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Limitations and mechanisms influencing the migratory performance of soaring birds

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Migration is costly in terms of time, energy and safety. Optimal migration theory suggests that individual migratory birds will choose between these three costs depending on their motivation and available resources. To test hypotheses about use of migratory strategies by large soaring birds, we used GPS telemetry to track 18 adult, 13 sub-adult and 15 juvenile Golden Eagles *Aquila chrysaetos* in eastern North America. Each age-class had potentially different motivations during migration. During spring, the migratory performance (defined here as the directness of migratory flight) of adults was higher than that of any other age-classes. Adults also departed earlier and spent less time migrating. Together, these patterns suggest that adults were primarily time-limited and the other two age-classes were energy-limited. However, adults that migrated the longest distances during spring also appeared to take advantage of energy-conservation strategies such as decreasing their compensation for wind drift. During autumn, birds of all age-classes were primarily energy-minimizers; they increased the length of stopovers, flew less direct routes and migrated at a slower pace than during spring. Nonetheless, birds that departed later in autumn flew more directly, indicating that time limitations may have affected their decision-making. During both seasons, juveniles had the lowest performance, sub-adults intermediate performance and adults the highest performance. Our results show age- and seasonal variation in time and energy-minimization strategies that are not necessarily exclusive of one another. Beyond time and energy, a complex suite of factors, including weather, experience and navigation ability, influences migratory performance and decision-making.

Keywords: Golden Eagle, migration, migration phenology, migratory wandering, movement ecology, path sinuosity.

Migration allows birds to exploit spatially and temporally available resources (Dingle 1996) and ultimately to improve survival and fitness (Alerstam & Lindström 1990, Clark & Butler 1999). However, in terms of both survival and fitness, migration can be one of the most costly periods of a bird's life (Sillett & Holmes 2002, Newton 2008, Harrison *et al.* 2011). To deal with these costs, birds often employ time-, energy- or predation-minimizing strategies. In general, these strategies have been

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presented as being exclusive of one another (Hedenström 1993), each with different consequences for migratory performance. More recently, however, it has been suggested that birds may use components of multiple strategies during a single migration period (Alerstam 2011).

Defining migratory performance can be challenging because the goals of migration vary with individual characteristics. For example, time-limited migrants should maximize their rate of travel and minimize the amount of time spent migrating (Hedenström 2008, Alerstam 2011). This can be done, for example, by limiting stopover time, by flying longer each day, or by increasing compensation for wind drift and thus flying along a more direct path. Conversely, energy-limited migrants maximize energy intake by increasing stopovers and food intake, and minimize the cost of flight by travelling during optimal conditions (e.g. flying with tailwinds) and by decreasing compensation for wind drift. Finally, in the case of predation-minimizers, an effective strategy may be to reduce energy intake to remain more agile when faced with predators.

Hypotheses about time and energy limitation are more straightforward to test in the case of apex predators, for which (non-anthropogenic) predation risk is negligible. Because apex predators are large and thus comparatively easy to track over long distances, it is also possible to test alternative hypotheses explaining behaviour. Conceivable alternatives to time- and energy-exclusive hypotheses may be selective pressures that push individuals (a) to incorporate multiple strategies during a single migratory season, (b) to incorporate different strategies during different seasons or (c) to incorporate different strategies based on breeding status and experience. For example, it has been shown that migratory performance (measured as how directly a bird flies during migration) improves with experience (age) as individuals learn the landscape (Fagan *et al.* 2013), as individuals improve navigation and orientation skills (Thorup *et al.* 2007, Mueller *et al.* 2013) and as individuals learn how to minimize energetic costs (Maransky & Bildstein 2001) and compensate for wind drift (Thorup *et al.* 2003).

The role of these alternative explanations for the evolution of migratory behaviour has not been well studied. To test hypotheses about the suite of potential factors driving migratory strategies and performance, we studied a small population of Golden Eagles *Aquila chrysaetos* in eastern North America. These birds are well suited to testing hypotheses about migration for three primary reasons. First, populations of Golden Eagles are highly age-structured and individuals have a prolonged pre-adult, pre-breeding phase. This means that spatial learning by individuals may be prolonged and behaviour may change significantly with experience (Fagan *et al.* 2013, Mueller *et al.* 2013). Secondly, this population is almost entirely migratory, with some individuals migrating two to three times as far as other individuals (Miller *et al.* 2010), providing an ideal test case to understand the influence of movement distance on migratory strategies and performance. Finally, Golden Eagles are top predators and, as noted above, predation risk during migration should therefore be low, reducing the number of potential selective pressures.

In the initial evaluation of migration behaviour, we observed that Golden Eagles that flew more directly also completed migration in less time. Moreover, straightness of migration paths has been used as a reasonable proxy for migratory performance (Desholm 2003, Benhamou 2004, Bonadonna *et al.* 2005, Mueller *et al.* 2013). We used the measure of straightness of migratory flight paths, in combination with measures of timing, migratory speed and length of stopover, to test whether Golden Eagles were time- or energy-limited during different life stages (age) and during different times of the annual cycle (season). We assumed that birds using a time-minimization strategy would exhibit higher migratory performance than would an energy-minimizer. Thus time-minimizers would, relative to energy-minimizers, minimize the time spent migrating by flying relatively more direct routes between start and end points. Energy-minimizers, in contrast, would minimize energy use by compensating less for wind drift and thereby flying relatively less direct routes (Liechti 2006, Alerstam 2011). We also assumed that energy-minimizers would spend longer periods of time at stopover areas and, subsequently, spend relatively more time migrating. To test the hypothesis that mechanisms beyond time and energy (e.g. experience) influence migratory performance, we built statistical models to account for individual characteristics including age, distance travelled, rate of travel, season and departure day, and for environmental characteristics including terrain and weather. This approach

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allowed us to evaluate the influence of each of these characteristics on migratory performance.

METHODS

Study species

Golden Eagles in eastern North America spend the summer in the provinces of Québec and Labrador and Newfoundland, Canada (Morneau *et al.* 2015). They winter mainly in the central Appalachian Mountains in the USA (Katzner *et al.* 2012). However, the species is found throughout the eastern USA and at least one individual in this study did not migrate each year. Like other large-bodied soaring raptors, Golden Eagles rely primarily on slope or thermal soaring and gliding when migrating (Kerlinger 1989, Duerr *et al.* 2012). Individuals tend to migrate alone or in pairs and migration is concentrated in both autumn and spring along the ridges of central Pennsylvania, where hundreds of Golden Eagles are counted at hawk watches each year (Hawk Migration Association of North America, hawkcount.org).

Study area

We studied Golden Eagles over most of their wintering and breeding range in eastern North America, from North Carolina to far northern Québec and Labrador (34°–60°N, 84°–62°W; Fig. 1). We examined daily movements of birds only in a core study area of Pennsylvania, northern West Virginia (WV), Virginia (VA) and Maryland (MD), and southern New York State (NY) (39°–42.8°N, 74°–80.5°W). Topography differs among physiographic provinces within this core study area (Bailey 1993). The Ridge and Valley physiographic

