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RESEARCH ARTICLE

Topographic drivers of flight altitude over large spatial and temporal scales

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ABSTRACT

Bird movements vary spatially and temporally, but the primary drivers that explain such variation can be difficult to identify. For example, it is well known that the availability of updraft influences soaring flight and that topography interacts with weather to produce these updrafts. However, the influences of topography on flight are not well understood. We determined how topographic characteristics influenced flight altitude above ground level (AGL) of a large soaring bird, the Golden Eagle (*Aquila chrysaetos*), over several regions within the State of California, USA. Primary drivers of flight AGL, those to which eagles showed the same response at all spatial scales, were topographic roughness, ground elevation and the east-west component of aspect (eastness). Each of these is related to formation of thermal updrafts. Secondary drivers, those to which eagles showed region-specific patterns, included topographic position, percent slope, and the north-south component of aspect (northness). In contrast to primary drivers, these secondary drivers were related to formation of both thermal and orographic updrafts. Overall, drivers of flight altitudes that were related to thermal updrafts showed different levels of complexity due to spatial and temporal variation of those drivers than did flight altitudes related to orographic updrafts.

Keywords: Aquila chrysaetos, Golden Eagles, movement, orographic updraft, soaring, spatial variation, temporal variation, thermal updraft

Determinantes topográficas de la altitud de vuelo a lo largo de grandes escalas espaciales y temporales

RESUMEN

Los movimientos de las aves varían espacial y temporalmente, pero los determinantes primarios que explican esta variación pueden ser difíciles de identificar. Por ejemplo, es bien sabido que la disponibilidad de corrientes ascendentes influencia el vuelo de planeo y que la topografía interactúa con el clima para producir estas corrientes. Sin embargo, no se entienden bien las influencias de la topografía en el vuelo. Determinamos cómo las características topográficas influenciaron la altitud de vuelo sobre el nivel del suelo (SNS) de una gran ave planeadora, el águila *Aquila chrysaetos*, a lo largo de varias regiones dentro del Estado de California, EEUU. Los determinantes primarios del vuelo SNS, aquellos a los cuales las águilas mostraron la misma respuesta a todas las escalas espaciales, fueron la rugosidad topográfica, la elevación del suelo y el componente este-oeste de la orientación. Cada uno de estos está relacionado con la formación de las corrientes ascendentes térmicas. Los determinantes secundarios, aquellos a los cuales las águilas mostraron patrones específicos por región, incluyeron la posición topográfica, el porcentaje de pendiente y el componente norte-sur de la orientación. En contraste con los determinantes primarios, estos determinantes secundarios estuvieron relacionados con la formación de corrientes ascendentes térmicas y orográficas. En general, los determinantes de las altitudes de vuelo que estuvieron relacionados con las corrientes ascendentes térmicas mostraron diferentes niveles de complejidad debido a la variación espacial y temporal de estos determinantes, más que las altitudes de vuelo relacionadas con las corrientes ascendentes orográficas.

Palabras clave: Aquila chrysaetos, corriente ascendente orográfica, corriente ascendente térmica, movimiento, planeo, variación espacial, variación temporal

INTRODUCTION

Ecological patterns vary spatially and temporally. As an example, animal movements are often seasonally and regionally segregated (Kjellen et al. 2001, Alerstam et al. 2006, Duerr et al. 2015). Additionally, movement of animals is expected to vary temporally, both at a daily scale (i.e. with hour) and at a monthly scale (i.e. during nonbreeding and breeding seasons; Rivrud et al. 2010, Braham et al. 2015, Vansteelant et al. 2015, Miller et al. 2017). Likewise, those same movements are expected to vary spatially and in conjunction with other behaviors, for example, an animal that stays on its breeding range year-round may move less than an animal that migrates and occupies different regions in different seasons. When there is this level of complexity in animal movement among seasons and regions, it is often easier to describe variation of movement than it is to explain the spatio-temporal drivers of that movement. That said, understanding the drivers of movement aids both ecological understanding and improved management.

The complexity inherent in animal movements and the linkages of that complexity to spatial and temporal environmental variation is apparent in the flight behavior of large birds. For example, flight behavior changes in response to ecological barriers, geography, and weather (Alerstam 2001, Klaassen et al. 2011, Vansteelant et al. 2017). For large soaring birds, flight behaviors (e.g., soaring, speed, altitude) are known to change in response to both variation of weather conditions and to variation of topography (Katzner et al. 2012, Panuccio et al. 2013, Katzner et al. 2015, Panuccio et al. 2016, Poessel et al. 2016). This is largely because weather and topography interact to form environmental updrafts that soaring birds rely on to subsidize flight over land. Orographic updrafts are air currents (wind) that are deflected upward by topography (Kerlinger 1989, Alerstam and Hedenstrom 1998). Thermal updrafts are currents of warm air that rise because of differential heating of the earth's surface (Hardy and Ottersten 1969, Kerlinger 1989). Surfaces over which thermals form tend to be smooth, with flat or gentle slopes that face the sun (Reichmann 1978). These environmental updrafts vary dramatically over time and space because topography varies spatially, and because weather varies both spatially and temporally (Kerlinger 1989, Alerstam and Hedenstrom 1998, Bohrer et al. 2012, Dennhardt et al. 2015). As such, variation in either topography or weather may explain spatial and temporal variation of updraft formation and its use by soaring birds.

