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ARTICLE

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, nonroutine 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

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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.

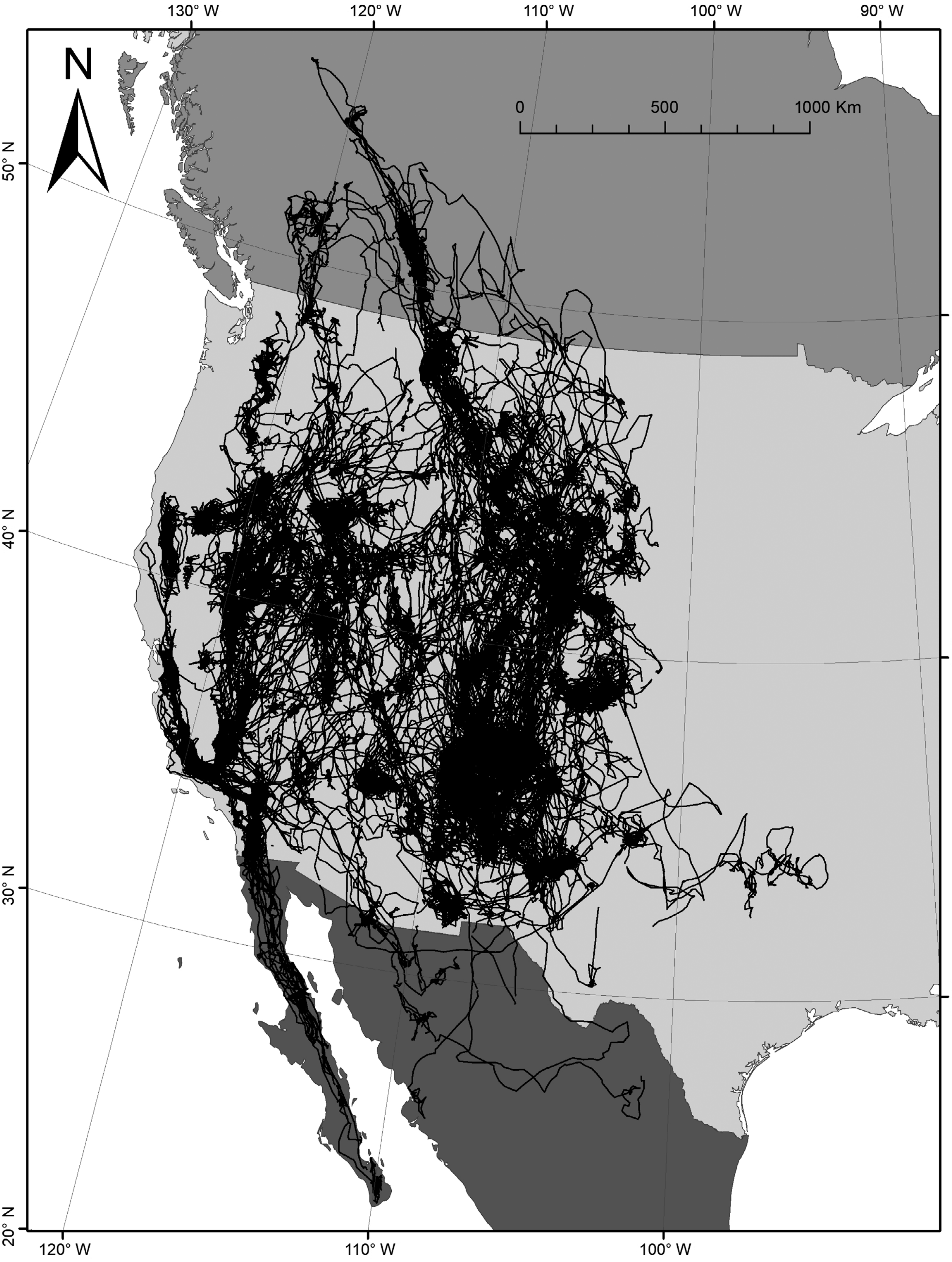

FIGURE 1 Map of western North America and composite of 88,093 daily tracks flown by 160 golden eagles tracked by telemetry devices, 2007–2017

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° 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°, 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°, 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° and ≤45°), east (>45° and ≤135°), south (>135° and ≤225°), or west (>225° and ≤315°).

