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DRIVERS OF FLIGHT PERFORMANCE OF CALIFORNIA CONDORS (*GYMNOGYPS CALIFORNIANUS*)

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Abstract.—Flight behavior of soaring birds depends on a complex array of physiological, social, demographic, and environmental factors. California Condors (*Gymnogyps californianus*) rely on thermal and orographic updrafts to subsidize extended bouts of soaring flight, and their soaring flight performance is expected to vary in response to environmental variation and, potentially, with experience. We collected 6298 flight tracks described by high-frequency GPS telemetry data from five birds ranging in age from 1 to 19 yr old and followed over 32 d in summer 2016. Using these data, we tested the hypothesis that climb rate, an indicator of flight performance, would be related to the topographic and meteorological variables the bird experienced, and also to its age. Climb rate was greater when condors were flying in faster winds and during environmental conditions that were conducive to updraft development. However, we found no effect of age on climb rate. Although many of these relationships were expected based on flight theory, the lack of an effect of age was unexpected. Our work expands understanding of the relationship condors have with the environment, and it also suggests the potential for as-yet unexplored complexity to this relationship. As such, this study provides insight into avian flight behavior and, because flight performance influences bird behavior and exposure to anthropogenic risk, it has potential consequences for development of conservation management plans.

Key Words: *California Condor*; Gymnogyps californianus; *climb rate*; *experience*; *GPS-GSM telemetry*; *meteorology*; *soaring*; *topography*; *updraft.*

CONDICIONANTES DEL DESEMPEÑO DEL VUELO EN *GYMNOGYPS CALIFORNIANUS*

Resumen.—El comportamiento de vuelo de las aves que planean depende de una compleja serie de factores fisiológicos, sociales, demográficos y ambientales. El cóndor *Gymnogyps californianus* depende de las corrientes ascendentes térmicas y orográficas para sustentar los episodios prolongados de planeo, por lo que

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es de esperar que su desempeño en vuelo varíe en respuesta a la variación del ambiente y, potencialmente, a la experiencia. Recopilamos 6298 trayectorias de vuelo registradas con telemetría GPS de alta frecuencia provenientes de cinco aves con edades comprendidas entre 1 y 19 años, seguidas durante 32 días en el verano de 2016. Con estos datos, evaluamos la hipótesis de que la tasa de ascenso, un indicador de desempeño del vuelo, estaría relacionada con las variables topográficas y meteorológicas que experimentó el ave y también con su edad. La tasa de ascenso fue mayor cuando los cóndores volaron con vientos más rápidos y durante condiciones ambientales propicias para el desarrollo de corrientes ascendentes. Sin embargo, no encontramos ningún efecto de la edad sobre la tasa de ascenso. Aunque muchas de estas relaciones se esperaban a partir de la teoría del vuelo, la falta del efecto de la edad fue inesperado. Nuestro trabajo amplía la comprensión de la relación que los cóndores tienen con el medio ambiente, y también sugiere una complejidad potencial de esta relación aún inexplorada. Como tal, este estudio proporciona información sobre el comportamiento de vuelo de las aves y, dado que el rendimiento de vuelo influye en el comportamiento de las aves y en la exposición al riesgo antropogénico, tiene consecuencias potenciales para el desarrollo de planes de manejo de conservación.

[Traducción del equipo editorial]

INTRODUCTION

Movements of animals are affected by internal and external factors (Dodge et al. 2013, Martin et al. 2013). Characteristics such as age, experience, sex, reproductive or social status (internal), and weather, topography, land cover, and predators (external), can alter the efficiency and energetic cost of movement (Nathan et al. 2008). These factors together can inhibit or enhance the speed of movement of an animal across a landscape (Shepard et al. 2013). They also can influence the path taken, time in motion, the number of interruptions in movement, and even the demographic consequences of movements (Nathan et al. 2008).

In the case of soaring animals, environmental conditions conducive to the formation of atmospheric updrafts are important influences on movement (Shamoun-Baranes et al. 2006, Scacco et al. 2019). Soaring birds rely on thermal or orographic updrafts to ascend and to move through the airspace (Kerlinger 1989, Alerstam and Hedenström 1998, Diehl 2013, Williams et al. 2020). Thermal updrafts develop from uneven heating of the Earth's surface that produces vertical air movements, whereas orographic updrafts form from wind deflecting upward off topographic features (Kerlinger 1989, Sage et al. 2019). The strength of updrafts is influenced by multiple external meteorological and topographic factors, all of which may affect flight performance of soaring animals. Likewise, flight performance is also influenced by experience and age, often over many years (Mueller et al. 2013, Sergio et al. 2014, Harel et al. 2016, Williams et al. 2020).