The type of updraft used by soaring birds both defines their flight mode (orographic soaring, thermal soaring) and can be interpreted by measuring flight altitude. Orographic updraft occurs at or near the peak of topographic features (e.g., steep slopes, ridgelines). Winds that create these updrafts also curtail them at higher elevations; therefore, orographic updrafts typically extend only up to a maximum of 300 m above the ground (Reichmann 1978). In contrast, thermal updrafts are limited by atmospheric conditions of the boundary layer and therefore may extend from the ground up to thousands of meters in height (Kerlinger 1989). Past work demonstrates that flight altitude above ground level (AGL) is a strong proxy for the flight mode (Lanzone et al. 2012, Katzner et al. 2015, Murgatroyd et al. 2018).

We studied the spatial and temporal variation in drivers of flight AGL, of the Golden Eagle (*Aquila chrysaetos*), a large soaring bird that uses both orographic and thermal updrafts (Duerr et al. 2012, 2015, Katzner et al. 2012). We measured flight AGL throughout 5 topographically diverse regions across California, USA, and over multiple seasons and years. Our objective was to determine how flight altitude varied in response to topographic features. Our hypothesis was that variation of flight altitude would reflect variation of topographic features. We therefore expected flight altitude to be higher at places where thermal updrafts form (i.e. over smooth topography that is flat or has gentle slopes and that faced eastward or southward) and lower at places where orographic updrafts form (i.e. over steep slopes and ridges). Additionally, if certain topographic features alone explain updraft formation, then we expect altitudinal responses to those topographic features to be consistent over both the large spatial extent of our study area and the large temporal frame of our study.

METHODS

Study Area

Our study area included all 5 bird conservation regions (BCRs) within the State of California, USA (Figure 1; U.S. NABCI Committee 2000). The 5 BCRs of California differ by terrain and climate (Commission for Environmental Cooperation 1997, 2011). The Sonoran and Mojave Deserts BCR has terrain with broad basins, valleys and ancient lakebeds separated by low elevation ranges and a subtropical desert climate of hot summers and relatively warm winters. The Coastal California BCR has varied terrain that includes coastal terraces, foothills, rugged mountains, tablelands and plains with a Mediterranean climate of hot summers and mild, slightly wet winters. The Sierra Nevada BCR has the highest mountains in California, which are hilly to steep, and has mild to hot dry summers and wet winters. The Great Basin BCR has terrain characterized by gently to steeply sloping mountains and plateaus separated by broad basins and valleys with warm to hot and dry summers and mild to cold winters. The Northern Pacific Rainforest BCR has rugged mountains with moderate to

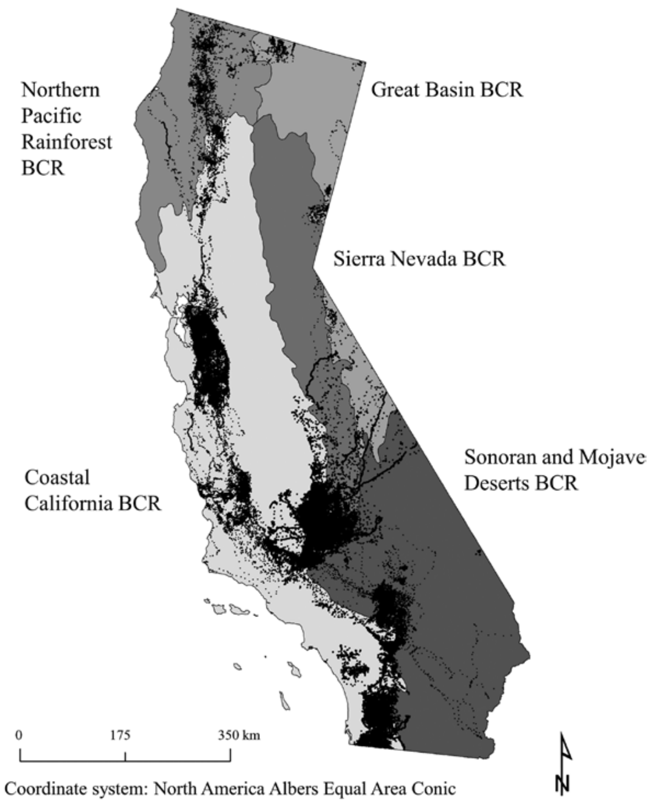

FIGURE 1. Flight locations of Golden Eagles throughout all Bird Conservation Regions (BCRs) within the State of California, USA, from 2012 to 2016.

steep slopes and includes plateaus and wide valleys. The climate is mid-latitude Mediterranean with warm dry summers and mild to cool winters that are wet along the coast.

Eagle Data Collection and Processing

We used bow nets (Jackman et al. 1994, Bloom et al. 2015), cannon nets (Bloom et al. 2007) or rocket nets set over carrion to capture resident Golden Eagles from 2012 to 2016 (months of November to March and May to July) at 5 locations in California, USA. Capture locations were in southern California (San Diego County, Granite and Tehachapi Mountains), in the Diablo Range, near Altamont Pass Wind Resource Area and in the Great Basin Desert of northeastern California. Captured eagles were outfitted with Cellular Tracking Technologies (Rio Grande, New Jersey, USA) CTT-1100 global positioning system (GPS) Global System for Mobile Communication (GSM) or Code Division Multiple Access (CDMA) telemetry systems attached as backpacks with Teflon ribbon (Dunstan 1972) and released. CTT-1100s collected a suite of data including latitude, longitude, altitude above geoid (mean sea level), and movement speed at intervals of 30 s and 15 min throughout daylight hours. We only used data collected at 15-min intervals for analyses because speed measurements collected at 30-s intervals were not accurate for some CTT firmware versions (Poessel et al. 2018a). AGL was calculated by subtracting ground elevation from a digital elevation model (DEM, 1-arc s; Gesch et al. 2002) from eagle altitude above mean sea level recorded by CTT-1100s. We classified eagles as flying when eagle AGL was >0 m above the earth's surface and movement speed was ≥1 knot (0.51 m s^{-1}; Poessel et al. 2018b).