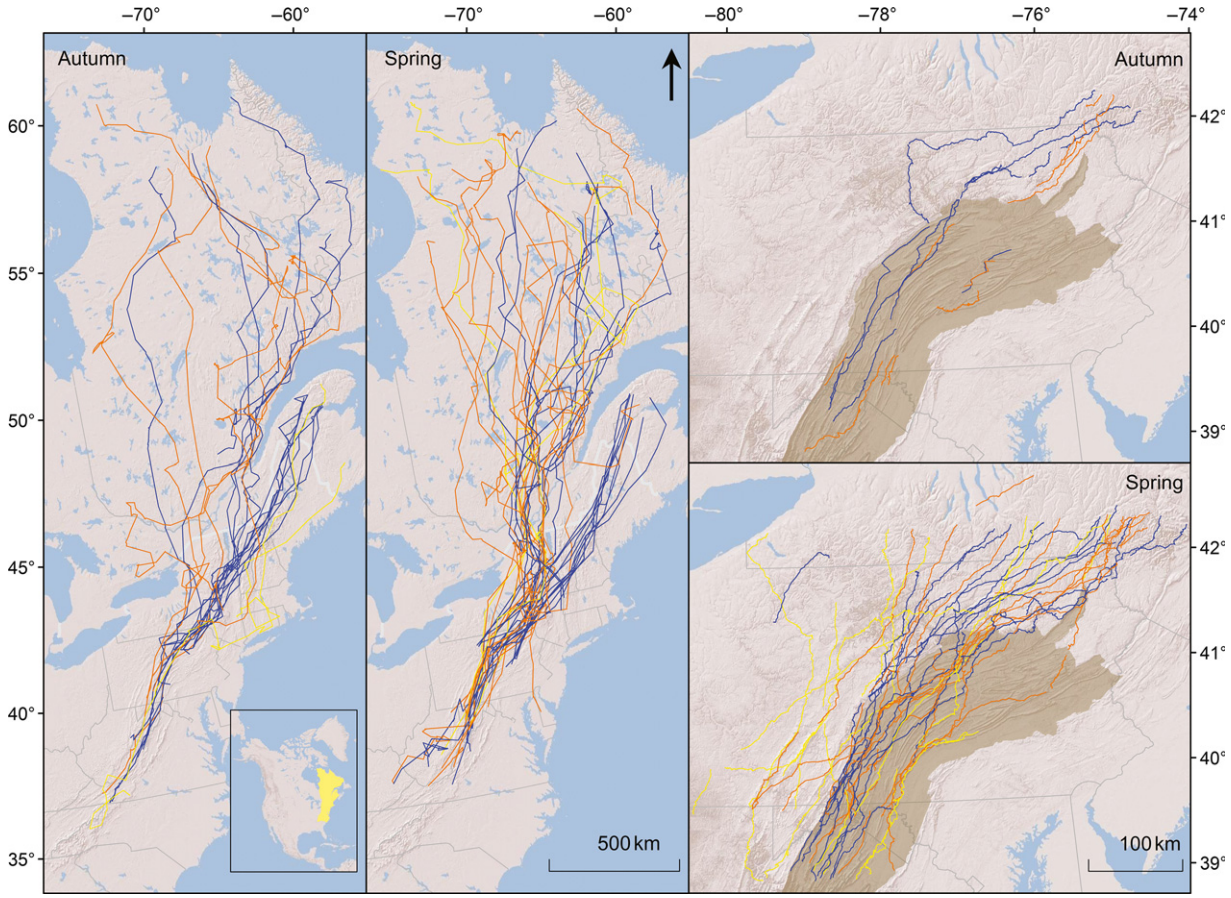

Figure 1. Complete (left) and daily (right) migratory tracks for adult (blue), sub-adult (orange) and juvenile (yellow) Golden Eagles *Aquila chrysaetos* in eastern North America during spring and autumn (2007–2013). Shaded region is the Ridge and Valley Province. Inset shows North America with study area highlighted in yellow.

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province of our core study area consists of very long ridges and valleys running along a southwest to northeast trajectory. Outside of this province and with the exception of coastal regions, the terrain over which eagles fly in eastern North America is generally hilly to mountainous, but terrain is poorly structured or randomly orientated.

Data collection

From November 2006 to March 2013, we deployed telemetry units on 18 adults, 13 sub-adults and 15 juveniles in the USA and Canada (Table 1), with several individuals tracked over multiple years. We used two types of solar-powered GPS telemetry units. These included nine PTT-100s (45 g or 100 g; Microwave Telemetry Inc., Columbia, MD, USA), which transmit data via the ARGOS satellite systems, and 38 CTT-1100s (80–95 g; Cellular Tracking Technologies, Somerset, PA, USA), which transmit data via the GSM (Global System for Mobile Communications) network. Satellite units provided GPS data at 1-, 3- or 4-h intervals and the GSM units provided GPS locations every 30 s within the core study area and every 15 min elsewhere.

Table 1. Total number of each age and sex of Golden Eagles *Aquila chrysaetos* tracked during spring and autumn migration in eastern North America (2007–2013) and the number of tracks obtained for each age and sex class.

		Complete track		Daily track	
Season	Age-Sex	Individuals	Tracks	Individuals	Tracks
Autumn	AdF	2	2	3	11
	AdM	6	12	2	7
	S-F			2	4
	S-M	3	5	4	10
	J-F	1	1		
	J-M	1	1		
	Total*	13 (12)	21	11 (10)	32
Spring	AdF	4	5	4	15
	AdM	8	15	9	35
	S-F	3	3	2	9
	S-M	6	10	10	49
	J-F			6	18
	J-M	4	4	6	16
	Total*	25 (22)	37	37 (34)	142

*Total individuals represents the sum of individuals across age-classes; the number in parentheses is the number of unique individuals. Some individuals were tracked over multiple years and fell into different age-classes over the study period and therefore are represented more than once in the sum of individuals.

We attached telemetry units in a backpack style using non-abrasive Teflon ribbon (Bally Ribbon Mills, Bally, PA, USA) harnesses (Kenward 1985). We ringed each bird with an aluminium USGS ring, except for several females whose legs were too large for existing ring sizes. We collected standard morphological measurements and determined sex using DNA extracted from blood samples (Fridolfsson & Ellegren 1999). We estimated age using moult patterns (Jollie 1947, Bloom & Clark 2001) and classified ages as follows: juvenile (first autumn or spring migration), sub-adult (2nd–4th autumn or spring migration) and adult (> 4th autumn or spring migration).

Data analysis

We used two types of migration tracks for our study: seasonal (long-distance) migration tracks between summer and winter locations, and daily (i.e. 30-s, shorter distance) migration tracks within the core study area. We used seasonal migration tracks to examine broad-scale movement patterns of Golden Eagles. We used daily migration tracks to examine fine-scale movement patterns and the influence of weather, topography and individual characteristics on flight performance (Fig. 1).

To create seasonal tracks, we selected birds for which we had collected data for at least one entire northbound or southbound migration (Fig. 1). To make consistent comparisons among individual paths for which data were collected at different intervals (Turchin 1998), we created lines from points for each bird in each season and year that were approximately 3–4 h apart (Tracking Analyst, ArcGIS 10.1; ESRI, Redlands, CA, USA).

To create daily migration tracks, we selected birds from the core study area for which we had collected data at 30-s intervals. For a subset of these birds, we also had complete migration tracks. We created paths from points for each bird/day. We segmented daily paths if they crossed physiographic boundaries, i.e. inside or outside the Ridge and Valley Province during a single day, so that we could assign each path to the appropriate physiographic province. Additionally, we created separate segments when a gap of > 15 km in continuous data collection occurred. We did this because a large gap between points results in a straight line connecting points on either end of a gap; the inclusion of long straight lines in a high-resolution track will cause the straightness index to

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artificially increase. Because we were specifically interested in migratory flight patterns of daily movements, rather than patterns of short-distance movements, we removed from the analysis data collected during stopovers, which we defined as stays of ≥ 24 h in one area, and tracks that were shorter than 30 km.

For all tracks, we calculated track length (km) and a straightness index, which we defined as the ratio of the total track length to the distance between the start and end points (ArcGIS 10.1; ESRI). This straightness index ranges from 0 to 1, where 1 is a straight line. For seasonal tracks we also calculated duration of migration including stopover, number of days actively migrating, first calendar day of migration, rate of travel including stopover days (km/day) and rate of travel on migratory days (km/day) excluding stopover (see Table S1). We defined active migration as days when total movements were ≥ 30 km in the primary direction of migration. For daily tracks, we calculated calendar day, rate of travel (km/h), and the centroid of each track (Table S2).

We used the centroid of each daily track to assign spatially interpolated National Centers for Environmental Protection (NCEP) Reanalysis II weather data (Kanamitsu *et al.* 2002) to each point at 18:00 h UTC, which is mid-day in the study area (RNCEP; Kemp *et al.* 2011) in R (R Development Core Team 2011). We considered surface variables that are expected to influence thermal development and orographic lift. These were temperature (°C), pressure (Pa), humidity, best lifted index (°K), downward short-wave radiation flux (W/m^2), sensible heat flux (W/m^2), the east–west component of wind (u-wind, m/s) and the north–south component of wind (v-wind, m/s). We calculated average tailwind and side wind speeds for each daily track using the mean track bearing and the u- and v-wind components (CircStats and circular; Jammalamadaka and Sengupta (2001); NCEP. Tailwind; Kanamitsu *et al.* (2002), Kemp *et al.* (2011); RNCEP) in R and included those values in our models rather than the raw wind components. To avoid multicollinearity, we created a correlation matrix among all variables. For each pair of variables with a correlation > 0.5, we removed the one we considered biologically less relevant.

