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RESEARCH ARTICLE

Counterintuitive roles of experience and weather on migratory performance

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ABSTRACT

Migration allows animals to live in resource-rich but seasonally variable environments. Because of the costs of migration, there is selective pressure to capitalize on variation in weather to optimize migratory performance. To test the degree to which migratory performance (defined as speed of migration) of Golden Eagles (*Aquila chrysaetos*) was determined by age- and season-specific responses to variation in weather, we analyzed 1,863 daily tracks ($n = 83$ migrant eagles) and 8,047 hourly tracks ($n = 83$) based on 15 min GPS telemetry data from Golden Eagles and 277 hourly tracks based on 30 s data ($n = 37$). Spring migrant eagles traveled 139.75 ± 82.19 km day^{-1} (mean ± SE; $n = 57$) and 25.59 ± 11.75 km hr^{-1} ($n = 55$). Autumn migrant eagles traveled 99.14 ± 59.98 km day^{-1} ($n = 26$) and 22.18 ± 9.18 km hr^{-1} ($n = 28$). Weather during migration varied by season and by age class. During spring, best-supported daily and hourly models of 15 min data suggested that migratory performance was influenced most strongly by downward solar radiation and that older birds benefited less from flow assistance (tailwinds). During autumn, best-supported daily and hourly models of 15 min data suggested that migratory performance was influenced most strongly by south–north winds and by flow assistance, again less strongly for older birds. In contrast, models for hourly performance based on data collected at 30 s intervals were not well described by a single model, likely reflecting eagles' rapid responses to the many weather conditions they experienced. Although daily speed of travel was similar for all age classes, younger birds traveled at faster hourly speeds than did adults. Our analyses uncovered strong, sometimes counterintuitive, relationships among weather, experience, and migratory flight, and they illustrate the significance of factors other than age in determining migratory performance.

Keywords: Aquila chrysaetos, Golden Eagle, GPS telemetry, migratory performance

Rôles contre-intuitifs de l'expérience et des conditions météorologiques sur la performance migratoire

RÉSUMÉ

La migration permet aux animaux de vivre dans des environnements riches en ressources mais variables d'une saison à l'autre. En raison des coûts de la migration, il existe une pression sélective pour tirer profit des variations météorologiques afin d'optimiser la performance migratoire. Afin d'examiner à quel degré la performance migratoire (définie comme étant la vitesse de migration) d'*Aquila chrysaetos* est déterminée par des réponses spécifiques à l'âge et aux saisons face aux variations météorologiques, nous avons analysé 1863 tracés quotidiens ($n = 83$ aigles migrateurs) et 8047 tracés horaires ($n = 83$) provenant de données télémétriques GPS aux 15 min de cette espèce, et 277 tracés horaires basés sur des données aux 30 s ($n = 37$). Au printemps, les aigles migrateurs se sont déplacés sur 139,75 ± 82,19 km/jour (±SE; $n = 57$) et 25,59 ± 11,75 km/h ($n = 55$). À l'automne, les aigles migrateurs ont parcouru 99,14 ± 59,98 km/jour ($n = 26$) et 22,18 ± 9,18 km/h ($n = 28$). Les conditions météorologiques au cours de la migration ont varié par saison et classe d'âge. Au printemps, les meilleurs modèles quotidiens et horaires des données aux 15 min suggèrent que la performance migratoire était influencée plus fortement par le rayonnement solaire descendant et que les oiseaux plus âgés profitaient moins d'un support de l'écoulement de l'air (vent arrière). À l'automne, les meilleurs modèles quotidiens et horaires des données aux 15 min suggéraient que la performance migratoire était influencée plus fortement par les vents orientés sud-nord et par le support de l'écoulement de l'air, d'une façon associée à l'âge similaire au printemps. Néanmoins, les modèles de performance horaire basés sur les données recueillies à des intervalles de 30 s n'étaient bien décrits par aucun modèle, ce qui reflète vraisemblablement les réponses rapides des aigles aux diverses conditions météorologiques auxquelles ils ont fait face. Bien que la vitesse de déplacement quotidienne soit similaire pour toutes les classes d'âge, les oiseaux plus jeunes se déplaçaient à des vitesses horaires plus rapides que les adultes. Nos analyses ont dévoilé des relations fortes, parfois contre-intuitives, entre les conditions météorologiques, l'expérience et le vol migratoire, et elles illustrent l'importance de facteurs autres que l'âge pour déterminer la performance migratoire.

Mots-clés : Aquila chrysaetos, télémétrie GPS, performance migratoire

INTRODUCTION

Migratory behavior likely evolved because animals face trade-offs associated with use of resource-rich but seasonally variable environments (Newton 2008, LaSorte et al. 2016). In spite of the fitness benefits associated with migration, the behavior itself can incur substantial costs to fecundity or survivorship. Therefore, there is selective pressure to evolve mechanisms to minimize such costs and maximize migratory performance (Åkesson and Hedenström 2007).

There are a number of strategies that migratory birds use to improve their migratory performance. Perhaps most intuitively, they can evaluate the individual-specific trade-offs they face (Miller et al. 2016b) and choose to fly in weather conditions that allow them to best address the evolutionary pressures they face (Duerr et al. 2014). Likewise, when they do choose to fly, birds can try to cover as much ground as possible to shorten time spent migrating (Åkesson and Hedenström 2007, Alerstam 2011). These and other strategies that birds adopt to improve migratory performance are reflected in metrics such as the straightness of their flight (Åkesson and Hedenström 2007, Mellone et al. 2014) and the distance or speed they travel (Hedenström and Alerstam 1998, Åkesson and Hedenström 2007, Vansteelant et al. 2015). The specific strategy a bird chooses also appears to be influenced by individual experience and a suite of factors linked to weather, seasonality, and social behavior (Mueller et al. 2013, Sergio et al. 2014, Miller et al. 2016b).

Variation in weather, in particular, creates site- and species-specific challenges for flying migrants (Kerlinger 1989, Chapman et al. 2016, Miller et al. 2016a). Although all flying migrants must cope with weather (Horvitz et al. 2014), because it determines their ability to migrate, obligate soaring migrants may be especially responsive to meteorological fluctuations (Shamoun-Baranes et al. 2006). Therefore, soaring species have evolved season- and individual-specific approaches to subsidize their migration (Alerstam and Hedenström 1998, Duerr et al. 2012), to respond to meteorological fluctuations (Duerr et al. 2014, Miller et al. 2016b), and to switch flight modes to take advantage of prevailing conditions (Lanzone et al. 2012, Katzner et al. 2015).