We associated each eagle flight location with several measures of the topography over which eagles flew. Topographic measures included aspect, elevation, slope, topographic position and topographic roughness, all of which influence ranging of soaring birds (Braham et al. 2015, Poessel et al. 2016, Miller et al. 2017). We determined aspect, elevation and slope based on DEMs. We then converted circular (i.e. 1–360°) measures of aspect into Euclidean vectors (on unitless scale of –1 to 1) for analysis, termed eastness (positive values face east, negative values face west) and northness (positive values face north, negative values face south; Roberts 1986). We calculated topographic position index (TPI) following techniques outlined elsewhere (Jenness et al. 2013). We then created 4 topographic position categories based on TPI values: valleys (TPI ≤ –1), gentle slopes (TPI between –1 and 1 and slope < 6%), steep slopes (TPI between –1 and 1 and slope > 6%) and ridges (TPI ≥ 1). We calculated topographic roughness index (TRI) following Riley et al. (1999) and created 5 categories of topographic roughness based on TRI: smooth areas (TRI: 0 to 80) and slight (TRI: >80 to 160), low (TRI: >160 to 240), moderate (TRI: >240 to 500) and high roughness (TRI: >500). We defined region as the BCR over which eagles flew. Finally, we defined hour of day as integers that corresponded with the hour value of Pacific Standard Time (e.g., 0600 hours = 6).

Statistical Analysis

We used generalized linear mixed models (GLMMs; package lme4; Bates et al. 2015) in R (3.3.2; R Core Team 2012) within an information theoretic framework (Burnham and Anderson 2002, Doherty et al. 2012) to assess support for our hypothesis that variation of flight altitude reflects variation of topographic features. We transformed variables with functions that allowed them to best match assumptions of homogeneity of variances. We used the natural logarithm to transform flight AGL and used ln(AGL) as the response variable in the analysis. Topographic variables included as predictors in models were eastness, northness, elevation at ground level, slope (square root transformed), topographic roughness, and topographic position. Correlation coefficients for continuous variables were all <|0.1|. To test whether responses of Golden Eagles to topography were consistent or varied over space, we included, as fixed effects, interactions of all topographic variables with region (BCR). To test whether responses of eagles were consistent or varied over time, we included both fixed and random effects for measures of time. Flight AGL of Golden Eagles peak mid-day and is lower early and late in the day (Poessel et al. 2016); therefore, to model this quadratic pattern, we included, as fixed effects, both hour of day and squared hour of day. We also included interactions of these time variables with BCR. All models included month and year as random effects to account for temporal variation and bird id as a random effect to account for autocorrelation within individuals. We developed a model set (MuMIn package; Barton 2016) that included all possible combinations of fixed explanatory variables (Doherty et al. 2012).

We illustrated how fixed explanatory variables influenced flight AGL by modeling AGL across the range of values for each variable included in the final model set (effects package; Fox 2003). We allowed only 1 variable to differ at a time and held all other variables constant. We held time of day constant at a value of 12 (noon local time) and held other continuous variables to values of 0. For categorical variables, instead of modeling each category as present (1) or absent (0), we modeled them as the proportion of all eagle locations that were classified in each category (e.g., for topographic position, we used the proportion of all eagle locations with topographic positions of valley, gentle slope, steep slope, and ridge). We illustrated the distribution of data across the range of values for topographic measures with either rug plots for continuous variables or jitter plots for categorical variables from a random subsample of 2.5% of the raw datapoints (ggplot2 package; Wickham 2017).

RESULTS

We identified 178,515 flight locations from 91 Golden Eagles monitored from 2012–2016. Eagles were tracked for an average of 305 days (SD = 342). Numbers of eagles captured differed by BCR; there were 68 captured within the Coastal California BCR (21 at Altamont, 24 at Tehachapi, 23 in San Diego County), 11 captured in the Sonoran and Mojave Desert BCR (all from the Mojave Desert), and 12 in the Great Basin BCR (in northeastern California). Eagle locations were predominantly recorded in the Coastal California (140,829 locations from 80 birds) and Sonoran and Mojave Desert (28,866 from 21 birds) BCRs, but also in Sierra Nevada (4,361 from 15 birds), Northern Pacific Rainforest (3,029 from 4 birds), and Great Basin (1,430 from 18 birds) BCRs (Figure 1).

From the set of models that we compared to describe flight AGL response to topography, there was support in the data for only 1 model (AICc $\omega = 0.994$). This model included fixed effects for all topographic factors (Table 1). It also included, as fixed effects, terms for hour, hour^2, and interactions of region with northness, slope, topographic position, hour, and hour^2. It did not include terms for interactions between eastness and BCR, elevation and BCR, or topographic roughness and BCR. We do not provide details for other models as they had no support in the data (AICc $\omega \le 0.005$, ΔAICc ≥ 10.6).

Topographic Influences of Flight AGL

Flight AGL of Golden Eagles differed by region. When all other variables were held constant, mean flight AGL was highest in the Sonoran and Mojave Desert, and lowest in the Sierra Nevada BCRs (Table 1, Figure 2A).

