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Flight response of slope-soaring birds to seasonal variation in thermal generation

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Summary

1. Animals respond to a variety of environmental cues, including weather conditions, when migrating. Understanding the relationship between weather and migration behaviour is vital to assessing time- and energy limitations of soaring birds. Different soaring modes have different efficiencies, are dependent upon different types of subsidized lift and are weather dependent.

2. We collected GPS locations from 47 known-age golden eagles that moved along 83 migration tracks. We paired each location with weather to determine meteorological correlates of migration during spring and fall as birds crossed three distinct ecoregions in north-east North America.

3. Golden eagle migration was associated with weather conditions that promoted thermal development, regardless of season, ecoregion or age. Eagle migration showed age- and season-specific responses to weather conditions that promoted orographic lift.

4. In spring, adult eagles migrated earlier, over fewer days, and under more variable weather conditions than did pre-adults, suggesting that adults were time limited and pre-adults made choices to conserve energy. In fall, we found no difference in the time span of migration or when each age class migrates; however, we saw evidence that pre-adults were less efficient migrants than adults.

5. The decision by soaring birds to migrate when thermals developed allowed individuals to manage trade-offs between migratory speed and migratory efficiency. When time was limited (i.e. spring movement of adults speeding towards nesting territories), use of whatever lift was available decreased the time span of migration. When migration was not time limited (e.g. spring movements by pre-adults, all movements in fall), eagles avoided suboptimal flight conditions by pausing migration, thus increasing the time span of migration while reducing energetic costs.

Key-words: *Aquila chrysaetos*, energy-limited, golden eagle, migration, orographic lift, soaring, thermal lift, time-limited, weather

Introduction

Animals respond to cues about environmental condition or habitat quality when they move. Habitat quality, measured as forage availability, forage quality or habitat permeability, influences movement through terrestrial

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environments (Lyons, Collazo & Guglielmo 2008; Avgar *et al.* 2013). Movement through air, such as flight by birds, often is related to weather conditions that support efficient flapping flight (Mitchell *et al.* 2012) or soaring flight (Shamoun-Baranes *et al.* 2006). Thus, for birds, airspace is habitat (Diehl 2013) and weather conditions define habitat quality.

The flight of large birds is restricted by weather conditions and topography that favour development of supplemental lift (Leshem & Yom-Tov 1996; Yates *et al.* 2001; Shannon *et al.* 2002; Shamoun-Baranes *et al.* 2003; Katzner *et al.* 2012a). Supplemental lift for soaring land birds primarily is in the forms of thermal and orographic lift, which corresponds to flight modes of thermal soaring and gliding and orographic soaring (Kerlinger 1989; Alerstam & Hedenstrom 1998). Thermal lift occurs when differential heating of the earth's surface warms air, causing it to rise, sometimes to thousands of metres (type I thermal cells; Hardy & Ottersten 1969; Kerlinger 1989). Orographic lift depends upon upward deflection of horizontal winds by structures, such as trees or ridgelines, and occurs at relatively low altitudes above ground level (Kerlinger 1989; Alerstam & Hedenstrom 1998). Other flight modes that depend on supplemental lift are also weather dependent and include dynamic soaring (e.g. Sachs *et al.* 2012) and use of thermal streets (thermals aligned such that circling is not needed to regain lift; type II thermal cells; Hardy & Ottersten 1969; Kerlinger 1989). Although general weather patterns associated with each flight mode are understood, knowledge is nascent of how soaring birds respond to variation in weather.

Understanding sources of variation in flight behaviour requires pairing weather conditions with animal locations throughout flight (Shamoun-Baranes, Bouten & van Loon 2010; Mandel *et al.* 2011). Soaring birds show different responses to weather conditions in different regions, which show how continental-scale differences in weather affect soaring (Shamoun-Baranes *et al.* 2003; Klaassen *et al.* 2011; Mandel *et al.* 2011). Studies that pair animal locations recorded at high frequencies (up to two locations per minute) with high-resolution environmental data sets provide detailed understanding of variation of flight modes. For example, flight modes shift from thermal soaring and gliding to orographic soaring as wind speeds increase (Lanzone *et al.* 2012). We also know that for some species, thermal soaring and gliding is faster, more direct and energetically more efficient than orographic soaring (Duerr *et al.* 2012). Observations of active selection of one of these flight modes over the other suggest soaring birds may make trade-offs during flight in response to ecological and evolutionary constraints.

Birds face age-specific time and energy constraints that may be especially apparent during migration (Hedenstrom 1993; Hedenstrom & Alerstam 1995, 1997). Adults often are time limited as they face strong selective pressures to arrive at breeding sites early, so they can acquire and defend territories (Sergio *et al.* 2007; Newton 2008); in some cases, arriving before food is abundant (van Wijk *et al.* 2012). Arrival of non-territorial birds onto breeding grounds is not constrained by time because they do not need to arrive early to claim a breeding site. These inexperienced non-breeders also are likely less efficient at obtaining food, thus may be energy limited.

Several predictions follow the time- and energy-limited hypotheses for soaring migrants. First, time limitation should be correlated with decreased migratory efficiency because time-limited animals would migrate whenever conditions permit (e.g. use both orographic and thermal lift; Duerr *et al.* 2012). This would allow time-limited migrants to reduce the number of days spent migrating between wintering and breeding grounds, although they would spend a large proportion of each season migrating. The consequence of such migratory shifts for time-limited animals would be a change in migration timing (e.g. migrate earlier in calendar year), especially relative to energy-limited migrants. Animals that conserve energy during migration should migrate only during conditions that promote the most efficient flight modes (i.e. thermal soaring) and pause migration when less optimal conditions exist (i.e. not use orographic soaring). Pausing migration to wait for optimal weather would increase the total number of days spent in migration while decreasing the proportion of time spent migrating each season.

Golden eagles (*Aquila chrysaetos*) in eastern North America are a useful model both to understand soaring flight responses to changes in weather conditions during migration and to test hypotheses about time- and energy-limited migration. This species is the largest soaring migrant in eastern North America (Allen, Goodrich & Bildstein 1996), and they take advantage of a variety of lift types (Duerr *et al.* 2012; Lanzone *et al.* 2012). Lift types used by eagles may vary throughout their migratory range as they cross several ecological regions with marked differences in topography (Commission for Environmental Cooperation 1997) from the Appalachian Mountains to Quebec, Canada (Katzner *et al.* 2012b). Golden eagle populations are age structured, with breeding generally delayed until at least their fifth year (Watson 2010); thus, we expect that individuals of different ages will have different levels of experience and be under different time and energy constraints.

We tested hypotheses about time- and energy-limited migration of golden eagles with a several step (objectives) process. To do this, we first (Objective 1) determined meteorological correlates of migration and described how these correlates change with season, eagle age and region. Meteorological correlates allow inference about flight modes used by eagles. Second, we placed meteorological correlates into the context of selection of migratory conditions and flight modes by (Objective 2) describing prevailing weather patterns experienced by golden eagles in spring and fall. Third, we (Objective 3) determined how the time span of migration (number of days spent migrating), proportion of season spent in active migration and timing of

migration differed by eagle age and season. Addressing these objectives provides ecological and evolutionary contexts for differences in migratory behaviour that we identify.