Although the linkages among weather, experience, and migratory flight behavior are well studied, the way these parameters interact to determine time spent in migration is less well understood. To address this knowledge gap, we used GPS telemetry data collected at 2 different temporal scales to evaluate interacting external and internal drivers of migratory performance of Golden Eagles (*Aquila chrysaetos*) in eastern North America. For the purposes of this analysis, we defined migratory performance as the speed of migration—distance traveled per unit time. We expected that the daily and hourly rates of travel by eagles would be influenced by age- and season-specific responses to variation in weather. In particular, we predicted that more experienced eagles would fly faster and in better weather conditions than less experienced eagles. We tested these predictions with a two-step research approach. First, we calculated the daily and hourly rates of travel by migratory eagles. Second, we evaluated, by season, how age and weather interacted to drive migratory performance at these same temporal scales. We then interpret these data to better understand the trade-offs individuals face as a consequence of long-distance migration.

METHODS

Study Area

Golden Eagles in eastern North America breed in the Canadian provinces of Québec, Labrador, and Ontario and winter in the central Appalachian Mountains and surrounding lowlands (Katzner et al. 2012). Each spring and autumn these birds migrate long distances along Appalachian ridgelines between their summering and wintering grounds. Migratory decisions, straightness of flight, and flight modes used are strongly influenced by weather, topography, and the experience of the bird (Duerr et al. 2014, Katzner et al. 2015, Miller et al. 2016b). The northern portion of the migratory routes of these eagles is over hilly terrain, boreal forest, and in areas characterized by long cold winters and short summers (Duerr et al. 2014). The southern portion of their migratory route takes them over more diverse landscapes of mountain ridges and dendritic valleys, plateaus, and coastal plains. Land cover is generally mixed conifer and deciduous temperate forest. The climate in southern portions of migratory routes is more mild than farther north.

Data Collection

Golden Eagles were captured on wintering grounds during 2008–2015 and fitted with 80–95 g CTT-1100 (Cellular Tracking Technologies, Rio Grande, New Jersey, USA) solar-powered GPS telemetry units. The units weighed <2.5% of body mass and were attached to the eagles as a backpack using a nonabrasive Teflon ribbon harness (Kenward 1985). Telemetry units collected, at 30 s or 15 min intervals, GPS data on location, instantaneous speed, fix quality, course over ground, and altitude (Lanzone et al. 2012). Data at 30 s intervals were collected predominantly in or near the long and linear ridges of Pennsylvania (Lanzone et al. 2012), whereas 15 min interval data were collected across the entire migratory route, spanning dramatically more diverse topography. Data were stored on the units and, at regular intervals when in mobile phone coverage, sent across the GSM (Global System for Mobile Communications) network.

We estimated the age of captured eagles using molt patterns (Jollie 1947, Bloom and Clark 2001). We classified birds as juvenile (first year of migration), sub-adult (2nd–4th autumn or spring migration), or adult ($>$ 4th autumn or spring migration).

Data Processing

We focused statistical analyses exclusively on "migratory" movements (Duerr et al. 2014, Miller et al. 2016b). We identified the start of migration when an eagle left a summer or winter home range and made a directed flight toward its ultimate winter or summer range (Duerr et al 2014). We identified the end of migration when an eagle stopped making continuous northward or southward progress. During these periods, we only considered "migratory flight," which we defined as occasions when eagles moved $>$10 km hr^{-1} (Katzner et al. 2012, Duerr et al. 2014). We filtered data separately for hourly and daily scale analyses. For daily scale analyses we considered only days on which we could clearly identify a roosting site (i.e. repeated points at one spot with zero speed and altitude above ground level generally $<$50 m) in the morning and evening and in which there were no data gaps $>$1 hr in duration. For hourly scale analyses, we considered only hours with at least 3 GPS points (for 15 min data) or with at least 30 GPS telemetry points (for 30 s data).

We measured distances eagles traveled using the Tracking Analyst "Points to Lines" tool (ArcGIS 10.1; ESRI, Redlands, California, USA) to connect sequential GPS locations and then to measure the length (in km) of tracks. At a daily scale, we calculated distance traveled for each bird by summing the lengths of all the tracks between the presumptive morning and evening roosts. Time in flight thus could vary considerably among days. At an hourly scale, we calculated the distance traveled for each bird-hour by summing the lengths of all the tracks between the points nearest to the start and end of each nominal hour (e.g., 0800–0900). We then calculated speed measurements (in km hr^{-1}) from these data. We calculated flight speed in 3 manners: (1) once at a daily scale, using only 15 min data (subsampling 30 s data where required); (2) once at an hourly scale, using only 15 min data (again, subsampling 30 s data when required); and (3) once again at an hourly scale, but this time using only 30 s data.

Data Associations

We linearly interpolated weather data at each eagle location using the RNCEP package (Kemp et al. 2011) in R (R Core Team 2012). RNCEP draws on meteorological data modeled by the National Centers for Environmental Prediction (NCEP; Kanamitsu et al. 2002). We focused on weather variables that we expected would most strongly influence migration of these Golden Eagles, per Duerr et al. (2014). These included surface temperature (°C), surface atmospheric pressure (Pa; mmHg), downward solar radiation flux (DSR; W per m^2), west–east surface wind vector (U-wind; m s^{-1}), south–north surface wind vector (V-wind; m s^{-1}), Omega, the vertical velocity of air (Pascals s^{-1}), thermal energy at flight altitude (°C per 100 m), and flow assistance, the support or resistance the bird experiences from the air flow (FA; calculated using the Tailwind function based on wind vectors at flight altitude and reported in m s^{-1}; Kemp et al. 2012). Data for each flight segment were then averaged among eagle locations across the segment.

Data Analysis

Because weather variables can be highly correlated, we calculated bivariate Pearson correlation coefficients among all possible pairs of weather variables for each migration season. For variables with $|r| > 0.5$, we kept the single variable of the pair that we thought provided the greatest ecological insight.