Certain correlates of flight AGL were consistent among regions (i.e. no region interactions; Table 1). In all regions, flight AGL increased the more a slope faced toward the east (eastness; Figure 2B). Likewise, in all regions, flight AGL decreased as both elevation (Figure 2C) and topographic roughness (Figure 2D) increased, although slight, low, and moderate roughness categories had similar flight altitudes.

Other correlates of flight AGL varied among regions (i.e. there was a regional interaction; Table 1). Flight AGL decreased as aspect faced more toward the north (northness) with the strongest effect in the Sierra Nevada BCR, intermediate in the Great Basin and Sonoran and Mojave Desert BCRs, and weakest in Coastal California BCR (Figure 3). In contrast to the other BCRs, flight AGL increased as aspect faced more toward the north in the Northern Pacific Rainforest BCR. Likewise, flight AGL decreased as percent slope increased, with the strength of the relationship differing by region (Figure 4). This pattern was strongest in the Sonoran and Mojave Desert and Coastal California BCRs, and weaker in the remaining BCRs.

Flight AGL also differed by topographic position and with region-specific variation (Figure 5). On average, and when holding other variables constant, flight AGL was lowest for ridges and steep slopes, and was higher in valleys and on gentle slopes. Exceptions included lower flight altitude for valleys in the Sierra Nevada BCR and similar flight altitudes for all topographic positions in the Northern Pacific Rainforest BCR.

Flight AGL differed by time of day with differences among regions (Table 1; Figure 6). Flight altitude increased with hour and decreased with hour^2, such that the combined effect formed an inverted parabolic pattern. Flight altitudes were lowest in the early morning (0600 hours), peaked between 1200 and 1400 hours, and decreased toward the end of the day (1800 hours), although they remained higher than during the morning. The exception to this pattern was for the Sierra Nevada BCR, where maximum flight altitudes were lower than in other regions and flight altitudes were similar early and late in the day.

Random factors accounted for some variation in flight AGL and were within the range of error estimates for other

TABLE 1. Factors that influenced flight altitude above ground level for Golden Eagles in California, USA, from 2012–2016. Reference categories (*) and effects without an interaction with Bird Conservation Region are blank. Values are estimates (±SE) from a generalized linear mixed model with the response of flight altitude above ground level on the natural log scale.

			Bird Conservation Region				
Variable	Category	Main effect	Coastal California*	Great Basin	Northern Pacific Rainforest	Sierra Nevada	Sonoran and Mojave Desert
Intercept		5.254 ± 0.088		0.019 ± 0.174	–0.151 ± 0.152	–0.526 ± 0.116	0.375 ± 0.049
Eastness (radians)		0.064 ± 0.005					
Northness (radians)		–0.033 ± 0.006		–0.102 ± 0.069	0.086 ± 0.040	–0.193 ± 0.033	–0.040 ± 0.015
Elevation (m)		–0.000214 ± 0.000012					
Slope (degrees)		–0.135 ± 0.008		0.104 ± 0.036	0.080 ± 0.029	0.104 ± 0.024	–0.031 ± 0.010
Topographic position	Valley*						
	Gentle	0.080 ± 0.022		–0.052 ± 0.154	–0.181 ± 0.267	0.725 ± 0.195	–0.304 ± 0.038
	Steep	–0.127 ± 0.013		–0.112 ± 0.123	0.210 ± 0.080	0.256 ± 0.065	–0.150 ± 0.033
	Ridge	–0.469 ± 0.009		–0.021 ± 0.099	0.346 ± 0.058	0.405 ± 0.049	–0.324 ± 0.024
Topographic roughness	Level*						
	Slight	–0.106 ± 0.014					
	Low	–0.179 ± 0.017					
	Moderate	–0.161 ± 0.020					
	High	–0.232 ± 0.026					
Hour		29.850 ± 1.613		61.680 ± 18.560	61.210 ± 11.840	–52.680 ± 8.191	31.470 ± 3.920
Hour^2		–161.400 ± 1.682		10.470 ± 21.370	–8.826 ± 12.070	30.810 ± 8.229	31.400 ± 4.006
Random factors							
Month		0 ± 0.184					
Year		0 ± 0.091					
Individual		0 ± 0.436					
Residual		0 ± 1.420					

