R package (Bartoń, 2018) to evaluate all possible submodels ($n = 320$ for the distances models, $n = 256$ for the long-distance events models; Doherty et al., 2012). We used Akaike information criterion corrected for small sample size to rank the models (Anderson, 2008; Burnham & Anderson, 2002), and we averaged the models with weights ≥ 0.01 .

Long-distance event timing and direction

We evaluated whether long-distance event timing was uniformly distributed throughout the year and whether long-distance event direction was uniformly distributed in all compass directions. We used a chi-squared test to compare the number of long-distance events that actually began in each month with that expected if the number of long-distance events was equal in every month. We used Watson’s goodness-of-fit test for circular uniformity (“CircStats” package in R; Lund & Agostinelli, 2018) to test the homogeneity of the compass direction of each long-distance event.

Eagle ages and sexes

To determine whether any of the different eagle age and sex classes were more or less likely to be long-distance movers than local movers, we ran a logistic regression model in R (R Core Team, 2018). The response variable was binary (i.e., 0 for local movers and 1 for long-distance movers), and the predictor variables were age at capture and sex. Age was not estimated for eight birds in our dataset, one of which was a long-distance mover. Further, sex was not determined for 11 birds, 2 of which were long-distance movers. We omitted these birds with unknown age or sex from this analysis.

RESULTS

Our initial dataset included 531 golden eagles associated with 8,036,564 GPS locations. After filtering locations and removing eagles that were migrants ($n = 32$) and local movers ($n = 339$), our final dataset of long-distance movers included 160 golden eagles (30% of original dataset; 78 female, 80 male, 2 unknown sex; 128 with PTTs, 32 with GPS/GSM units) with 950,955 GPS locations ($\bar{x} \pm \text{SD} = 5943 \pm 4179$ locations per bird; range = 112–17,406 locations) collected from June 2007 to August 2017 (558 ± 398 number of days of data per bird; range = 19–1815 days). We removed 1194 locations that represented the only location collected in a single

day. At the time of capture, 108 long-distance movers were juveniles (usually nestlings), 20 were subadults, and 31 were adults. During the study, 99 of these birds (88 juveniles and 11 subadults) advanced to the next age class. The one unaged bird was excluded from models in which age was a fixed effect.

Correlates of daily tracks

We identified 88,093 daily tracks ($\bar{x} \pm \text{SD} = 551 \pm 394$ tracks per bird; range = 19–1815), consisting of 949,761 locations (5936 ± 4178 locations per bird; range = 99–17,405 locations). Eagles traveled, on average, 28.3 (± 10.8) km each day (range of averages per bird = 7.2–69.1 km; Appendix S1: Table S4). The maximum distance any bird flew in a single day was 517.2 km. Throughout the period of each bird's data collection, eagles traveled, on average, 15,983.3 ($\pm 13,877.9$) km longer than the straight-line displacement distance (i.e., displacement distance was $\sim 5\%$ of the cumulative distance; Appendix S1: Table S4).

Age, month, and all landscape, topographic, and meteorological variables, except wind speed and the interaction between wind speed and direction, were associated with variation in daily distances traveled by eagles (Table 1). Adult and subadult eagles traveled longer distances than juveniles (Figure 2a), and all eagles flew longer distances, on average, during spring (March–May) and autumn (September–November) than during summer (June–August) and winter (December–February; Figure 2b). They traveled farther over grassland and shrubland habitats and, to a lesser degree, over croplands and forests (broadleaf + needleleaf; Figure 2c). Eagles also flew farther when TRI was more variable (Figure 3a), when DSR was higher (Figure 3b), and when precipitation was lower (Figure 3c).

The top-ranked model had 68% of model weights and included all variables except wind speed and the interaction between wind speed and direction (Appendix S1: Table S5). The second-ranked model, with 31% of weights, was the global model. Finally, the third-ranked model, with only 1% of weights, included all variables except the interaction between wind speed and direction (Appendix S1: Table S5).

Correlates of long-distance events

We identified 563 long-distance events by 153 long-distance movers ($\bar{x} \pm \text{SD} = 3.7 \pm 4.0$ long-distance events per bird; range = 1–26 long-distance events; 7 birds did not have a long-distance event per our definition; Appendix S1: Table S6). Eagles traveled, on average, 872 (± 368) km during a long-distance event (range of

averages per bird = 331–2459 km) for 10 (± 6) days (range = 2–38 days) at a speed of 116 (± 49) km per day (range = 24–284 km per day; Appendix S1: Table S6). The longest distance any bird flew during a long-distance event was 2955 km. During long-distance events, eagles flew, on average, 250 (± 174) km longer than the straight-line displacement distance (i.e., displacement distance was 71% of the cumulative distance).

Neither age, month, nor any of the landscape, topographic, or meteorological variables were associated with variation in how far eagles traveled during long-distance events. The null model was ranked first in the cumulative distances model set and second in the displacement distances model set (Appendix S1: Table S7). By contrast, in our third model, variation in number of days in a long-distance event was associated with parameters describing the ecoregion at the start and at the end of a long-distance event (Table 2). Eagles traveled for a longer time when travel began in the Interior Plains, Warm Deserts, and Western Cordillera ecoregions (Figure 4a) and when travel ended in the Mediterranean California and Western Cordillera ecoregions (Figure 4b). All top-ranked models (model weights ≥ 0.01) included these two variables, as well as month (Appendix S1: Table S7), although the CIs overlapped zero for each category of this last variable (Table 2).

Long-distance event timing and direction

Long-distance events did not occur uniformly throughout the year ($\chi^2_{10} = 154.66$, $p < 0.001$), with the greatest number of long-distance events beginning in May (101 events) and October (86 events; Appendix S1: Figure S2). Likewise, direction of movement within a long-distance event was not uniform ($U^2 = 1.70$, $p < 0.01$). The most common long-distance event directions were north and south, and the next most common were the intercardinal directions; easterly and westerly movements were rare (Figure 5).

Eagle ages and sexes

Age, but not sex, was related to the probability of eagles being long-distance movers. Juveniles and subadults were more likely than adults to be long-distance movers (Figure 6; Appendix S1: Table S8). By contrast, both males and females were equally likely to be long-distance movers (Appendix S1: Table S8).

DISCUSSION

Our analysis suggests that, when engaging in nonroutine, long-distance movements, golden eagles in western

TABLE 1 Model-averaged parameters, including 95% CIs, from the three best-performing, linear mixed-effects models (model weights ≥ 0.01) that explain the drivers of daily distances traveled by golden eagles in western North America, 2007–2017

Variable	Averaged coefficient	Adjusted SE	z	Lower CI	Upper CI
Intercept	2.08	0.44	4.68	1.21	2.95
Age					
Subadult	0.95	0.03	33.98	0.90	1.01
Adult	1.09	0.04	27.38	1.01	1.17
Month					
February	0.29	0.05	6.34	0.20	0.38
March	0.48	0.05	10.18	0.39	0.58
April	0.43	0.05	8.31	0.33	0.53
May	0.03	0.05	0.63	−0.07	0.14
June	−0.55	0.06	9.97	−0.66	−0.44
July	−0.71	0.05	13.20	−0.81	−0.60
August	−0.33	0.05	6.24	−0.43	−0.22
September	0.46	0.05	9.14	0.36	0.56
October	0.99	0.05	21.40	0.90	1.08
November	0.70	0.05	15.21	0.61	0.79
December	0.35	0.05	7.53	0.26	0.45
Land cover					
Barren	0.85	0.18	4.80	0.51	1.20
Broadleaf/mixed forest	1.90	0.16	11.61	1.58	2.22
Cropland	1.75	0.16	10.90	1.43	2.06
Grassland	2.06	0.14	15.14	1.80	2.33
Needleleaf forest	1.87	0.14	13.58	1.60	2.14
Shrubland	2.27	0.14	16.73	2.00	2.53
Terrain Ruggedness Index (SD)	1.33	0.02	67.82	1.29	1.37
Downward shortwave radiation	0.81	0.03	25.96	0.74	0.87
Precipitation	−0.42	0.02	22.79	−0.45	−0.38
Wind speed	0.02	0.05	0.45	−0.08	0.12
Wind direction					
East	−0.03	0.04	0.79	−0.12	0.05
South	0.09	0.03	2.71	0.03	0.16
West	0.18	0.03	5.50	0.12	0.25
Wind speed × wind direction					
East	−0.08	0.13	0.60	−0.32	0.17
South	−0.05	0.09	0.59	−0.22	0.12
West	0.00	0.04	0.09	−0.08	0.07

Note: Reference variables were juvenile for age, January for month, and other (including low vegetation, water/wetland, urban, and snow/ice) for land cover. Variables with CI ranges that did not overlap zero are important variables.

North America responded to their environment at relatively small spatial and temporal scales. However, at larger scales, these birds were not as likely to respond to the environmental conditions that we measured. As evidence of this, we found that movements within a given

day and at relatively small spatial scales were influenced by demographic, temporal, landscape, topographic, and meteorological factors that eagles encountered in their environment. By contrast, movements spanning multiple days and over large spatial scales were less likely to be

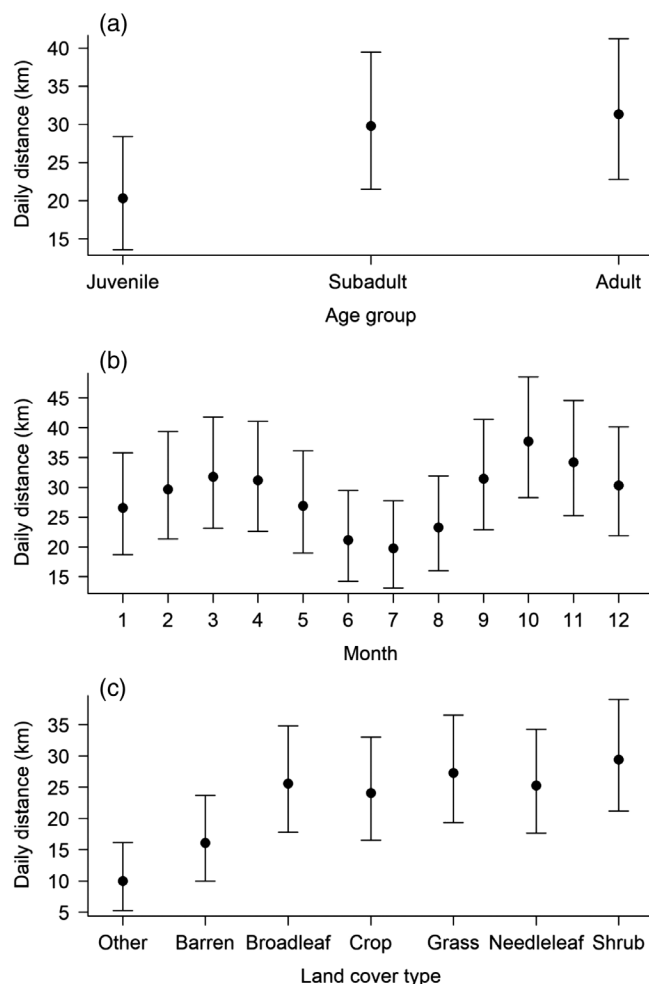


FIGURE 2 Plots of the back-transformed, model-fitted values of daily distances and (a) age group, (b) month, and (c) land cover type for golden eagles in western North America, 2007–2017. Bars represent 95% CIs

influenced by these factors. Interpreting these data patterns allows us to classify the long-distance movements we observed to gain insight into the potential drivers of these behaviors.

Impact of scale of measurement on interpretation of movement

During both local and migratory movements, soaring birds are known to respond to the updraft potential of the spatial and temporal landscape (Bohrer et al., 2012; Duerr, Miller, et al., 2019; Katzner et al., 2012, 2015; Poessel, Brandt, Mendenhall, et al., 2018; Shamoun-Baranes et al., 2016). In our study of non-migratory, long-distance movements, golden eagles flew farther on days when their environment was more conducive to the development of thermal and orographic updrafts.

