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LETTER

Estimating updraft velocity components over large spatial scales: contrasting migration strategies of golden eagles and turkey vultures

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Abstract

Soaring birds migrate in massive numbers worldwide. These migrations are complex and dynamic phenomena, strongly influenced by meteorological conditions that produce thermal and orographic uplift as the birds traverse the landscape. Herein we report on how methods were developed to estimate the strength of thermal and orographic uplift using publicly available digital weather and topography datasets at continental scale. We apply these methods to contrast flight strategies of two morphologically similar but behaviourally different species: golden eagle, *Aquila chrysaetos*, and turkey vulture, *Cathartes aura*, during autumn migration across eastern North America tracked using GPS tags. We show that turkey vultures nearly exclusively used thermal lift, whereas golden eagles primarily use orographic lift during migration. It has not been shown previously that migration tracks are affected by species-specific specialisation to a particular uplift mode. The methods introduced herein to estimate uplift components and test for differences in weather use can be applied to study movement of any soaring species.

Keywords

Behavioural ecology, flight, movement ecology, terrain, uplift, weather.

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INTRODUCTION

Millions of soaring birds, including raptors, storks and pelicans that breed in the northern hemisphere migrate southward in autumn to their wintering grounds. These birds are heavy and can only use flapping flight for short distances. Therefore, over very large migration distances these birds depend on vertical air motion (lift) to subsidise soaring and gliding flight (Spaar & Bruderer 1996; Shannon *et al.* 2002b; Bildstein *et al.* 2009; Sapir *et al.* 2010). Quantitative understanding and prediction of when and where concentrations of soaring birds occur during migration is important to conservation of migratory routes and stop-over habitat; and to reduce risk of collisions with aircraft, wind turbines and other infrastructure. Until recently, a quantitative understanding of this process has not been possible. Recent improvements in satellite tracking of soaring birds include remote telemetry, GPS, miniaturisation of the tags and on-board accelerometers and other sensors. These have provided a wealth of new high-resolution data on migratory movements of many species and can be used to map migration patterns (Wikelski *et al.* 2007; Tomkiewicz *et al.* 2010). Large volumes of migration-track data can be stored and processed automatically by on-line resources, such as MoveBank (http://www.movebank.org; Kranstauber *et al.* 2011) and annotated with publicly accessible on-line datasets of weather and environmental data (Kemp *et al.* 2011; Mandel *et al.* 2011).

With these data in hand, new insights can be achieved for some of the 'big questions' in integrative migration biology (Bowlin *et al.* 2010). For example: How do species interact with their environment? In particular, why do they fly through some places rather than others, and what sets the timing of migration and of particular location selections during flight? How will their flight patterns, energy expenditure during flight and survival of the migration event change if the environment changes due to human activities or natural variability?

Several models that describe responses to meteorological drivers exist (e.g., Beekman *et al.* 2002; Shamoun-Baranes *et al.* 2003a, 2006, 2010a,b; Thorup *et al.* 2003; Klaassen *et al.* 2004; Roshier *et al.* 2008; Gill *et al.* 2009; Chevallier *et al.* 2010; van Loon *et al.* 2011; Sapir *et al.* 2011a,b). However, only a few weather-driven models of raptor migration over long distances exist in the literature (Shamoun-Baranes *et al.* 2003b; Mandel *et al.* 2008, 2011). Some include models that are driven by direct or indirect estimates of the strength of uplift (Shannon *et al.* 2002a,b; Bowlin & Wikelski 2008). Integrating meteorological information into models of flight behaviour, and, in particular, of continental-scale migration, is therefore, one of the grand challenges in the study of avian movement ecology. This is

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particularly relevant for attempts to forecast bird response to climate change, as well as their interaction with human activity (Gill *et al.* 2009; Bowlin *et al.* 2010; Shamoun-Baranes *et al.* 2010a).