To better understand how environmental conditions affect the movement of soaring animals, we investigated flight performance, measured by climb rate, of California Condors (*Gymnogyps californianus*; hereafter condors). Condors are a large, obligate-scavenging and -soaring species in western North America. They are a suitable species for study of this topic because of their conservation status, their almost exclusive use of soaring during flight, and the previous lack of knowledge of their flight performance. The conservation status and consequent intensive management focused on the species have resulted in long-term monitoring and substantial GPS tracking data that can be used to study flight behavior. Also, as especially long-lived and large flying animals, condors are expected to be influenced by external factors in their environment, and to learn and adjust their response over time. Given these expectations, we used GPS data to test predictions that, during soaring flight, (1) condors would climb faster in conditions conducive to thermal (i.e., strong solar generation and low wind speed) and to orographic (i.e., rougher terrain and high wind speed) updrafts, and (2) older, more experienced condors would climb faster than younger, less experienced condors.

METHODS

Study Area. We studied condors in Los Angeles, Ventura, and Kern Counties in southern California, USA (Fig. 1). Elevations in the region extend from sea level to 3000 m above sea level (ASL). Land cover ranges from shrub and scrub at low elevations to barren rock at high elevations, and topography is generally rugged. For more details on the study site, see Poessel et al. (2018a, 2018b).

Trapping, Tagging, and Telemetry. Biologists from the California Condor Recovery Program at