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° and ≤22.5°), northeast (>22.5° and ≤67.5°), east (>67.5° and ≤112.5°), southeast (>112.5° and ≤157.5°), south (>157.5° and ≤202.5°), southwest (>202.5° and ≤247.5°), west (>247.5° and ≤292.5°), or northwest (>292.5° and ≤337.5°).

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 ≤2°), and slopes (>−30 and ≤30 TPI; slope >2°). 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 (±13,877.9) km longer than the straight-line displacement distance (i.e., displacement distance was ~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

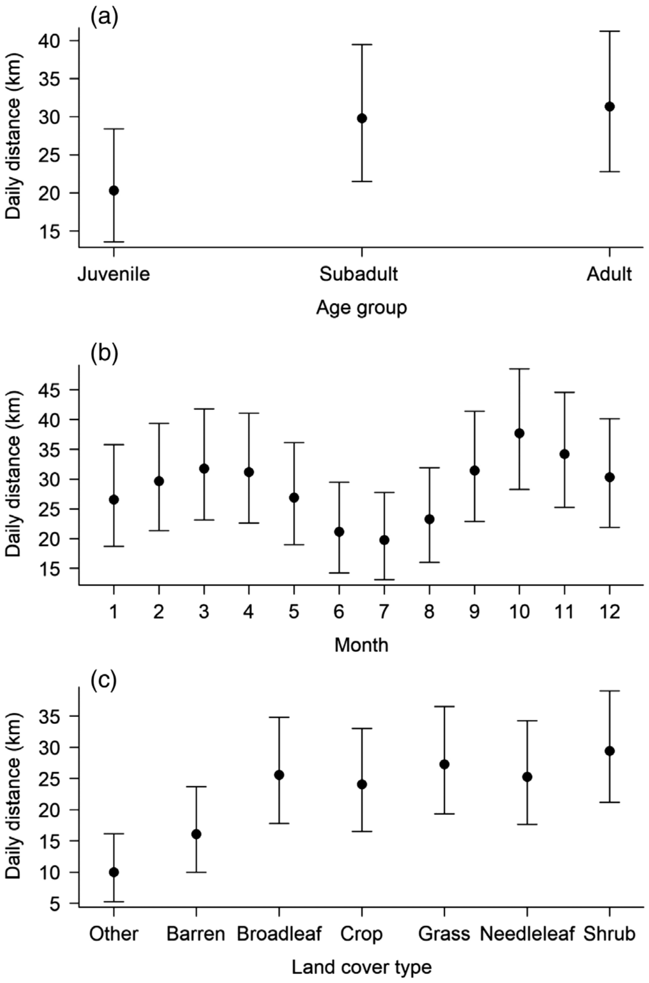

FIGURE 2 Plots of the back-transformed, model-fitted values of daily distances and (a) age group, (b) month, and (c) land cover type for golden eagles in western North America, 2007–2017. Bars represent 95% CIs