Materials and methods

STUDY AREA

Golden eagles are found in five ecoregions of eastern North America (Fig. 1; (Commission for Environmental Cooperation 1997; Katzner *et al.* 2012b). Their winter range includes mainly eastern temperate forest, despite some winter in northern forest, and their breeding range includes northern forest, taiga, tundra and Arctic cordillera. Eastern temperate forest is dominated by mixed broadleaf and evergreen forests. It has a mild climate with warm humid summers and cool to mild winters and a variety of landforms that range from the Appalachian Mountains, large plateaus, ridge and valley systems and coastal plains (Commission for Environmental Cooperation 1997). Northern forest is dominated by cover of boreal evergreen trees; it has many lakes, long cold winters and short warm summers and is characterized by hilly terrain of the Canadian Shield interspersed with shallow to deep moraine deposits. Taiga is dominated by rolling uplands and lowlands and has long and very cold winters and short cool summers, and vegetation varies from bogs, wetlands and boreal forests to open shrublands and sedge meadows. Tundra, with low forms of vegetation and similar topography to taiga, and Arctic cordillera, with bare rocky mountains, both have similar climate to taiga.

DATA COLLECTION FROM EAGLES

We used cannon or rocket nets and bow nets set over bait to capture 47 golden eagles during migration and winter November–March 2006–2012 in Pennsylvania, Virginia and West Virginia, USA and in May 2009 at a nest on the Gaspé Peninsula, Quebec, Canada. Each eagle was aged by plumage and moult characteristics (Jollie 1947; Bloom & Clark 2001) and classified as adult (less than or equal to age 5) or pre-adult (less than age 5). Eagles were outfitted with Cellular Tracking Technologies CTT-1100 GPS-GSM (CTT, Somerset, PA, USA; $n = 44$) or Microwave Telemetry GPS PTT-100s (PTT, Columbia, MD, USA; $n = 3$) telemetry systems attached as backpacks with Teflon ribbon (Bird & Bildstein 2007) and released. Both types of telemetry collect GPS data, but CTT-1100s transmit data through the Global System for Mobile Communication (GSM) network, whereas platform terminal transmitters (PTTs) transmit data through ARGOS weather satellites. Cellular terminal transmitters (CTT) transmitters collected data at 15-min intervals, and PTT transmitters collected data at 1-h intervals. We removed data points when CTTs recorded GPS locations, but other telemetry data (e.g. heading, altitude, speed) were not recorded. We collated and analysed eagle location data from spring and fall migration from November 2006 through December 2012 (Fig. 1).

DATA CLASSIFICATION

We classified each eagle location first by migration period and then as part of migratory or non-migratory flights. We identified migration periods as the series of GPS data points from each individual eagle that connected wintering and breeding ranges. Golden eagles in eastern North America have distinct wintering and breeding territories that encompass their southernmost and northernmost GPS locations (Miller 2012). Within each migration period, we grouped locations from the start to the end of each nominal hour (e.g. 08.00–09.00) and calculated the average tag-recorded flight speed for each nominal hour. 'Migratory' locations included average hourly flight speeds >10 km h^{-1}, and 'non-migratory' locations included flight speeds <5 km h^{-1} (Katzner *et al.* 2012a). Hours in which eagles averaged speeds between 5 and 10 km h^{-1} were classified as intermediate locations. Thus, on a given day, GPS locations from a single eagle could have been classified as migratory, non-migratory and intermediate locations.

We used migration classifications of eagle locations to calculate three measures of time related to migration. The first was time span of migration, which was calculated as the number of days between the first and last day of migration. The second was the proportion of season spent migrating, calculated as the number of migratory GPS locations divided by the total number of GPS locations (flying and perched, daytime and night-time) in a migration season. The third, the migration mid-point, was a measure of when eagles migrated and was calculated as the median calendar day from the time span of migration.

At each eagle location, we used the RNCEP package (Kemp *et al.* 2011) in R (R Core Team 2012) to interpolate weather conditions over space and time from the National Centers for Environmental Prediction/National Centers for Atmospheric

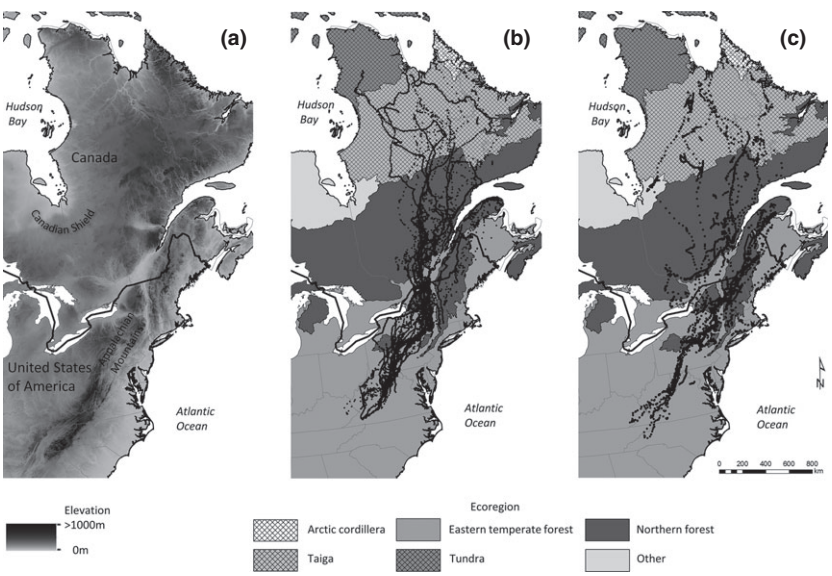

Fig. 1. Study area depicting (a) elevation and major geologic features and (b) spring and (c) fall locations of golden eagles as they migrated across ecoregions of eastern North America, March 2006 to December 2012. Northern ecoregions (Arctic cordillera, tundra and taiga) are cross-hatched and were combined for analyses.

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Research 40-year reanalysis project (Reanalysis II; Kalnay *et al.* 1996). Reanalysis II is a model that predicts values of weather variables (Table 1) at the surface and at four pressure levels above the surface (1000, 925, 850 and 700 mb) (see Appendix S1 in Supporting Information for definitions of select weather variables). At each eagle location, we modified wind variables by including the absolute values of west–east and south–north wind vectors, wind speed (i.e. without a directional component) and a modified value of thermal energy (Δ °C per 100 m; Chevallier *et al.* 2010), in which we substituted geopotential height of pressure levels for height of pressure levels in the standard atmosphere.

Calculating weather conditions at the flight altitude of eagles required an additional interpolation step because flight altitudes of eagles rarely corresponded exactly with altitudes (geopotential height) of pressure levels in the Reanalysis II data set. We linearly interpolated weather variables between geopotential height of pressure levels and the eagle's flight altitude as recorded by the telemetry unit. If the eagle flew below the lowest pressure level (1000 mb), we interpolated between values of weather variables at 1000 mb and at the earth's surface. Surface elevation was determined from the global Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) digital elevation model (produced jointly by US National Aeronautics and Space Administration and Japan's Ministry of Economy, Trade and Industry; http://gdex.cr.usgs.gov/gdex/).

We also classified eagle locations by the level I ecoregion (Commission for Environmental Cooperation 1997) in which they occurred using ArcGIS 10.1 (Esri [SIC], Redlands, CA, USA).