Assessing differences in behaviour (speed of travel, departure date, etc.) or environmental conditions (wind speed, atmospheric conditions, etc.) can provide key information to better understand whether a group is either time- or energy-limited. Such information can also provide insight into the specific mechanisms or responses that support these strategies. Therefore, we calculated univariate models to test the effect of age and season on each of the variables listed above. We ran a total of five models for each variable – autumn among ages, spring among ages, adult between seasons, sub-adult between seasons and juvenile between seasons. We ran multiple models rather than a single omnibus model for each variable so that the information could be more easily interpreted. Thus for each variable we modelled within-season age variation and within-age seasonal variation. All sets that included adults or sub-adults had repeated measures. We used linear mixed models (nlme; Pinheiro *et al.* 2011) in R with individual bird fitted as a random effect. For juvenile between-season models, we used generalized least squares models (gls; Pinheiro *et al.* 2011) in R. In the results we present modelled means from the within-season models.

We modelled factors influencing the straightness index using linear mixed models (nlme; Pinheiro *et al.* 2011). We tested the following random effects structures: bird, year and bird nested within year. We chose the random effects structure that best fit the data based on Akaike's information criterion (AIC) (Burnham & Anderson 2002, 2004, Zuur *et al.* 2009). For seasonal and daily tracks we built two separate models, one for each season, to give a total of four models (Table 2). We examined model residuals to verify that model assumptions had been met. In cases where residuals did not meet the assumption of homogeneity of variance, we tested various variance structures and applied the variance structure that AIC values indicated best fit the data (Zuur *et al.* 2009).

We used an information-theoretic approach for model selection (Burnham & Anderson 2002, 2004). We ran seasonal and daily models with all combinations of fixed effects and ranked each model using AIC_c (Burnham & Anderson 2002) using the R package MuMIn (Bartoń 2015). We used model averaging (Buckland *et al.* 1997) to derive our final models. Variable importance was calculated as the cumulative AIC_c weights for each variable from all models in each model set. We assumed that variables were important to the model if the cumulative variable weight (variable importance) was > 0.6.

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Table 2. Modelled means and 95% confidence intervals by age and season for univariate GLMMs of metrics measured for complete migration tracks for Golden Eagles *Aquila chrysaetos* migrating during autumn and spring in eastern North America (2006–2013). Tukey *post-hoc* multiple comparisons indicate within-season age-related differences among each metric.

					Post-hoc comparisons					
			Model estimates		Juvenile		Sub-adult		Adult	
Metric	Season	Age	Mean	95% CI	*z*	*P*	*z*	*P*	*z*	*P*
Straightness index	Autumn	Juvenile	0.60	0.19	–	–	0.95	0.604	−2.38	0.044
	Autumn	Sub-adult	0.66	0.14	0.95	0.604	–	–	−2.17	0.075
	Autumn	Adult	0.79	0.09	−2.38	0.04	−2.17	0.075	–	–
	Spring	Juvenile	0.68	0.16	–	–	0.63	0.800	−2.50	0.032
	Spring	Sub-adult	0.73	0.11	0.63	0.800	–	–	−2.76	0.016
	Spring	Adult	0.86	0.07	−2.50	0.032	−2.76	0.016	–	–
Departure day	Autumn	Juvenile	296.4	42.2	–	–	−1.62	0.233	0.28	0.957
	Autumn	Sub-adult	267.7	30.8	−1.62	0.233	–	–	−1.81	0.162
	Autumn	Adult	291.4	16.4	0.28	0.96	−1.81	0.162	–	–
	Spring	Juvenile	114.0	19.0	–	–	−3.00	0.007	5.43	< 0.001
	Spring	Sub-adult	86.8	12.7	−3.00	0.007	–	–	3.53	0.001
	Spring	Adult	66.2	7.9	5.43	< 0.001	3.53	0.001	–	–
Proportion of migration days	Autumn	Juvenile	0.58	0.19	–	–	−2.22	0.065	0.16	0.986
	Autumn	Sub-adult	0.43	0.14	−2.22	0.065	–	–	−2.31	0.053
	Autumn	Adult	0.57	0.10	0.16	0.99	−2.31	0.053	–	–
	Spring	Juvenile	0.66	0.19	–	–	0.22	0.974	−1.32	0.377
	Spring	Sub-adult	0.68	0.12	0.22	0.974	–	–	−1.67	0.210
	Spring	Adult	0.78	0.08	−1.32	0.377	−1.67	0.210	–	–
No. of days actively migrating	Autumn	Juvenile	22.9	17.0	–	–	5.89	< 0.001	−2.27	0.057
	Autumn	Sub-adult	55.1	12.2	5.89	< 0.001	–	–	3.07	0.006
	Autumn	Adult	39.3	12.0	−2.27	0.06	3.07	0.006	–	–
	Spring	Juvenile	38.1	16.2	–	–	−1.03	0.554	2.42	0.039
	Spring	Sub-adult	30.6	11.0	−1.03	0.554	–	–	2.09	0.090
	Spring	Adult	20.0	7.5	2.42	0.039	2.09	0.090	–	–
Travel rate (km/day)	Autumn	Juvenile	73.0	18.9	–	–	−9.85	< 0.001	0.58	0.820
	Autumn	Sub-adult	35.8	17.4	−9.85	< 0.001	–	–	−4.43	< 0.001
	Autumn	Adult	68.3	15.6	0.58	0.82	−4.43	< 0.001	–	–
	Spring	Juvenile	104.7	45.6	–	–	−0.29	0.953	−0.61	0.811
	Spring	Sub-adult	98.4	30.6	−0.29	0.953	–	–	−1.35	0.361
	Spring	Adult	117.6	19.5	−0.61	0.811	−1.35	0.361	–	–
Travel rate on days actively migrating (km/day)	Autumn	Juvenile	109.4	35.0	–	–	−1.64	0.227	0.83	0.683
	Autumn	Sub-adult	85.9	25.6	−1.64	0.227	–	–	−1.04	0.546
	Autumn	Adult	97.2	13.9	0.83	0.68	−1.04	0.546	–	–
	Spring	Juvenile	129.3	37.2	–	–	−0.18	0.408	−0.64	0.791
	Spring	Sub-adult	126.1	24.4	−0.18	0.408	–	–	−1.26	0.408
	Spring	Adult	140.3	14.9	−0.64	0.791	−1.26	0.408	–	–
Migrating distance (km)	Autumn	Juvenile	2067.5	850.2	–	–	2.43	0.038	−0.51	0.863
	Autumn	Sub-adult	2754.6	611.0	2.43	0.038	–	–	1.95	0.120
	Autumn	Adult	2250.7	506.4	−0.51	0.863	1.95	0.120	–	–
	Spring	Juvenile	3496.8	931.9	–	–	−2.15	0.077	3.31	0.003
	Spring	Sub-adult	2593.6	631.7	−2.15	0.077	–	–	1.79	0.169
	Spring	Adult	2070.5	436.2	3.31	0.003	1.79	0.169	–	–

RESULTS

Autumn migration

We collected 13 complete (seasonal) autumn tracks from 12 birds and 11 daily tracks from 10 birds (Table 1). Eagles departed from the summering grounds between 11 August and 17 December, with sub-adults departing earliest (n = 3; 24 September ± 30.8 days (95% confidence interval, CI)), followed by adults (n = 8; 18 October ± 16.4 days) and juveniles (n = 2; 23 October ± 42.2 days;

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Fig. 2). Eagles flew south through the daily study region between 28 October and 12 January (Fig. 2). Adults and juveniles took the shortest time to migrate south and sub-adults the longest time