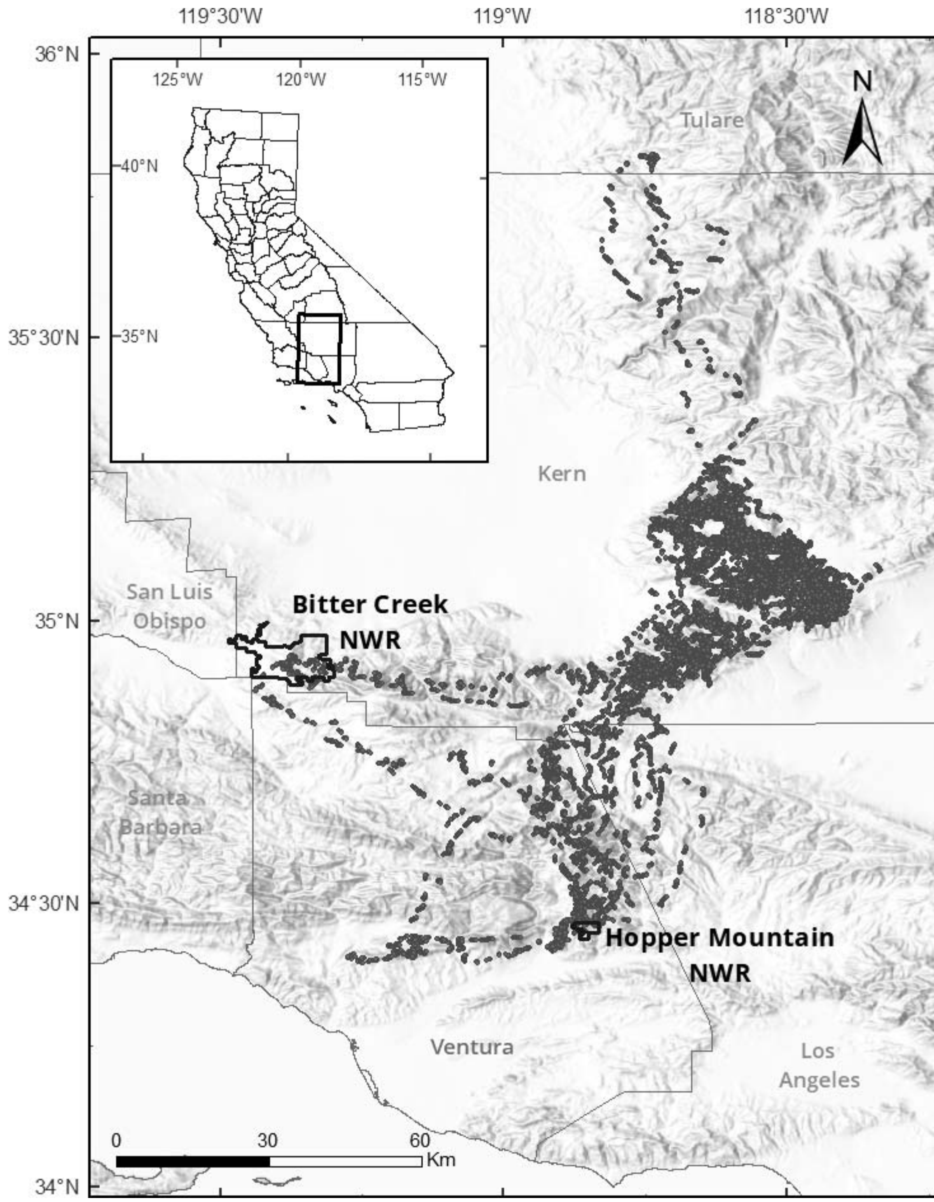

Figure 1. Map of GPS-recorded flight locations (gray dots) of five California Condors tracked in southern California, 2016, with names of counties and locations of the Bitter Creek and Hopper Mountain National Wildlife Refuges.

the US Fish and Wildlife Service (USFWS) trapped, tagged, and released condors at Bitter Creek National Wildlife Refuge (NWR) in Kern County and at Hopper Mountain NWR in Ventura County. Condors were outfitted with solar-powered Global Positioning System-Global System for Mobile Communications (GPS-GSM) patagial telemetry units manufactured by Cellular Tracking Technologies, LLC (Rio Grande, NJ, USA). These devices collected GPS locations at intervals ranging from 1 hr to <10 sec and sent them via the mobile phone network to a server from which they were downloaded. The GPS data included information on location (latitude and longitude), date, time, altitude (altitude ASL, in m), ground speed (knots), horizontal and vertical dilution of precision (HDOP and VDOP, respectively), and fix quality (2D or 3D). Exact age of all condors was known because they all either hatched in captivity or in the wild at monitored nests. For additional details on trapping, tagging, and telemetry, see Poessel et al. (2018b).

Data Management. GPS telemetry data were imported into a customized database and filtered to remove locations for which diagnostic or altitudinal data indicated errors (Poessel et al. 2018b). We also excluded GPS data that were collected at night (between 2000 H and 0430 H PST) or with fix intervals >10 s.

We used a two-step process to identify segments of the remaining data when birds were in continuous upward flight (i.e., flight tracks). First, we defined a flight track as a series of locations where the bird was ascending (defined here as a change in altitude between successive locations of >–2 m, or for which cumulative change in altitude over the track was >0 m). By defining continuous upward flight in this way, we allowed an ascent phase to be interrupted by short-term drops in altitude. Subsequently, we removed short flight tracks with a duration <30 sec as these may not be representative of general flight performance. For each remaining flight track, we then calculated the climb rate as the total change in altitude divided by the total flight time, and we report and analyze values in m/sec.

Data Associations. We used the Environmental-Data Automated Track Annotation system (Env-DATA; Dodge et al. 2013) in Movebank (http://www.movebank.org; Kranstauber et al. 2011, Wikelski and Kays 2016) to link each GPS location in a flight track to the values of four meteorological variables we believed were likely to influence updraft strength and condor flight performance. Downward shortwave radiation (DSR, W/m^2), pressure at the surface (Pa), and turbulent kinetic energy (TKE, J/kg) all influence thermal updraft in a landscape (Shamoun-Baranes et al. 2003, Chevallier et al. 2010, Sapir et al. 2011). Wind speed (m/sec) positively influences the strength of orographic updrafts and negatively influences the strength of thermal updrafts (Pennycuick 1989, Chevallier et al. 2010). We calculated wind speed from u-wind and v-wind vectors that we downloaded from Movebank (Poessel et al. 2018b). The spatial resolution of these weather variables was 32 km^2, their temporal granularity was 3 hr, and data were linearly interpolated to the location, time, and, in the case of wind speed, the altitude of the bird.

We used ArcGIS v.10.6 (Esri, Redlands, CA, USA) to link each GPS location in a flight track to three topographic variables (US Geological Survey 2015): terrain ruggedness index (TRI, 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), slope (in percent), and aspect (Pierce et al. 2005, Piedallu and Gégout 2013). Each of these variables influences formation of updrafts and thus, a condor's flight performance (Reichmann 1978, Shamoun-Baranes et al. 2003, Bohrer et al. 2012, Poessel et al. 2018a, 2018b, Duerr et al. 2019). Because aspect has a circular distribution, we converted it into two linear components: northness (cosine of aspect; ranging from –1 [south] to 1 [north]) and eastness (sine of aspect; ranging from –1 [west] to 1 [east]).