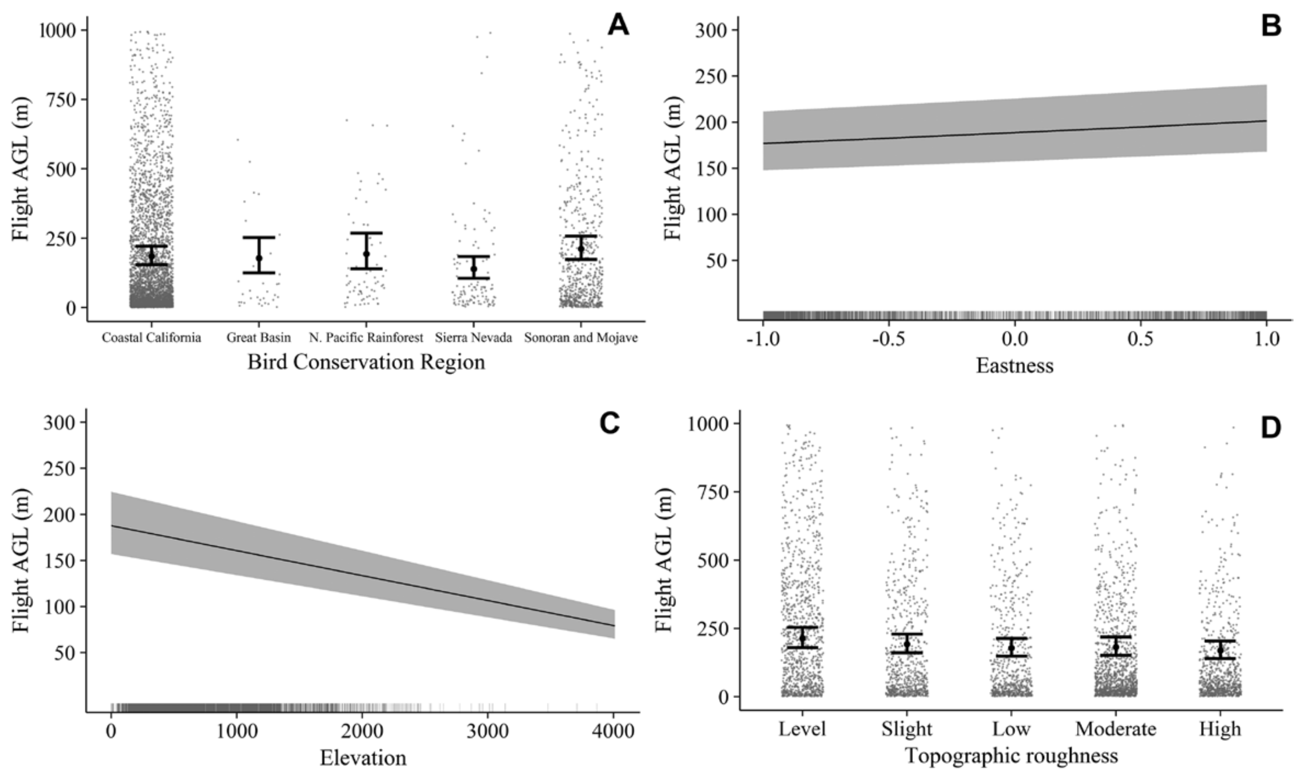

FIGURE 2. Variation of flight altitude above ground level (AGL) by (**A**) Bird Conservation Region, (**B**) the east-west component of aspect (eastness), (**C**) elevation and (**D**) topographic roughness for Golden Eagles in California, USA, from 2012 to 2016. Coastal California (**A**) and smooth roughness (**D**) were reference categories. Black dots (**A** and **D**) or black lines (**B** and **C**) are means and tails (**A** and **D**) or gray bands (**B** and **D**) are 95% CIs. Distribution of a random sample of the data (2.5% of 178,515 points) are shown as gray dots (**A** and **D**) or gray rugs (**B** and **C**). The distribution of flight altitudes (the *y* axis in panels **A** and **D**) was truncated at 1,000 m AGL; there are an additional 108 measurements above that altitude.

predictor variables (Table 1). Monthly and yearly factors accounted for little variation in the data. Likewise, of the random factors included in models, residual error, which accounted for variation not otherwise captured by random or fixed effects, had the greatest effect, followed by variation among individual eagles.

DISCUSSION

We found support for our hypothesis that topographic features are primary drivers of environmental updrafts and flight altitude. The strength of the driver depended, in part, on the specific topographic feature being considered. At a large spatial scale, variation in flight altitude reflected the spatial variation of certain topographic features. We refer to these features as “primary drivers” because they explain flight altitude, and presumably updraft development, consistently over space (across regions) and across time. However, flight altitude also varied both across a small temporal scale (hour of day) and, for other topographic features, over a large spatial scale (region). We refer to these as “secondary drivers” because they explain how flight altitude, and presumably updraft development, varied over space and across time, although they did not support our initial hypothesis. Our analysis shows that primary and secondary topographic drivers can both be used to model flight altitude and to understand the system of updraft formation.

The model that we developed can be used to predict flight altitude of Golden Eagles throughout California. Because of its simplicity, our approach is an improvement over other models. More complex models of updraft formation used to predict flight altitude require wind speed, wind direction, slope, and aspect to estimate orographic updraft (Brandes and Ombalski 2004, Bohrer et al. 2012, Dennhardt et al. 2015). Likewise, models of thermal formation include similar parameters as well as descriptors of land cover and albedo (Reichmann 1978, Bohrer et al. 2012). Updraft models are further complicated because they depend on weather models that include variables reported over short temporal intervals (3–6 hr) and over large spatial extents (32–210 km; Kalnay et al. 1996, Mesinger et al. 2006). An alternative may be to use state-space models to predict flight mode and updraft type (Pirotta et al. 2018). However, a limitation of these models