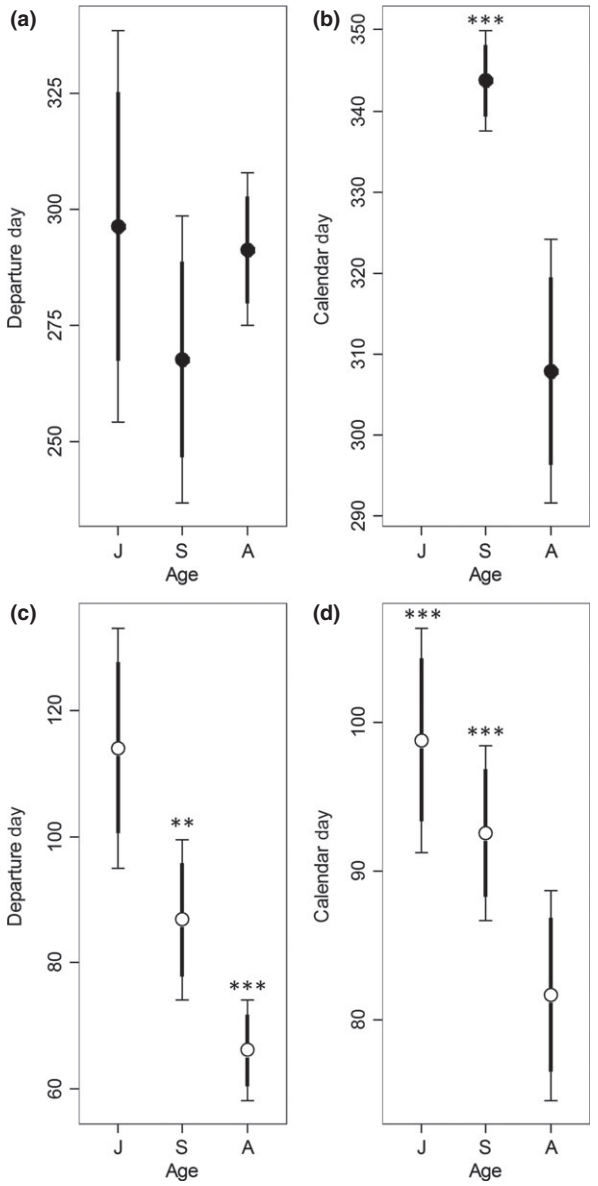

Figure 2. Modelled estimates of departure dates (shown as calendar day, with 1 January = day 1) with 85% (bold) and 95% confidence intervals for (a) autumn (black circles) and (c) spring (white circles) complete tracks and calendar day of daily tracks through the PA study area during (b) autumn and (d) spring of migration of Golden Eagles *Aquila chrysaetos* in eastern North America (2007–2013) by age-class (J = juvenile, S = sub-adult, A = adult). Asterisks indicate differences from adults: $*P < 0.1$, $**P < 0.5$, $***P < 0.001$.

(Table 2, Fig. 3). Juveniles were only tracked from the southern breeding grounds, which is likely to have had an effect on the number of days and distance travelled. Adult birds actively migrated (moved ≥ 30 km in the direction of migration) on 57 ± 10% of days (Table 2, Fig. 3). Sub-adults spent a slightly lower proportion of days actively migrating than did adults or juveniles. Juveniles spent about the same proportion of days actively migrating as did adults. During autumn, sub-adult Eagles travelled at a slower rate than adults or juveniles, whereas juveniles and adults travelled at similar rates over the entire migration route (Table 2, Fig. 3). When actively migrating, all age-classes travelled at similar rates (Table 2, Fig. S1). However, when we considered rates of daily movements (measured with 30-s data), adults migrated slightly slower than sub-adults (Table 3, Fig. 3). No juveniles were tracked at 30-s intervals through the core study area during autumn migration. The paths flown by adults were somewhat straighter than those flown by sub-adults or juveniles (Table 2, Fig. 3). Measured at a 30-s resolution (daily), adults and sub-adults flew along similarly straight flight paths (Table 3, Fig. 3).

Wind and weather conditions supportive of thermal convection were similar when adults and sub-adults migrated. Best lifted index, an indication of atmospheric stability, and the potential for thermal convection did not differ for adult migration and sub-adult migration (Table 3, Fig. 3). Downward solar radiation was only somewhat higher when sub-adults migrated than when adults migrated (Table 3, Fig. 3). Sensible heat flux was also similar when adults and sub-adults migrated (Table 3, Fig. S1). Tailwinds were similar between age groups (Table 3, Fig. S1). Similarly, side winds did not differ between age groups (Table 3, Fig. S1).

During autumn migration, departure day and distance travelled were positively correlated ($r = 0.92$), whereby for every 100 km increase in distance travelled, departure day was 2.4 days earlier. Because of the high correlation between these variables, we ran separate models including either departure day or distance travelled (Table 4). Comparison of the two models showed more support for departure day rather than distance ($AIC_{Day} = -9.1$, $AIC_{km} = -5.3$). Therefore, we report the model results only from the model including departure day.

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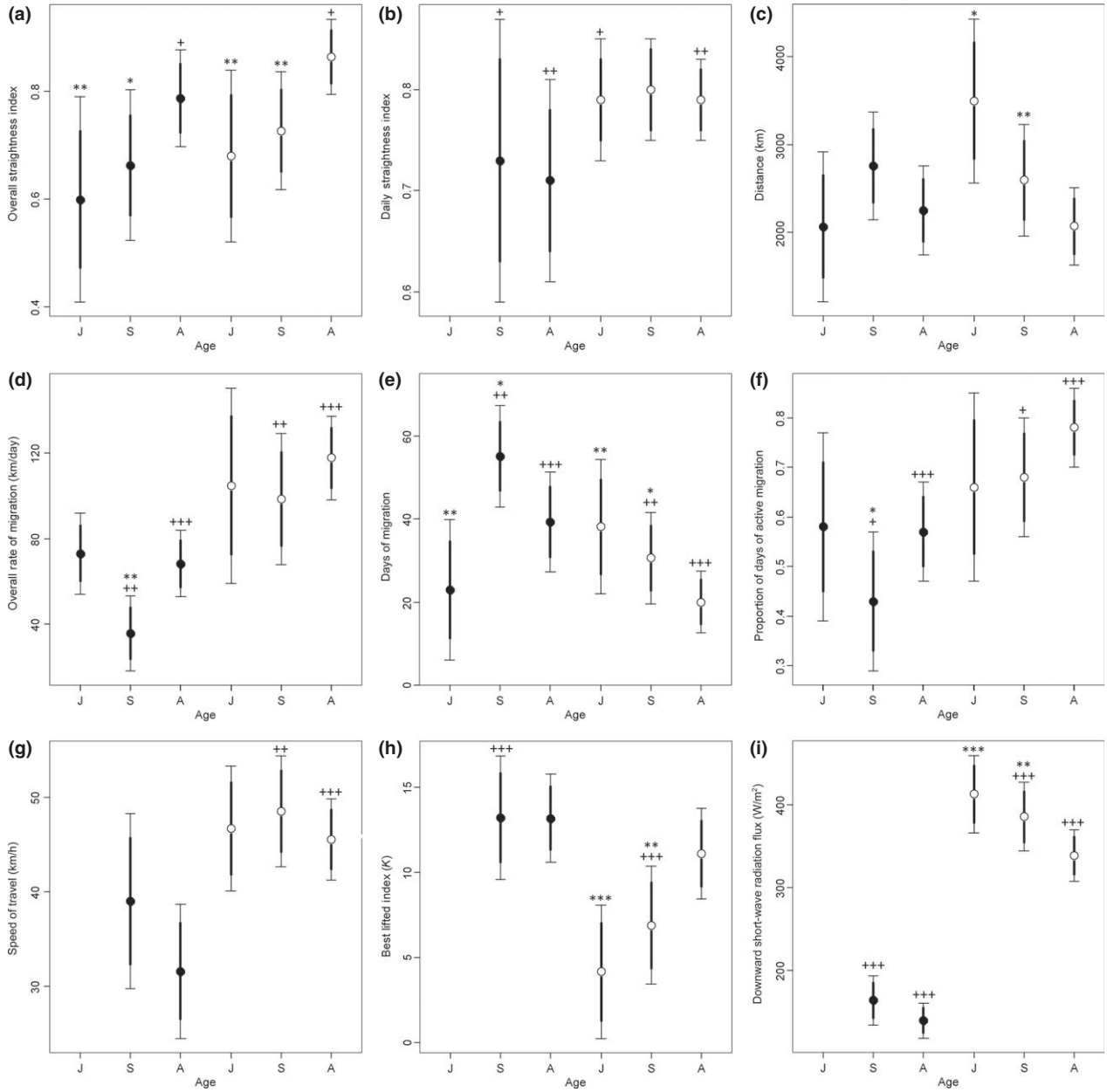

Figure 3. Modelled estimates with 85% (bold) and 95% confidence intervals for (a) straightness index of complete migration tracks, (b) straightness index of daily migration tracks, (c) total distance migrated (km), (d) rate of migration including stopover (km/day), (e) total number of migration days, (f) proportion of days spent actively migrating, (g) speed of travel (km/h) of daily migration tracks, (h) best lifted index (*K*) and (i) downward short-wave radiation flux (W/m^2) for autumn (black circles) and spring (white circles) for juvenile (J), sub-adult (S) and adult (A) Golden Eagles *Aquila chrysaetos* in eastern North America (2007–2013). Asterisks indicate modelled results of within-season differences from adults: $*P < 0.1$, $**P < 0.5$, $***P < 0.001$. Plus signs indicate between-season differences within each age group: $+P < 0.1$, $++P < 0.5$, $+++P < 0.001$.