We used one-way repeated measures ANOVA (package 'nlme' in R; Pinheiro et al. 2015) and Tukey's test for post-hoc multiple comparisons (package 'multcomp' in R; Hothorn et al. 2014) to compare weather conditions that birds of different age classes experienced during measured migration tracks. Subsequently, for each of the 2 migration seasons (spring and autumn), we created 3 different sets of candidate models to examine the potential effects of weather conditions on migratory performance. These 3 sets of candidate models evaluated performance at a daily scale (one model using 15 min data) and at an hourly scale (2 separate models, one each for 15 min and 30 s data) using migration speed as the metric of migratory performance (i.e. our response variable; see Data Processing). The 2 model sets that considered the 15 min data each had 23 models (described in Table 1), chosen based on our understanding of eagle biology and published information on eagle migration response to weather (Duerr et al. 2014). We used the same candidate models for the 30 s data except, because of the smaller sample size of birds measured at this temporal scale, we were unable to include bird age in models. This model set thus had 11 candidate models (Table 1).

TABLE 1. List of models in model sets used to evaluate migratory performance of Golden Eagles in eastern North America, 2008–2015, as measured at daily and hourly scales interpreted from 15 min GPS data and at hourly scales interpreted from 30 s GPS telemetry data. Variables used were south–north wind vector (V-wind), east–west wind vector (U-wind), flow assistance (FA), age of the bird (Age: juvenile, sub-adult, and adult), downward solar radiation (DSR), Omega (vertical wind velocity), and thermal energy.

Models	Model set 1 Daily distance (km day^{-1})	Model set 2 Hourly speed (15 min, km hr^{-1})	Model set 3 Hourly speed (30 s, km hr^{-1})
Thermal Energy	x	x	x
DSR	x	x	x
FA	x	x	x
U-wind	x	x	x
V-wind	x	x	x
Omega	x	x	x
Thermal Energy + FA	x	x	x
DSR + FA	x	x	x
U-wind + FA	x	x	x
V-wind + FA	x	x	x
Omega + FA	x	x	x
Thermal Energy + Age	x	x	
DSR + Age	x	x	
FA + Age	x	x	
U-wind + Age	x	x	
V-wind + Age	x	x	
Omega + Age	x	x	
FA + Age + FA × Age	x	x	
Thermal Energy + FA+ Age + (FA × Age)	x	x	
DSR + FA + Age + (FA × Age)	x	x	
U-wind + FA + Age + (FA × Age)	x	x	
V-wind + FA + Age + (FA × Age)	x	x	
Omega + FA + Age + (FA × Age)	x	x	

In each case we used linear mixed effects models (lmer, program R) to account for individuals with repeated measurements. At the daily scale, we included eagle ID and day of the year as categorical random effects and bird age (as a categorical variable) and continuous meteorological variables as fixed effects. At the hourly scale, models for the 15 min data included eagle ID, day of the year, and hour of the day as categorical random effects, and bird age and meteorological variables as categorical and continuous fixed effects, respectively. Day of the year and hour of the day were included as random effects in these models because flight behavior of different eagles can be correlated within a season or within a single day (Duerr et al. 2014, Katzner et al. 2015).

Prior to running mixed effects models, we scaled all explanatory and response variables to the range [0,1]. We also examined the residuals of each model and found that the response variable at both daily and hourly scales showed a high degree of heteroscedasticity. As a consequence we used a double square-root transformation of the response variable in models. We confirmed that this transformation removed the heteroscedasticity with a Breusch-Pagen test performed with the R package 'lmtest' (Hothorn et al. 2015).

We used an information–theoretic approach for model selection (Burnham and Anderson 2004). Within each model set we ranked each model based on its Akaike information criterion value, corrected for small sample sizes (AIC_c), and we considered the top model as best if its AIC_c weight (w_i) was $>$0.90 (Burnham and Anderson 2002, Grueber et al. 2011). If rankings showed several competing models ($w_i < 0.90$), we averaged models with $w_i > 0.01$ using 'MuMIn' package in R (Barton 2015). Means ± SE are provided unless indicated otherwise and sample sizes are provided in Appendix Table 6.

RESULTS

During northbound (spring) migration we collected 234,203 GPS points from 60 individual eagles; some of these birds were tracked across multiple years and age classes (Appendix Table 6). From these data, we identified 1,436 complete daily tracks from 57 eagles, 6,408 complete hourly tracks (15 min resolution) from 55 eagles, and 205 complete hourly tracks (30 s resolution) from 28 eagles.

During spring, eagles traveled at a speed of 139.75 ± 82.19 km day^{-1} (range: 12.72–508.46 km; Figure 1A) and 25.59 ± 11.57 km hr^{-1} (range: 10.00–80.86 km; Figure

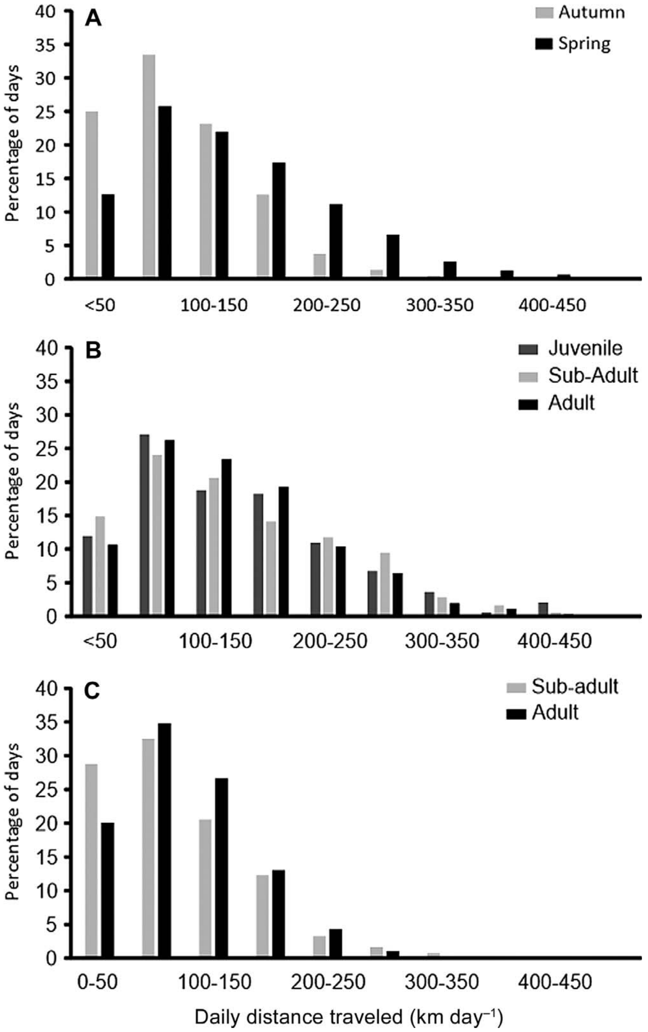

FIGURE 1. Frequency of daily distance (km day^{-1}) traveled by migratory Golden Eagles in eastern North America. Panels show comparison of (**A**) all eagles during spring vs. autumn; (**B**) 3 different age classes monitored during spring migration; and (**C**) 2 different age classes monitored during autumn migration. The *y* axis shows percentage of days recorded in each bin of total migration tracks in each season or age class. Because percentages were calculated across all birds (not by bird), we do not statistically compare by bins. Sample sizes are in Appendix Table 5.