Table 1. Weather variables from NCEP/NCAR Reanalysis II data set interpolated to space and time of golden eagle locations in northeast North America during migration, March 2006–December 2012

Weather variable	Measurement units	Atmospheric level
Air temperature	°C	Surface, 1000, 925, 850, 700 mb
Barometric pressure*	mm mercury	Surface
Best-lifted index	°K	Surface
Downward solar radiation flux†	W m^{-2}	Surface
Geopotential height	m	1000, 925, 850, 700 mb
Latent heat flux†	W m^{-2}	Surface
Omega (vertical velocity)	Pascal s^{-1}	Surface, 1000, 925, 850, 700 mb
Precipitable water	kg m^{-2}	Surface to 300 mb
Precipitation rate (>0)†	kg m^{-2} s^{-1}	Surface
Relative humidity	%	Surface, 1000, 925, 850, 700 mb
Sensible heat flux†	W m^{-2}	Surface
South–north wind vector	m s^{-1}	Surface, 1000, 925, 850, 700 mb
Water equivalent of snow	kg m^{-2}	Surface
West–east wind vector	m s^{-1}	Surface, 1000, 925, 850, 700 mb
Thermal energy‡	°C 100 m^{-1}	Average from 1000, 925, 850, 700 mb

*Units for barometric pressure converted from Pascals.
†Variables reported as 6 h averages and not interpolated over time.
‡Modification from Chevallier *et al.* (2010) using geopotential height at pressure levels instead of from standard atmosphere.

Due to the limited numbers of telemetry locations in tundra and Arctic cordillera, we combined these ecoregions with taiga and refer to them as northern ecoregions (Fig. 1).

CORRELATIONS AMONG METEROLOGICAL VARIABLES

Meteorological variables are often either positively or negatively correlated (e.g. downward solar radiation should be negatively correlated with cloud cover). We included only weather variables that were not correlated ($|R| < 0{\cdot}5$) with others in our analyses. When variables were correlated, we retained the weather variable that we expected would have provided the clearest ecological interpretation if associated with migration.

MIGRATION RESPONSE MODELS

We developed migration response models (so termed to distinguish from other analyses) to determine meteorological correlates of migration (Objective 1). We built these models separately for spring and fall, as prevailing weather patterns differ by season (Kerlinger & Moore 1989). These models included a binary response variable of migratory flight or non-migratory flight; we did not consider intermediate points in this analysis. Weather conditions (Table 1) were explanatory variables. We used generalized linear mixed models (GLMMs) with the binomial distribution, logit link and empirical sandwich estimators of covariance (PROC GLIMMIX; SAS 9.3, Cary, NC, USA). Fixed effects that we included were weather variables, eagle age, ecoregion and interactions of age and ecoregion with weather variables. We included two random effects in each model. These were a term for eagle individual that accounted for correlation among repeated measures on the same individual and a single-year/month term that accounted for temporal autocorrelation. We accounted for multiple comparisons within models using false discovery rates (Benjamini & Hochberg 1995; García 2004; Pike 2011). To assess the magnitude of weather effects on eagle migration, we calculated odds ratios for significant effects. Odds of an eagle migrating (O_A) during average weather conditions were calculated by applying average values of weather variables to the solutions for fixed effects (beta estimates) from the linear model. We also calculated the odds of an eagle migrating (O_S) when the significant weather effect was increased by 1 SD and all other weather variables were held at seasonal averages. The odds ratio for each significant effect was O_S/O_A and was interpreted as the multiplicative change in odds of migrating.

We developed three alternative migration response models for each of the two migration seasons (spring and fall, six models total). Our three models in each season incorporated weather variables from different altitudes above ground level, to understand eagle response to weather at the earth's surface, at eagle flight altitude, or somewhere in between. Each of the three alternatives used a set of weather variables (temperature, omega, relative humidity, south–north wind vector, west–east wind vector, thermal energy and modified wind variables) from different pressure levels (see Table 1). In the first model, all weather variables were from the earth's surface. In the second model, the set of variables were all from the 925-mb pressure level. In the third model, measurements of the set of variables were interpolated linearly to the eagle's flight altitude. Other variables from the Reanalysis II data set were from the earth's surface for all models (Table 1). We used pseudo-Akaike's information criteria (PAIC) to compare the three alternative models in separate model sets for spring and fall.

SEASONAL WEATHER COMPARISON MODELS

We developed seasonal weather comparison models to determine whether and how weather encountered by eagles differed by

season (Objective 2). In these models, we only considered those weather variables that were associated with migration in spring or in fall (as determined in Objective 1). When an interaction with age or ecoregion entered migration response models for either spring or fall (Objective 1), we also included these interactions in our seasonal weather comparison models (Objective 2). We combined migratory, intermediate and non-migratory locations to define weather conditions encountered by eagles in spring and in fall. Season and season–age and season–ecoregion interactions were explanatory variables. We used GLMMs with a Gaussian distribution, identity link and empirical sandwich estimators of covariance (PROC GLIMMIX; SAS 9.3). We included explanatory variables as fixed effects. Random effects were eagle individual and month/year term.

TIME RESPONSE MODELS

We developed three sets of time response models to determine whether and how migration timing differed by age or season. Measures of time were time span of migration (number of days), proportion of season spent migrating (proportion of GPS locations) and migration mid-point (calendar day), and each included migratory, intermediate and non-migratory locations.

The first model compared time span of migration between adults and pre-adults in spring and in fall. The response variable was time span of migration, and explanatory variables were age, season and age–season interaction. We used GLMMs with a Gaussian distribution, the identity link and empirical sandwich estimators of covariance (PROC GLIMMIX; SAS 9.3). We included explanatory variables as fixed effects and random effects of eagle individual and year.

The second time response model compared proportion of season spent migrating between adults and pre-adults in spring and in fall. The response variable was proportion of season spent migrating and explanatory variables were age, season and age–season interaction. We used GLMMs with a binomial distribution, logit link and empirical sandwich estimators of covariance (PROC GLIMMIX; SAS 9.3). We included explanatory variables as fixed effects and random effects of eagle individual and year.

The third time response model compared the migration mid-point between adult and pre-adult eagles. The response variable was migration mid-point, and the explanatory variable was eagle age. We built separate models for spring and fall as calendar days differ between seasons. We used GLMMs, a Gaussian distribution, identity link and empirical sandwich estimators of covariance (PROC GLIMMIX; SAS 9.3). The fixed effect was age, and random effects were eagle individual and year.

Results

DATA COLLECTED FROM EAGLES

We tracked 47 eagles moving along 83 migration tracks (Table 2). Telemetry devices collected 87 029 GPS locations transmitted from CTT/GSM systems ($n = 44$) and 2233 GPS locations transmitted from PTT/ARGOS systems ($n = 3$). Birds contributed data exclusively for spring migration ($n = 27$), exclusively for fall migration ($n = 1$) or for both seasons ($n = 19$). Eagle ages included 20 pre-adults, 24 adults and three eagles that provided data as both a pre-adult and an adult.

DATA CLASSIFICATION

In spring, CTTs ($n = 44$ birds) transmitted 44 680 GPS points from non-migratory locations (flight speed <5 km h^{-1}), 19 617 points from migratory locations (flight speed >10 km h^{-1}) and 2418 points from intermediate (flight speed 5–10 km h^{-1}) locations. PTTs ($n = 3$ birds) transmitted 372 non-migratory, 226 migratory and 29 intermediate points. In fall, CTTs ($n = 17$ birds) transmitted 13 484 non-migratory, 5688 migratory and 778 intermediate locations and PTTs ($n = 3$ birds) transmitted 1248, 260 and 98 points from non-migratory, migratory and intermediate locations, respectively.