Finally, we linked each GPS location to flight altitude above ground level (altitude AGL, in m) because altitude can influence flight performance of soaring birds (Poessel et al. 2018a). We obtained altitude AGL by subtracting the ground elevation below a condor's flight location (determined using a 30-m resolution digital elevation model; US Geological Survey 2015) from the altitude ASL of the condor (as measured by the GPS). For each meteorological, topographic, and flight altitude variable, we averaged all values within a flight track for analysis. Additionally, for each of the three topographic variables, we calculated the standard deviation of all values within a flight track to account for variation within the flight track.

The coarse spatial and temporal resolutions of the meteorological variables limit how accurately weather data reflect microscale conditions that condors may actually experience. Furthermore, additional uncertainty occurs because Movebank linearly interpolates environmental variables to condor locations and because the topographic data are averaged over a 30 m^2 area, meaning that any drastic elevation changes within that area may have been lost. Finally, our dataset was limited in the number and age of condors, which may have affected our analysis of the effect of age on condor flight performance. In our study, we attempted to interpret our outputs in the context of these biases, as well as those induced by spatial mismatch between datasets and by measurement errors (Katzner and Arlettaz 2020, Péron et al. 2020).

Table 1. Summary statistics (post-filtering) describing data for five California Condors of different ages and their tracks of ascending flight used in an analysis of flight performance in southern California, 2016. AGL is altitude above ground level, DSR is downward shortwave radiation, TKE is turbulent kinetic energy, and TRI is terrain ruggedness index.

Parameter	Condor Identification Number				
	#156	#161	#480	#507	#791
Age	19	19	8	7	1
Number of tracks	1239	1195	1484	1260	1120
AGL (m; $\bar{x} \pm$ SE)	320.5 ± 7.43	269.2 ± 7.29	284.6 ± 6.33	330.9 ± 6.03	271.8 ± 8.59
Wind speed (m/sec; $\bar{x} \pm$ SE)	5.1 ± 0.05	5.1 ± 0.06	4.3 ± 0.05	4.3 ± 0.05	4.3 ± 0.07
Pressure (Pa; $\bar{x} \pm$ SE)	89,973.2 ± 22.60	90,270.9 ± 24.35	90,191.7 ± 22.45	90,261 ± 22.45	91,112.3 ± 49.07
DSR (W/m^2; $\bar{x} \pm$ SE)	820.4 ± 4.72	823.9 ± 4.98	830.6 ± 4.93	827.8 ± 4.12	788.5 ± 5.43
TKE (J/kg; $\bar{x} \pm$ SE)	2.2 ± 0.04	2.3 ± 0.04	2.0 ± 0.35	2.2 ± 0.03	1.6 ± 0.04
Northness ($\bar{x} \pm$ SE)	0.11 ± 0.02	0.10 ± 0.02	0.03 ± 0.02	0.07 ± 0.01	0.09 ± 0.02
Eastness ($\bar{x} \pm$ SE)	−0.01 ± 0.02	−0.04 ± 0.02	0.02 ± 0.02	0.02 ± 0.01	−0.09 ± 0.02
TRI ($\bar{x} \pm$ SE)	314.7 ± 7.39	337.1 ± 7.38	299.2 ± 6.76	297.9 ± 6.12	375.9 ± 9.94
Slope (%; $\bar{x} \pm$ SE)	18.2 ± 0.25	19.4 ± 0.23	18.1 ± 0.23	17.9 ± 0.21	19.6 ± 0.29
Climb rate (m/sec; $\bar{x} \pm$ SE)	1.1 ± 0.02	1.1 ± 0.02	1.3 ± 0.02	1.1 ± 0.02	1.1 ± 0.02
Track duration (s; $\bar{x} \pm$ SE)	88.2 ± 1.90	83.0 ± 1.73	93.9 ± 1.85	85.5 ± 1.68	94.6 ± 2.19
Days of flights	29	14	18	19	19
Time period	14 Aug–11 Sept	11–24 Aug	14–31 Aug	11–29 Aug	11–29 Aug