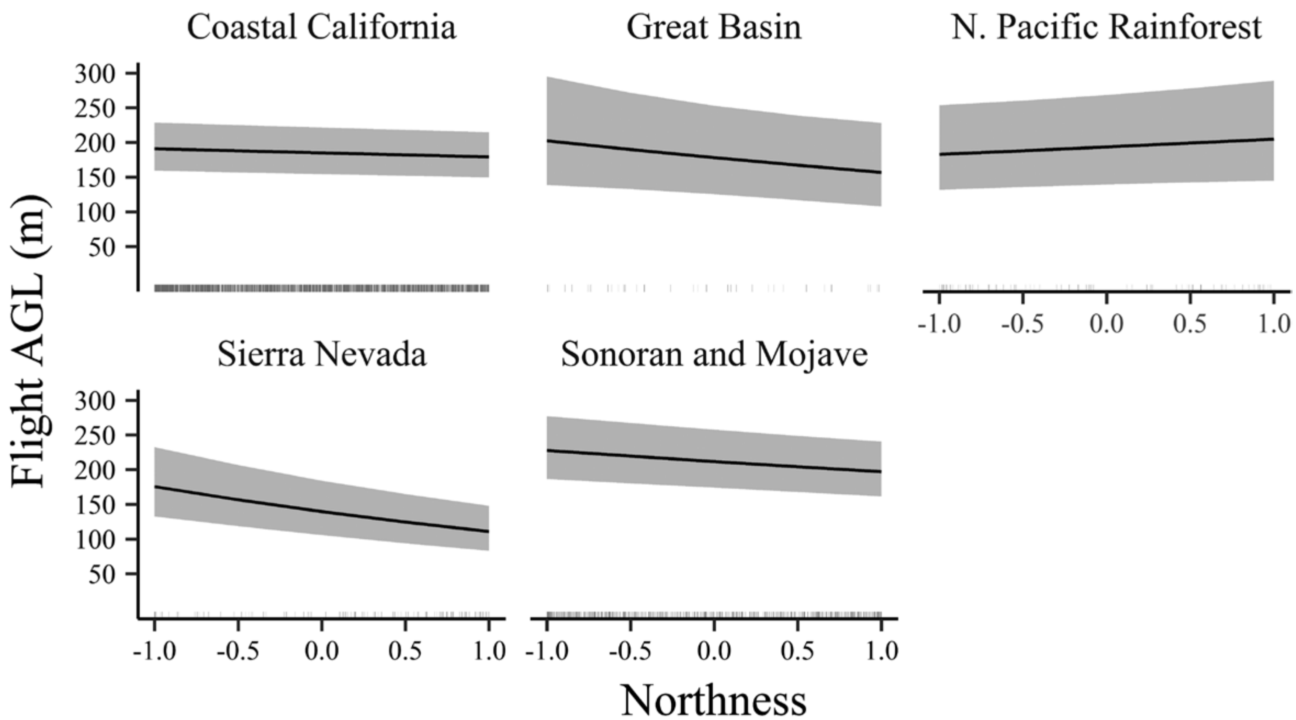

FIGURE 3. Variation of flight altitude above ground level (AGL) by the north-south component of aspect (northness) for Golden Eagles in 5 Bird Conservation Regions in California, USA, from 2012 to 2016. Black line is the mean and gray bands are 95% CI. Distribution of a random sample of the data (2.5% of 178,515 points) are shown in gray rugs.

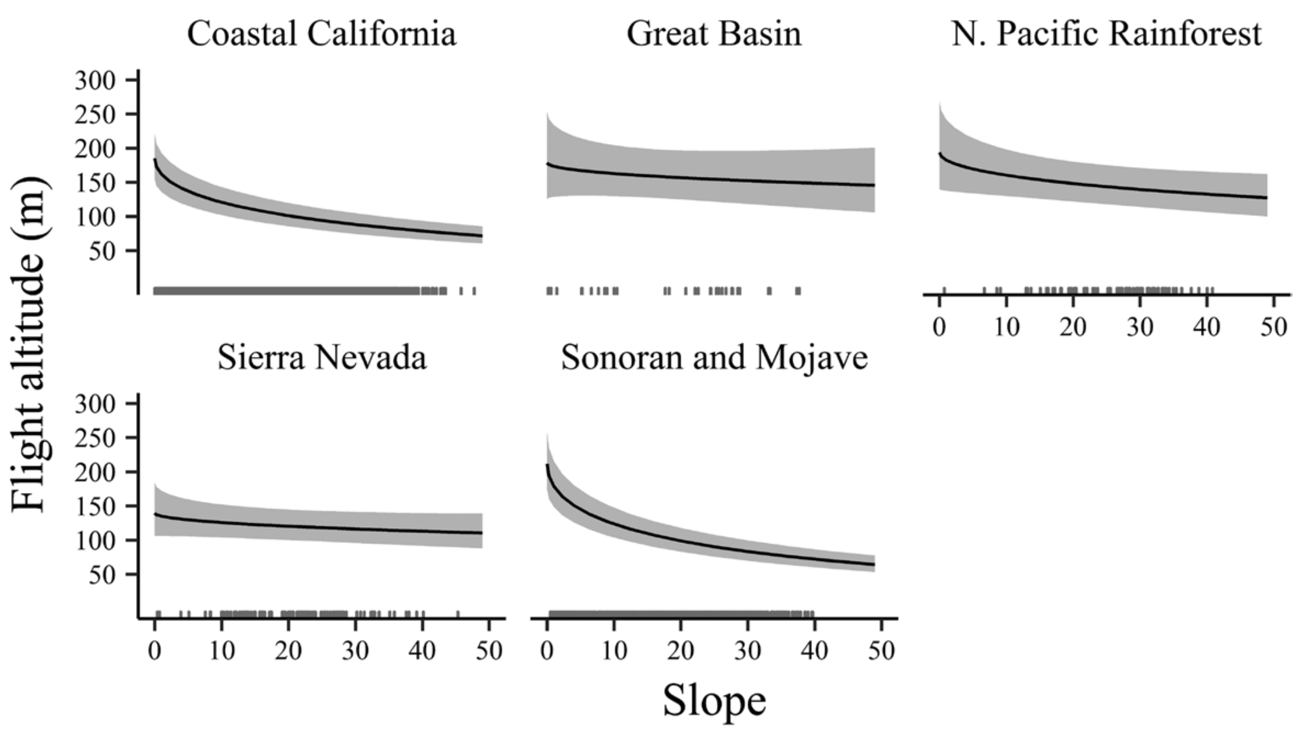

FIGURE 4. Variation of flight altitude above ground level (AGL) by percent slope for Golden Eagles in 5 Bird Conservation Regions in California, USA, from 2012 to 2016. Black line is the mean and gray bands are 95% CI. Distribution of a random sample of the data (2.5% of 178,515 points) are shown in gray rugs.