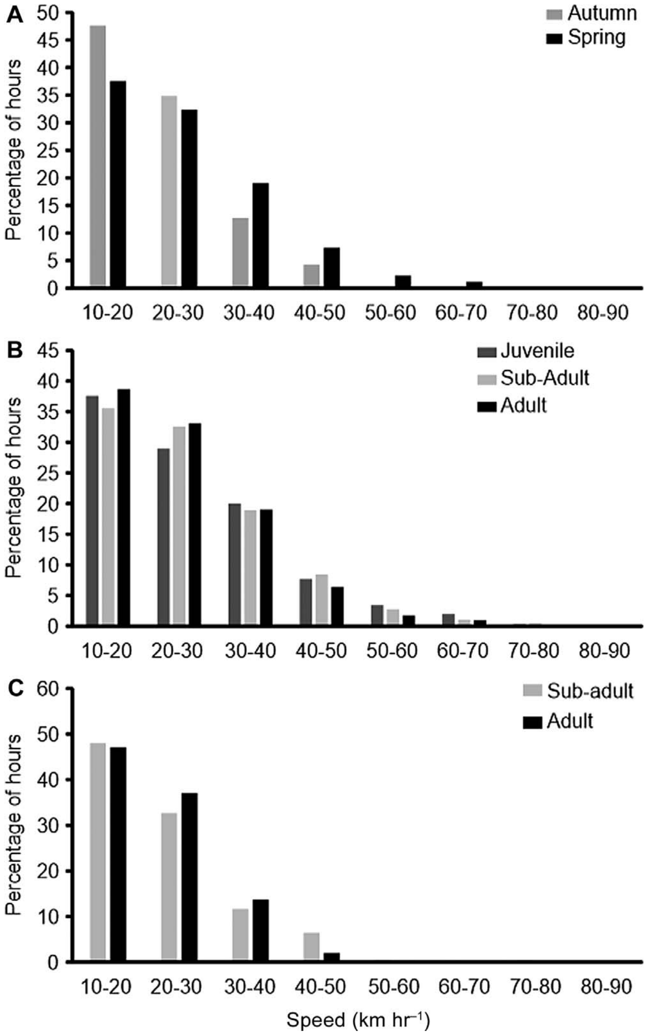

FIGURE 2. Frequency of speed of travel (km hr^{-1}) of migratory Golden Eagles in eastern North America. Panels show comparison of (**A**) all eagles during spring vs. autumn; (**B**) 3 different age classes monitored during spring migration; and (**C**) 2 different age classes monitored during autumn migration. The *y* axis shows percentages in each bin of total migration tracks in each season or age class. Because percentages were calculated across all birds (not by bird), we do not statistically compare by bins. Sample sizes are in Appendix Table 5.

2A). Binned data suggested limited differences in speed of migration by age class (Figures 1B and 2B).

During southbound (autumn) migration we collected 75,498 GPS points from 29 sub-adult and adult eagles (no first-year birds were telemetered on breeding grounds); again some eagles were tracked across multiple years and age classes (Appendix Table 6). These data allowed us to identify 427 complete daily tracks from 26 eagles, 1,639 complete hourly tracks (15 min resolution) from 28 eagles, and 72 complete hourly tracks (30 s resolution) from 9 eagles.

During autumn migration eagles traveled at speeds of 99.14 ± 59.98 km day^{-1} (range: 13.75–412.02 km day^{-1}; Figure 1A) and 22.18 ± 9.18 km h^{-1} (range: 10.02–79.41 km h^{-1}; Figure 2A). Binned data for autumn migrants also showed limited differences between age classes in rate of migration (Figures 1C and 2C).

Maps and tables showing age- and season-specific differences in routes, timing and other parameters associated with migration are published elsewhere (Miller et al. 2016b).

TABLE 2. Summary of model selection results for models describing migratory performance as a function of meteorological factors during spring migration by Golden Eagles in eastern North America, 2008–2015. We used linear mixed effects models ranked by ascending ΔAIC (the top 5 models are shown). Random effects were bird ID, day of the year, and hour of the day; fixed effects included the east–west wind vector (U-wind), flow assistance (FA), age of the bird (Age: juvenile, sub-adult, and adult), downward solar radiation (DSR), Omega (vertical wind velocity), and Thermal Energy. See Methods: Data Associations for units and additional details on meteorological factors.

Model	K^a	AIC_c	ΔAIC_c	w_i^b	Deviance^c
Daily distance traveled					
DSR + FA + Age + (FA × Age)	10	−1965.70	0.00	0.78	992.93
DSR + FA	6	−1963.14	2.56	0.22	987.60
DSR	5	−1909.29	56.41	0.00	959.66
DSR + Age	7	−1906.03	59.67	0.00	960.06
Thermal Energy + FA + Age + (FA × Age)	10	−1857.33	108.37	0.00	938.74
Speed (15 min data)					
DSR + FA + Age + (FA × Age)	11	−7489.81	0.00	0.99	3755.92
DSR + FA	7	−7481.27	8.54	0.01	3747.64
Thermal Energy + FA + Age + (Age × FA)	11	−7392.16	97.65	0.00	3707.10
Thermal Energy + FA	7	−7384.16	105.65	0.00	3699.09
U-wind + FA + Age + (Age × FA)	11	−7355.43	134.38	0.00	3688.74
Speed (30 s data)					
DSR + FA	6	−432.88	0.00	0.47	222.65
U-wind + FA	6	−431.61	1.28	0.25	222.02
Thermal Energy + FA	6	−431.05	1.84	0.19	221.74
Omega + FA	6	−429.45	3.43	0.08	220.94
FA	5	−425.68	7.21	0.01	217.99

[a] Number of parameters.