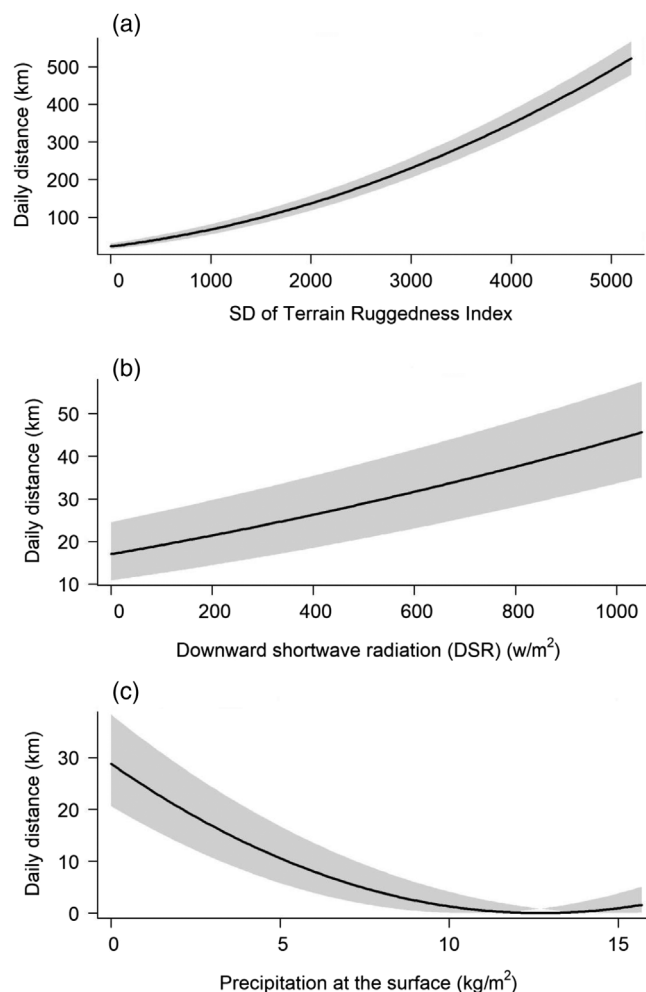


FIGURE 3 Plots of the back-transformed, model-fitted values of daily distances and (a) SD of Terrain Ruggedness Index, (b) downward shortwave radiation, and (c) precipitation at the earth's surface for golden eagles in western North America, 2007–2017. Gray bands represent 95% CIs. The y-axes of the plots are on different scales to clearly discern the pattern of each variable

Specifically, eagles flew farther when over open landscapes, when solar radiation was higher, and when precipitation was lower, all conditions associated with thermal updraft formation. Eagles also generally flew farther when terrain ruggedness was more variable, conditions favoring orographic updrafts. Both types of updrafts are heavily relied upon by soaring birds, allowing them to fly farther over the landscape with minimal energetic costs (Hedenström, 1993; Lish et al., 2016; Pennycuik, 1972).

Adult and subadult eagles flew farther in their daily movements than did juvenile birds, a finding that likely reflects the biology and flight skills associated with these different life stages. Adult and subadult eagles were wide-ranging and regularly moved long distances. By contrast, when juveniles first fledged, their flight skills were not

TABLE 2 Model-averaged parameters, including 95% CIs, from the 22 best-performing, linear mixed-effects models (model weights ≥ 0.01) that explain the drivers of number of days in a long-distance event for golden eagles in western North America, 2007–2017

Variable	Averaged coefficient	Adjusted SE	z	Lower CI	Upper CI
Intercept	2.43	0.28	8.70	1.88	2.98
Age					
Subadult	0.00	0.03	0.13	−0.06	0.07
Adult	0.00	0.04	0.08	−0.08	0.07
Month					
February	0.03	0.26	0.10	−0.48	0.53
March	−0.20	0.25	0.79	−0.70	0.30
April	−0.26	0.25	1.03	−0.76	0.23
May	−0.25	0.26	0.97	−0.75	0.25
June	−0.42	0.27	1.59	−0.94	0.10
July	−0.29	0.28	1.04	−0.85	0.26
August	−0.28	0.29	0.98	−0.85	0.28
September	0.03	0.28	0.10	−0.52	0.58
October	0.11	0.26	0.43	−0.40	0.62
November	−0.11	0.27	0.39	−0.65	0.43
December	0.37	0.37	1.01	−0.35	1.09
Ecoregion-start					
Cold Deserts	−0.31	0.09	3.34	−0.49	−0.13
Warm Deserts	−0.14	0.16	0.88	−0.44	0.17
Upper Gila Mountains	−0.49	0.13	3.84	−0.74	−0.24
Western Cordillera	−0.13	0.10	1.33	−0.33	0.06
Mediterranean California	−0.25	0.14	1.83	−0.52	0.02
Ecoregion-end					
Cold Deserts	−0.02	0.10	0.26	−0.21	0.16
Warm Deserts	0.03	0.14	0.20	−0.25	0.30
Upper Gila Mountains	−0.17	0.12	1.37	−0.41	0.07
Western Cordillera	0.23	0.10	2.28	0.03	0.42
Mediterranean California	0.21	0.14	1.49	−0.07	0.48
Landform					
Flat	−0.05	0.07	0.77	−0.19	0.08
Slopes	0.00	0.03	0.10	−0.05	0.06
Precipitation	−0.02	0.04	0.42	−0.10	0.06
Maximum temperature	−0.09	0.11	0.80	−0.30	0.13

Note: Reference variables were juvenile for age, January for month, and Interior Plains for ecoregion-start and ecoregion-end. Variables with CI ranges that did not overlap zero are important variables.

well developed, and they only made short-distance flights near their nest sites. Few juveniles made long-distance movements before September of their hatch-year, likely because of their inexperience and the short period of time since fledging. Additionally, juveniles may not have made long-distance movements because they were still procuring food from their parents after fledging. Juveniles progressively decrease their dependence on parents for food

(Watson, 2010), and this changing dietary strategy may affect how they move in response to the distribution of resources. These differing behaviors between juveniles and older eagles likely influenced the difference in mean daily travel distances among age classes.

In contrast to daily movements, none of the factors we measured influenced the overall distances of long-distance events, and only landscape type affected the

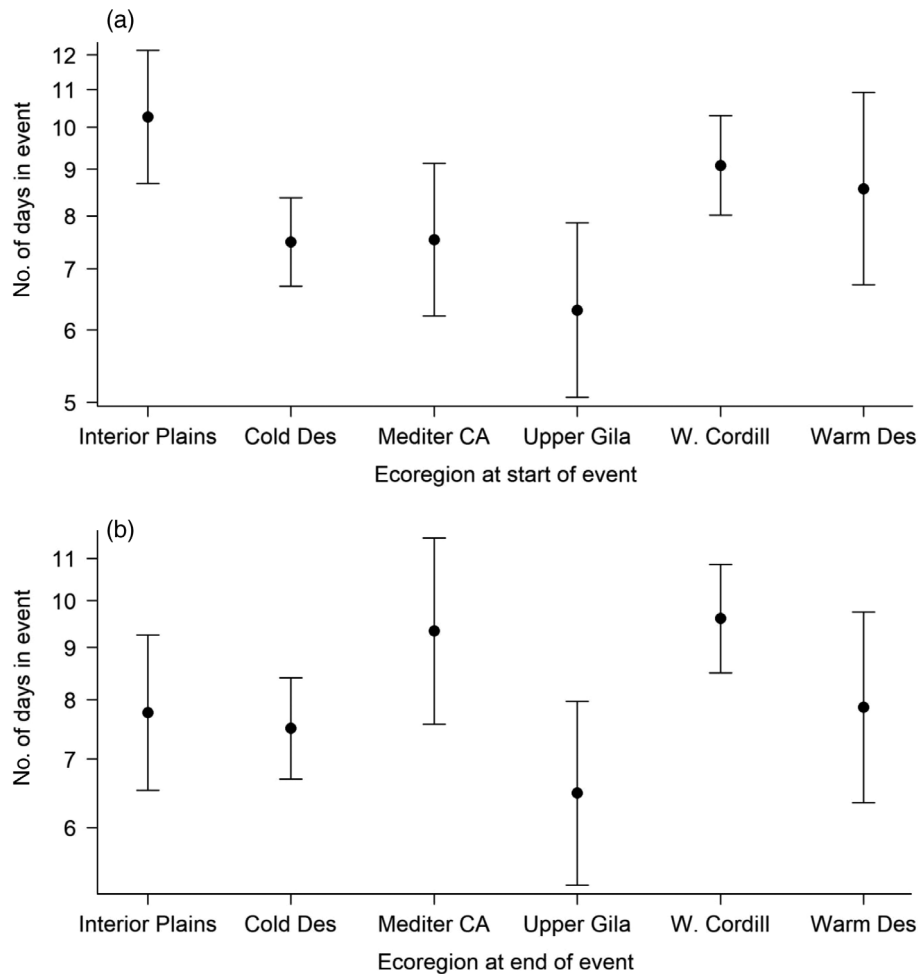


FIGURE 4 Plots of the model-fitted values of number of days in a long-distance event and (a) ecoregion at the start of the long-distance event and (b) ecoregion at the end of the long-distance event for golden eagles in western North America, 2007–2017. Bars represent 95% CIs

length of time spent flying in a long-distance event. Eagles spent more time in long-distance events when they began flying over open and warm landscapes, as these habitats readily create thermals that can aid in soaring and increase travel speeds. Eagles also spent less time in long-distance events when they ended in these same open landscapes. For some of these long-distance events, eagles appeared to stay in or return to these landscapes during the event. This short-term residency may indicate that eagles were searching for future nest sites, or it may have been a regional response by eagles to peaks in the population cycles of high-quality prey resources, such as leporids, in the Interior Plains and Warm Deserts ecoregions (Bedrosian et al., 2017).

Although older eagles flew farther in their daily movements, juvenile and subadult birds were more likely than adults to engage in long-distance movements (which may be related to behavioral development; Jenkins et al., 2017). This was not surprising because

young golden eagles are known to make putatively dispersing, nomadic, or prospecting movements that take them long distances away from natal areas (Murphy et al., 2017; Soutullo et al., 2006). These movement behaviors become less frequent as the birds age (Miller et al., 2017; Watson, 2010).

Our results showed that the decisions made by eagles on how far to fly were likely based on their immediate environment and on the local conditions they encountered. However, the metrics affecting eagle responses on a broader spatial scale were less clear. At this scale, eagles were likely responding to (1) environmental factors that we did not measure, (2) genetic adaptations that override variation in environmental conditions (Pulido, 2011), (3) internal motivations for making these sporadic, irregular movements, such as avoiding competition with resident eagles for scarce resources (Poessel et al., 2016) or prospecting for future foraging or breeding opportunities (Weston, 2014), or (4) some combination of 1, 2, or 3.

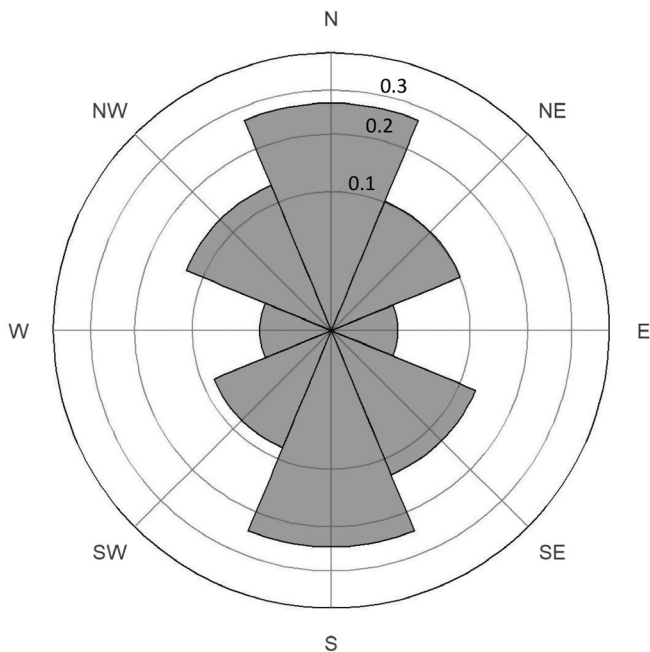


FIGURE 5 Rose plot of generalized directions of long-distance events by golden eagles in western North America, 2007–2017. Numbers above lines represent the proportion of long-distance events in each general direction sector. The square roots of frequencies were plotted to obtain the true area of each direction sector (Zar, 1999)

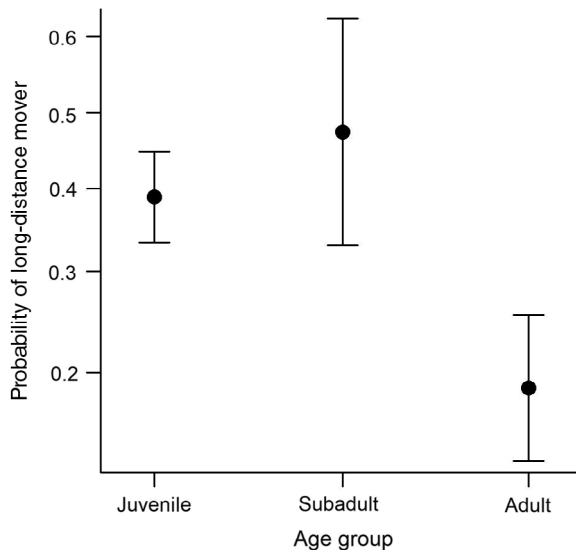


FIGURE 6 Plot of the probability of different age classes being long-distance movers for golden eagles in western North America, 2007–2017. Bars represent 95% CIs

Movement types

Definitions for the terms describing movement types are fluid. As such, teasing apart the difference between truly routine and nonroutine movements is both a difficult

and important component of understanding movements of any species. For example, we removed migratory individuals from our dataset by using an established definition within published literature (Katzner et al., 2020). However, after post hoc examination, we found that long-distance events for ~12% of the birds in our dataset of long-distance movers could have been reasonably classified either as nonroutine movements or as routine, intermediate-distance migration. These movements seemed to exhibit some typical characteristics of migration; that is, they were north–south in orientation, they were seasonally paired (one in spring and one in autumn), and the eagles tended to return near to their respective points of origin. Analysis of our dataset without these birds suggested no differences in the movement patterns we report (Appendix S1: Additional Models). Closer examination of these particular atypical movements is therefore a research priority.