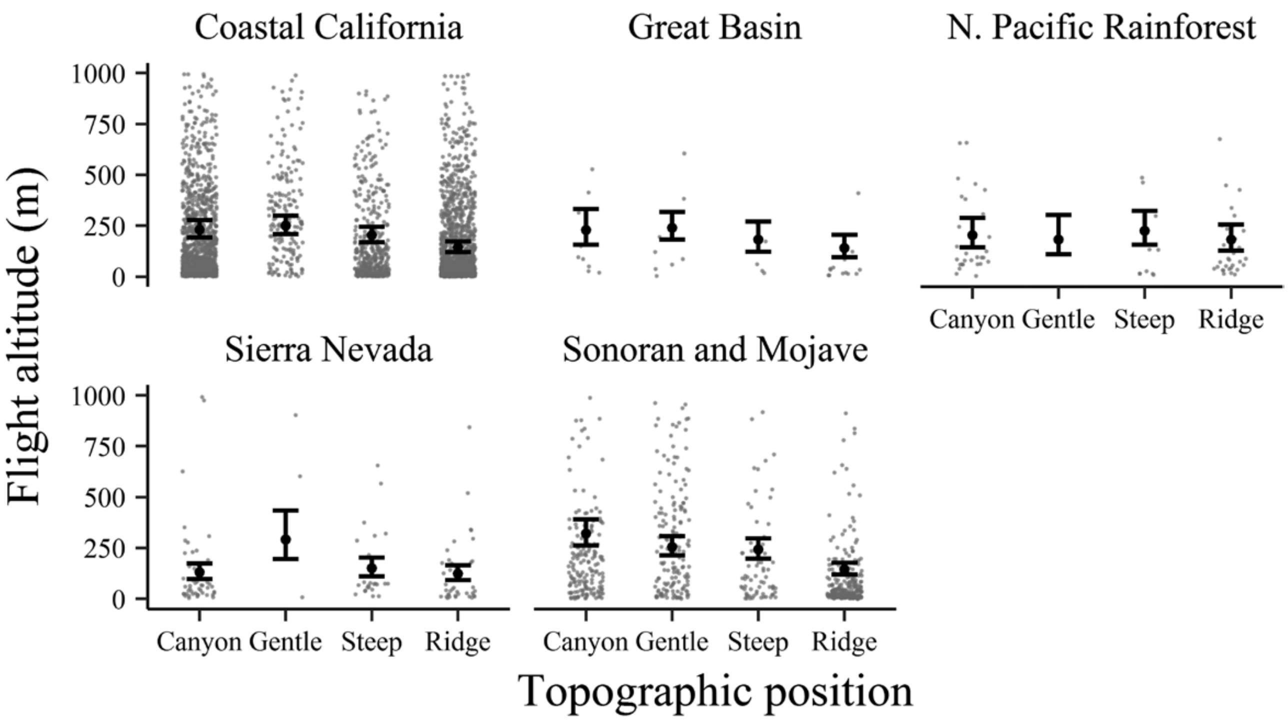

FIGURE 5. Variation of flight altitude above ground level (AGL) by categories of topographic position for Golden Eagles in 5 Bird Conservation Regions in California, USA, from 2012 to 2016. Valley was the reference category. Black dots are means and error bars are 95% CI. Distribution of a random sample of the data (2.5% of 178,515 points) are shown in gray dots, although flight altitudes (the *y* axis) were truncated at 1,000 m AGL. There were 108 measurements above that altitude.