[b] Akaike's Information Criterion weight.

[c] Deviance is computed as $-2[\log_e(L(\theta)) - 2\log_e(L_s(\theta))]$.

Meteorological Associations of Migration

In both spring and autumn, cloud cover and downward solar radiation (DSR) were negatively correlated with each other (Appendix Table 7A and 7B). Likewise, flow assistance was correlated with V-wind during spring migration. We therefore removed cloud cover and, in the case of spring models, V-wind, from models. We retained for analysis all other variables.

Adult eagles encountered lower levels of solar radiation and flow assistance during spring migration than did either juveniles or sub-adults (DSR: $F = 12.65$, df = 2 and 1,302, $P < 0.001$; FA: $F = 6.76$, df = 2 and 1,302, $P < 0.01$; Figure 3A and 3B) and faster west–east wind speeds compared to sub-adults ($F = 7.75$, df = 2 and 1,302, $P < 0.001$; Figure 3C). In spite of this, all age classes of eagles traveled at similar daily rates ($F = 0.52$, df = 2 and 1,302, $P = 0.59$; Figure 3E). However, hourly speed differed among the age classes ($F = 13.36$, df = 2 and 6,405, $P < 0.001$; Figure 3F). A post-hoc comparison suggested that adult eagles traveled at slower hourly speeds than did juveniles or sub-adults (difference of means: juvenile vs. adult: 1.80 km hr^{-1}, 95% CI: 0.50–3.09 95% CI; sub-adult vs. adult: 1.37 km hr^{-1}, 95% CI: 0.51–2.23).

During autumn, adult eagles encountered lower levels of flow assistance and greater levels of south–north wind than did sub-adults (FA: $F = 8.49$, df = 2 and 1,302, $P < 0.01$; V-wind: $F = 5.38$, df = 2 and 1,302, $P = 0.02$; Figure 3B and 3D). There were no statistical differences between the 2 age classes in any of the other meteorological variables associated with migration ($P > 0.05$ in all other cases; Figure 3). As was the case for spring migration, during autumn the daily rate of travel was similar for both age groups ($F = 1.44$, df = 2 and 1,302, $P = 0.23$; Figure 3E) but adult eagles traveled at slower hourly speeds compared to sub-adults ($t_{1,637} = 3.89$; $P = 0.049$; Figure 3F).

Determinants of Migratory Performance in Spring

During spring migration, daily and hourly migratory performance of eagles, as measured with 15 min GPS data, were most strongly influenced by downward solar radiation, flow assistance, and the interaction between flow assistance and age (Table 2). There was no support for a role of any of the other environmental parameters we considered. Daily migratory performance improved with increasing age, but the response to flow assistance was strongest for juveniles and weakest for adults (Table 3). Hourly migratory performance showed relationships to weather nearly identical to those at a daily scale (Table 2), again with response to flow assistance inversely correlated with age (Table 3).

Speed based on data collected at 30 s intervals was not well described by a single model (Table 2). Instead, there were 5 models with support in the data, each with a flow assistance term and, in 4 cases, one other term. The 4 other