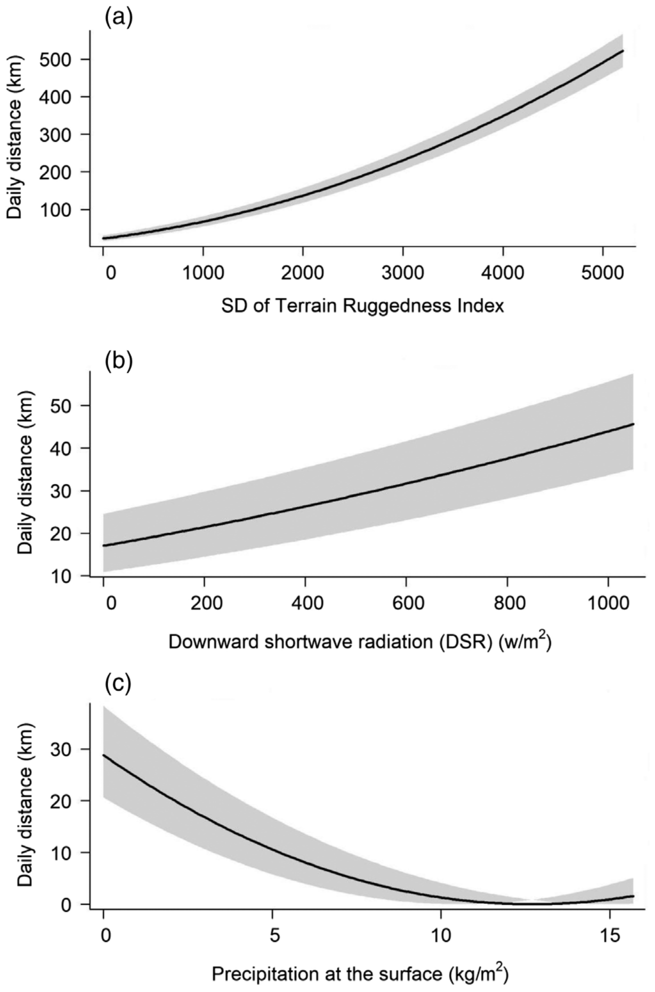

FIGURE 3 Plots of the back-transformed, model-fitted values of daily distances and (a) SD of Terrain Ruggedness Index, (b) downward shortwave radiation, and (c) precipitation at the earth's surface for golden eagles in western North America, 2007–2017. Gray bands represent 95% CIs. The *y*-axes of the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

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. 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; Pennycuick, 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