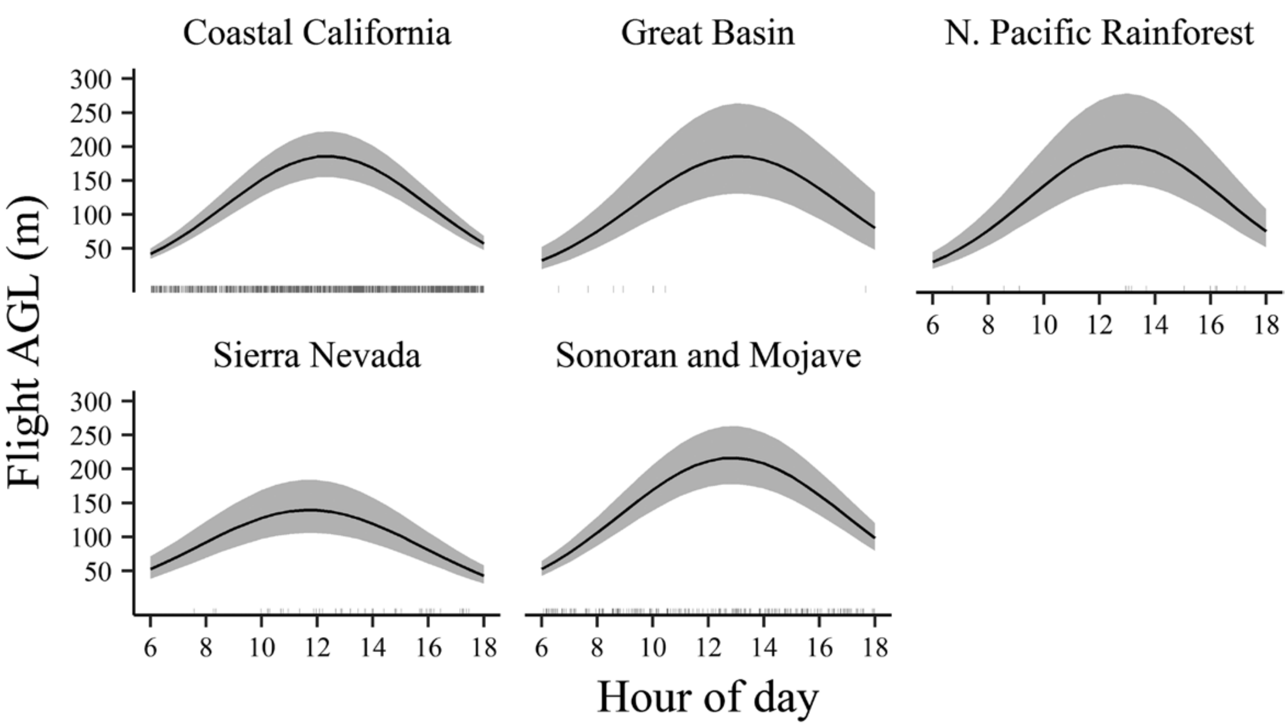

FIGURE 6. Variation of flight altitude above ground level (AGL) by hour of day for Golden Eagles in 5 Bird Conservation Regions in California, USA, from 2012 to 2016. Black line is the mean and gray bands are 95% CI. Distribution of a random sample of the data (2.5% of 178,515 points) are shown in gray rugs.

is that they predict altitude at specific animal locations and require collection of locations at high frequencies (30-s to 1-min intervals). In contrast, our model uses measures of primary and secondary topographic drivers, region and hour, with only hour changing at any given location.

Primary topographic drivers of flight AGL are important features because they directly explain flight mode. Primary drivers—eastness, ground elevation, and topographic roughness—are either themselves causal factors determining use of updraft, or they are directly and positively correlated with the weather–topography interactions that are those causal factors. In contrast, interpreting secondary drivers requires understanding more complex interactions among environmental variables. In fact, the relationships between secondary topographic drivers—northness, slope, topographic position, and hour of day—and movement, were different for each region in our study. These region-specific patterns could have been a function of topographic variation that we did not capture or regional differences in climate, and thus weather (Commission for Environmental Cooperation 1997, 2011). Interpreting the details of primary and secondary drivers provides important insights into how environmental updrafts affect flight altitude.

In general, primary topographic drivers of flight AGL described features where thermal updrafts could have formed and where soaring altitudes were highest. For example, when exposed to solar radiation, a rough surface does not heat evenly (Reichmann 1978), which both limits heating of the earth's surface at the scale required for development of thermal updraft, and explains why topographic roughness was a primary driver. The rain shadow created by the Coast Range and Sierra Nevada Mountains creates a cooler and moister climate, which in turn decreases thermal convection (Moran 2009) on west-facing slopes compared with east-facing slopes, which is why eastness is a primary driver. Thermal convection also becomes stronger as the temperature gradient between rising air masses and surrounding air increases (Moran 2009). Such temperature gradients decrease as one goes up in elevation, which is why elevation is a primary driver.

Secondary drivers of flight AGL described features where both thermal and orographic updrafts could have formed. As described above, thermal updrafts are more likely to form, and their development will be strongest where solar radiation at the earth's surface is greatest, for instance over south-facing slopes compared with north-facing slopes. Solar radiation also changes throughout the day, with the greatest levels during mid-day. The fact that thermal updraft requires differential heating of the earth's surface, which could be driven by climate (thus weather patterns) or land cover (Bohrer et al. 2012), likely explains why northness and time of day were secondary drivers. In contrast, orographic updrafts are more likely to form where topography deflects wind currents (Kerlinger 1989, Alerstam and Hedenstrom 1998). Slope, the measure of the steepness of terrain, influences potential development of orographic updrafts, such that greater updrafts develop where and when suitable winds flow over steeper slopes. Likewise, orographic updrafts are more likely to develop over certain topographic positions, especially ridges. The fact that orographic updraft requires wind and topography likely explains why slope and topographic position were secondary drivers of flight AGL. Based on the patterns of secondary topographic drivers, solar radiation and wind are possible candidates of primary drivers of updraft and flight altitude.

Identifying primary drivers of flight AGL may be more complex than finding single variables that are most correlated with flight altitude, and there are likely primary drivers that are independent of topography. In the case of soaring birds, updrafts form when weather and topography interact; therefore, the primary driver of movement could be such an interaction between measures. Additionally, to understand drivers of movement behavior, it may be important to include other features that affect use of a given area, such as land use or habitat types over which animals move.

Conclusions

Drivers of flight AGL that were related to thermal updrafts showed different levels of complexity due to spatial and temporal variation of those drivers than did flight AGL related to orographic updrafts. Primary topographic drivers were only related to thermal updrafts, while secondary topographic drivers were related to both thermal and orographic updrafts. Thus, flight AGL related to orographic updraft was driven by both topography and by other factors that varied spatially and temporally. Although spatial and temporal variation had some role in driving flight AGL that was related to thermal updraft, this behavior was more consistent over space and time.

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