Statistical Analysis. To test the effects of our predictors on flight performance, we evaluated multivariate relationships within the data with linear mixed-effects models (LMMs) using the *lme4* package (Bates et al. 2015) in R (R Core Team 2018). First, we evaluated the potential for multicollinearity among covariates by examining pairwise Pearson correlations between weather, topographic, and flight altitude variables. When two variables were highly correlated ($r \geq 0.60$), we removed one member of the pair. Mean slope, mean TRI, and the standard deviation of TRI were all highly correlated (Supplemental Material Table S1). The standard deviation of TRI was also highly correlated with the standard deviation of slope (Table S1). Thus, we removed from consideration the mean slope and the standard deviation of TRI. To meet distributional assumptions of statistical tests, we square-root-transformed the response variable (climb rate of a flight track), and we rescaled predictor variables by subtracting the mean of the data and dividing by two standard deviations (Gelman 2008).

Next, we evaluated a global LMM that included transformed climb rate as the response variable and condor identification (ID) as a random effect. Topographic predictors in the model included means for northness, eastness, and TRI, and standard deviations for northness, eastness, and slope as fixed effects. Meteorological predictors included DSR, TKE, wind speed, and pressure at the surface as fixed effects. We also included continuous predictors for age and altitude AGL as fixed effects. We then used the *dredge* function (MuMIn package in R; Barton 2015) to evaluate performance of models based on all possible combinations of variables (Doherty et al. 2012). We used Akaike's Information Criterion corrected for small sample size (AIC_c) to rank the models, and we averaged the top-ranked sub-models (model weight >0.01; Burnham and Anderson 2002). We used the highest-ranked model to construct plots (*effects* package in R; Fox 2003) illustrating the effects on climb rate of each predictor variable. When plotted, both climb rate and each predictor variable were back-transformed to their original scales.

Results

Condor Telemetry. Data were collected at 10-sec intervals during the day only during the period between 11 August 2016 and 11 September 2016 (Table 1). After filtering and conducting quality control on the data, we retained 92,804 GPS locations from five condors aged 1, 7, 8, 19, and 19 yr. These locations defined 6298 flight tracks, of which there was a range of 1120–1484 per condor, with a mean of 14.6 locations per track (range = 5–107 locations per track) and a mean flight duration of 88.9 sec per track (range: 30–669 sec per track; Table 1). Average climb rates for each

Table 2. Summary of selection process for the model set describing climb rate of California Condors as a function of age and environmental effects. We used linear mixed effects models ranked by ΔAIC_c (Akaike's Information Criterion corrected for small sample size), and we show the top five models, plus the model with all explanatory variables (8th-ranked model). Explanatory variables in models included age, the means of altitude above ground level (AGL), downward shortwave radiation (DSR), pressure at the surface (Pressure), turbulent kinetic energy (TKE), wind speed (WS), eastness (East), northness (North), and terrain ruggedness index (TRI), and the standard deviations of northness (North SD), eastness (East SD), and slope (Slope SD). K refers to the number of parameters (including intercept and error terms) in a model, adjusted R^2 is the percentage of explained deviance, and w_i is the model weight.

MODEL	K	ΔAICc	ADJUSTED R^2	w_i
AGL + DSR + Pressure + TKE + WS + North + TRI + East SD + North SD + Slope SD	13	0.00	0.551	0.77
AGL + DSR + Pressure + WS + North + TRI + East SD + North SD + Slope SD	12	2.81	0.549	0.19
AGL + DSR + Pressure + TKE + WS + East + North + TRI + East SD + North SD + Slope SD	14	6.19	0.552	0.03
AGL + DSR + Pressure + TKE + WS + North + TRI + East SD + North SD + Slope SD + Age	14	9.47	0.552	0.01
AGL + DSR + Pressure + WS + East + North + TRI + East SD + North SD + Slope SD	13	11.43	0.549	0.00
AGL + DSR + Pressure + TKE + WS + East + North + TRI + East SD + North SD + Slope SD + Age	15	15.59	0.553	0.00

condor ranged from 1.1 ± 0.02 to 1.3 ± 0.02 m/sec ($\bar{x}$ ± SE; Table 1).

Factors Affecting Climb Rate. Our top ranked model, which had 77% of model weights, included terms for mean altitude AGL, DSR, pressure, TKE, wind speed, northness, TRI, and the standard deviations of eastness, northness, and slope (Table 2). The second-ranked model (19% of weights) was similar to the top model, except it did not include a term for TKE. Age was not included until the fourth-ranked model.