The remaining 88% of the golden eagles in our dataset of long-distance movers also generally moved in north and south directions and did so during spring and autumn. However, these movements were not seasonally paired, nor did they return the bird to its region of origin, as would be expected of migration. Likewise, we had insufficient information to assess whether these movements had characteristics of natal dispersal (Greenwood, 1980; Greenwood & Harvey, 1982). In fact, we had continuous data from hatch-year to breeding age (typically 5 years old; Watson, 2010) for only five birds, none of which bred during this study. Finally, based on our observations of the telemetry data and locations of the birds across multiple breeding seasons, none of the 31 adults we tracked appeared to engage in breeding dispersal during our study. As such, studies that address natal and breeding dispersal are therefore also priorities for this and other species.

The nonroutine, long-distance movements we evaluated were irregular, and although we have found no empirically based ways to define prospecting or nomadism, by process of elimination, these movements seem most similar to those behaviors. We were unable to link these movements to drivers typically associated with these two movement types, such as potential territory recruitment, or highly variable prey abundance or habitat conditions (Reed et al., 1999; Teitelbaum & Mueller, 2019). Nevertheless, we interpreted these movements as prospecting and nomadism based on their characteristics and their remarkable variability. Some eagles in our dataset flew back and forth between two general areas repeatedly in a single year (i.e., more than twice, so they were not seasonal migratory movements). Although we cannot understand the motives for such movement behavior, the eagles may have been assessing certain

qualities of these areas (i.e., they were prospecting). Some of these movements also may have been influenced by memory or spatial learning, which can reinforce the repeated use of patches containing high-quality resources (Gautestad, 2011). Certain other eagles we studied arrived in new areas, became short-term residents in some of those areas, and then moved on, in a wandering manner, to new landscapes to become short-term residents (see our earlier note about eagles in the Interior Plains and Warm Deserts ecoregions). Although none of these eagles appeared to be breeding, their movements were consistent with many definitions of nomadism (Newton, 2008; Teitelbaum & Mueller, 2019).

CONCLUSIONS

Characterizing the movement behavior of animals is important for understanding their management, ecology, and conservation. In western North America, management of golden eagles largely focuses on birds that make routine movements (e.g., year-round home range use or seasonal migrations; USFWS, 2013). Although relevant to all eagles in a given population, such management does not target the large proportion of the population that is most likely to make nonroutine movements (e.g., nonterritorial birds; Hunt, 1998). For example, the US Fish and Wildlife Service generally requires proponents of wind energy projects to identify areas that might be affected by a proposed development that are important to nesting and migratory eagles (e.g., nests, foraging areas, roost sites, and migration concentration sites; USFWS, 2013). This requirement overlooks nonterritorial and non-migratory eagles, such as those we studied here.

Long-distance movements by animals of many species can expose them to new environments where novelty may create disproportionate risk from negative interaction with anthropogenic structures and other threats such as habitat fragmentation (Trakhtenbrot et al., 2005; Watson, 2010). Further, these long movements may cause energy deficits, which may lead younger individuals to take greater risks to increase food intake (e.g., Gjershaug et al., 2019). Understanding these trade-offs can also influence management of these species. For example, conservation actions directed at reducing these risks may improve the recruitment of younger animals into the breeding population and the long-term stability of populations of these species.

Our study is unusual because of the large number of tagged golden eagles we studied that made long-distance prospecting or nomadic movements. We observed clear patterns that characterized external environmental drivers of these movements at small, local scales. However, we were unable to identify consistent patterns in

larger, regional-scale correlates of these movements, suggesting that at this scale, movements were likely driven by internal factors, such as the need to investigate breeding or foraging opportunities, or to avoid competition with conspecifics (Nathan et al., 2008). Because few studies identify and describe prospecting and nomadism for large numbers of individuals of any species, our findings lay the foundation for subsequent study into the drivers of these movements.

AUTHOR CONTRIBUTIONS

Sharon A. Poessel, Brian Woodbridge, Brian W. Smith, Robert K. Murphy, and Todd E. Katzner conceived the design of the study and secured funding; Bryan E. Bedrosian, Douglas A. Bell, David Bittner, Peter H. Bloom, Ross H. Crandall, Robert Domenech, Robert N. Fisher, Steven J. Slater, Jeff A. Tracey, and James W. Watson provided eagle telemetry data from their respective projects; Sharon A. Poessel analyzed the data; Patricia K. Haggerty compiled the land cover data for the daily tracks and assisted with electronic data collection; and Sharon A. Poessel and Todd E. Katzner led the writing of the manuscript. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data used in the analyses of daily distances and long-distance events of golden eagles (Poessel et al., 2022) are available in the ScienceBase digital repository: <https://doi.org/10.5066/P91T2VMO>.

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REFERENCES

- Åkesson, S., and A. Hedenström. 2007. "How Migrants Get There: Migratory Performance and Orientation." *Bioscience* 57: 123–33.
- Anderson, D. R. 2008. *Model Based Inference in the Life Sciences: A Primer on Evidence*. New York, NY: Springer Science+Business Media LLC.
- Bartoń, K. 2018. MuMIn: Multi-Model Inference. R package version 1.42.1. <https://cran.r-project.org/web/packages/MuMIn/index.html>.
- Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67(1): 1–48.
- Bedrosian, B. E., R. Domenech, A. Shreading, M. M. Hayes, T. L. Booms, and C. R. Barger. 2018. "Migration Corridors of Adult Golden Eagles Originating in Northwestern North America." *PLoS One* 13: e0205204.
- Bedrosian, G., J. W. Watson, K. Steenhof, M. N. Kochert, C. R. Preston, B. Woodbridge, G. E. Williams, K. R. Keller, and R. H. Crandall. 2017. "Spatial and Temporal Patterns in Golden Eagle Diets in the Western United States, with Implications for Conservation Planning." *Journal of Raptor Research* 51: 347–67.
- Bevanda, M., E. A. Fronhofer, M. Heurich, J. Müller, and B. Reineking. 2015. "Landscape Configuration Is a Major Determinant of Home Range Size Variation." *Ecosphere* 6: 195.
- Bloom, P. H., and W. S. Clark. 2001. "Molt and Sequence of Plumages of Golden Eagles and a Technique for In-Hand Ageing." *North American Bird Bander* 26: 97–116.
- Bohrer, G., D. Brandes, J. T. Mandel, K. L. Bildstein, T. A. Miller, M. Lanzone, T. Katzner, C. Maisonneuve, and J. A. Tremblay. 2012. "Estimating Updraft Velocity Components over Large Spatial Scales: Contrasting Migration Strategies of Golden Eagles and Turkey Vultures." *Ecology Letters* 15: 96–103.
- Boulinier, T., S. Kada, A. Ponchon, M. Dupraz, M. Dietrich, A. Gamble, V. Bourret, et al. 2016. "Migration, Prospecting, Dispersal? What Host Movement Matters for Infectious Agent Circulation?" *Integrative and Comparative Biology* 56: 330–42.
- Braham, M., T. Miller, A. E. Duerr, M. Lanzone, A. Fesnock, L. LaPre, D. Driscoll, and T. Katzner. 2015. "Home in the Heat: Dramatic Seasonal Variation in Home Range of Desert Golden Eagles Informs Management for Renewable Energy Development." *Biological Conservation* 186: 225–32.
- Brown, J. L., B. Bedrosian, D. A. Bell, M. A. Braham, J. Cooper, R. H. Crandall, J. DiDonato, et al. 2017. "Patterns of Spatial Distribution of Golden Eagles across North America: How Do they Fit into Existing Landscape-Scale Mapping Systems?" *Journal of Raptor Research* 51: 197–215.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed. New York, NY: Springer.
- CEC [Commission for Environmental Cooperation]. 2018. Terrestrial Ecoregions: Level II. <http://www.cec.org/north-american-environmental-atlas/terrestrial-ecoregions-level-ii/>.
- Chevallier, D., Y. Handrich, J.-Y. Georges, F. Baillon, P. Brossault, A. Aurouet, Y. Le Maho, and S. Massemin. 2010. "Influence of Weather Conditions on the Flight of Migrating Black Storks." *Proceedings of the Royal Society B* 277: 2755–64.
- Cooper, N. W., and P. P. Marra. 2020. "Hidden Long-Distance Movements by a Migratory Bird." *Current Biology* 30: 4056–62.
- Coyle, J. R., A. H. Hurlbert, and E. P. White. 2013. "Opposing Mechanisms Drive Richness Patterns of Core and Transient Bird Species." *The American Naturalist* 181: E83–90.
- Craig, T. H., and E. H. Craig. 1984. "A Large Concentration of Roosting Golden Eagles in Southeastern Idaho." *The Auk* 101: 610–3.
- Data East, LLC. 2017. *XTools Pro 17.0*. Novosibirsk, Russia: Data East, LLC.
- D'Eon, R. G., and R. Serrouya. 2005. "Mule Deer Seasonal Movements and Multiscale Resource Selection Using Global Positioning System Radiotelemetry." *Journal of Mammalogy* 86: 736–44.
- Dodge, S., G. Bohrer, R. Weinzierl, S. C. Davidson, R. Kays, D. Douglas, S. Cruz, J. Han, D. Brandes, and M. Wikelski. 2013. "The Environmental-Data Automated Track Annotation (EnvDATA) System: Linking Animal Tracks with Environmental Data." *Movement Ecology* 1: 3.
- Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. "Greater Sage-Grouse Nesting Habitat: The Importance of Managing at Multiple Scales." *Journal of Wildlife Management* 74: 1544–53.
- Doherty, P. F., G. C. White, and K. P. Burnham. 2012. "Comparison of Model Building and Selection Strategies." *Journal of Ornithology* 152: S317–23.
- Domenech, R., B. E. Bedrosian, R. H. Crandall, and V. A. Slabe. 2015. "Space Use and Habitat Selection by Adult Migrant Golden Eagles Wintering in the Western United States." *Journal of Raptor Research* 49: 429–40.
- Duerr, A. E., M. A. Braham, T. A. Miller, J. Cooper, J. T. Anderson, and T. E. Katzner. 2019. "Roost- and Perch-Site Selection by Golden Eagles (*Aquila chrysaetos*) in Eastern North America." *Wilson Journal of Ornithology* 131: 310–28.
- Duerr, A. E., T. A. Miller, L. Dunn, D. A. Bell, P. H. Bloom, R. N. Fisher, J. A. Tracey, and T. E. Katzner. 2019. "Topographic