CORRELATIONS AMONG METEOROLOGICAL VARIABLES

Several weather variables were correlated. Downward solar radiation was correlated with sensible heat flux and latent heat flux ($r > 0{\cdot}57$). We retained downward solar radiation and excluded sensible heat flux and latent heat flux as downward solar radiation is a complete measure of incident solar radiation onto the earth's surface, whereas sensible and latent heat fluxes are partial measures of energy transferred back to the atmosphere from the ground. Best-lifted index was correlated with precipitable water

Table 2. Number of migratory golden eagles, migration tracks and global positioning system locations recorded by cellular terminal transmitters (CTT) and platform terminal transmitters (PTT) from north-eastern North America, March 2006 to December 2012

					Number of locations by ecoregion		
Season	Age	Transmitter type	Number of individuals	Number of tracks	Eastern temperate forest	Northern forest	Northern regions*
Spring	Adult	CTT	24	25	6990	11 549	2602
		PTT	2	3	201	159	64
	Pre-adult	CTT	22	28	9976	20 856	14 742
		PTT	1	1	0	92	111
Fall	Adult	CTT	8	10	1687	4025	1749
		PTT	3	5	421	1000	185
	Pre-adult	CTT	9	11	2499	7115	3239
		PTT	0	0	0	0	0

*Taiga, tundra and Arctic cordillera were combined into northern regions.

($r = -0{\cdot}73$) and air temperatures at all but the highest pressure level ($r < -0{\cdot}69$). We included best-lifted index and excluded precipitable water and air temperatures because best-lifted index is a measure of atmospheric stability that more directly relates to lift experienced by birds than either precipitable water or temperature. The modified wind variables were correlated (i.e. wind speed was correlated with absolute values of both the south–north wind vector and the west–east wind vector; $R > 0{\cdot}64$). We retained absolute values of south–north and west–east vectors of wind as these provided detail on wind effects along two axes. Unmodified wind variables (south–north and west–east wind) were not correlated with other weather variables and were retained in all models.

MIGRATION RESPONSE MODELS

The best migration model for spring included variables measured only at the earth's surface (Table 3), while the best fall migration model included measurements at the 925-mb pressure level (mean altitude above ground level for the 925 mb pressure level during fall was 325 m ± 222; SD). Fit of the data for alternative models in spring was poor when weather variables were measured at eagle flight altitude (ΔPAIC = 508) or at the 925-mb pressure level (ΔPAIC = 4579). Likewise, fit of the data for alternative fall models was poor when weather was measured at the earth's surface (ΔPAIC = 1015) or at eagle flight altitude (ΔPAIC = 1847). Alternative models for spring and fall are not presented.

The most important factors that influenced migration of golden eagles in spring and fall were those associated with increased thermal formation – downward solar radiation and thermal energy (ranked 1 and 2 in spring and fall migration response models; Tables 3 and 4; Fig. 2; Tables S1 and S2). Furthermore, this relationship was always positive, indicating that probability of an eagle being recorded as engaged in migratory flight in a given hour (hereafter probability of migration) increased as downward solar radiation and thermal energy increased. This pattern held regardless of season, age or ecoregion (Tables 3–5).

In spring, adult and pre-adult eagles responded differently to variation in weather (age interactions in migration response models; Table 3). Although probability of migration increased with increasing values of the south–north wind vector and increasing thermal energy, these responses were stronger for pre-adults than for adults (Table 5). These responses suggest that in spring, pre-adults track these weather conditions more tightly than do adults (Table 5).

Eagles responded to certain spring weather conditions differently in each ecoregion through which they migrated (ecoregion interactions in migration response models; Table 3). Probability of migratory flight was positively correlated with barometric pressure in eastern temperate forests and northern forests. In northern regions in spring, probability of migration was negatively correlated with barometric pressure.

Eagles also responded differently to relative humidity and precipitation rates in each ecoregion. As humidity levels increased, probability of migration by eagles increased in northern regions but decreased in northern and eastern temperate forests. In temperate forests, eagles increased probability of migration as precipitation rates increased, which contradicts with the response to relative humidity. In other ecoregions, probability of migration decreased as precipitation increased.

Table 3. Migration response model. Spring weather variables and interactions with eagle age and ecoregion used in generalized linear mixed model (logit link) to compare locations of migratory and non-migratory movements for golden eagles in eastern North America, March 2006 to December 2012. Weather variables measured at the earth's surface fit data better than variables measured at eagle flight altitude (ΔPAIC = 508) or at 925 mb pressure level (ΔPAIC = 4579). We used false discovery rates to correct for multiple comparisons and identify variables associated with migration (significant *P*-values are bold)

Effect	*F*-value	*P*
Downward solar radiation	252·46	**< 0·0001**
Thermal energy	74·25	**< 0·0001**
Barometric pressure × Ecoregion	12·74	**< 0·0001**
Ecoregion	9·59	**< 0·0001**
South–north wind vector	9·5	**0·0021**
Thermal energy × Age	8·56	**0·0034**
South–north wind vector × Age	5·13	**0·0235**
Relative humidity × Ecoregion	5·05	**0·0064**
Precipitation rate × Ecoregion	4·8	**0·0083**
Downward solar radiation × Ecoregion	3·62	0·0269
Downward solar radiation × Age	4·58	0·0324
Thermal energy × Ecoregion	3·09	0·0454
Best-lifted index × Ecoregion	3·03	0·0484
West–east wind vector × Age	2·31	0·1283
Best-lifted index	2·09	0·148
Age	1·93	0·1647
Precipitation rate	1·77	0·1835
Barometric pressure × Age	1·59	0·207
Omega	1·47	0·2247
Water equivalent of snow × Age	1·26	0·2617
West–east wind vector × Ecoregion	1·06	0·3468
Omega × Ecoregion	1·04	0·3543
Relative humidity × Age	0·83	0·3614
Water equivalent of snow	0·82	0·3664
Omega × Age	0·73	0·3934
|South–north wind vector| × Ecoregion	0·68	0·5058
Barometric pressure	0·54	0·464
|West–east wind vector| × Ecoregion	0·5	0·6074
|West–east wind vector|	0·39	0·5301
Water equivalent of snow × Ecoregion	0·37	0·6939
|West–east wind vector| × Age	0·33	0·5666
Precipitation rate × Age	0·28	0·5939
Relative humidity	0·23	0·6297
South–north wind vector × Ecoregion	0·21	0·8111
Best-lifted index × Age	0·18	0·6748
|South–north wind vector|	0·15	0·7004
|South–north wind vector| × Age	0·13	0·7227
West–east wind vector	0	0·9886

PAIC, pseudo-Akaike's information criteria.

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Table 4. Migration response model. Fall weather variables and interactions with eagle age and ecoregion used in generalized linear mixed model (logit link) to compare locations of migratory and non-migratory movements for golden eagles in eastern North America, March 2006 to December 2012. Weather variables measured at the 925-mb pressure level fit data better than variables measured at eagle flight altitude (ΔPAIC = 1847) or at the earth's surface (ΔPAIC = 1015). We used false discovery rates to correct for multiple comparisons and identify variables associated with migration (significant *P*-values are bold)