Climb rate of condors was positively influenced most heavily by altitude AGL and DSR (i.e., z-values were high, confidence interval bands were narrow, and both variables were included in each of the top five sub-models; Tables 2, 3; Fig. 2a, 2b). Other influential predictors with positive effects included mean TRI (Table 3; Fig. 2c), the standard deviation of eastness, the standard deviation of slope, wind speed, and the standard deviation of northness (Table 3; Fig. 3a–d). Climb rate was negatively associated with mean northward aspects and increasing pressure at the surface (Table 3; Fig. 3e, 3f). We

Table 3. Model-averaged coefficients, standard errors, z-values, and 95% confidence intervals (CI) from the three best-performing linear mixed models (with standardized predictor variables) explaining the environmental factors influencing the climb rate (square-root transformed) of California Condors in southern California, 2016. SD is the standard deviation of a variable.

PARAMETER	COEFFICIENT	SE	z-VALUE	LOWER 95% CI	UPPER 95% CI
Intercept	1.00	0.01	75.57	0.98	1.03
Altitude above ground level (AGL)	0.26	0.01	27.34	0.24	0.28
Downward shortwave radiation (DSR)	0.14	0.01	16.69	0.12	0.15
Terrain ruggedness index (TRI)	0.09	0.01	9.87	0.07	0.10
Eastness SD	0.09	0.01	9.19	0.07	0.11
Slope SD	0.09	0.01	9.05	0.07	0.11
Northness	−0.06	0.01	7.52	−0.08	−0.05
Wind speed	0.07	0.01	7.19	0.05	0.09
Pressure at the surface	−0.06	0.01	6.84	−0.08	−0.05
Northness SD	0.05	0.01	4.91	0.03	0.07
Turbulent kinetic energy (TKE)	0.02	0.01	1.73	0.00	0.05
Eastness	0.00	0.00	0.17	−0.01	0.01

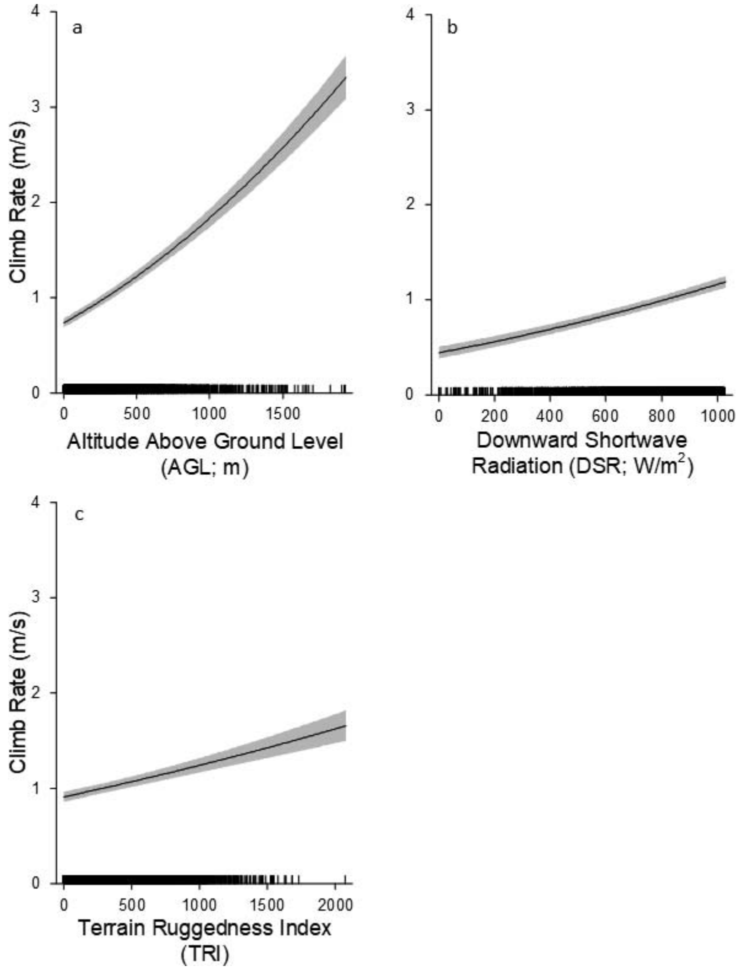

Figure 2. Plots of the back-transformed, model-fitted values of climb rate and (a) altitude above ground level, (b) downward shortwave radiation, and (c) mean terrain ruggedness index for five California Condors tracked in southern California in 2016. Gray bands represent 95% confidence intervals. Black rug plots on the x-axis show the distribution of data.

did not find a strong effect of TKE or mean eastward aspects on climb rate (i.e., the confidence intervals for the averaged effect estimates of these variables overlapped 0; Table 3).