Departure day and juvenile age had the greatest effects on straightness of complete migratory tracks (Fig. 4, Table S7). Birds that left later flew shorter distances and had straighter flight paths than birds that left earlier. This was consistent among age-classes. However, juveniles followed much less direct paths than adults or sub-adults.

For the daily flight path analysis, we found that some weather variables were correlated with each other and so kept only those variables that we

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Table 3. Modelled means and 95% confidence intervals by age and season for univariate GLMMs of metrics measured for daily migration tracks for Golden Eagles *Aquila chrysaetos* migrating during autumn and spring in eastern North America (2009–2012). Tukey *post-hoc* multiple comparisons indicate within-season age-related differences among each metric.

					Post-hoc comparisons					
			Model results		Juvenile		Sub-adult		Adult	
Metric	Season	Age	Mean	95% CI	*z*	*P*	*z*	*P*	*z*	*P*
Straightness index	Autumn	Juvenile	–	–	–	–	–	–	–	–
	Autumn	Sub-adult	0.73	0.14	–	–	–	–	0.23	0.817
	Autumn	Adult	0.71	0.10	–	–	0.23	0.817	–	–
	Spring	Juvenile	0.79	0.06	–	–	0.49	0.875	−0.09	0.996
	Spring	Sub-adult	0.80	0.05	0.49	0.875	–	–	0.43	0.902
	Spring	Adult	0.79	0.04	−0.09	0.996	0.43	0.902	–	–
Calender day	Autumn	Juvenile	–	–	–	–	–	–	–	–
	Autumn	Sub-adult	343.7	6.2	–	–	–	–	11.96	<0.001
	Autumn	Adult	307.9	16.2	–	–	11.96	< 0.001	–	–
	Spring	Juvenile	98.8	7.5	–	–	−2.30	0.053	4.51	<0.001
	Spring	Sub-adult	92.5	5.8	−2.30	0.053	–	–	3.70	<0.001
	Spring	Adult	81.7	7.1	4.51	< 0.001	3.70	< 0.001	–	–
Travel rate (km/h)	Autumn	Juvenile	–	–	–	–	–	–	–	–
	Autumn	Sub-adult	39.0	9.3	–	–	–	–	1.67	0.110
	Autumn	Adult	31.6	7.1	–		1.67	0.110	–	–
	Spring	Juvenile	46.7	6.6	–		0.56	0.840	0.36	0.933
	Spring	Sub-adult	48.5	5.9	0.56	0.840	–	–	1.01	0.569
	Spring	Adult	45.5	4.3	0.36	0.933	1.01	0.569	–	–
Best lifted index	Autumn	Juvenile	–	–	–	–	–	–	–	–
	Autumn	Sub-adult	13.2	3.7	–	–	–	–	0.02	0.985
	Autumn	Adult	13.2	2.6	–	–	0.02	0.985	–	–
	Spring	Juvenile	4.2	3.9	–		1.50	0.289	−3.51	0.001
	Spring	Sub-adult	6.9	3.5	1.50	0.289	–	–	−2.42	0.041
	Spring	Adult	11.1	2.7	−3.51	0.001	−2.42	0.041	–	–
Downward solar radiation (W/m^2)	Autumn	Juvenile	–	–	–	–	–	–	–	–
	Autumn	Sub-adult	163.8	29.5	–	–	–	–	1.71	0.103
	Autumn	Adult	139.7	21.1	–	–	1.71	0.103	–	–
	Spring	Juvenile	412.6	46.7	–	–	−1.24	0.432	3.14	0.005
	Spring	Sub-adult	385.2	41.6	−1.24	0.432	–	–	2.22	0.067
	Spring	Adult	338.7	31.0	3.14	0.005	2.22	0.067	–	–
Sensible heat flux (W/m^2)	Autumn	Juvenile	–	–	–	–	–	–	–	–
	Autumn	Sub-adult	−21.4	32.3	–	–	–	–	−0.04	0.965
	Autumn	Adult	−20.7	21.4	–	–	−0.04	0.965	–	–
	Spring	Juvenile	44.7	49.7	–	–	−1.76	0.183	0.83	0.681
	Spring	Sub-adult	3.8	44.1	−1.76	0.183	–	–	−0.90	0.638
	Spring	Adult	23.8	33.3	0.83	0.681	−0.90	0.638	–	–
Side winds (m/s)	Autumn	Juvenile	–	–	–	–	–	–	–	–
	Autumn	Sub-adult	3.7	2.7	–	–	–	–	−0.18	0.086
	Autumn	Adult	4.0	1.9	–	–	−0.18	0.086	–	–
	Spring	Juvenile	2.7	1.1	–	–	1.01	0.571	−0.22	0.973
	Spring	Sub-adult	3.2	0.9	1.01	0.571	–	–	0.86	0.665
	Spring	Adult	2.8	0.7	−0.22	0.973	0.86	0.665	–	–
Tailwinds (m/s)	Autumn	Juvenile	–	–	–	–	–	–	–	–
	Autumn	Sub-adult	0.2	2.7	–	–	–	–	−0.93	0.362
	Autumn	Adult	1.4	1.8	–	–	−0.93	0.362	–	–
	Spring	Juvenile	1.9	1.6	–	–	−0.06	0.998	0.08	0.996
	Spring	Sub-adult	1.8	1.4	−0.06	0.998	–	–	0.3	0.999
	Spring	Adult	1.8	1.0	0.08	0.996	0.03	0.999	–	–

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Table 4. Fixed and random effects of initial linear mixed-models of flight path straightness for migratory Golden Eagles *Aquila chrysaetos* migrating in eastern North America (2007–2013). Variance structures were defined when there was heterogeneity of the residuals.

Model	Fixed effects	Random effects	Variance structure
Complete			
Autumn[a]	Juvenile + sub-adult + male + departure day + migration rate	Bird	None
Spring[a]	Juvenile + sub-adult + male + departure day + distance + migration rate + juvenile [a] distance + sub-adult [a] distance	Bird	varExp ~ Migration Rate
Daily			
Autumn[a]	Sub-adult + male + region + calendar day + distance + speed + best lifted index + downward solar radiation + sensible heat flux + | side wind | + tail wind	Bird nested in year	None
Spring Pre-adult[b]	Sub-adult + male + region + calendar day + distance + speed + best lifted index + downward solar radiation + sensible heat flux + | side wind | + tail wind	Bird	None
Spring Adult[a]	Male + region + calendar day + distance + speed + best lifted index + downward solar radiation + sensible heat flux + | side wind | + tail wind	Bird	None

[a]Reference category is adult female. [b]Reference category is juvenile female.

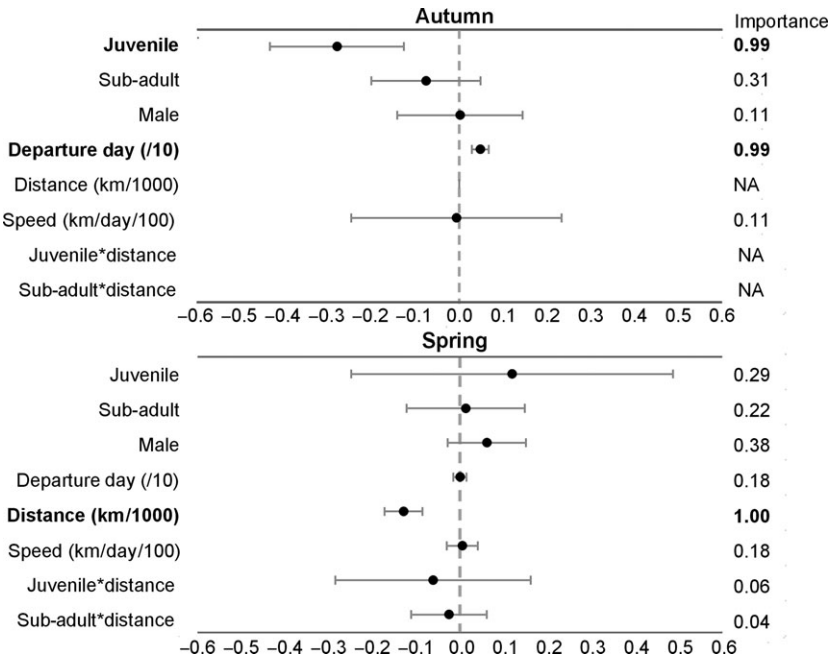

Figure 4. Effect sizes, confidence intervals and variable importance for response variables of complete flight path straightness for Golden Eagle *Aquila chrysaetos* spring and autumn migratory tracks. Bold variables have moderate to strong relative variable importance, which is the sum of AIC_c weights for all models in which the variable was included.

expected to influence flight behaviour most. We removed from the analysis temperature, pressure and relative humidity (these were correlated with best lifted index, $r = -0.60$; sensible heat flux, $r = 0.59$; and downward solar radiation, $r = -0.54$, respectively). Straightness of daily flight paths during autumn was influenced by region ($w = 0.65$) and path length ($w = 0.72$) and somewhat influenced by best lifted index ($w = 0.56$; Fig. 5, Table S8). Flight paths through the Ridge and Valley province were more direct than those through other regions, and the length of daily tracks was positively correlated with straighter flight paths. More stable atmospheric conditions, those less conducive to thermal convection, were associated with more direct flight paths.