- Drivers of Flight Altitude over Large Spatial and Temporal Scales." *The Auk: Ornithological Advances* 136: 1–11.
- Duerr, A. E., T. A. Miller, M. Lanzone, D. Brandes, J. Cooper, K. O'Malley, C. Maisonneuve, J. Tremblay, and T. Katzner. 2012. "Testing an Emerging Paradigm in Migration Ecology Shows Surprising Differences in Efficiency between Flight Modes." *PLoS One* 7: e35548.
- Duerr, A. E., T. A. Miller, M. Lanzone, D. Brandes, J. Cooper, K. O'Malley, C. Maisonneuve, J. A. Tremblay, and T. Katzner. 2015. "Flight Response of Slope-Soaring Birds to Seasonal Variation in Thermal Generation." *Functional Ecology* 29: 779–90.
- Eisaguirre, J. M., M. Auger-Méthé, C. P. Barger, S. B. Lewis, T. L. Booms, and G. A. Breed. 2019. "Dynamic-Parameter Movement Models Reveal Drivers of Migratory Pace in a Soaring Bird." *Frontiers in Ecology and Evolution* 7: 317.
- Evans, J. S., J. Oakleaf, S. A. Cushman, and D. Theobald. 2014. *An ArcGIS Toolbox for Surface Gradient and Geomorphometric Modeling, Version 2.0-0*. <https://evansmurphy.wixsite.com/evansspatial>.
- Fernandez, E. S. 2014. Johnson: Johnson Transformation. R package version 1.4. <https://CRAN.R-project.org/package=Johnson>.
- Gautestad, A. O. 2011. "Memory Matters: Influence from a Cognitive Map on Animal Space Use." *Journal of Theoretical Biology* 287: 26–36.
- Gelman, A. 2008. "Scaling Regression Inputs by Dividing by Two Standard Deviations." *Statistics in Medicine* 27: 2865–73.
- Gjershaug, J. O., D. Halley, and B. G. Stokke. 2019. "Predefinitive Plumage in the Golden Eagle (*Aquila chrysaetos*): A Signal of Aggression or Submission?" *Journal of Raptor Research* 53: 431–5.
- Greenwood, P. J. 1980. "Mating Systems, Philopatry and Dispersal in Birds and Mammals." *Animal Behaviour* 28: 1140–62.
- Greenwood, P. J., and P. H. Harvey. 1982. "The Natal and Breeding Dispersal of Birds." *Annual Review of Ecology, Evolution, and Systematics* 13: 1–21.
- Hedenström, A. 1993. "Migration by Soaring or Flapping Flight in Birds: The Relative Importance of Energy Cost and Speed." *Philosophical Transactions of the Royal Society of London B* 342: 353–61.
- Hunt, W. G. 1998. "Raptor Floaters at Moffat's Equilibrium." *Oikos* 82: 191–7.
- Jenkins, J. M. A., F. R. Thompson, III, and J. Faaborg. 2017. "Behavioral Development and Habitat Structure Affect Post-fledging Movements of Songbirds." *Journal of Wildlife Management* 81: 144–53.
- Jenness, J. 2006. *Topographic Position Index (tpi_jen.avx) Extension for ArcView 3.x, v.1.3a*. Flagstaff, AZ: Jenness Enterprises. <http://www.jennessent.com/arcview/tpi.htm>.
- Katzner, T. E., D. Brandes, T. Miller, M. Lanzone, C. Maisonneuve, J. A. Tremblay, R. Mulvihill, and G. T. Merovich, Jr. 2012. "Topography Drives Migratory Flight Altitude of Golden Eagles: Implications for On-Shore Wind Energy Development." *Journal of Applied Ecology* 49: 1178–86.
- Katzner, T. E., M. N. Kochert, K. Steenhof, C. L. McIntyre, E. H. Craig, and T. A. Miller. 2020. "Golden Eagle (*Aquila chrysaetos*), Version 2.0." In *Birds of the World*, edited by P. G. Rodewald and B. K. Keeney. Ithaca, NY: Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.goleag.02>.
- Katzner, T. E., P. J. Turk, A. E. Duerr, T. A. Miller, M. J. Lanzone, J. L. Cooper, D. Brandes, J. A. Tremblay, and J. Lemaître. 2015. "Use of Multiple Modes of Flight Subsidy by a Soaring Terrestrial Bird, the Golden Eagle *Aquila chrysaetos*, When on Migration." *Journal of the Royal Society Interface* 12: 20150530.
- Lish, J. W., R. Domenech, B. E. Bedrosian, D. H. Ellis, and M. Payton. 2016. "Wing Loading in North American Golden Eagles (*Aquila chrysaetos*)." *Journal of Raptor Research* 50: 70–5.
- Lohmann, K. J. 2018. "Animal Migration Research Takes Wing." *Current Biology* 28: R952–5.
- Lund, U., and C. Agostinelli. 2018. CircStats: Circular Statistics. R package version 0.2-6. <https://CRAN.R-project.org/package=CircStats>.
- McCrary, M. D., P. H. Bloom, S. Porter, and K. J. Sernka. 2019. "Facultative Migration: New Insight from a Raptor." *Journal of Raptor Research* 53: 84–90.
- Michalak, J. L., C. Carroll, S. E. Nielsen, and J. J. Lawler. 2018. "Land Facet Data for North America at 100m Resolution." Zenodo Dataset. <https://doi.org/10.5281/zenodo.1344637>.
- Miller, T. A., R. P. Brooks, M. Lanzone, D. Brandes, J. Cooper, K. O'Malley, C. Maisonneuve, J. Tremblay, A. Duerr, and T. Katzner. 2014. "Assessing Risk to Birds from Industrial Wind Energy Development Via Paired Resource Selection Models." *Conservation Biology* 28: 745–55.
- Miller, T. A., R. P. Brooks, M. J. Lanzone, D. Brandes, J. Cooper, J. A. Tremblay, J. Wilhelm, A. Duerr, and T. E. Katzner. 2016. "Limitations and Mechanisms Influencing the Migratory Performance of Soaring Birds." *Ibis* 158: 116–34.
- Miller, T. A., R. P. Brooks, M. J. Lanzone, J. Cooper, K. O'Malley, D. Brandes, A. Duerr, and T. E. Katzner. 2017. "Summer and Winter Space Use and Home Range Characteristics of Golden Eagles (*Aquila chrysaetos*) in Eastern North America." *The Condor: Ornithological Applications* 119: 697–719.
- Millsap, B. A., E. R. Bjerre, M. C. Otto, G. S. Zimmerman, and N. L. Zimpfer. 2016. *Bald and Golden Eagles: Population Demographics and Estimation of Sustainable Take in the United States, 2016 Update*. Washington, DC: U.S. Fish and Wildlife Service, Division of Migratory Bird Management.
- Murphy, R. K., J. R. Dunk, B. Woodbridge, D. W. Stahlecker, D. W. LaPlante, B. A. Millsap, and K. V. Jacobson. 2017. "First-Year Dispersal of Golden Eagles from Natal Areas in the Southwestern United States and Implications for Second-Year Settling." *Journal of Raptor Research* 51: 216–33.
- NALCMS [North American Land Change Monitoring System]. 2013. *2010 North American Land Cover at 250 m Spatial Resolution*. Natural Resources Canada/The Canada Centre for Mapping and Earth Observation (NRCan/CCMEO), United States Geological Survey (USGS), Instituto Nacional de Estadística y Geografía (INEGI), Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Comisión Nacional Forestal (CONAFOR).
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. "A Movement Ecology Paradigm for Unifying Organismal Movement Research." *Proceedings of the National Academy of Sciences of the USA* 105: 19052–9.
- Newton, I. 2008. *The Migration Ecology of Birds*. London, UK: Academic Press.
- Pennycuik, C. J. 1972. "Soaring Behavior and Performance of some East African Birds, Observed from a Motor-Glider." *Ibis* 114: 178–218.
- Poessel, S. A., P. H. Bloom, M. A. Braham, and T. E. Katzner. 2016. "Age- and Season-Specific Variation in Local and Long-Distance Movement Behavior of Golden Eagles." *European Journal of Wildlife Research* 62: 377–93.

- Poessel, S. A., J. Brandt, L. Mendenhall, M. A. Braham, M. J. Lanzone, A. J. McGann, and T. E. Katzner. 2018. "Flight Response to Spatial and Temporal Correlates Informs Risk from Wind Turbines to the California Condor." *The Condor: Ornithological Applications* 120: 330–42.
- Poessel, S. A., J. Brandt, T. A. Miller, and T. E. Katzner. 2018. "Meteorological and Environmental Variables Affect Flight Behaviour and Decision-Making of an Obligate Soaring Bird, the California Condor *Gymnogyps californianus*." *Ibis* 160: 36–53.
- Poessel, S. A., B. Woodbridge, B. W. Smith, R. K. Murphy, B. E. Bedrosian, D. A. Bell, D. Bittner, et al. 2022. "Long-Distance Movements of Non-Migratory Golden Eagles in Western North America, 2007–2017." Dataset. U.S. Geological Survey. <https://doi.org/10.5066/P91T2VMO>.
- Pulido, F. 2011. "Evolutionary Genetics of Partial Migration – The Threshold Model of Migration Revis(it)ed." *Oikos* 120: 1776–83.
- R Core Team. 2018. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org>.
- Reed, J. M., T. Boulonier, E. Danchin, and L. W. Oring. 1999. "Informed Dispersal: Prospecting by Birds for Breeding Sites." In *Current Ornithology*, Vol 15, edited by V. Nolan, Jr., E. D. Ketterson, and C. Thompson, 189–259. New York, NY: Kluwer Academic/Plenum Publishers.
- Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. "A Terrain Ruggedness Index That Quantifies Topographic Heterogeneity." *Intermountain Journal of Sciences* 5: 23–7.
- Riotte-Lambert, L., S. Benhamou, and S. Chamaillé-Jammes. 2017. "From Randomness to Traplining: A Framework for the Study of Routine Movement Behavior." *Behavioral Ecology* 28: 280–7.
- Riotte-Lambert, L., and J. Matthiopoulos. 2020. "Environmental Predictability as a Cause and Consequence of Animal Movement." *Trends in Ecology & Evolution* 35: 163–74.
- Rivers, J. W., J. M. Johnson, S. M. Haig, C. J. Schwarz, L. J. Burnett, J. Brandt, D. George, and J. Grantham. 2014. "An Analysis of Monthly Home Range Size in the Critically Endangered California Condor *Gymnogyps californianus*." *Bird Conservation International* 24: 492–504.
- Sergio, F., A. Tanferna, R. De Stephanis, L. López Jiménez, J. Blas, G. Tavecchia, D. Preatoni, and F. Hiraldo. 2014. "Individual Improvements and Selective Mortality Shape Lifelong Migratory Performance." *Nature* 515: 410–3.
- Shamoun-Baranes, J., W. Bouten, E. E. van Loon, C. Meijer, and C. J. Camphuysen. 2016. "Flap or Soar? How a Flight Generalist Responds to Its Aerial Environment." *Philosophical Transactions of the Royal Society of London B* 371: 20150395.
- Shamoun-Baranes, J., E. van Loon, F. Liechti, and W. Bouten. 2007. "Analyzing the Effect of Wind on Flight: Pitfalls and Solutions." *Journal of Experimental Biology* 210: 82–90.
- Soutullo, A., V. Urios, M. Ferrer, and S. G. Peñarrubia. 2006. "Dispersal of Golden Eagles *Aquila chrysaetos* during Their First Year of Life." *Bird Study* 53: 258–64.
- Squires, J. R., L. E. Olson, Z. P. Wallace, R. J. Oakleaf, and P. L. Kennedy. 2020. "Resource Selection of Apex Raptors: Implications for Siting Energy Development in Sagebrush and Prairie Ecosystems." *Ecosphere* 11: e03204.
- Studds, C. E., and P. P. Marra. 2011. "Rainfall-Induced Changes in Food Availability Modify the Spring Departure Programme of a Migratory Bird." *Proceedings of the Royal Society B* 278: 3437–43.
- Teitelbaum, C. S., and T. Mueller. 2019. "Beyond Migration: Causes and Consequences of Nomadic Animal Movements." *Trends in Ecology & Evolution* 34: 569–81.
- Thornton, P. E., M. M. Thornton, B. W. Mayer, Y. Wei, R. Devarakonda, R. S. Vose, and R. B. Cook. 2016. *Daymet: Daily Surface Weather Data on a 1-Km Grid for North America, Version 3*. Oak Ridge, TN: ORNL DAAC. <https://doi.org/10.3334/ORNLDAAC/1328>.
- Trakhtenbrot, A., R. Nathan, G. Perry, and D. M. Richardson. 2005. "The Importance of Long-Distance Dispersal in Biodiversity Conservation." *Diversity and Distributions* 11: 173–81.
- USFWS [U.S. Fish and Wildlife Service]. 2013. *Eagle Conservation Plan Guidance: Module 1 – Land-Based Wind Energy, Version 2*. Washington, DC: U.S. Fish and Wildlife Service, Division of Migratory Bird Management.
- Watson, J. 2010. *The Golden Eagle*, 2nd ed. New Haven, CT: Yale University Press.
- Watson, J. W., U. Banasch, T. Byer, D. N. Svingen, R. McCready, D. Hanni, and R. Gerhardt. 2019. "First-Year Migration and Natal Region Fidelity of Immature Ferruginous Hawks." *Journal of Raptor Research* 53: 266–75.
- Watson, J. W., A. A. Duff, and R. W. Davies. 2014. "Home Range and Resource Selection by GPS-Monitored Adult Golden Eagles in the Columbia Plateau Ecoregion: Implications for Wind Power Development." *Journal of Wildlife Management* 78: 1012–21.
- Watson, J. W., and I. N. Keren. 2019. "Repeatability in Migration of Ferruginous Hawks (*Buteo regalis*) and Implications for Nomadism." *Wilson Journal of Ornithology* 131: 561–70.
- Weston, E. 2014. "Juvenile Dispersal Behaviour in the Golden Eagle (*Aquila chrysaetos*)." Dissertation, University of Aberdeen, Aberdeen, Scotland.
- Weston, E. D., D. P. Whitfield, J. M. J. Travis, and X. Lambin. 2013. "When Do Young Birds Disperse? Tests from Studies of Golden Eagles in Scotland." *BMC Ecology* 13: 42.
- Wikelski, M., S. C. Davidson, and R. Kays. 2020. *Movebank: Archive, Analysis and Sharing of Animal Movement Data*. Radolfzell, Germany: Max Planck Institute of Animal Behavior. <https://www.movebank.org>.
- Zar, J. H. 1999. *Biostatistical Analysis*, 4th ed. Upper Saddle River, NJ: Prentice-Hall, Inc.