DISCUSSION

Flight performance of the condors we monitored was influenced by meteorological and topographic factors, but not by age of the bird. Although based on a small sample size, these observations are consistent with our expectation that the vertical climb rate of condors would be faster in conditions conducive to thermal and orographic updraft generation. That said, the lack of relevance of age-related variation in flight performance was unexpected.

Condors rely on thermal and orographic updrafts to achieve energy-efficient soaring flight (Poessel et al. 2018b). Data from this study provide the first descriptions of flight performance of condors and, despite the small number of birds, they give insight into the general trends underpinning drivers of condor flight behavior. Thermal formation is linked to both solar radiation and atmospheric instability, the latter of which is higher when low pressure systems are present (Hertenstein 2005). One way condors use these updrafts is to rapidly gain altitude.

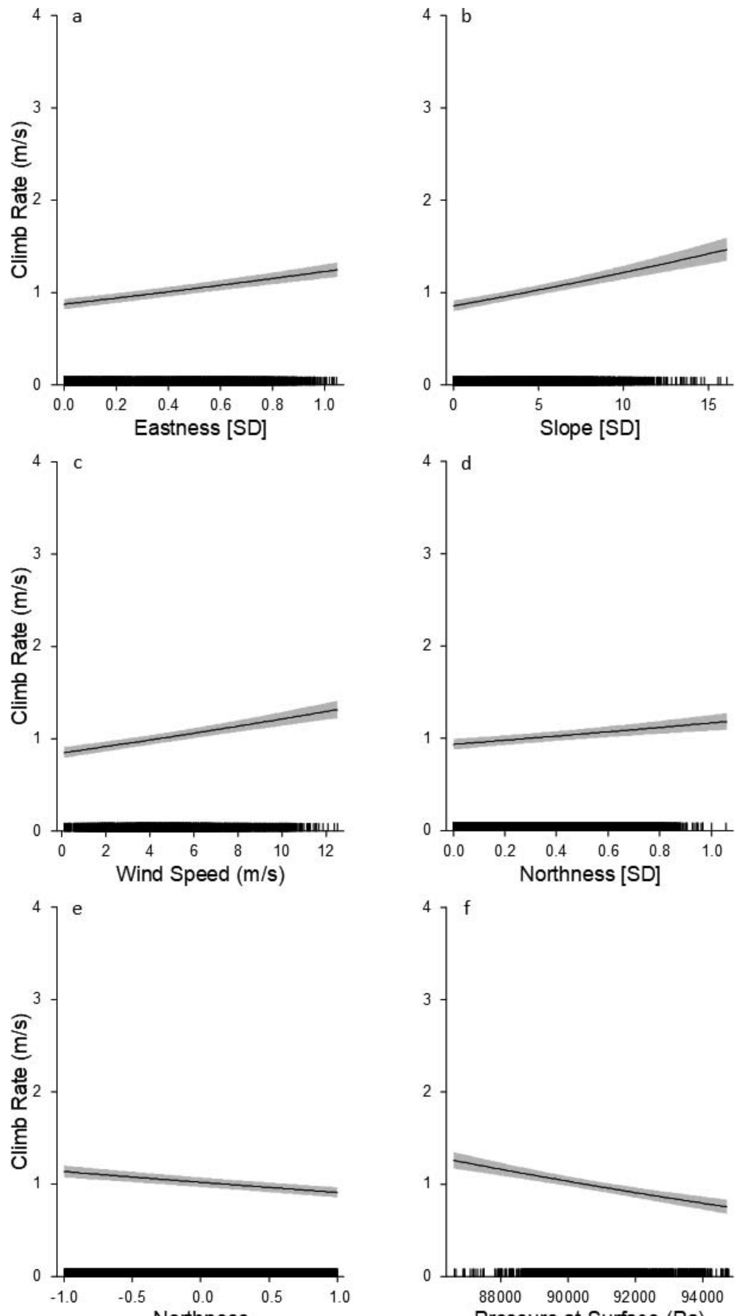

Figure 3. Plots of the back-transformed, model-fitted values of climb rate and (a) standard deviation of eastness, (b) standard deviation of slope, (c) wind speed, (d) standard deviation of northness, (e) mean northness, and (f) pressure at the surface for five California Condors tracked in southern California in 2016. Gray bands represent 95% confidence intervals. Black rug plots on the x-axis show the distribution of data.