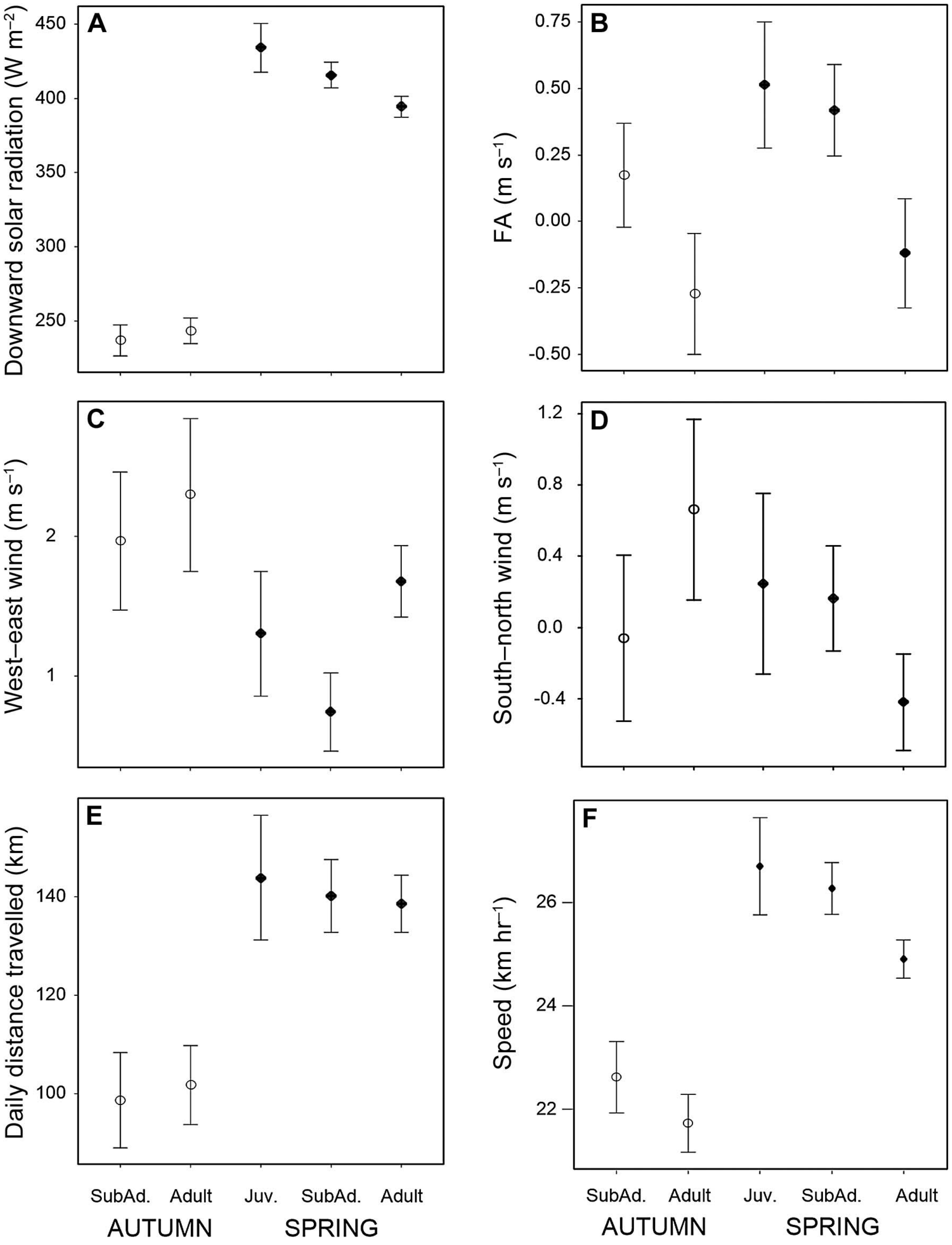

FIGURE 3. Mean (± 95% CI) for meteorological variables associated with daily migration of and for distances traveled by Golden Eagles in eastern North America, 2008–2015. Plots show (**A**) downward solar radiation, (**B**) flow assistance, (**C**) west–east surface wind vector, (**D**) south–north surface wind vector, (**E**) daily distance traveled, (**F**) hourly distance traveled. Autumn migration is represented by open circles and spring migration by filled circles. Sample sizes are in Appendix Table 5. Age classes of eagles are Juvenile (Juv.), sub-adult (SubAd.), and Adult; for details see Methods.

TABLE 3. Coefficient estimates of top model (daily and hourly, 15 min data) and from model averaging (hourly distance 30 s) for models in Table 1 describing migratory performance as a function of meteorological factors during spring migration by Golden Eagles in eastern North America, 2008–2015. Adult eagles were used as a base comparison between the different age groups. Parameters were downward solar radiation (DSR), flow assistance (FA), east–west wind vector (U-wind), and age (AgeS = sub-adult eagles). See Methods: Data Associations for units and additional details on meteorological factors. Prior to analysis, variables were rescaled and double square root transformed.

Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI
Daily distance traveled				
DSR	0.32	0.02	0.27	0.37
FA	0.21	0.05	0.12	0.31
AgeJ	−0.17	0.11	−0.36	−0.08
AgeS	−0.06	0.05	−0.15	0.01
FA × AgeJ	0.31	0.20	0.13	0.66
FA × AgeS	0.09	0.08	−0.03	0.26
Speed (15 min data)				
DSR	0.20	0.02	0.17	0.23
FA	0.40	0.02	0.35	0.44
AgeJ	−0.10	0.03	−0.17	−0.04
AgeS	−0.04	0.02	−0.08	0.01
FA × AgeJ	0.22	0.06	0.10	0.33
FA × AgeS	0.09	0.04	0.01	0.16
Speed (30 s data)				
DSR	0.06	0.07	0.05	0.21
FA	0.21	0.05	0.12	0.30
U-wind	0.02	0.04	0.03	0.16
Thermal Energy	−0.02	0.04	−0.14	−0.02
Omega	0.01	0.03	0.02	0.18

terms (one in each model) were for DSR, U-wind, thermal energy, and Omega. The fifth model only had a flow assistance term and very little support in the data. Speed was most strongly influenced by flow assistance (model-averaged estimates; Table 3). DSR was also influential but east–west winds, thermal energy, and Omega were all relatively less important to speed (Table 3).

Determinants of Migratory Performance in Autumn

During autumn migration, daily and hourly migratory performance, as measured with 15 min GPS data, were most strongly influenced by south–north wind, flow assistance, eagle age, and an interaction between flow assistance and age (Table 4). At a daily scale, eagle migratory performance was negatively affected by age and flow assistance. V-wind also influenced migration speed; winds from the south (positive V-wind) slowed the speed of migration and winds from the north (negative V-winds) increased the speed of migration. Once again, younger birds responded more strongly to flow assistance than did adults (Table 5). At an hourly scale, V-winds had a similar effect on migratory performance as in the daily-scale model (positive V-winds reduced migratory performance), flow assistance improved migratory performance, and younger birds performed worse than adults but again responded more strongly to flow assistance.

No single model described hourly speed of travel calculated using data collected at 30 s intervals (Table 4). Instead, a suite of models was supported. Of the 5 models with the most support in the data, all included a flow assistance term. Four of these models also included one other term, either DSR, Omega, thermal energy, or V-wind. The fifth model had the most support in the data and included only the flow assistance term. Hourly speed of travel was most strongly influenced by flow assistance. Other environmental parameters had relatively little influence on speed of migration. Thus, eagles flew faster especially in response to changes in tailwinds (Table 5).

DISCUSSION

Our analyses suggest that a complex suite of age- and season-specific factors interacted with weather to shape migratory performance of Golden Eagles. In general, eagles flew faster and farther with tailwinds and the strong solar radiation that produces thermals (i.e. conditions well suited to long-distance flight; Duerr et al. 2012, 2014). However, we also observed unexpected relationships between experience and migratory performance that provide important insight into the drivers of migration behavior.

The Golden Eagles we monitored occasionally flew >80 km in a single hour and >500 km in a single day (Figures 1 and 2). This is far above the expected or observed migration speed of typical terrestrial migrants (Hedenström and Alerstam 1998, Åkesson and Hedenström 2007). However, although it is similar to maximum speeds for other species soaring over land (Chevallier et al. 2010, Klaassen et al. 2011, Mellone et al. 2012, Vansteelant et al. 2015), it is well short of the speed recorded for an oceanic soaring albatross (*Thalassarche chrystostoma*; up to 950 km day^{-1}; Croxall et al. 2005). That soaring eagles travel so quickly attests to their ability to capitalize on atmospheric variation to maximize the subsidy they draw from environmental updraft. However, eagles did not travel long distances every day. Instead, there were dramatic inter-seasonal and age-specific differences in response to meteorological variables (Figure 3). We also observed differences in fixed effects in the best-supported statistical models describing hourly movement as measured at 15 min vs. 30 s intervals. Together, these patterns demonstrate the role of multiple interacting factors in determining migratory performance.

Seasonal Variation in Migratory Performance

The strong inter-seasonal differences in responses of eagles to meteorological variables are consistent with

TABLE 4. Summary of model selection results for models describing migratory performance as a function of meteorological factors during autumn migration by Golden Eagles in eastern North America, 2008–2015. We used linear mixed effects models ranked by ascending ΔAIC and we only show the top 5 models. Random effects were bird ID and day of the year; fixed effects included south–north wind vector (V-wind), flow assistance (FA), age of the bird (Age: sub-adult and adult), downward solar radiation (DSR), Omega (vertical wind velocity), and Thermal Energy. See Methods: Data Associations for units and additional details on meteorological factors.