SUPPORTING INFORMATION

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**Interpreting long-distance movements of non-migratory golden eagles:
prospecting and nomadism?**

Ecosphere

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Appendix S1

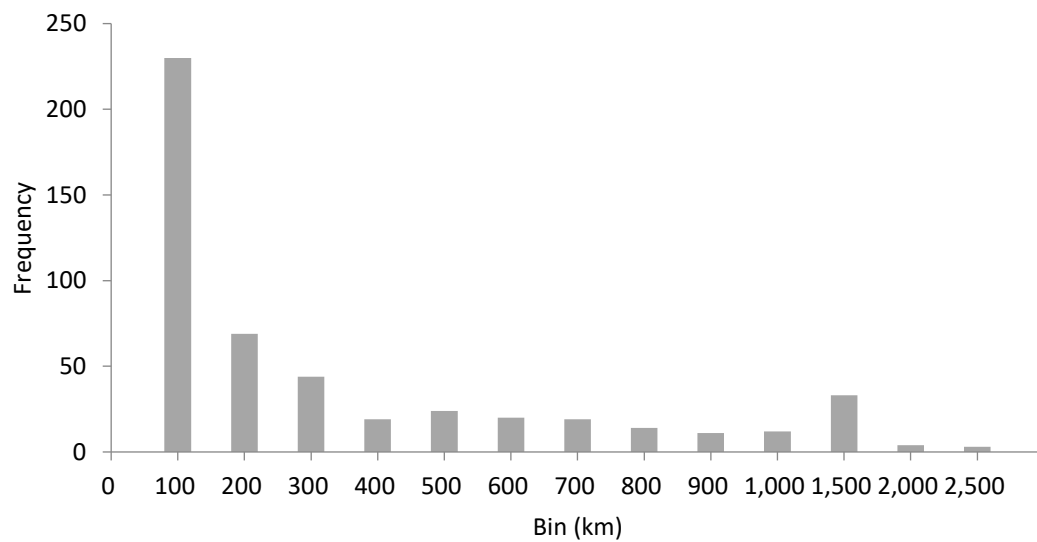


Fig. S1. Histogram of maximum distances moved by golden eagles in western North America, 2007-2017. Frequencies begin to stabilize after the 300-km bin.

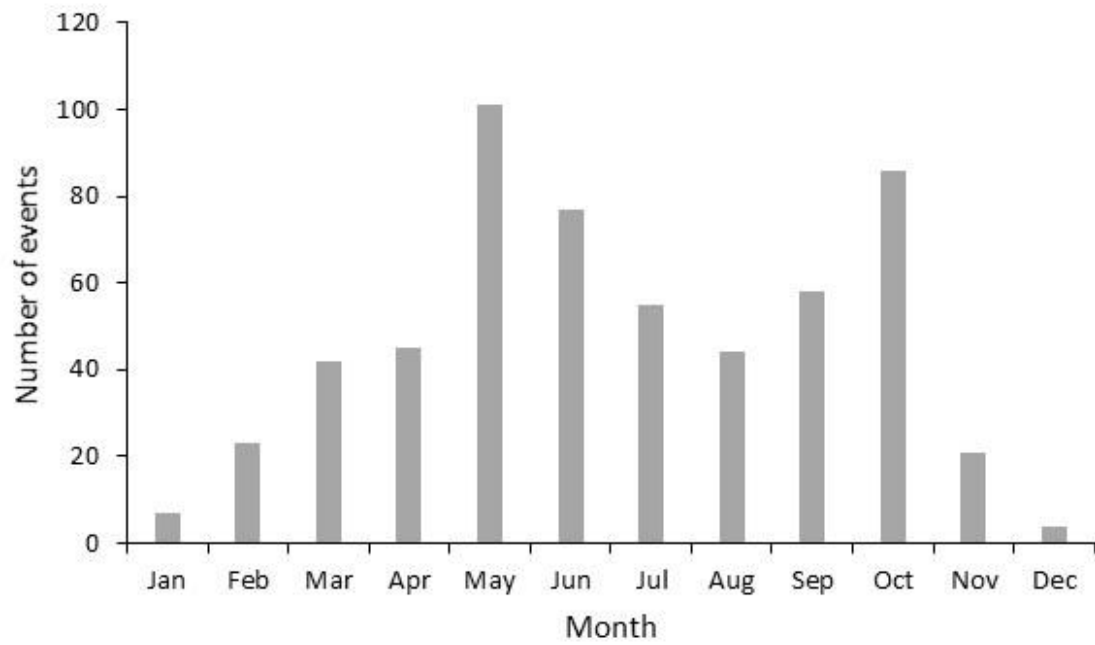


Fig. S2. Number of events, by month, traveled by golden eagles in western North America, 2007-2017.

Table S1. Land cover classes associated with daily tracks of golden eagles in western North America, 2007-2017.

Land cover class	Description
Needleleaf forest	Forests with trees >3 m tall and crown cover consisting of $\geq 75\%$ needleleaved species
Broadleaf/mixed forest	Forests with trees >3 m tall, >20% total vegetation cover, and crown cover >75% broadleaved evergreen or deciduous species; includes mixed forests where needleleaf and broadleaf species co-dominate
Shrubland	Areas dominated by woody perennial plants with persistent woody stems <5 m tall and >20% total vegetation cover
Grassland	Areas dominated by graminoid or herbaceous vegetation with >80% total vegetation cover
Low vegetation [†]	Areas dominated by dwarf shrubs, grassland, or bare areas with lichen and moss and $\geq 20\%$ total vegetation cover
Water/wetland [†]	Areas dominated by perennial herbaceous and woody wetland vegetation or areas of open water
Cropland	Areas dominated by intensively managed crops with >20% total vegetation cover
Barren	Areas characterized by bare rock, gravel, sand, silt, clay, or other earthen material with <10% vegetation cover
Urban [†]	Areas with $\geq 30\%$ urban constructed materials for human activities
Snow/ice [†]	Areas with >25% cover of ice and/or snow

Notes: We obtained land cover data from the North American Land Change Monitoring System, 250-m resolution 2010 data, and reclassified the data from 19 classes to 10 classes.

[†] Land cover class was combined into an "other" category for modeling purposes.

Table S2. Weather variables associated with GPS locations in daily tracks of golden eagles in western North America, 2007-2017.

Weather variable	Measurement units	Atmospheric level	Definition
Downward shortwave radiation flux	W/m ²	Surface	Measure of the reflection of incident solar radiation by the surface
Temperature	K	Surface	Air temperature
Precipitation	kg/m ²	Surface	3-hour accumulation of total precipitation at the surface
u-wind	m/s	10 m above ground	Velocity of east-west winds (positive value is wind from the west)
v-wind	m/s	10 m above ground	Velocity of north-south winds (positive value is wind from the south)

Notes: Data for each weather variable have a 3-hour temporal resolution and were provided by the National Centers for Environmental Prediction/National Center for Atmospheric Research North American Regional Reanalysis program.

Table S3. Ecological regions associated with events of golden eagles in western North America, 2007-2017.

Ecoregion Category	Description
Western Cordillera	High-elevation mountains and plateaus in U.S. and Canada
Interior Plains	Western Great Plains, including West-Central and South-Central Semiarid Prairies, and Boreal Plain in U.S. and Canada
Cold Deserts	Sagebrush-steppe ecosystems of high-elevation intermountain basins and plateaus in U.S. and Canada
Warm Deserts	Arid region in southern U.S. and Mexico
Mediterranean California	Mixed chaparral, grassland, and oak woodlands in California, U.S., and northern Baja California, Mexico
Upper Gila Mountains	Forested hills, scrublands, and grassland valleys in southern U.S., between cold desert and warm desert regions

Notes: Level II ecoregion data were obtained from the Commission for Environmental Cooperation and condensed into six categories.

Table S4. Summary data of daily tracks (distances traveled in km) flown by 160 golden eagles in western North America, 2007-2017.

Bird ID	Age at capture [†]	Start date	End date	# Tracks	Mean daily distance	Maximum daily distance	Minimum daily distance	Cumulative distance	Displacement distance
778	HY	11-Jun-2013	31-Aug-2016	1,018	12.64	176.97	0.003	13,805.41	494.58
1196	HY	10-Jun-2013	24-Sep-2014	464	11.01	176.48	0.010	5,321.58	445.01
1834	A5Y	2-Mar-2015	3-Jul-2017	771	21.61	268.53	0.004	17,552.43	975.34
1883	A5Y	8-Feb-2017	4-Jul-2017	141	39.16	252.56	0.333	6,186.44	1,058.63
2097	SY	24-Mar-2017	27-Jun-2017	95	45.50	264.23	1.930	4,489.06	749.94
4517	HY	17-Jun-2014	4-Apr-2016	554	12.14	224.58	0.004	7,443.45	830.26
4899	SY	8-Feb-2017	3-Jul-2017	146	32.83	194.44	0.145	4,858.69	556.83
4931	HY	3-Jun-2016	14-Dec-2016	193	13.67	147.03	0.004	2,683.57	861.58
5186	5Y	12-Jan-2014	1-Dec-2016	970	27.74	188.28	0.004	28,107.60	621.14
5196	SY	18-Dec-2012	20-Dec-2016	1,047	9.66	227.76	0.005	10,994.05	497.45
5298	A4Y	1-Dec-2015	19-Dec-2015	19	69.12	242.06	0.001	1,321.63	1,174.32
6696	TY	13-Jan-2017	4-Jul-2017	173	22.21	211.97	0.196	3,901.23	713.29
6846	4Y	9-Jan-2013	26-Mar-2014	409	39.07	326.73	0.019	16,981.61	851.78
6994	TY	16-Jan-2013	6-Apr-2014	414	41.07	313.78	0.007	18,295.57	916.45
7132	A5Y	21-Jan-2017	4-Jul-2017	105	17.17	259.39	0.051	2,114.17	844.74
7199	4Y	26-Dec-2015	26-Jul-2016	211	35.24	465.43	0.009	7,837.73	1,012.35
7224	TY	10-Mar-2014	20-Dec-2015	633	29.53	262.40	0.028	19,398.12	1,301.57
7364	SY	15-Jan-2013	24-Jan-2015	696	40.30	385.40	0.000	29,157.47	1,794.70
7448	5Y	3-Jan-2013	9-Jan-2016	688	32.30	302.67	0.005	25,901.68	1,038.02
7463	HY	6-Dec-2012	29-Jun-2015	755	30.21	262.63	0.002	24,907.23	1,184.61
7546	TY	23-Jan-2012	4-Nov-2015	1,245	26.22	252.68	0.004	34,383.21	423.10
7652	A5Y	11-Feb-2016	4-Jul-2017	494	16.67	398.01	0.002	8,606.68	844.79
7837	HY	18-May-2012	16-Dec-2012	185	21.84	217.34	0.002	4,263.60	746.89
8008	HY	17-May-2012	25-Nov-2012	185	22.06	213.64	0.005	4,179.99	1,017.06
8114	A5Y	11-Feb-2016	4-Jul-2017	502	25.73	313.81	0.003	13,183.04	1,478.82
8221	SY	29-Jan-2017	4-Jul-2017	149	25.95	334.50	0.129	4,123.33	1,193.85
8478	A5Y	29-May-2016	5-Jul-2017	390	23.49	393.78	0.014	9,537.26	954.46