Furthermore, thermals bring birds high in the air where air density and resistance are lower, reducing the amount of effort it takes to soar (Buffo et al. 1972, Williams et al. 2020). Thus, it is not surprising that altitude AGL was a significant predictor of climb rate. In contrast, thermals tend to be broken down by the higher winds that create orographic updrafts (Murgatroyd et al. 2018). As such, wind speed has opposing effects on the two updraft types. The strong positive effect of this variable that we observed indicates that faster winds during orographic updrafts have a stronger influence on climb rate than do slower winds during thermal updrafts. These factors combined illustrate the complex ways that both thermal and orographic updrafts are used by condors to enhance flight performance.

Flight behavior of soaring birds also is strongly linked to topography (Katzner et al. 2012, Poessel et al. 2018a, Scacco et al. 2019, Sur et al. 2019). In the northern hemisphere, south-facing slopes generally receive higher solar radiation, and thus are more conducive to thermal generation, than north-facing slopes (Buffo et al. 1972). In fact, the climb rates we measured were positively associated with TRI and southward aspects, and with variation in slope and aspect. Although classifying behavioral modes was not a research objective, these data indicate that condors were likely using orographic updrafts when flying over rougher terrain with varying slopes. This supposition is further supported because our data collection occurred at a time of the year when winds in southern California blow perpendicular to east-facing slopes (e.g., the east-west Santa Ana winds).

Contrary to expectations, we did not detect an effect of age on flight performance. Improvement in flight performance may be greatest in the first year of life but can extend well beyond that (e.g., Mueller et al. 2013), sometimes into a bird's second decade of life (Sergio et al. 2014). These patterns suggest that from the perspective of learning and flight performance, if we had used the usual system of breaking age into two categories (juvenile and adult), it likely would have been simplistic, as some birds learn continuously over time. The fact that we did not detect an age effect in this study may be a result of our small sample size or of the importance of rapid learning of flight by condors. Future studies of this topic may wish to focus especially on comparisons between birds of multiple age classes, including those <1 yr old, when flight skills are still developing and wing shape is most different.

The limited temporal scope of our study simplified our analysis by allowing us to ignore seasonal variation in weather. However, despite this advantage, there are also costs to this limited scope. In particular, the data we considered were all collected during a time period with high thermal strength and a relatively constant solar declination angle. Data collected in winter, when the sun is lower in the sky and weather patterns are different, may tell a different story about the relationship of flight performance and environmental variation.

Understanding flight performance of obligate-soaring birds under different demographic and environmental conditions has important implications for understanding individual fitness, ecology, and behavior. Movement behavior also interacts with risk to condors and other soaring birds from wind turbines (e.g., Miller et al. 2014, Reid et al. 2015, Poessel et al. 2018a), and wind energy generation is rapidly expanding within California (US Energy Information Administration 2020). Flight performance of condors may influence this risk because some of the factors that influence flight performance (e.g., altitude AGL, landscapes, DSR, and wind speed) may also be associated with higher or lower risk. Our work here expands understanding of the relationship condors have with the environment and it also suggests the potential for as-yet unexplored complexity to this relationship.

SUPPLEMENTAL MATERIAL (available online). Table S1: Pearson correlation (*r*) matrix for meteorological, topographic, and flight altitude variables associated with California Condor soaring flight in southern California, 2016.

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Species Division. The use of GPS transmitters was authorized as a recovery action under section 10(a)(1)(A) of the Endangered Species Act with a permit issued to the Hopper Mountain NWR Complex (#TE-108507 HMNWR-0). This work also was authorized by the state of California under a Memorandum of Understanding between managers of the Hopper Mountain NWR Complex and the California Department of Fish and Wildlife under sections 650 and 670.7, Title 14, California Code of Regulations. We thank the many people at the US Fish and Wildlife Service who assisted with condor monitoring, trapping, and telemetry. We also thank A. Punzalan for her review of the manuscript. SRB, SAP, TEK, and JRB designed the study; JCB and MTA handled and telemetered condors; SRB performed the analysis with supervision from SAP and TEK; SRB, SAP, and TEK led the writing; and all authors contributed to revising and improving the manuscript. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

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