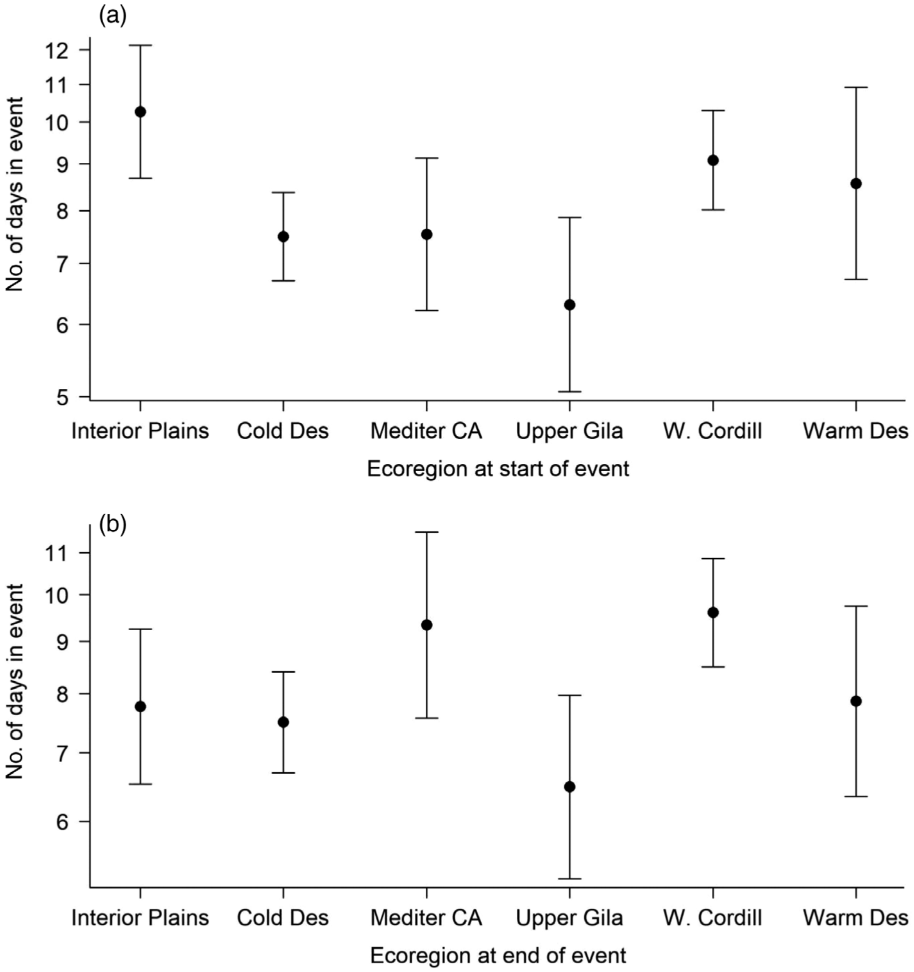

FIGURE 4 Plots of the model-fitted values of number of days in a long-distance event and (a) ecoregion at the start of the long-distance event and (b) ecoregion at the end of the long-distance event for golden eagles in western North America, 2007–2017. Bars represent 95% CIs

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.

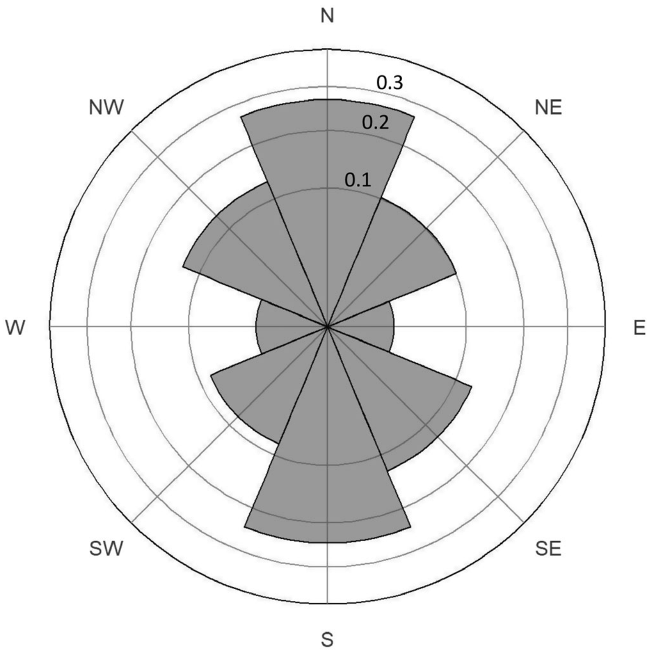

FIGURE 5 Rose plot of generalized directions of long-distance events by golden eagles in western North America, 2007–2017. Numbers above lines represent the proportion of long-distance events in each general direction sector. The square roots of frequencies were plotted to obtain the true area of each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

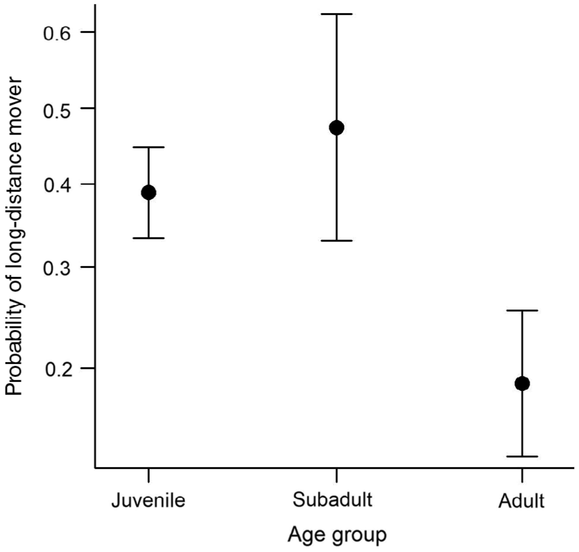

FIGURE 6 Plot of the probability of different age classes being long-distance movers for golden eagles in western North America, 2007–2017. Bars represent 95% CIs

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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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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