Bird ID	Age at capture [†]	Start date	End date	# Tracks	Mean daily distance	Maximum daily distance	Minimum daily distance	Cumulative distance	Displacement distance
0629-30628	HY	8-Jun-2007	24-Nov-2007	116	10.92	141.35	0.000	1,541.27	1,076.73
0629-30639	HY	5-Jun-2007	29-Nov-2008	398	19.44	226.34	0.000	9,073.08	1,202.28
0629-30658	HY	21-May-2009	12-Jul-2016	1,470	15.05	181.31	0.000	33,329.21	488.07
0629-30697	A4Y	13-Oct-2009	13-May-2013	1,275	21.06	219.96	0.000	28,128.86	857.79
0629-43430	HY	2-Jun-2016	9-Aug-2017	434	25.49	330.88	0.000	12,059.95	1,013.61
0629-46167	HY	11-May-2011	26-Jun-2012	393	10.76	255.06	0.000	4,485.20	998.93
0629-46170	HY	3-Jun-2011	31-Dec-2012	553	16.84	200.07	0.000	9,940.66	1,294.44
0629-46185	HY	3-Jun-2011	10-Oct-2012	481	9.94	141.45	0.000	5,083.06	376.02
0629-46187	HY	4-Jun-2011	3-Sep-2012	445	14.38	153.88	0.000	7,053.08	465.41
0629-46195	HY	29-May-2012	19-Aug-2013	436	26.03	275.27	0.017	11,600.11	1,837.58
0629-46200	HY	30-May-2012	17-Aug-2016	1,395	26.23	231.46	0.000	39,558.76	1,059.33
0629-46318	A4Y	9-Oct-2008	18-Jul-2009	28	20.03	382.19	0.013	1,766.81	1,084.38
0629-46326	A4Y	24-Oct-2007	27-May-2008	149	34.12	293.60	0.000	6,856.97	2,819.67
0629-46365	HY	22-May-2010	25-Jul-2011	402	26.89	310.19	0.000	11,109.70	1,802.93
0629-46366	HY	22-May-2010	1-Jul-2011	390	14.32	221.50	0.000	5,752.92	923.62
0629-46391	HY	1-Jun-2010	30-Oct-2011	508	16.30	222.01	0.000	8,687.60	475.54
0629-46394	HY	1-Jun-2010	24-Feb-2013	996	11.37	183.19	0.000	11,886.54	591.92
0629-46395	HY	1-Jun-2010	17-Dec-2010	195	15.15	139.59	0.000	3,035.71	559.46
0679-02134	HY	28-Jun-2013	8-Sep-2013	68	50.63	267.39	0.033	3,478.35	456.39
0679-02141	HY	26-Jun-2013	5-Nov-2013	127	39.75	287.75	0.024	5,264.97	1,498.19
0679-02142	HY	25-Jun-2013	4-Jan-2014	176	16.60	212.82	0.000	3,136.83	450.17
0679-02149	HY	27-Jun-2013	20-Nov-2014	508	10.26	206.53	0.000	5,505.53	523.54
0679-03484	HY	3-Jul-2013	21-Nov-2014	474	30.56	296.31	0.020	15,175.28	1,544.68
0679-04367	5Y	14-May-2014	12-Aug-2017	1,172	47.53	430.49	0.020	59,682.63	2,429.86
0679-04387	SY	20-Mar-2015	12-Feb-2017	610	19.38	157.95	0.001	12,626.88	456.71
0679-04388	TY	21-Mar-2015	5-Apr-2016	249	31.08	282.08	0.013	8,235.90	503.76
0679-04393	TY	3-Mar-2016	12-Aug-2017	528	40.55	492.67	0.097	23,738.74	723.24
0679-04947	HY	23-May-2014	20-Jun-2017	948	23.66	313.78	0.000	25,536.21	1,084.51
0679-04948	HY	23-May-2014	24-Apr-2015	265	32.51	226.41	0.000	9,750.69	486.34

Bird ID	Age at capture [†]	Start date	End date	# Tracks	Mean daily distance	Maximum daily distance	Minimum daily distance	Cumulative distance	Displacement distance
0679-04950	HY	30-May-2014	26-Nov-2015	512	37.03	384.15	0.000	20,047.57	1,525.90
0679-04982	HY	10-Dec-2014	8-Sep-2016	263	17.06	153.69	0.016	8,798.40	547.12
0679-04984	HY	17-Jun-2014	15-Feb-2017	898	36.20	329.39	0.000	35,387.39	792.97
0679-04985	HY	17-Jun-2014	10-Aug-2017	1,145	33.55	390.88	0.019	42,211.42	681.43
0709-01053	HY	3-Jun-2014	20-Nov-2014	140	25.74	197.64	0.066	3,916.55	509.82
0709-01059	HY	10-Jun-2014	21-Nov-2014	137	32.28	266.47	0.000	4,537.63	721.13
0709-01062	HY	12-Jun-2014	21-Oct-2014	123	31.03	250.77	0.014	4,175.59	381.51
0709-01064	HY	12-Jun-2014	10-Aug-2017	1,086	33.36	355.84	0.000	39,707.67	941.13
0709-01065	HY	12-Jun-2014	2-Sep-2015	361	32.35	338.60	0.000	12,958.76	507.73
0709-02278	HY	6-Jun-2014	26-Jan-2015	212	26.66	263.27	0.000	6,002.85	768.38
0709-02351	HY	4-May-2014	8-Dec-2014	91	18.53	147.80	0.039	2,099.02	303.82
0709-02824	HY	28-Jun-2014	6-Dec-2014	157	20.15	299.68	0.015	3,332.85	1,005.07
0709-02825	HY	15-Jun-2014	27-Jul-2015	406	41.61	410.10	0.000	17,940.16	466.65
0709-02829	HY	11-Jun-2014	25-Aug-2016	801	58.27	321.70	0.035	49,893.66	894.65
0709-02830	HY	16-Jun-2014	22-Oct-2014	96	20.70	243.18	0.000	2,105.00	528.53
0709-02962	HY	20-Jul-2013	28-Jul-2015	713	33.70	366.20	0.014	25,526.18	568.72
0709-02963	HY	21-Jul-2013	27-Jul-2015	729	35.27	310.92	0.000	26,963.53	887.94
0709-02969	HY	5-Jun-2014	11-Aug-2017	1,157	33.09	517.17	0.000	40,267.25	775.42
0709-02970	HY	11-Jul-2014	28-Jul-2015	333	33.34	319.34	0.013	12,358.75	661.96
0709-02972	HY	9-Mar-2015	27-Jul-2015	138	46.94	282.13	0.269	6,869.90	1,242.88
0709-02973	U	3-Jan-2015	20-Apr-2016	226	43.91	214.69	0.014	15,035.41	1,069.61
0709-02974	SY	9-Dec-2014	30-Jun-2016	570	38.58	287.99	0.025	23,246.69	508.99
0709-02983	HY	4-Jun-2015	12-Aug-2017	711	19.74	419.93	0.000	15,409.62	914.00
0709-03781	4Y	22-Aug-2015	10-Aug-2017	175	19.11	140.68	0.129	7,870.60	783.97
0709-03851	HY	5-Aug-2014	21-Apr-2015	221	32.49	341.86	0.015	7,604.09	849.85
0709-03855	HY	24-Jul-2014	8-Feb-2015	198	33.05	259.34	0.041	6,802.58	938.28
0709-03858	HY	21-Jun-2014	14-Aug-2017	1,014	31.69	299.76	0.000	34,296.16	1,093.80
0709-03864	HY	27-Jun-2014	12-Aug-2017	1,096	25.68	206.05	0.013	30,628.11	544.89
0709-03881	HY	6-Jun-2016	12-Aug-2017	429	30.88	364.23	0.099	14,060.00	1,192.28

Bird ID	Age at capture [†]	Start date	End date	# Tracks	Mean daily distance	Maximum daily distance	Minimum daily distance	Cumulative distance	Displacement distance
0709-03886	HY	15-Jun-2016	12-Aug-2017	403	30.43	247.16	0.000	13,100.15	756.08
0709-04003	HY	23-May-2014	7-Aug-2017	1,098	38.93	229.03	0.000	46,686.07	454.29
0709-04022	HY	19-Aug-2015	9-Aug-2017	719	33.37	227.11	0.013	26,161.29	741.60
0709-04170	HY	6-Jun-2014	10-Aug-2017	1,106	28.50	246.15	0.012	34,050.53	498.97
0719-00657	A5Y	18-Oct-2011	31-Jul-2016	556	9.78	244.90	0.000	8,686.14	777.00
0719-00677	HY	29-May-2012	14-Jul-2013	354	18.79	309.88	0.080	6,830.51	1,542.63
0719-00678	HY	7-Jun-2012	24-Aug-2013	431	23.77	280.28	0.000	10,611.67	454.72
0799-00096	HY	4-Jun-2014	12-Aug-2017	1,113	32.60	257.61	0.059	38,018.51	772.71
0799-00097	HY	8-Jul-2013	27-Jul-2015	739	38.54	345.04	0.103	30,042.90	555.73
0799-00098	HY	11-Jul-2013	28-Jul-2015	704	19.64	354.80	0.024	14,579.95	437.18
0799-00662	HY	23-May-2014	26-Jun-2017	551	35.36	385.87	0.000	22,764.12	620.34
0799-00735	HY	29-Jun-2014	12-Aug-2017	1,090	16.13	237.49	0.000	18,636.61	365.86
0799-00737	HY	3-Jun-2015	12-Aug-2017	794	22.81	237.98	0.000	19,725.51	716.44
0799-00750	HY	5-Jun-2016	12-Aug-2017	405	26.90	251.13	0.020	11,659.59	985.25
0799-00751	HY	6-Jun-2016	12-Aug-2017	422	24.81	175.90	0.000	11,155.39	380.17
0799-00752	HY	24-Jun-2014	13-Aug-2017	971	15.93	383.17	0.000	16,868.49	1,209.04
0799-01253	HY	8-Jun-2016	12-Aug-2017	401	23.73	263.70	0.000	10,198.86	1,271.29
0799-01254	HY	10-Jun-2016	12-Aug-2017	299	17.15	146.00	0.012	5,552.57	312.62
0907-03866	HY	30-Jun-2014	11-Aug-2017	1,133	22.46	387.44	0.000	28,630.64	870.78
1098-00904	5Y	22-May-2014	19-May-2015	362	45.93	376.29	0.113	17,366.30	1,083.07
1098-00908	TY	20-Mar-2017	12-Aug-2017	145	41.94	409.77	0.036	6,322.54	979.19
629-33469	HY	29-May-2014	10-Aug-2017	1,049	34.89	311.47	0.013	40,010.83	927.95
629-33473	HY	28-May-2014	12-Mar-2017	889	24.83	290.86	0.013	24,640.54	654.72
629-33479	HY	5-Jun-2014	10-Aug-2017	910	20.28	248.12	0.000	20,829.51	619.54
629-43411	HY	19-Jun-2014	10-Aug-2017	858	28.53	302.84	0.011	26,770.16	557.68
629-43412	HY	27-Jun-2014	8-Aug-2017	1,126	38.74	338.21	0.019	46,341.44	2,014.58
629-43413	HY	27-Jun-2014	18-Nov-2014	127	26.93	264.36	0.020	3,542.57	1,421.79
629-43417	HY	20-Nov-2014	10-Aug-2017	821	29.54	364.97	0.012	26,523.85	566.76
629-48075	A5Y	25-Feb-2011	10-May-2012	398	32.33	344.35	0.000	13,663.82	2,013.26