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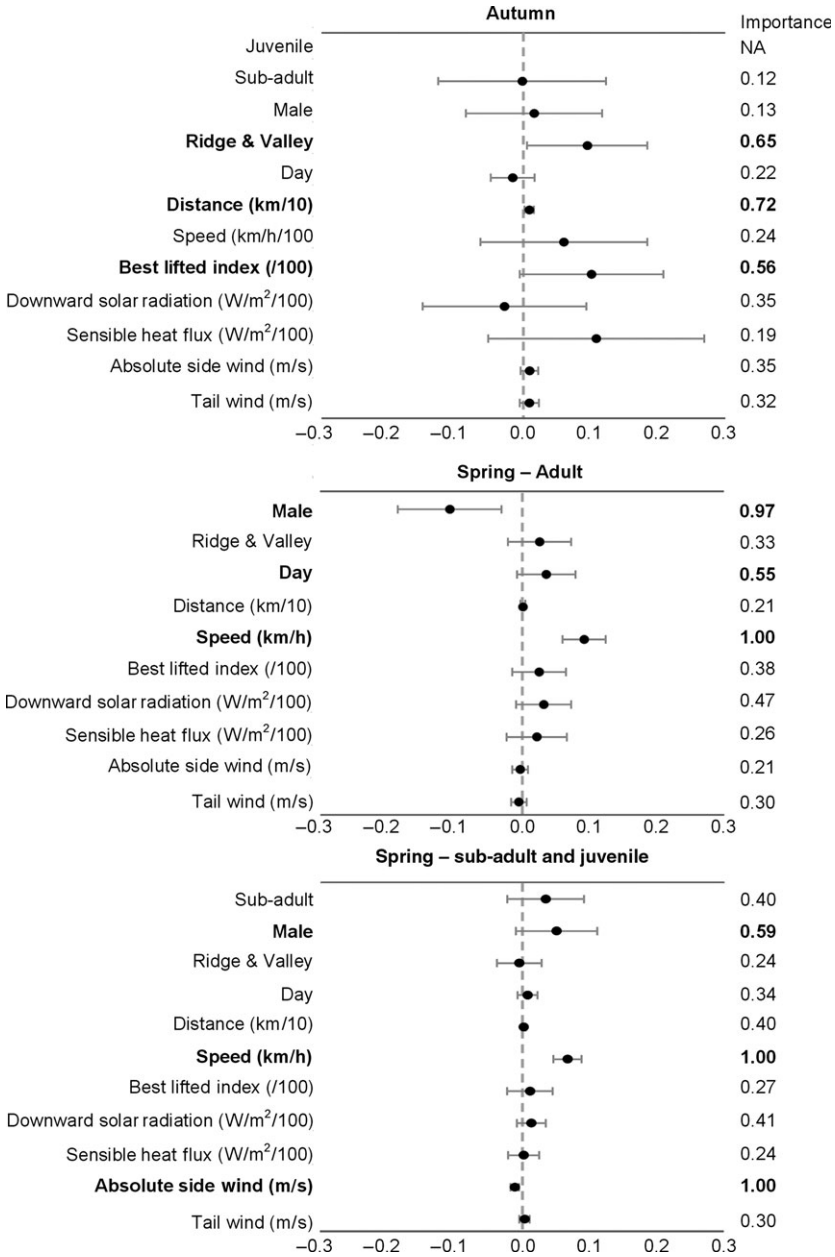

Figure 5. Effect sizes, confidence intervals and variable importance for response variables of flight path straightness for Golden Eagle *Aquila chrysaetos* autumn and spring daily migratory tracks. Autumn model includes adults and sub-adults. Results for two spring models, one for adults and one for non-adults, are shown. Variables in bold have moderate to strong relative variable importance, which is the sum of AIC_c weights for all models in which the variable was included.

Spring migration

During spring migration, we collected 37 complete tracks from 22 birds and 142 daily tracks from 34 birds (Table 1). Eagles departed the wintering grounds between 12 February and 11 May. Departure day was strongly staggered by age-class, with adults departing the earliest (n = 12; 7 March ± 7.9 days), followed by sub-adults (n = 9; 27 March ± 12.7 days) and then juveniles (n = 4; 24 April ± 19.0 days; Table 2, Fig. 2). Eagles flew through the daily study area from 15 February to 18 May (Fig. 2). It took adults far less time to reach their northern destination (20.0 ± 7.5 days) than it

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took sub-adults (30.6 ± 11.0 days) or juveniles (38.1 ± 16.2 days; Fig. 3). All age-classes spent about the same proportion of days actively migrating; adults actively migrated on 78 ± 8% of days, sub-adults on 68 ± 12% of days and juveniles on 66 ± 19% of days (Table 2, Fig. 3). Rate of travel over the course of the entire migration and rate of travel during active migration were similar among all age-classes (Table 2, Fig. 3, Fig. S1). Likewise, speed of daily flights varied little among age-classes (Table 3, Fig. 3). As in autumn, adults flew along straighter paths than did sub-adults and juveniles (Table 2, Fig. 3). Daily flight path straightness did not differ among age-classes (Table 3, Fig. 3).

During migration, weather conditions supportive of thermal convection differed among age-classes, whereas winds did not. Downward solar radiation was much higher when juveniles and sub-adults migrated than when adults migrated (Table 3, Fig. 3). There was a similar trend for best lifted index, an indication of atmospheric stability. The atmosphere was much less stable (more conducive to thermal development) when juveniles and sub-adults migrated than when adults migrated (Table 3, Fig. 3). Conversely, sensible heat flux was highly variable and did not differ among age groups (Table 3, Fig. S1). Both tailwinds and side winds were similar among all age groups (Table 3, Fig. S1).

The most important factor influencing migratory performance (straightness) of complete spring migratory tracks was the distance travelled between wintering and summering grounds (w = 1.0, Fig. 4, Table S7). Those birds that flew longer distances had less direct flight paths than those that travelled shorter distances.

The strong temporal segregation of migration among age-classes and the differences in weather variables related to thermal convection suggested that there could be variation in the influence of weather on migratory performance. Therefore, rather than including complex age–weather interactions, we ran two separate models, one for adults, which migrated early in spring, and one for sub-adults and juveniles, which migrated later in spring (Table 4). As was the case in autumn, temperature, pressure and relative humidity were removed from the spring daily models. All three variables were correlated with best lifted index (r = 0.84, r = 0.67, r = −0.59, respectively). Relative humidity was also correlated with downward solar radiation (r = −0.60). Straightness of sub-adult and juvenile flight paths were strongly associated with speed (w = 1.0) and weather where higher side wind speeds resulted in less direct paths (w = 1.0; Fig. 5, Table S8). Path straightness was moderately associated with sex (w = 0.59), whereby young males flew more directly than young females.

Straightness of adult flight paths was not affected by weather, but was strongly associated with speed of travel (w = 1.0) and sex (w = 0.97; Fig. 5, Table S8). Adults that flew faster followed more direct routes. The effect of sex was opposite that of younger birds, in which adult females flew along more direct paths than adult males. There was a weak association with calendar day (w = 0.55), whereby flights later in the season were more direct than those earlier in the season.

Seasonal differences

Adult and sub-adult Golden Eagles spent more time migrating south during autumn than they did migrating north during spring, whereas juveniles took about the same amount of time (Fig. 3, Table S3). Rate of migration by adults was much slower during autumn than during spring, but it was only somewhat slower in autumn for sub-adults, and did not differ among seasons for juveniles (Fig. 3, Table S3). Adults also travelled at a higher rate of speed on days of active migration during spring than during autumn. However, there were no seasonal differences for sub-adults or juveniles (Table S3, Fig. S1). Adults spent about 20% fewer days actively migrating during autumn than during spring, whereas sub-adults spent about 12% fewer days and juveniles showed no seasonal differences in the proportion of days actively migrating (Fig. 3, Table S3).