Model	K[a]	AIC_c	ΔAIC_c	w_i[b]	Deviance[c]
Daily distance traveled					
V-wind + FA + Age + (FA × Age)	8	−496.64	0.00	0.61	256.49
V-wind + Age	6	−494.15	2.50	0.17	253.17
V-wind	5	−493.61	3.03	0.13	251.88
V-wind + FA	6	−492.76	3.89	0.09	252.48
DSR + FA	6	−476.35	20.29	0.00	244.28
Speed (15 min data)					
V-wind + FA + Age + (FA × Age)	9	−2078.24	0.00	0.53	1048.18
V-wind + FA	7	−2077.96	0.28	0.47	1046.02
DSR + FA	6	−2021.78	56.46	0.00	1016.92
DSR + FA + Age + (FA × Age)	7	−2019.77	58.48	0.00	1016.92
V-wind	7	−2014.38	63.86	0.00	1014.22
Speed (30 s data)					
FA	5	−148.86	0.00	0.33	79.89
DSR + FA	6	−147.22	1.64	0.15	80.25
Omega + FA	6	−146.83	2.04	0.12	80.06
Thermal Energy + FA	6	−146.60	2.26	0.11	79.95
V-wind + FA	6	−146.58	2.29	0.11	79.93

[a] Number of parameters

[b] Akaike's Information Criterion weight

[c] Deviance is computed as $-2[\log_e(L(\theta)) - 2\log_e(L_s(\theta))]$

TABLE 5. Coefficient estimates of top model (daily and hourly, 15 min data) and model averaging (hourly distance 30 s) for models in Table 1 describing migratory performance as a function of meteorological factors during autumn migration by Golden Eagles in eastern North America, 2008–2015. Adult eagles were used as a base comparison between the different age groups. Parameters were downward solar radiation (DSR), flow assistance (FA), south–north wind vector (V-wind), Thermal Energy, and age (AgeS = sub-adult eagles). See Methods: Data Associations for units and additional details on meteorological factors. Prior to analysis, variables were rescaled and double square root transformed.

Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI
Daily distance traveled				
V-wind	−0.26	0.04	−0.34	−0.18
FA	−0.04	0.08	−0.23	0.11
AgeS	−0.12	0.10	−0.31	0.01
FA × AgeS	0.15	0.14	0.03	0.44
Speed (15 min data)				
V-wind	−0.21	0.02	−0.25	−0.17
FA	0.18	0.05	0.08	0.27
AgeS	−0.03	0.03	−0.10	0.00
FA × AgeS	0.06	0.07	0.01	0.21
Speed (30 s data)				
FA	0.09	0.06	0.01	0.21
DSR	0.01	0.03	−0.05	0.14
Omega	0.00	0.01	−0.08	0.05
Thermal Energy	0.00	0.01	−0.08	0.06
V-wind	0.00	0.02	−0.09	0.09

these birds taking advantage of prevailing conditions to maximize migratory performance. The weather these eagles experience varies between seasons (Duerr et al. 2014), the birds switch between different flight modes in response to weather (Katzner et al. 2015), and their use of those different flight modes has consequences for flight speed (Duerr et al. 2012). Seasonal, daily, and hourly responses of flight behavior are well understood for birds migrating through Europe and Africa, where variation in migratory performance has been linked to spatial variation in tailwinds and thermal convection, especially over arid deserts (Liechti et al. 1996, Shamoun-Baranes et al. 2003, Klaassen et al. 2008, Chevallier et al. 2010, Vansteelant et al. 2015). In eastern North America, in contrast, where humidity is higher and there are no deserts, spatial and seasonal variation in thermal availability is dramatically different. Our analyses show that behavior and performance of eagles in this region responded to this interseasonal variation. In particular, in spring, solar radiation, flow assistance, and age helped determine hourly and daily-scale migratory performance, whereas in autumn performance was shaped by wind availability and age.

Influence of Scale of Measurement on Interpretation of Migratory Performance

Although flight data have been collected at intervals as short as 10 s (Vansteelant et al. 2015), we know of no other study that explicitly compares migration performance as recorded with shorter- vs. longer-interval telemetry data. In this case, because our starting models differed slightly (i.e. we were unable to include an age term in the 30 s data) and because the data collected at 30 s intervals were collected only in one region, we were unable to make direct statistical comparisons between measurements at these 2 scales. However, qualitative comparisons that recognize the differences in model starting points can still be informative. For example, it is clear that the 30 s tracks that we collected are a more precise measure than the 15 min data of the distance traveled by the bird. Because of this, the 30 s tracks averaged ~12% longer than the tracks derived from 15 min data.

Those highly detailed data that we collected were from eagles flying through a predefined geographic area in the central Appalachian Mountains in Pennsylvania (Lanzone et al. 2012). In this region, the landscape is composed predominantly of long, linear ridges and hilly terrain (Bailey 1993). Such a topographic backdrop creates spatial variation in updrafts, and the 30 s data appear to capture a suite of micro-scale responses eagles used to migrate through such a variable landscape. In contrast, the 15 min data were collected across a much greater spatial extent (the entire geographic range of this subpopulation) and eagle responses are almost certainly more variable across this region than within the area where 30 s data were collected. Thus, the topographic consistency in the area where 30 s data were collected likely explains a large part of the differences in model results. Nevertheless, comparison of these 2 datasets is useful because it highlights the importance of the spatial and temporal scales of measurement when evaluating migratory performance. Similar data sets from other species, especially where age is accounted for more completely than we could do here, would provide insight into the comparative details of soaring birds' responses to variable updraft environments.

Inverse Age Effects on Migratory Performance

Migratory performance of birds typically improves with age (Thorup et al. 2003, Mueller et al. 2013, Sergio et al. 2014). Therefore, we expected experienced adult eagles to migrate in optimal weather conditions, to orient more effectively, and consequently to travel more quickly than younger, more inexperienced, eagles. This was not the case. In fact, although daily distances traveled did not differ among age classes, hourly migratory performance of young eagles was better than that of older eagles (younger eagles flew more quickly than did older eagles; Figure 3F). These patterns run contrary to those in much of the previously published literature (Thorup et al. 2003, Mueller et al. 2013, Sergio et al. 2014). We believe that the explanation for this counterintuitive observation is tied to age-specific timing of migration. In particular, younger eagles migrated later in spring and earlier in autumn than did older eagles (Miller et al. 2016b). As such, they migrated when solar incidence angles are higher, solar radiation was more intense, and thermals were relatively more available. Such conditions are positively associated with higher cross-country soaring speeds (Reichmann 1978). In contrast, adult eagles flew earlier in spring and later in autumn, when thermals were relatively less available and flight speeds consequently slower. These patterns indicate that factors other than experience likely help determine migratory performance in this system.