Effect	*F*-value	*P*
Thermal energy	39·82	**< 0·0001**
Downward solar radiation	32·32	**< 0·0001**
|South–north wind vector at 925 mb|	9·58	**0·0020**
Age	9·08	**0·0026**
Barometric pressure × Age	8·57	**0·0034**
Best-lifted index	8·19	**0·0042**
Ecoregion	7·36	**0·0006**
Omega at 925 mb	6·76	**0·0093**
Barometric pressure × Ecoregion	6·23	**0·002**
West–east wind vector at 925 mb × Ecoregion	4·45	**0·0117**
West–east wind vector at 925 mb	4·37	0·0365
Precipitation rate	3·82	0·0507
Relative humidity at 925 mb × Age	3·8	0·0514
Thermal energy × Ecoregion	2·77	0·0625
Water equivalent of snow	2·72	0·0992
|South–north wind vector at 925 mb| × Ecoregion	2·63	0·0722
Precipitation rate × Ecoregion	2·41	0·0897
|West–east wind vector at 925 mb| × Ecoregion	2·37	0·0932
Relative humidity at 925 mb	2·26	0·1325
Downward solar radiation × Ecoregion	1·89	0·1505
Downward solar radiation × Age	1·76	0·1845
South–north wind vector at 925 mb × Ecoregion	1·51	0·2207
Omega at 925 mb × Ecoregion	1·3	0·2719
Barometric pressure	0·77	0·3807
Water equivalent of snow × Ecoregion	0·73	0·4828
|South–north wind vector at 925 mb| × Age	0·64	0·4235
Omega at 925 mb × Age	0·63	0·4288
Water equivalent of snow × Age	0·6	0·44
Precipitation rate × Age	0·46	0·4988
|West–east wind vector at 925 mb| × Age	0·29	0·5925
Best-lifted index × Ecoregion	0·27	0·7642
|West–east wind vector at 925 mb|	0·22	0·6406
Best-lifted index × Age	0·2	0·6529
Relative humidity at 925 mb × Ecoregion	0·19	0·8254
South–north wind vector at 925 mb	0·08	0·774
West–east wind vector at 925 mb × Age	0·04	0·8362
Thermal energy × Age	0·03	0·8644
South–north wind vector at 925 mb × Age	0	0·9962

PAIC, pseudo-Akaike's information criteria.

In fall, along with downward solar radiation and thermal energy, probability of migratory flight increased as best-lifted index (atmospheric stability), omega (vertical velocity) measured at 925 mb and absolute value of the vector for south–north wind at 925 mb increased (Tables 4 and 5).

Fall migration differed by ecoregion for two weather variables (ecoregion interactions in migration response models; Tables 4 and 5). Golden eagles increased probability of migration as the west–east wind vector measured at the 925-mb pressure level decreased in eastern temperate forests and northern regions, but the opposite was true in northern forests. Probability of migration varied by ecoregion and age for barometric pressure. In fall, adult eagles increased probability of migration as barometric pressure increased for all ecoregions, with the greatest effect observed in northern forests. Probability of pre-adult migration increased with decreasing pressure in all ecoregions, with the magnitude of this effect increasing as they migrated south.

SEASONAL WEATHER COMPARISON MODELS

Certain weather conditions that eagles encountered and that were identified as important from migration response models differed between seasons (Table 6). Eagles encountered more than twice the levels of downward solar radiation in spring than in fall (Tables 6 and 7; Fig. 2). Best-lifted index encountered by eagles was twice as high in fall as in spring (atmosphere more stable in fall) and omega measured at 925 mb was slightly higher in fall than in spring. The south–north wind vector encountered by eagles was greater in fall in spring. Seasonal differences in the south–north wind vector corresponded to shifts in prevailing wind patterns (Table 7; Fig. 2) with predominant winds from the north in spring and from the south in fall.

Other weather conditions experienced by eagles differed among ecoregions by season (season–ecoregion interactions), but did not differ seasonally between adults and pre-adults (season–age interactions; Table 6). Eagles encountered lower precipitation rates in eastern temperate forests and northern regions, but higher precipitation rates in northern forests in fall compared to spring. The west–east wind vector measured at the 925-mb pressure differed in magnitude between seasons and among ecoregions; however, prevailing wind in all ecoregions and during both seasons was from the west (Fig. 2). Barometric pressure experienced by tagged eagles was higher in fall than in spring in forested regions but lower in fall than spring in northern regions.

TIME RESPONSE MODELS

Time span of migration (number of days from start to end of migration) differed by season (first time response model; $F_{1,32} = 11{\cdot}07$, $P = 0{\cdot}002$) but not by age ($F_{1,32} = 1{\cdot}84$, $P = 0{\cdot}185$) or by the age–season interaction ($F_{1,32} = 0{\cdot}03$, $P = 0{\cdot}870$). Eagles spent less time migrating in spring (26·1 ± 2·6, SE, days) than in fall (70·9 ± 17·3 days).

The proportion of season spent migrating (proportion of the GPS locations classified as migratory) differed by age (first time response model; $F_{1,50} = 5{\cdot}43$, $P = 0{\cdot}02$) and season ($F_{1,50} = 25{\cdot}62$, $P < 0{\cdot}001$), but not by the age–season interaction ($F_{1,50} = 2{\cdot}45$, $P = 0{\cdot}124$). Adults spent a greater proportion of each season migrating that did

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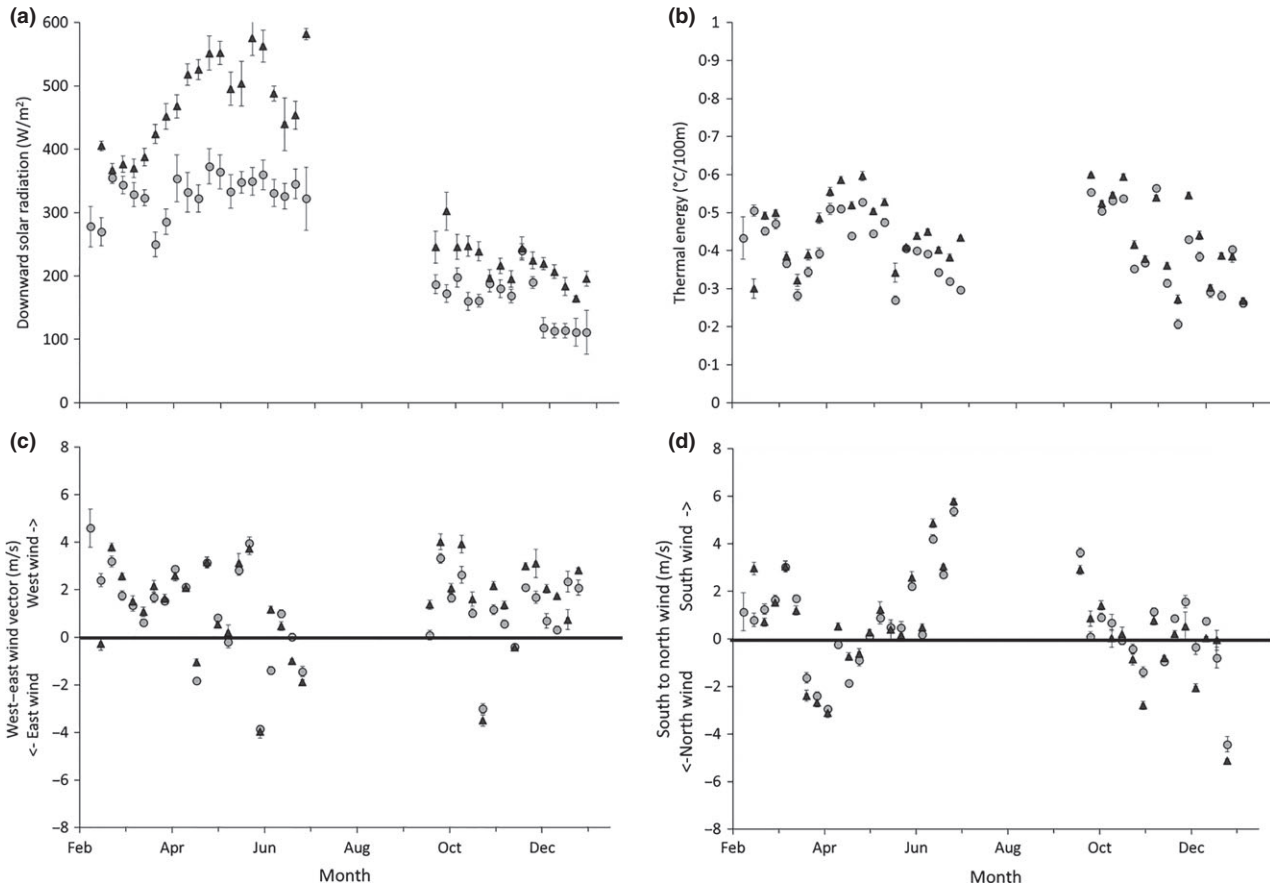