Adults and sub-adults travelled similar distances during each season (Fig. 3, Table S3). Juveniles travelled slightly further during spring than during autumn, but this trend could have been affected by the fact that the two juveniles that we tracked during autumn were telemetered in the nest on the Gaspé Peninsula, QC, in the southern-most part of the breeding range and spring migrant juveniles were not always of known origin. Nonetheless, the autumn migrant juvenile that retained its transmitter over winter and was tracked during spring did not return to his natal area. Instead, he bypassed this area and migrated to the northern part of the breeding range, over 1000 km north of his natal area on the Gaspé Peninsula.

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Adults flew along slightly straighter paths during spring than during autumn, whereas juvenile and sub-adults flew similarly straight paths between seasons (Fig. 3, Table S3). For daily routes, adults flew more directly during spring than during autumn, and sub-adults somewhat more directly (Fig. 3, Table S3).

Weather conditions that are supportive of thermal convection also differed seasonally. Best lifted index, an indication of atmospheric stability, did not differ between seasons for adults, but was much higher (more stable) during autumn than spring migration of sub-adults (Fig. 3, Table S4). Downward solar radiation was much higher during spring than during autumn migration of both adults and sub-adults (Fig. 3, Table S4). Conversely, sensible heat flux was only slightly lower during autumn than spring and did not differ for sub-adult migrations. Adults used similarly supportive tailwinds each season, whereas sub-adults used somewhat more supportive tailwinds during spring than during autumn (Table S4, Fig. S1). Conversely, adults flew on days with somewhat high lateral wind speeds during autumn than during spring, whereas sub-adults flew on days with similar lateral wind speeds during both seasons (Table S4, Fig. S1).

Grand means generated from the raw data are presented in Tables S5 and S6.

DISCUSSION

Time and energy demands on animals living at high latitudes are great and may be particularly constraining for species that migrate (Greenberg 2005, Helm *et al.* 2005). Although studies of migration ecology typically suggest that animals are either time- or energy-limited (Hedenström 1993), it is becoming more apparent that there exists a continuum of limitations (Alerstam 2011). Correspondent with the hypothesis that birds face different limitations at different times of their lives and of the year, we found multiple time and energy constraints on the migratory behaviour of Golden Eagles. Where an individual fell along this continuum depended on a suite of intrinsic and extrinsic factors. Although this continuum was apparent during both seasons, energetic constraints appeared to be more important to all birds migrating during autumn and to young birds during spring. Conversely, implied time limitations had greater importance for migratory behaviour and performance of adults during spring. This seasonal and age-specific variation in movement strategies has direct consequences for our understanding of how and why birds make migration decisions.

The importance of time

Time-minimization strategies are used by birds when early arrival at the destination is thought to be important, such as when it will improve survival or increase the potential for successful reproduction (Sergio *et al.* 2014). Such selective pressures should result in higher migratory performance – decreased compensation for wind drift (more direct flight paths) and decreased time spent in stopover (faster overall travel rate). Rate of migration is determined by a combination of the fuelling rate (the time spent at stopover; Alerstam & Lindström 1990), the speed of travel while actively migrating, the number of hours travelled per day and the directness of flight paths (Sergio *et al.* 2014). For soaring birds, the speed of travel while actively migrating is directly affected by the sources, strength and availability of updrafts, where use of thermal updrafts results in higher cross-country speeds than does the use of orographic (deflected) updrafts (Duerr *et al.* 2012). Orographic updrafts are dependent on a combination of topography and wind conditions and consequently constrain route choice. In contrast, thermal updrafts are dependent on solar heating and, although they subject birds to wind drift, they provide more freedom to choose a more direct route (Sergio *et al.* 2014). Due to the position of the sun relative to the earth, thermals are stronger and more available during spring, especially later in spring, than during autumn migration (Kerlinger 1989, Duerr *et al.* 2014), thus providing a subsidy for faster travel rates during spring.

All the Golden Eagles in all age-classes travelled much faster during spring than during autumn, probably because weather conditions then were more supportive of the development of thermals. However, during spring, adult birds travelled earlier, when convective updrafts were less available than they were when younger birds migrate. Despite this, spring migrating adults had the highest migratory performance of any group (they travelled along the straightest routes) and they were the only age-class that appeared to minimize flight time. In fact, spring migrating adults flew along

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straighter flight paths than they did during autumn, they departed the earliest, had low variability of departure dates and flew straighter than any other age-class. Moreover, they spent far less time migrating north than south. They did this by spending more days actively migrating, spending fewer days in stopover, and by travelling faster. In spring, adults increased their hourly travel rate by 12 km/h over their rate in autumn. Furthermore, on days actively migrating, adults increased their rate by over 45 km/day, and they increased their overall travel rate by more than 63 km/day. Based on the evaluation of directness of flight paths, speed and timing of migration, it appears that adult Golden Eagles migrating in spring mainly used a time-minimization strategy.

Survival and lifetime reproductive output are the two most approximate measures of true fitness (Hedenström 2008). The time spent migrating during spring may be minimized if there is high pressure to arrive early on the breeding grounds or if the probability of survival increases with decreased time spent migrating (Alerstam & Lindström 1990). As Golden Eagles are apex predators and predation is unlikely, pressure to arrive early on breeding grounds seems the most likely driver of the behaviour we observed. In fact, Golden Eagles actively defend nest-sites and territories, where males are the primary territory holder (Watson *et al.* 2010). They tend to nest solitarily, unless nest-sites are limited. Moreover, in eastern North America, they nest at high latitudes, where seasonally abundant food is almost certainly limited during the winter. Departure times, therefore, probably evolved in a balanced response to intense pressure to arrive early (when breeding territories are still available) but not too early (before food is available).

The importance of energy

Energy-minimization strategies are thought to be selected for when food is scarce, relative to energetic needs (Alerstam & Lindström 1990). Energy use is minimal when the cost of flying is reduced (Hedenström & Alerstam 1995). During flight, the amount of energy used can be reduced by limiting flying to times when optimal conditions exist and, when in flight, by not compensating fully for wind drift until near the destination (Alerstam 1979, Spaar & Bruderer 1996). Both of these behaviours result in less direct flight paths, which is equated with lower migratory performance. Many species of birds have been found to use an energy-minimization strategy during migration.

Duerr *et al.* (2014) found that Golden Eagles migrating south during autumn selected optimal conditions for flight, i.e. tailwinds and conditions supportive of thermal updraft. This is consistent with previously published work suggesting that good soaring conditions may be the most important constraint on migratory performance and speed of migration (Newton 2008). In this case, the biggest constraint on the migration rates we observed is likely to be day length, because this has the greatest effect on thermal strength and availability. In addition to flying when conditions were best for soaring flight, birds may spend relatively more time feeding during autumn than spring. Eagles in our study spent just over half of days during the migration period travelling south and therefore slightly less than half of migration time at stopover sites. This pattern was consistent across age-classes, suggesting that during autumn migration all age-classes of eagles benefit from use of energy-minimization strategies. These behaviours are consistent with reducing energetic costs of flight and increasing energy intake and logically would be selected for if there is no fitness benefit to reaching the wintering grounds early. Such behaviours might be especially important if there is selective pressure to reach the wintering grounds in optimal physical condition. This could occur if food is limited, sparsely distributed or difficult to find during migration or on wintering grounds (Newton 2008).

Our data highlight important differences between spring and autumn flight conditions and correspondent migration speeds. However, they also suggest that during autumn migration the effects of energy and time may be confounded. Staying later on the summering grounds (which has benefits if it appears feasible to overwinter on breeding grounds, a strategy Golden Eagles sometimes use) may cause these later departing birds to become more time-limited. For instance, food availability may rapidly decrease after a certain point in time. Those birds that we studied that departed later flew more directly than those departing earlier. Additionally, birds travelling longer distances left earlier (2.4 days for every 100 km) than did those travelling shorter distances. However, travel rate (km/day) did not vary

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by either distance travelled or departure date. Because there are fewer daylight hours as autumn progresses, birds that departed later had less time available each day to migrate. Thus, the only way that late-departing birds may be able to decrease the amount of time they spend migrating is by travelling along more direct routes.

There are energetic consequences to travelling along more direct routes. Eagles typically reduce energetic costs of migration by subsidizing migratory flight with updrafts, especially thermal updrafts (Lanzone *et al.* 2012, Katzner *et al.* 2015). However, autumn migration occurred when the atmosphere was relatively stable (best lifted index is high), resulting in weaker thermal convection than during spring migration (Kerlinger 1989). Other species that use subsidy to reduce costs of flight show behavioural plasticity in responses to variation in available updrafts (Maransky *et al.* 1997), and Golden Eagles are no exception (Lanzone *et al.* 2012). In addition to switching from thermal soaring to slope soaring as conditions permit, birds may use powered flight after other sources of lift are no longer available. This behavioural plasticity in flight response incurs energetic costs but would allow birds to extend the amount of time that they can migrate each day. Such a strategy is an indication of time limitations (Hedenström 1993).