There may be season-specific selective pressures that cause factors other than experience to determine migratory performance. In this case, adult eagles may see fitness benefits by migrating earlier in the spring season, allowing them to return early to establish breeding territories. Early in the spring, thermals are limited in this region, birds must rely more on orographic updraft or powered flight, and hourly travel speeds are consequently lower (Duerr et al. 2012, 2014). These and other analyses suggest that adults not only are traveling less quickly, but they are also following a less direct migratory pathway (Miller et al. 2016b). However, because daily migratory performance is similar in each age class, we expect that on a daily basis, adult eagles spend more time actively migrating than do younger birds (i.e. they have longer travel days and take fewer breaks en route); previous analyses also support this notion (Miller et al. 2016b).

In contrast, younger birds (juveniles and subadults) do not need to find and defend nesting territories during spring. As they do not breed, they do not face the same fitness pressures as adults to migrate early. Indeed, arriving later in the breeding season may provide adaptive benefit because territory defense by adults grows weaker as the nesting season progresses (Watson 2010). In autumn, non-territorial younger birds also are usually able to leave summering grounds earlier than territorial adults, especially those with dependent young. In both seasons, these strategies allow younger eagles to have more flexibility in choosing the timing of their migration, such that they can choose only to migrate when weather conditions are most suitable for long-distance travel. These timing-based strategies are also likely the mechanism by which a younger, inexperienced bird, whose orientation and weather-compensation abilities are weaker, may still fly farther than an older, more experienced bird that better orients and compensates for poor weather conditions.

Although age is often used as the single proxy for migratory experience and as the only predictor of migratory performance, our data suggest that such a single-faceted approach may cloud interpretation of migratory performance. In fact, our results suggest complex linkages among timing of migration, weather, experience, and stage- or age-specific selective pressures that may drive migratory performance. Key to understanding these patterns is comparing across seasons, when selection may operate differently on age classes, comparing within seasons, when weather may operate differently on age classes, and understanding the effect of the spatial and temporal scales at which migratory performance is measured.

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Ethics statement: Use of Golden Eagles for this research was approved by the West Virginia University Institutional Animal Care and Use Committee (IACUC) protocol no. 11-0304, and trapping was conducted with a number of different state (West Virginia, Pennsylvania, Virginia, etc.) and US federal bird banding permits. At the time telemetry systems were deployed, TEK was a co-owner of Cellular Tracking Technologies, the company that manufactured the telemetry units used in this study.

Author contributions: JRB raised funds for this research, TEK, TAM, AIR, and JRB conceived of the research; AIR, AED, and TEK designed and implemented the statistical analyses; AIR and TEK wrote the initial draft of the manuscript and all authors revised the document. 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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APPENDIX TABLE 6. Number of individual migratory Golden Eagles, number of individual eagles tracked across more than one year and age class (repeat years), and the number of tracks during (**A**) spring and (**B**) autumn migration in Eastern North America, 2008–2015. Total number of eagles represent the sum of the number of individual eagles monitored (less than the number of eagles in each age class, since some eagles occurred in multiple age classes).

Track interval	Age	Number of eagles	Repeat years	Number of tracks
(A) Spring migration				
Daily	Juvenile	8	–	182
	Sub-adult	25	11	553
	Adult	35	10	701
	Total	**57**	**22**	**1436**
Hourly (15 min)	Juvenile	6	–	725
	Sub-adult	22	10	2246
	Adult	40	13	3437
	Total	**55**	**23**	**6408**
Hourly (30 s)	Juvenile	5	–	22
	Sub-adult	11	5	70
	Adult	16	6	113
	Total	**28**	**11**	**205**
(B) Autumn migration				
Daily	Sub-adult	15	4	243
	Adult	11	7	184
	Total	**25**	**11**	**427**
Hourly (15 min)	Sub-adult	17	5	802
	Adult	13	8	837
	Total	**28**	**13**	**1639**
Hourly (30 s)	Sub-adult	4	1	19
	Adult	6	3	53
	Total	**9**	**4**	**72**

APPENDIX TABLE 7A. Pearson correlation (*r*) matrix for meteorological variables associated with migration during spring migration by Golden Eagles in eastern North America. Bold values indicate variables with a correlation $>$0.5. Variables are downward solar radiation (DSR), U- and V- vectors of wind at ground level (U-wind, V-wind), cloud cover (C-cover), vertical velocity of wind (Omega), Thermal Energy, and flow assistance (FA); see text for additional details.

	DSR	U-wind	V-wind	C-cover	Omega	Thermal Energy	FA
DSR	1.00	0.06	−0.16	−**0.58**	0.06	0.18	0.05
U-wind		1.00	−0.18	−0.09	−0.04	0.46	0.05
V-wind			1.00	0.22	0.00	−0.27	**0.57**
C-cover				1.00	−0.16	0.04	0.12
Omega					1.00	−0.02	0.00
Thermal Energy						1.00	−0.02
FA							1.00

APPENDIX TABLE 7B. Pearson correlation (*r*) matrix for meteorological variables associated with migration during autumn migration by Golden Eagles in eastern North America. Bold values indicate variables with a correlation $>$0.5. Variables are downward solar radiation (DSR), U- and V- vectors of wind at ground level (U-wind, V-wind), cloud cover (C-cover), vertical velocity of wind (Omega), Thermal Energy, and flow assistance (FA); see text for additional details.

	DSR	U-wind	V-wind	C-cover	Omega	Thermal Energy	FA
DSR	1.00	0.05	−0.02	−**0.50**	−0.03	0.03	−0.09
U-wind		1.00	−0.07	0.05	−0.11	**0.55**	0.11
V-wind			1.00	0.19	−0.20	−0.06	−0.17
C-cover				1.00	−0.23	0.28	0.00
Omega					1.00	−0.12	0.03
Thermal Energy						1.00	0.02
FA							1.00