Fig. 2. Average weekly values (SE bars) of weather variables for 2012 that differed for migratory (dark triangles) and non-migratory locations (grey circles) or between seasons (spring February to July, fall September to January) for golden eagles migrating in eastern North America. Downward solar radiation was measured as 6 h averages, while thermal energy and wind variables were interpolated to times when eagle locations were recorded (15-min to 1-h intervals). For downward solar radiation (a) migration > non-migratory locations and spring > fall (see Tables 3–5). For thermal energy (b) migratory > non-migratory locations. Prevailing winds measured by the west–east wind vector (c) were from the west regardless of season. Winds measured by the south–north wind vector (d) were greater in spring than fall, with a shift in prevailing direction between seasons.

pre-adults (both seasons combined, adults 0·296 ± 0·016, SE; pre-adults 0·241 ± 0·014). Eagles spent a greater proportion of each season migrating in spring (0·314 ± 0·013) than in fall (0·210 ± 0·013).

Migration mid-point (middle day of time span of migration) differed by age in spring (third time response model; $F_{1,9} = 52{\cdot}08$, $P < 0{\cdot}001$) but not fall ($F_{1,4} = 1{\cdot}28$, $P = 0{\cdot}321$; Fig. 3). During spring, median calendar day for adult migration was 82 ± 2 (SE) days (22 March) and 116 ± 4 days (25 April) for pre-adults. During fall migration, median calendar day for migration was 315 ± 5 days (10 November).

Discussion

Migratory flight of a model soaring migrant was positively associated with weather conditions that promoted thermal lift. This response was prominent during both spring and fall migration, across all ecoregions, and for all age classes. Migration is faster and more direct when birds soar and glide in and out of thermals, and migration is slower when birds use orographic lift to travel along ridgelines (Duerr *et al.* 2012). The response of eagles choosing to migrate preferentially when conditions existed for thermal development shows that eagles were seeking to maximize flight efficiency and minimize energetic expenditures whenever possible. However, migratory responses to weather conditions that promote orographic lift differed by age and season. This contrast highlights the contradictory temporal and energetic constraints faced by eagles of different ages and different reproductive statuses.

Many breeding raptors are time limited during spring migration (Sergio *et al.* 2007; Newton 2008). Timing of migration in spring is constrained by age-specific breeding behaviour. During spring, adult golden eagles migrated earlier, when solar radiation levels were lower, and they showed a weaker response (measured as increased probability of engaging in migration) to thermal energy than did later migrating pre-adults. Adults migrated when conditions were conducive to both thermal lift and less efficient orographic lift, and a greater proportion of their season was spent migrating, compared to pre-adults. These

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Table 5. Odds ratios are multiplicative changes in the odds of migration of golden eagles during spring or fall due to an increase in the value of that variable by 1 SD from migration response models. Eagle data were collected in eastern North America from March 2006 to December 2012

	Odds ratios					
Effect	Spring			Fall		
Downward solar radiation	2·89			1·26		
Thermal energy				1·69		
|South–north wind vector at 925 mb|				1·26		
Best-lifted index				1·15		
Omega at 925 mb				1·15		
Age interactions	Adult			Pre-adult		
South–north wind vector × Age	1·00			1·26		
Thermal energy × Age	1·19			1·62		
Ecoregion interactions	ETF	NF	NR	ETF	NF	NR
Precipitation rate × Ecoregion	1·04	0·73	0·99			
Barometric pressure × Ecoregion	1·34	1·28	0·85			
Relative humidity × Ecoregion	0·86	0·98	1·46			
West–east wind vector at 925 mb × Ecoregion				0·63	1·07	0·90
Age and ecoregion interactions	ETF	NF	NR	ETF	NF	TAI
Barometric pressure × Ecoregion (adult)*				1·01	1·33	1·02
Barometric pressure × Ecoregion (pre-adult)				0·64	0·84	0·98

ETF, Eastern temperate forest; NF, Northern forest; NR, northern regions (Taiga/tundra/Arctic cordillera combined) are ecoregion-specific odds ratios.
*Adult and pre-adult are age-specific odds ratios.

patterns indicate time limitation and a potential advantage to adults to return to northern breeding territories as quickly as possible. In contrast, pre-adult migration in spring was correlated with increasing thermal energy and south to north winds (i.e. tailwinds), both of which contribute to migratory efficiency. Pre-adults also spent a smaller proportion of their season migrating, but the time span of migration (number of days) was greater, suggesting that they waited for weather conditions that promoted efficient flight modes. These two factors together provide strong evidence that pre-adults, in contrast to adults, act to minimize energetic expenditures during spring migration.

Evaluating temporal and energetic limitations is relatively more complex during fall migration. Adult eagles typically begin migration in October and November, after successful breeders complete the 18–20-week breeding cycle (Watson 2010). Breeding activities did not delay southbound migration by adults, and there was no difference in time span that adults and pre-adults spent in migration (although adults appeared to spend a greater proportion of their season migrating in both spring and fall than did pre-adults). Thus, adults were not time limited. Adults encountered lower levels of downward solar radiation in fall than in spring. This likely reduced their migratory efficiency by forcing them to use orographic soaring or flapping flight. However, they were more likely to migrate as barometric pressure increased, when type I thermals develop (Kerlinger 1989), and solar radiation and thermal energy are on the rise. Therefore, adults appeared to have migrated more efficiently than pre-adults and were not time limited during fall migration.

In fall, pre-adults migrated during conditions of lower barometric pressure than adults, which better corresponds to the development of orographic lift than of thermal lift. They appeared to have used less efficient lift types and flight modes than did adults. This pattern might suggest pre-adults were time limited. However, there was no

Table 6. Tests to determine whether weather variables (including interaction terms) that were associated with migratory movements of golden eagles differed between spring and fall from seasonal weather comparison models. Data were collected in eastern North America, March 2006 to December 2012. We used false discovery rates to correct for multiple comparisons (significant *P*-values are bold)

Variable	Effect	*F*-value	d.f.	*P*
Downward solar radiation	Season	296·77	1	**< 0·001**
Precipitation rate	Season × Ecoregion	12·6	2	**< 0·001**
Omega at 925 mb	Season	9·7	1	**0·002**
South–north wind vector	Season	5·6	1	**0·018**
West–east wind vector at 925 mb	Season × Ecoregion	5·51	2	**0·004**
Best-lifted index	Season	5·38	1	**0·020**
Barometric pressure × ecoregion	Season × Ecoregion	5·3	2	**0·005**
Thermal energy	Season	3·49	1	0·062
Thermal energy	Season × Age	2·1	1	0·147
Relative humidity	Season × Ecoregion	2·08	2	0·125
|South–north wind vector at 925 mb|	Season	1·27	1	0·260
South–north wind vector	Season × Age	0·46	1	0·499
Barometric pressure	Season × Age	0·36	1	0·546

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Table 7. Average values (±SD) of weather variables that were associated with migration (identified in migration response models) of golden eagles and that differed between spring and fall migrations (from seasonal weather comparisons)

Variable	Spring				Fall			
Downward solar radiation	346·78 ± 236·72				162·63 ± 129·88			
Omega at 925 mb	0·01 ± 0·07				0·027 ± 0·078			
South to north wind vector	−0·26 ± 3·78				0·33 ± 3·74			
Best-lifted index	9·44 ± 5·73				11·18 ± 4·92			
Ecoregion interactions	ETF	NF	NR	ETF	NF	NR		
Precipitation rate	0·0000414 ± 0·0001009	0·0000307 ± 0·0000688	0·0000243 ± 0·000056	0·0000151 ± 0·000077	0·0000334 ± 0·0000825	0·0000292 ± 0·0000823		
West to east wind at 925 mb	3·6 ± 5·15	2·33 ± 5·32	1·56 ± 5·45	3·65 ± 5·9	1·93 ± 6·44	4·1 ± 6·56		
Barometric pressure	733·22 ± 6·43	728·41 ± 9·16	730·77 ± 12·81	736·8 ± 5·76	730·01 ± 10·43	724·65 ± 10·26		

ETF, Eastern temperate forest; NF, Northern forest; NR, Northern regions (taiga/tundra/Arctic cordillera combined).