Spring migrants appeared to respond differently to temporal limitations than did autumn migrants. While time limitation was most important for adults during spring, some migrating adult Golden Eagles also appeared to employed energy-minimization strategies. In particular, adults that travelled longer distances during spring took less direct routes than those travelling shorter distances. These less direct routes may be a result of birds attempting to conserve energy by decreasing compensation for wind drift (Alerstam & Lindström 1990, Alerstam 2011).

Beyond time and energy

Migratory performance is likely to be influenced by other mechanisms beyond time and energy, possibly including orientation ability, experience, exploration and weather. Like other species (Mueller *et al.* 2013, Sergio *et al.* 2014), Golden Eagles showed a clear pattern of improvement of migratory performance with age, which suggests learning (Thorup *et al.* 2003, Mueller *et al.* 2013). Learning can play out in many different ways for eagles. Familiarity with migratory routes is an essential component of spatial learning and is necessary for the navigation and orientation techniques used by older birds (Perdeck 1958, Mettke-Hofmann & Gwinner 2003). Because of route familiarity, orientation ability also is expected to differ between adult and juvenile birds (Drost 1938). Juvenile Golden Eagles in autumn make their first migratory journey along a novel route to an unknown destination. Of all the birds we studied, these had the lowest migratory performance. During this life stage, juveniles are likely to be vector-orientated – they migrate in a specific direction (Perdeck 1958). In contrast, older birds are goal-orientated migrants – they travel toward a specific, known destination (Alerstam & Lindström 1990, Alerstam 2011). Although our sample size was small, the two juvenile birds orientated more-or-less south and their migration paths did not coincide with those of the adults that occupied the same general breeding area. During spring, juveniles also appeared to be vector-orientated, travelling more-or-less north. The slight improvement they showed in performance during spring may have been due to a combination of experience gained during autumn migration and the more supportive weather conditions they experienced.

Exploration may also affect migratory performance, especially by altering timing of departure, duration of migration and directness of flight. However, there may be more important long-term fitness benefits that favour exploration. These may be especially significant during southbound migration of sub-adults that are facing an increasing pressure to find breeding territories. In autumn, those birds may thus benefit by departing early from their summering areas and exploring for territories while migrating southbound. Exploration at this time may bring multiple benefits because it allows birds extensive time to make their way south while simultaneously prospecting for high-quality territories. Prospecting during late summer and early autumn increases the odds of encountering locally fledged juveniles whose presence can indicate quality of a local breeding territory (Cadiou 1999, Schjørring *et al.* 1999). Although prospecting may be essential for survival, spatial learning and ultimately higher reproductive output, it also results in lower migratory performance. In the end, lower migratory performance during

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the pre-adult stage may be more important to the overall fitness of the individual, as spatial learning in this period should lead to higher migratory performance later in life when migratory performance should have more profound effects on reproductive output.

Weather conditions, especially winds (Spaar & Bruderer 1996), also can affect migratory performance (Alerstam 1979, Spaar & Bruderer 1997, Klaassen *et al.* 2008, Kemp *et al.* 2010). Winds may be used selectively to reduce energetic costs. We found that during spring, faster side winds reduced daily migratory performance of young birds. This is likely to be because thermal development was stronger when young eagles migrated and lateral winds drift thermals, pushing birds off course (Kerlinger 1989). Likewise, during autumn, birds flew more directly when atmospheric conditions were more stable (best lifted index was higher). This is likely to be because stable conditions (higher pressure, lower temperature, lower relative humidity) generally suppress thermal convection or only allow weak thermal development (Kerlinger 1989). Under such conditions, birds must rely more on other sources of uplift, such as orographic updrafts, powered flight or even mountain waves (Reichmann 1978). Flight in such conditions is more closely tied to topography and consequently slower (Duerr *et al.* 2012, 2014). The resulting flight paths are therefore more tortuous in broken terrain but more direct in regions with long, linear ridges (e.g. the Ridge and Valley Province of the Appalachians).

We found differences between males and females with respect to daily migratory performance. Adult females migrated more directly than adult males, whereas young females migrated less directly than young males. Others have found differences between the sexes in duration and timing of migration, which are thought to be adaptive traits under endogenous control (Ketterson & Nolan 1983, Terrill & Berthold 1989, Holberton 1993). Timing alone could result in variation in flight behaviour if there are strong differences in weather conditions. However, there may be other reasons (e.g. morphology, feeding/hunting behaviour en route) for the differences that we observed.

Interestingly, within each season, when birds chose to migrate, daily migratory performance did not differ among age-classes and it was not reflective of overall migratory performance. However, although mean daily performance of all birds was similar, those of different ages responded differently to the same environmental conditions. For example, weather influenced daily migratory performance of birds that behaved in an energy-limited manner (all autumn migrants and non-adult spring migrants) such that when conditions were stable, routes were more direct. This may be because energy-limited migrants and those that are less experienced may not compensate fully for drift that occurs when using thermal uplift (Alerstam 1979, Spaar & Bruderer 1996, Thorup *et al.* 2003). In contrast, weather did not influence daily performance of time-limited adults, whose routes were similarly direct regardless of atmospheric stability. These birds appeared more capable or perhaps more driven to compensate for drift or other performance-reducing weather conditions over the course of the entire migration period. Together, these trends suggest that the scale at which performance is measured has important implications for how we understand influences of time, energy and other factors on migration.

CONCLUSION

Optimal migration theory suggests that birds employ strategies to minimize time spent migrating, to balance energetic costs or to maximize safety (Alerstam & Lindström 1990, Alerstam 2011). Hypotheses about time and energy limitation are often presented as mutually exclusive (Hedenström 1993) but the existence of a continuum of limitations is more realistic (Alerstam 2011). We found evidence supporting this non-exclusive alternative, in that Golden Eagles appeared to use a mix of both time- and energy-minimization strategies and that the balance between the two was affected by age, location and timing. Adult Golden Eagles migrating during autumn, and sub-adults and juveniles migrating in all seasons appeared to minimize the energetic costs of migration. In spite of this energy-minimization strategy, as the autumn progresses, individuals of all age-classes also become time-limited. During spring, adults switch to a time-limited strategy. Unexpectedly, however, the trade-off between time and energy was evident also during spring, when longer distance migrants apparently engage in some form of energy-minimization.

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Although migration strategies fall along a continuum of time and energy optimization, this study also shows that migratory performance cannot be disentangled from mechanisms beyond time and energy.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Data from 58 complete migration tracks of Golden Eagles *Aquila chrysaetos* in eastern North America (2007–2013).

Table S2. Data from 174 daily migration tracks of Golden Eagles *Aquila chrysaetos* in the mid-Appalachian Mountains, USA (2009–2012).

Table S3. Modelled means and 95% confidence intervals by age and season for univariate GLMMs of metrics measured for complete migration tracks for Golden Eagles *Aquila chrysaetos* migrating during autumn and spring in eastern North America (2007–2013).

Table S4. Modelled means and 95% confidence intervals by age and season for univariate GLMMs of metrics measured for daily migration tracks for Golden Eagles *Aquila chrysaetos* migrating during autumn and spring in eastern North America (2009–2012).

Table S5. Grand means of raw data for complete migration tracks of Golden Eagles *Aquila chrysaetos* in eastern North America (2007–2013). *N* indicates the number of unique individuals of each age-class.

Table S6. Grand means of raw data for daily migration tracks of Golden Eagles *Aquila chrysaetos* in eastern North America (2009–2012). *N* indicates the number of unique individuals of each age-class.

Table S7. Mixed model results of straightness index for complete migration tracks of Golden Eagles *Aquila chrysaetos* in eastern North America during autumn and spring (2007–2013).

Table S8. Mixed model results of straightness index for daily migration tracks of Golden Eagles *Aquila chrysaetos* in eastern North America during autumn and spring (2009–2012).

Figure S1. Modelled estimates with 85% and 95% confidence intervals for rate of migration on days actively migrating distance (km/day), number of days spent actively migrating, sensible heat flux (W/m^2), speed of tailwinds (m/s) and absolute speed of side winds (m/s) for each age-class and season of Golden Eagles *Aquila chrysaetos* in eastern North America (2007–2013).

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