Bird ID	Age at capture [†]	Start date	End date	# Tracks	Mean daily distance	Maximum daily distance	Minimum daily distance	Cumulative distance	Displacement distance
629-50752	HY	5-Jul-2012	28-Jul-2015	1,089	45.70	364.07	0.014	52,411.71	1,898.03
629-50755	HY	9-Jul-2012	27-Jul-2015	1,102	28.33	317.09	0.019	33,321.42	747.76
629-50756	HY	17-Jul-2012	23-Aug-2013	365	39.68	312.18	0.058	15,526.79	528.80
629-50759	HY	11-Jul-2012	27-Jul-2015	1,098	37.87	432.28	0.025	43,442.32	1,293.43
629-50760	HY	9-Jun-2012	21-Dec-2012	191	30.39	251.33	0.042	6,149.87	815.71
629-50762	HY	13-Jul-2012	30-Oct-2013	448	23.70	282.35	0.076	11,581.35	1,210.47
629-50765	HY	21-Jul-2012	4-Sep-2013	375	30.93	421.70	0.014	12,602.86	967.93
629-50772	HY	21-Jul-2012	27-Jul-2015	1,051	39.04	309.24	0.000	44,881.60	752.20
629-50774	HY	10-Aug-2012	27-Jul-2015	1,046	28.93	345.66	0.122	32,393.77	1,492.94
629-50793	HY	1-Aug-2013	16-Jul-2015	696	24.37	274.81	0.000	17,887.77	821.72
629-50796	HY	8-Jul-2013	28-Mar-2014	256	43.42	394.97	0.052	11,327.98	1,669.64
629-50799	HY	1-Aug-2013	27-Jul-2015	708	33.33	277.72	0.015	24,626.20	742.17
679-02261	HY	30-Jul-2010	27-Jul-2015	1,815	25.77	308.12	0.000	55,249.05	1,217.30
679-02267	HY	2-Jul-2011	14-Jun-2014	1,069	44.39	434.34	0.088	50,364.95	818.15
679-02271	HY	3-Jul-2011	10-Dec-2013	883	44.98	382.39	0.014	42,343.96	1,039.40
679-02273	HY	4-Jul-2011	28-Jul-2015	1,472	15.43	330.36	0.000	25,537.71	850.74
679-02275	HY	12-Jul-2011	17-Nov-2011	124	25.86	175.55	0.102	3,462.79	578.07
679-02280	HY	16-Jul-2011	25-Aug-2014	1,130	36.28	270.57	0.130	42,216.54	576.13
679-02283	HY	24-Jul-2011	28-Jul-2015	1,455	27.02	457.50	0.167	40,397.34	1,112.99
679-02297	A4Y	13-Jan-2011	28-Jul-2015	1,647	33.51	393.03	0.019	57,433.49	1,364.73
679-02299	A4Y	8-Jan-2011	15-Jun-2011	158	33.25	254.67	0.024	5,351.04	1,087.07
679-02300	A4Y	15-Jan-2011	18-May-2012	481	27.52	416.63	0.106	13,881.86	722.59
679-03084	HY	20-Jul-2012	7-Aug-2013	376	27.94	264.28	0.114	11,005.61	993.40
709-01852	A5Y	3-Oct-2011	11-Mar-2013	522	29.70	348.15	0.101	16,184.47	1,976.17
709-01856	A5Y	10-Oct-2011	2-Jan-2012	85	23.51	393.92	0.859	2,038.20	799.95
709-01858	A5Y	10-Oct-2011	18-Aug-2013	673	41.12	361.95	0.275	29,635.67	2,504.88
709-02493	A5Y	28-Feb-2014	18-Feb-2015	252	15.48	62.86	0.063	4,557.46	302.42
709-02744	SY	10-Feb-2015	30-Apr-2015	80	43.02	350.90	0.628	3,575.86	1,211.17
709-02801	HY	17-Jul-2013	28-Jul-2015	732	34.86	310.59	0.020	27,013.15	731.01

Bird ID	Age at capture [†]	Start date	End date	# Tracks	Mean distance	Maximum distance	Minimum distance	Cumulative distance	Displacement distance
709-02802	HY	23-Jul-2013	5-Nov-2013	99	52.15	258.77	0.024	5,474.54	1,485.57
709-02803	HY	22-Jul-2013	7-Nov-2013	109	39.63	332.27	0.143	4,425.86	971.98
719-00363	A5Y	13-Oct-2012	11-May-2013	28	38.69	182.30	0.006	6,968.21	2,099.72
799-00055	A5Y	21-Oct-2013	14-Mar-2014	136	14.30	159.36	0.019	2,056.32	457.89
b57d	SY	3-Feb-2017	2-Jul-2017	148	33.61	259.55	0.115	5,150.14	659.11
BM11	A4Y	3-Apr-2011	18-Jan-2012	261	8.41	135.46	0.000	3,465.37	867.91
Broadus_Sub_Female2_2014	SY	23-Feb-2014	30-Apr-2015	418	27.06	241.95	0.012	12,058.68	368.14
Butte_Creek_Sub_Female_2014	SY	2-Feb-2014	30-Apr-2015	449	29.58	297.10	0.103	14,223.44	1,322.52
cf61	A5Y	4-Feb-2016	28-Jul-2016	154	38.76	271.03	0.020	6,749.89	338.81
CPNF13	HY	21-Jun-2013	8-Feb-2015	595	23.82	212.78	0.031	15,135.76	807.79
CPNM13	HY	21-Jun-2013	9-Feb-2015	598	24.21	195.55	0.156	15,480.02	957.42
dc1b	TY	5-Jan-2016	19-May-2017	478	40.39	221.23	0.007	20,493.73	643.39
e148	TY	1-Jan-2016	20-Jun-2017	375	16.39	110.84	0.009	7,410.78	721.48
ERNF13	HY	20-Jun-2013	8-Feb-2015	509	14.69	167.56	0.000	8,660.45	767.64
ERNF14	HY	2-Jul-2014	8-Feb-2015	220	13.45	155.56	0.050	3,230.46	696.88
PNM12	HY	30-Jun-2012	31-Dec-2012	144	7.22	148.29	0.073	2,295.50	839.80
Roundup_Sub_Male2_2014	4Y	21-Feb-2014	1-Apr-2014	40	25.23	86.44	0.813	1,028.90	358.26
Total tracks/average distances				88,093	28.31			16,895.95	912.67

[†] HY = hatch-year, SY = second-year, TY = third-year, 4Y = fourth-year, 5Y = fifth-year, A4Y = after fourth-year, A5Y = after fifth-year, U = unknown bird age.

Table S5. Top models (model weights ≥ 0.01) that explain influences on daily distances flown by golden eagles in western North America, 2007-2017.

Model	<i>K</i>	logLik	$\Delta AICc$	Model Weight
Age, month, land cover, TRI-SD, DSR, precipitation, wind direction	29	-205,954	0.00	0.68
Age, month, land cover, TRI-SD, DSR, precipitation, wind speed*wind direction interaction	33	-205,951	1.60	0.31
Age, month, land cover, TRI-SD, DSR, precipitation, wind speed, wind direction	30	-205,957	8.00	0.01

Notes: TRI-SD is the standard deviation of the terrain ruggedness index and DSR is downward shortwave radiation. *K* refers to the number of parameters in a model, logLik is the log-likelihood, and $\Delta AICc$ is the distance from the top model in Akaike's information criterion corrected for small sample size.

Table S6. Summary data of events (distances traveled in km) flown by 153[†] golden eagles in western North America, 2007-2017.

Bird ID	Age at capture [‡]	# Events	Mean # days	Mean distance flown	Mean speed	Mean displacement distance
778	HY	1	18.00	571.51	31.75	415.94
1196	HY	2	10.00	517.59	55.68	374.09
1834	A5Y	2	8.50	1,005.69	122.04	920.91
1883	A5Y	2	12.00	1,042.51	94.00	890.84
2097	SY	2	9.50	969.82	98.16	415.95
4517	HY	3	8.33	497.51	59.48	385.39
4899	SY	1	5.00	416.93	83.39	367.56
4931	HY	1	13.00	1,056.68	81.28	859.51
5186	5Y	1	8.00	483.04	60.38	332.14
5196	SY	2	6.00	518.61	117.34	383.54
5298	A4Y	1	14.00	1,275.19	91.09	1,167.04
6696	TY	1	7.00	826.66	118.09	686.68
6846	4Y	2	10.50	700.82	90.12	610.13
6994	TY	2	15.00	1,109.74	73.69	689.77
7132	A5Y	1	6.00	588.14	98.02	487.59
7199	4Y	3	5.33	997.04	208.69	891.57
7224	TY	6	10.17	979.17	111.49	718.90
7364	SY	9	8.33	1,051.60	134.84	790.49
7448	5Y	2	7.50	1,078.08	161.05	958.99
7463	HY	11	7.18	700.22	108.98	551.64
7546	TY	26	6.12	446.92	85.97	325.55
7652	A5Y	3	5.00	589.02	139.62	529.87
7837	HY	1	26.00	1,986.30	76.40	682.01
8008	HY	1	17.00	1,405.46	82.67	996.87
8114	A5Y	11	11.45	706.03	72.76	511.95
8221	SY	3	5.67	592.25	105.45	412.60
8478	A5Y	3	7.00	736.12	135.13	594.75
0629-30628	HY	1	24.00	1,287.94	53.66	1,035.98

Bird ID	Age at capture [‡]	# Events	Mean # days	Mean distance flown	Mean speed	Mean displacement distance
0629-30639	HY	3	19.33	1,251.50	68.60	786.62
0629-30658	HY	2	14.50	473.30	33.34	308.57
0629-30697	A4Y	8	23.88	776.23	37.47	549.11
0629-43430	HY	3	11.67	904.79	90.65	541.79
0629-46167	HY	1	11.00	1,299.05	118.10	955.71
0629-46170	HY	1	10.00	1,404.53	140.45	1,222.30
0629-46185	HY	1	14.00	570.60	40.76	345.42
0629-46187	HY	1	3.00	421.73	140.58	381.41
0629-46195	HY	4	8.25	723.12	97.52	518.65
0629-46200	HY	5	12.00	658.88	72.43	482.98
0629-46318	A4Y	1	18.00	1,191.94	66.22	1,072.24
0629-46326	A4Y	4	19.00	1,472.45	74.01	1,239.88
0629-46365	HY	6	7.17	848.64	123.83	580.48
0629-46366	HY	1	12.00	1,349.58	112.46	890.24
0629-46391	HY	2	12.00	667.08	55.22	394.56
0629-46394	HY	2	15.00	699.77	47.24	487.51
0629-46395	HY	1	24.00	805.02	33.54	494.26
0679-02134	HY	1	4.00	585.17	146.29	314.63
0679-02141	HY	3	6.33	1,038.52	177.36	683.98
0679-02142	HY	1	7.00	595.10	85.01	448.31
0679-02149	HY	2	10.50	683.11	68.46	485.95
0679-03484	HY	5	6.00	919.13	165.86	674.17
0679-04367	5Y	11	12.55	1,628.82	133.56	1,342.07
0679-04387	SY	2	11.50	652.10	56.68	373.36
0679-04388	TY	2	17.00	626.91	117.80	384.26
0679-04393	TY	4	3.25	643.64	225.38	498.06
0679-04947	HY	2	5.50	927.06	169.74	761.70
0679-04948	HY	1	4.00	358.53	89.63	354.19
0679-04950	HY	3	11.33	1,421.00	140.61	960.79
0679-04982	HY	2	10.50	575.47	67.92	410.49
0679-04984	HY	3	10.00	771.44	133.85	445.45