Fig. 3. The per cent of GPS tagged golden eagles that were migrating for each day of the year. This illustrates the timing of spring (February to July) and fall (August to January) migration for adult and pre-adult ages. Eagles were tracked from March 2006 to December 2012 in eastern North America.

difference in time span of migration or migration midpoint between adults and pre-adults. That pre-adults used less efficient flight modes but took similar amounts of time as adults suggest that pre-adults responded to similar temporal pressures as adults but were simply less efficient migrants than were adults.

In spite of the near-universal response to thermal lift, adult and pre-adult eagles showed different responses to temporal and energetic constraints that reflected seasonal differences in the weather conditions that they encountered in spring but not in fall. In spring, levels of downward solar radiation were lower when adults migrated than when pre-adults migrated. The lower solar radiation encountered by adults may be a consequence of differences in weather relative to conditions when pre-adults migrate, or it may be an artefact of shorter day length when adults migrate. In either case, lower levels of solar radiation corresponded to a weaker migratory response to thermal energy in spring by time-limited adults than by pre-adults. In contrast, pre-adults showed a greater dependence upon orographic lift in fall than did adults, which reflected prevailing weather conditions during that period.

Seasonal differences in weather showed that eagles encounter less thermal development in fall than in spring throughout migration. The subsidized lift that fall-migrating eagles use primarily occurred in the form of orographic lift. Probability of migration in the fall increased as winds along the south–north vector became stronger (i.e. greater north or greater south winds measured at 925 mb). Migrating into headwinds may seem counterintuitive, but because of the topography along the migration route (e.g. in New York and eastern Pennsylvania), such winds are frequently deflected upward along ridgelines and provide supplemental lift (Kerlinger 1989). Although not well documented, birds also may use dynamic soaring to gain altitude over land; this form of lift also requires turning into the wind (Kerlinger 1989; Sachs & Mayrhofer 2001). The combination of these multiple forms of subsidized lift creates a system where each lift type could be used by eagles individually or together to provide a synergistic effect to reduce the costs of migration.

In fall, pre-adult eagles were more likely to migrate as pressure levels dropped and adult eagles were more likely to migrate as pressure levels increased. Age-specific migratory response under different pressure regimes may appear to contrast with patterns observed at Hawk Mountain Sanctuary, Pennsylvania, where eagle counts tend to double within 3 days following the passage of a cold front (Allen, Goodrich & Bildstein 1996). However, cold fronts are followed by high-pressure air masses, with corresponding increases in barometric pressure, increases in type I thermal lift and, in our study, increased adult migration. Most cold fronts passed by Hawk Mountain within 5 days of one another (Allen, Goodrich & Bildstein 1996), with a warm front, decreasing barometric pressure, and pre-adult migration passing between cold fronts. Therefore, it is likely that increased counts in the days following a cold front at Hawk Mountain actually include adults migrating within high pressure behind a cold front and pre-adults migrating within low pressure with a cold front. By migrating following a cold front, adults appear to supplement orographic lift, the prevailing lift type in fall, with thermal lift to a greater degree than pre-adults. These patterns strongly suggest that adult eagles respond more rapidly to changing weather conditions, providing additional evidence that adults migrate more efficiently than pre-adults.

Differences in pressure systems also account for differences in migration patterns among ecoregions. This seems intuitive because weather patterns and topography can differ dramatically among regions (Commission for Environmental Cooperation 1997; Strandberg *et al*. 2009). In spring, migration in forested ecoregions was associated with higher pressure, but migration in northern regions was associated with lower pressure. This is a logical consequence of trends in prevailing weather patterns, as subpolar low pressure generally prevails to the north, and is separated from southerly higher pressure by the jet stream (Moran 2009).

Golden eagles appeared to be generalists with regard to selection of migratory conditions. Raptors, including eagles, are regularly observed from hawk-watch sites located on mountain peaks or ridgelines (Allen, Goodrich & Bildstein 1996). These observations create an apparently false impression that soaring birds depend on orographic lift to migrate. Although eagles showed a consistent response to thermal development, they readily migrated under conditions supporting both thermal and orographic lift. Eagles also showed season- and ecoregion-specific differences in migratory responses to weather conditions. Generalist behaviour in response to migratory conditions is very likely a result of evolutionary pressures related to variable time and energy constraints to migration that eagles experience over the course of their long lives.

A consistent response to thermal development allows soaring birds to both reduce time spent migrating and to conserve energy during migration. Thermal lift represents high-quality habitat for migration in which eagles can conserve both time and energy (Duerr *et al*. 2012). Use of thermal lift increases flight speed and reduces the time span of migration, which is especially important when migration is time limited. When eagles are conserving energy on migration, they can wait out periods of bad weather and return to migration when conditions are more conducive to flight. Knowing responses to optimal migratory conditions is important when assessing the trade-off between time- and energy limitations. However, to understand this problem, it is also vital to consider migratory responses to less optimal weather conditions (i.e. orographic lift is lower-quality habitat for migration) and time span of migration. By doing so, we able to provide evidence that (i) adult eagles are more strongly time limited in spring, (ii) pre-adult eagles show behaviours consistent with energy limitation in spring, (iii) adults and pre-adults attempt to conserve energy in fall and (iv) pre-adults appear to be less efficient migrants than adults in fall. Thus, we conclude that golden eagles show age- and season-specific responses to variation in habitat quality of airspace that corresponds directly to time and energy conservation.

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References

Alerstam, T. & Hedenstrom, A. (1998) The development of bird migration theory. *Journal of Avian Biology*, **29**, 343–369.

Allen, P.E., Goodrich, L.J. & Bildstein, K.L. (1996) Within- and among-year effects of cold fronts on migrating raptors at hawk mountain, Pennsylvania, 1934–1991. *The Auk*, **113**, 329–338.

Avgar, T., Mosser, A., Brown, G.S. & Fryxell, J.M. (2013) Environmental and individual drivers of animal movement patterns across a wide geographical gradient. *Journal of Animal Ecology*, **82**, 96–106.

Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, **57**, 289–300.

Bird, D.M. & Bildstein, K.L. (2007) *Raptor Research and Management Techniques*. Hancock House, Surrey, British Columbia and Blane, Washington.

Bloom, P.H. & Clark, W.S. (2001) Molt and sequence of plumages of golden eagles and a technique for in-hand ageing. *American Bird Bander*, **26**, 97–116.

Chevallier, D., Handrich, Y., Georges, J.Y., Baillon, F., Brossault, P., Aurouet, A. *et al.* (2010) Influence of weather conditions on the flight of migrating black storks. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2755–2764.

Commission for Environmental Cooperation (1997) *Ecoregions of North America, Level I, II, and III Maps*. Available at [http://www.epa.gov/wed/pages/ecoregions/na_eco.htm] from the United States Environmental Protection Agency (EPA), Office of Research and Development, National Health and Environmental Effects Research Laboratory, Western Ecology Division, Corvallis, Oregon, USA and at [http://www.cec.org/pubs_docs/documents/index.cfm?varlan = english&id = 344] from the Commission for Environmental Cooperation (CEC), Montréal (Québec), Canada.

Diehl, R.H. (2013) The airspace is habitat. *Trends in Ecology & Evolution*, **28**, 377–379.

Duerr, A.E., Miller, T.A., Lanzone, M., Brandes, D., Cooper, J., O'Malley, K. *et al.* (2012) Testing an emerging paradigm in migration ecology shows surprising differences in efficiency between flight modes. *PLoS ONE*, **7**, e35548.

García, L.V. (2004) Escaping the Bonferroni iron claw in ecological studies. *Oikos*, **105**, 657–663.

Hardy, K.R. & Ottersten, H. (1969) Radar investigations of convective patterns in the clear atmosphere. *Journal of the Atmospheric Sciences*, **26**, 666–672.

Hedenstrom, A. (1993) Migration by soaring or flapping flight in birds – the relative importance of energy-cost and speed. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **342**, 353–361.

Hedenstrom, A. & Alerstam, T. (1995) Optimal flight speed of birds. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **348**, 471–487.

Hedenstrom, A. & Alerstam, T. (1997) Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. *Journal of Theoretical Biology*, **189**, 227–234.

Jollie, M. (1947) Plumage changes in the golden eagle. *The Auk*, **64**, 549–576.

Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L. *et al.* (1996) The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological Society*, **77**, 437–471.

Katzner, T.E., Brandes, D., Miller, T., Lanzone, M., Maisonneuve, C., Tremblay, J.A. *et al.* (2012a) Topography drives migratory flight altitude of golden eagles: implications for on-shore wind energy development. *Journal of Applied Ecology*, **49**, 1178–1186.

Katzner, T., Smith, B., Miller, T., Brandes, D., Cooper, J., Lanzone, M. *et al.* (2012b) Status, biology, and conservation priorities for North America's Eastern Golden Eagle (*Aquila chrysaetos*) Population. *The Auk*, **129**, 168–176.

Kemp, M.U., Emiel van Loon, E., Shamoun-Baranes, J. & Bouten, W. (2011) RNCEP: global weather and climate data at your fingertips. *Methods in Ecology and Evolution*, **3**, 65–70.

Kerlinger, P. (1989) *Flight Strategies of Migrating Hawks*. University of Chicago Press, Chicago, Illinois.

Kerlinger, P. & Moore, F.R. (1989) Atmospheric structure in avian migration. *Current Ornithology*, **6**, 109–142.

Klaassen, R.H.G., Hake, M., Strandberg, R. & Alerstam, T. (2011) Geographical and temporal flexibility in the response to crosswinds by migrating raptors. *Proceedings of the Royal Society B-Biological Sciences*, **278**, 1339–1346.

Lanzone, M.J., Miller, T.A., Turk, P., Brandes, D., Halverson, C., Maisonneuve, C. *et al.* (2012) Flight responses by a migratory soaring raptor to changing meteorological conditions. *Biology Letters*, **8**, 710–713.

Leshem, Y. & Yom-Tov, Y. (1996) The use of thermals by soaring migrants. *The Ibis*, **138**, 667–674.

Lyons, J.E., Collazo, J.A. & Guglielmo, C.G. (2008) Plasma metabolites and migration physiology of semipalmated sandpipers: refueling performance at five latitudes. *Oecologia*, **155**, 417–427.

Mandel, J.T., Bohrer, G., Winkler, D.W., Barber, D.R., Houston, C.S. & Bildstein, K.L. (2011) Migration path annotation: cross-continental study of migration-flight response to environmental conditions. *Ecological Applications*, **21**, 2258–2268.

Miller, T.A. (2012) *Movement ecology of golden eagles (*Aquila chrysaetos*) in eastern North America*. PhD Dissertation, Pennsylvania State University, State College, Pennsylvania.

Mitchell, G.W., Newman, A.E.M., Wikelski, M. & Ryan Norris, D. (2012) Timing of breeding carries over to influence migratory departure in a songbird: an automated radiotracking study. *Journal of Animal Ecology*, **81**, 1024–1033.

Moran, J.M. (2009) *Weather Studies Introduction to Atmospheric Science*, 4th edn. American Meteorological Society, Boston, Massachusetts.

Newton, I. (2008) *The Migration Ecology of Birds*. Academic Press, London.

Pike, N. (2011) Using false discovery rates for multiple comparisons in ecology and evolution. *Methods in Ecology and Evolution*, **2**, 278–282.

R Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Sachs, G. & Mayrhofer, M. (2001) Shear wind strength required for dynamic soaring at ridges. *Technical Soaring*, **25**, 209–215.

Sachs, G., Traugott, J., Nesterova, A.P., Dell'Omo, G., Kümmeth, F., Heidrich, W. *et al.* (2012) Flying at no mechanical energy cost: disclosing the secret of wandering albatrosses. *PLoS ONE*, **7**, e41449.

Sergio, F., Blas, J., Forero, M.G., Donázar, J.A. & Hiraldo, F. (2007) Sequential settlement and site dependence in a migratory raptor. *Behavioral Ecology*, **18**, 811–821.

Shamoun-Baranes, J., Bouten, W. & van Loon, E.E. (2010) Integrating meteorology into research on migration. *Integrative and Comparative Biology*, **50**, 280–292.

Shamoun-Baranes, J., Liechti, O., Yom-Tov, Y. & Leshem, Y. (2003) Using a convection model to predict altitudes of white stork migration over central Israel. *Boundary-Layer Meteorology*, **107**, 673–681.

Shamoun-Baranes, J., van Loon, E., Alon, D., Alpert, P., Yom-Tov, Y. & Leshem, Y. (2006) Is there a connection between weather at departure sites, onset of migration and timing of soaring-bird autumn migration in Israel? *Global Ecology and Biogeography*, **15**, 541–552.

Shannon, H.D., Young, G.S., Yates, M.A., Fuller, M.R. & Seegar, W.S. (2002) American White Pelican soaring flight times and altitudes relative to changes in thermal depth and intensity. *Condor*, **104**, 679–683.

Strandberg, R., Klaassen, R.H.G., Olofsson, P. & Alerstam, T. (2009) Daily travel schedules of adult Eurasian Hobbies Falco subbuteo – variability in flight hours and migration speed along the route. *Ardea*, **97**, 287–295.

Watson, J. (2010) *The Golden Eagle*, 2nd edn. Yale University Press, New Haven, Connecticut.

van Wijk, R.E., Kölzsch, A., Kruckenberg, H., Ebbinge, B.S., Müskens, G.J.D.M. & Nolet, B.A. (2012) Individually tracked geese follow peaks of temperature acceleration during spring migration. *Oikos*, **121**, 655–664.

Yates, R.E., McClelland, B.R., McClelland, P.T., Key, C.H. & Bennets, R.E. (2001) The influence of weather on golden eagle migration in northwestern Montana. *The Journal of Raptor Research*, **35**, 81–90.

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Supporting Information

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

Appendix S1. Definitions of select weather variables.
Table S1. Spring migration response model.
Table S2. Fall migration response model.