Bird ID	Age at capture [‡]	# Events	Mean # days	Mean distance flown	Mean speed	Mean displacement distance
0679-04985	HY	6	4.17	620.69	183.98	466.27
0709-01053	HY	1	16.00	1,003.43	62.71	439.72
0709-01059	HY	3	4.00	654.49	170.09	467.73
0709-01062	HY	1	2.00	330.67	165.33	321.44
0709-01064	HY	5	5.00	621.28	124.66	391.33
0709-01065	HY	2	3.00	421.03	140.34	315.29
0709-02278	HY	1	14.00	1,133.69	80.98	698.31
0709-02824	HY	1	9.00	1,337.07	148.56	991.24
0709-02825	HY	13	3.92	508.33	139.99	369.44
0709-02829	HY	9	3.33	604.24	185.36	434.78
0709-02830	HY	1	8.00	696.86	87.11	501.11
0709-02962	HY	2	3.50	730.62	228.03	503.69
0709-02963	HY	4	6.50	759.06	135.26	468.84
0709-02969	HY	2	6.00	1,074.66	216.82	705.40
0709-02970	HY	1	8.00	785.69	98.21	531.26
0709-02972	HY	3	3.67	585.65	161.26	459.62
0709-02973	U	3	7.67	647.57	121.31	557.41
0709-02974	SY	7	3.57	451.51	147.95	372.48
0709-02983	HY	6	8.17	808.08	120.71	632.57
0709-03851	HY	2	11.00	1,133.89	103.35	766.88
0709-03855	HY	2	8.50	1,103.91	127.30	635.32
0709-03858	HY	2	9.00	1,595.84	175.78	1,031.93
0709-03864	HY	2	2.00	347.75	173.88	313.90
0709-03881	HY	5	5.60	686.69	117.38	476.04
0709-03886	HY	5	3.80	479.51	129.46	338.36
0709-04003	HY	4	6.75	536.55	95.84	317.11
0709-04022	HY	5	6.80	546.96	114.63	395.88
0709-04170	HY	1	5.00	485.15	97.03	385.20
0719-00657	A5Y	3	19.33	706.04	63.92	524.37
0719-00677	HY	2	12.50	1,126.15	84.38	762.88
0719-00678	HY	1	7.00	701.81	100.26	370.76

Bird ID	Age at capture [‡]	# Events	Mean # days	Mean distance flown	Mean speed	Mean displacement distance
0799-00096	HY	2	4.00	716.88	186.07	633.74
0799-00097	HY	11	3.73	509.75	155.76	357.34
0799-00098	HY	2	2.50	379.27	227.87	321.82
0799-00662	HY	6	5.33	673.34	154.17	459.66
0799-00737	HY	3	7.67	621.25	100.13	477.87
0799-00750	HY	2	6.00	657.95	150.23	540.76
0799-00751	HY	2	6.00	499.57	102.33	327.04
0799-00752	HY	4	9.00	1,401.28	174.99	809.78
0799-01253	HY	1	13.00	1,820.71	140.05	1,171.74
0907-03866	HY	2	4.00	1,142.88	283.60	664.77
1098-00904	5Y	2	6.50	1,176.40	191.66	956.79
1098-00908	TY	4	6.50	974.22	155.77	651.83
629-33469	HY	2	16.50	1,396.71	84.27	817.65
629-33473	HY	2	5.50	565.53	101.62	360.94
629-33479	HY	4	5.50	589.31	115.33	419.05
629-43411	HY	4	17.50	972.35	62.88	380.57
629-43412	HY	17	9.24	986.18	127.50	752.86
629-43413	HY	1	23.00	1,844.71	80.20	1,342.08
629-43417	HY	6	7.17	598.50	101.45	365.07
629-48075	A5Y	7	16.29	1,234.63	80.47	818.85
629-50752	HY	20	7.75	804.27	125.13	599.60
629-50755	HY	2	3.50	697.07	202.40	625.97
629-50756	HY	2	6.00	701.83	170.13	443.55
629-50759	HY	5	10.20	1,204.78	133.16	782.26
629-50760	HY	1	12.00	1,135.99	94.67	725.39
629-50762	HY	7	10.29	707.00	94.85	510.60
629-50765	HY	3	6.33	774.63	169.02	639.18
629-50772	HY	2	9.00	823.55	92.63	584.95
629-50774	HY	4	13.75	1,286.09	127.90	970.00
629-50793	HY	2	20.00	982.60	59.09	667.61
629-50796	HY	3	9.33	1,515.17	171.40	846.98

Bird ID	Age at capture [‡]	# Events	Mean # days	Mean distance flown	Mean speed	Mean displacement distance
629-50799	HY	3	4.33	535.09	132.21	476.13
679-02261	HY	12	7.08	794.68	122.32	624.00
679-02267	HY	25	5.00	626.98	158.11	415.60
679-02271	HY	8	3.75	725.15	196.66	552.97
679-02273	HY	6	7.33	597.34	108.13	482.75
679-02275	HY	1	7.00	589.43	84.20	401.27
679-02280	HY	2	4.50	558.18	142.79	478.35
679-02283	HY	11	10.64	801.00	123.81	660.77
679-02297	A4Y	9	5.89	684.94	155.66	555.35
679-02299	A4Y	3	8.67	673.41	83.76	508.31
679-02300	A4Y	2	4.00	732.84	239.07	687.97
679-03084	HY	3	8.00	700.69	93.04	452.57
709-01852	A5Y	3	18.33	1,800.42	99.05	1,507.37
709-01856	A5Y	1	4.00	840.01	210.00	770.68
709-01858	A5Y	4	28.00	2,459.20	96.14	2,118.53
709-02744	SY	1	9.00	1,421.16	157.91	1,167.39
709-02801	HY	3	4.00	547.98	146.66	441.35
709-02802	HY	2	9.00	1,519.04	174.39	795.53
709-02803	HY	2	8.50	1,242.68	166.07	824.64
719-00363	A5Y	1	19.00	1,195.86	62.94	992.35
799-00055	A5Y	1	6.00	591.92	98.65	447.99
b57d	SY	2	8.50	797.77	90.24	483.04
BM11	A4Y	1	34.00	812.39	23.89	563.39
Broadus_Sub_Female2_2014	SY	2	15.50	626.84	40.92	319.85
Butte_Creek_Sub_Female_2014	SY	5	7.80	821.64	126.02	646.38
CPNF13	HY	2	16.00	958.86	67.88	724.15
CPNM13	HY	3	16.33	1,128.21	71.79	604.70
dc1b	TY	8	13.50	757.70	61.97	473.62
e148	TY	1	15.00	842.66	56.18	670.45
ERNF13	HY	2	18.50	691.07	37.26	497.67
ERNF14	HY	1	38.00	1,527.95	40.21	681.70

Bird ID	Age at capture[‡]	# Events	Mean # days	Mean distance flown	Mean speed	Mean displacement distance
PNM12	HY	1	19.00	1,094.41	57.60	817.72
Total events/average days and distances		563	10.00	871.88	115.86	622.19

[†] Seven eagles did not have any long-distance movements that met our definition of an event.

[‡] HY = hatch-year, SY = second-year, TY = third-year, 4Y = fourth-year, 5Y = fifth-year, A4Y = after fourth-year, A5Y = after fifth-year, U = unknown bird age.

Table S7. Top models (model weights ≥ 0.01) that explain influences on (a) cumulative distances flown, (b) displacement distances, and (c) number of days during events for golden eagles in western North America, 2007-2017.

Model	K	logLik	$\Delta AICc$	Model Weight
<u>(a) Cumulative distances</u>				
Intercept only	3	-343.37	0.00	0.74
Maximum temperature	4	-344.33	3.94	0.10
Age	5	-344.40	6.12	0.03
Landform-flat	4	-345.45	6.18	0.03
Precipitation	4	-345.61	6.50	0.03
Landform-slopes	4	-345.67	6.63	0.03
<u>(b) Displacement distances</u>				
Landform-flat	4	-734.74	0.00	0.26
Intercept only	3	-735.84	0.17	0.24
Landform-flat, maximum temperature	5	-734.44	1.44	0.13
Maximum temperature	4	-735.85	2.23	0.09
Age	5	-735.26	3.08	0.06
Age, landform-flat	6	-734.64	3.87	0.04
Landform-flat, landform-slopes	5	-735.93	4.42	0.03
Landform-flat, precipitation	5	-736.27	5.10	0.02
Landform-slopes	4	-737.32	5.16	0.02
Landform-flat, landform-slopes, maximum temperature	6	-735.35	5.30	0.02
Precipitation	4	-737.40	5.32	0.02
Age, maximum temperature	6	-735.65	5.90	0.01
Landform-flat, precipitation, maximum temperature	6	-735.66	5.93	0.01
Age, landform-flat, maximum temperature	7	-734.86	6.36	0.01
<u>(c) Number of days</u>				
Month, ecoregion-start, ecoregion-end, landform-flat	25	-1,628.15	0.00	0.12
Month, ecoregion-start, ecoregion-end, maximum temperature	25	-1,628.26	0.21	0.11
Month, ecoregion-start, ecoregion-end, landform-flat, maximum temperature	26	-1,627.22	0.33	0.10
Month, ecoregion-start, ecoregion-end	24	-1,629.57	0.64	0.09
Month, ecoregion-start, ecoregion-end, precipitation, maximum temperature	26	-1,627.55	0.98	0.07
Month, ecoregion-start, ecoregion-end, landform-flat, precipitation, maximum temperature	27	-1,626.63	1.35	0.06
Month, ecoregion-start, ecoregion-end, landform-flat, precipitation	26	-1,627.99	1.87	0.05
Month, ecoregion-start, ecoregion-end, landform-flat, landform-slopes	26	-1,628.10	2.09	0.04
Month, ecoregion-start, ecoregion-end, landform-slopes, maximum temperature	26	-1,628.26	2.41	0.04
Month, ecoregion-start, ecoregion-end, landform-flat, landform-slopes, maximum temperature	27	-1,627.18	2.46	0.03

Model	K	logLik	ΔAICc	Model Weight
Month, ecoregion-start, ecoregion-end, precipitation	25	-1,629.39	2.46	0.03
Month, ecoregion-start, ecoregion-end, landform-slopes	25	-1,629.56	2.82	0.03
Month, ecoregion-start, ecoregion-end, landform-slopes, precipitation, maximum temperature	27	-1,627.54	3.19	0.02
Age, month, ecoregion-start, ecoregion-end, landform-flat	27	-1,627.60	3.29	0.02
Month, ecoregion-start, ecoregion-end, landform-flat, landform-slopes, precipitation, maximum temperature	28	-1,626.60	3.51	0.02
Age, month, ecoregion-start, ecoregion-end, landform-flat, maximum temperature	28	-1,626.74	3.80	0.02
Age, month, ecoregion-start, ecoregion-end, maximum temperature	27	-1,627.88	3.86	0.02
Month, ecoregion-start, ecoregion-end, landform-flat, landform-slopes, precipitation	27	-1,627.93	3.97	0.02
Age, month, ecoregion-start, ecoregion-end	26	-1,629.08	4.05	0.02
Month, ecoregion-start, ecoregion-end, landform-slopes, precipitation	26	-1,629.38	4.65	0.01
Age, month, ecoregion-start, ecoregion-end, precipitation, maximum temperature	28	-1,627.18	4.68	0.01
Age, month, ecoregion-start, ecoregion-end, landform-flat, precipitation, maximum temperature	29	-1,626.16	4.87	0.01

Notes: *K* refers to the number of parameters in a model, logLik is the log-likelihood, and Δ AICc is the distance from the top model in Akaike's information criterion corrected for small sample size.

Table S8. Model parameters, including 95% confidence intervals (CI), from the logistic regression model that explains the probability of long-distance movement by age and sex classes of golden eagles in western North America, 2007-2017.

Variable	Coefficient	SE	z-value	Lower CI	Upper CI
Intercept	-0.39	0.16	-2.44	-0.71	-0.08
Age-Sub-adult	0.35	0.33	1.05	-0.31	1.00
Age-Adult	-1.02	0.24	-4.33	-1.49	-0.57
Sex-Male	-0.10	0.20	-0.52	-0.50	0.29

Notes: Reference variables were juvenile for age and female for sex. Variables with CI ranges that did not overlap zero are important variables.

Additional Models. Because 19 of the golden eagles in our dataset had long-distance movements that could have been classified as migratory, we re-ran the six models for long-distance events without these 19 birds: three models describing environmental correlates of the events (with response variables cumulative distances, displacement distances, and number of days), one model describing event timing, one model describing event direction, and one model comparing non-migratory long-distance movers to local movers. For all six of these models, the results, including important variables, were identical to the original models.