The vertical component of wind velocity is rarely reported in meteorological datasets and in regional and global-scale models. It is, however, physically necessary for extended flight of soaring birds, and required to understand flight behaviour and strategy. On a large scale, long-term average vertical wind speed, and thus uplift, is close to zero. Turbulent phenomena, and particularly thermally buoyant eddies and orographic updrafts, create small-scale persistent updrafts in particular locations and over short to intermediate timescale (seconds–hours). The small scale of persistent uplift modes and their turbulent nature means that they are impossible to resolve explicitly in regional-scale atmospheric models. That said, regional – or even larger, continental-scale models are needed for simulating the atmospheric conditions over a large domain that includes the long migration tracks and migration season of continental soaring migratory birds.

Orographic updrafts result from deflection of horizontal winds by sloping terrain. In some cases migrating raptors soar and glide for 100 s of km along terrain features that produce updrafts, for example, along the parallel ridges of the Appalachian Mountains (Brandes & Ombalski 2004; Bildstein 2006; Mandel *et al.* 2011). Thermally buoyant eddies, known as 'thermals' and sometimes outlined by circles of soaring birds, are formed due to heating of the land surface by solar radiation during the day. Large thermals may be up to a few km in diameter. Migrating soaring birds can target these local updrafts to generate upward motion with minimal energy expenditure (Sapir *et al.* 2010). Several studies of soaring birds have found a correlation between flight-leg distance or energy expenditure and parameters that are indicative of uplift but were derived from coarse-scale weather data (Shamoun-Baranes *et al.* 2003b; Bowlin & Wikelski 2008; Mandel *et al.* 2008, 2011; Sapir *et al.* 2011a). These parameters include boundary layer depth, turbulence kinetic energy and the upward rate of change of pressure levels.

Two different modelling approaches have been used to incorporate updraft directly in bird movement models. Brandes and Ombalski (2004) used a continuum fluid flow analogy to predict flow-paths of migrating raptors through a heterogeneous landscape, where the conductivity function is determined by orographic updraft strength. Mandel *et al.* (2008, 2011) and others (Shamoun-Baranes *et al.* 2003a,b, Shamoun-Baranes *et al.* 2008) used an empirical autoregressive linear model to relate migratory movements of particular species to model-resolved wind speed, and updraft surrogates that are available from model data. Both models are limited in scope and generality. In the first case, the model explicitly applies only to conditions where orographic updrafts are the dominant source of lift. In the second case the model applies only to the study species and the regional model data. The paucity of such models is likely due in part to the computational challenge of estimating lift over relevant space and time scales of migration, which can extend over thousands of kilometres and several months time. More general methods and models for quantitative, spatially explicit prediction of avian migration behaviour are needed.

Herein we report on a novel integrative framework to enhance the understanding of avian flight behaviour, migration-route determination and inter-specific differences in flight behaviour and travel paths. We do this by simplifying the analysis of vertical wind movement and by providing two matrices for estimation of the vertical wind component in the atmosphere, based on common meteorological data and topographical information. We then apply the track-annotation approach (Mandel *et al.* 2011) to estimate the distributions of the thermal, w^*, and orographic, w_o, components of uplift along tracks of observed migrating raptors tracked with GPS tags during southward fall migrations in eastern North America (Fig. 1). We compare these distributions with the background distribution of uplift components at a large domain (in space and time) of the migration movement for each population. The results are used to contrast the preferential use of thermal and orographic uplift by two morphologically similar species, golden eagle (*Aquila chrysaetos*) and turkey vulture (*Cathartes aura*).

Although these species are not particularly closely related they are similar in size and shape and both migrate long distances over a variety of terrains. Both species are primarily soaring migrants, and both are known to use both thermal and orographic uplift. There are, however, several important differences. The two have different foraging and flight behaviour. Also, wing loading (mass/wing area) of golden eagles (7.2 kg m^{-2}) is greater than that of turkey vultures (3.9 kg m^{-2}) (Pennycuick 2008). In part, this is because golden eagles have more muscle mass and thus stronger flapping flight than turkey vultures, which presumably use soaring all-but exclusively in migration. The higher wing loading of golden eagles is consistent with faster cross-country flight and a predatory lifestyle. The lower wing loading of turkey vultures is consistent with use of relatively weak updrafts and also with their scavenging (non-predatory) lifestyle, which selects for

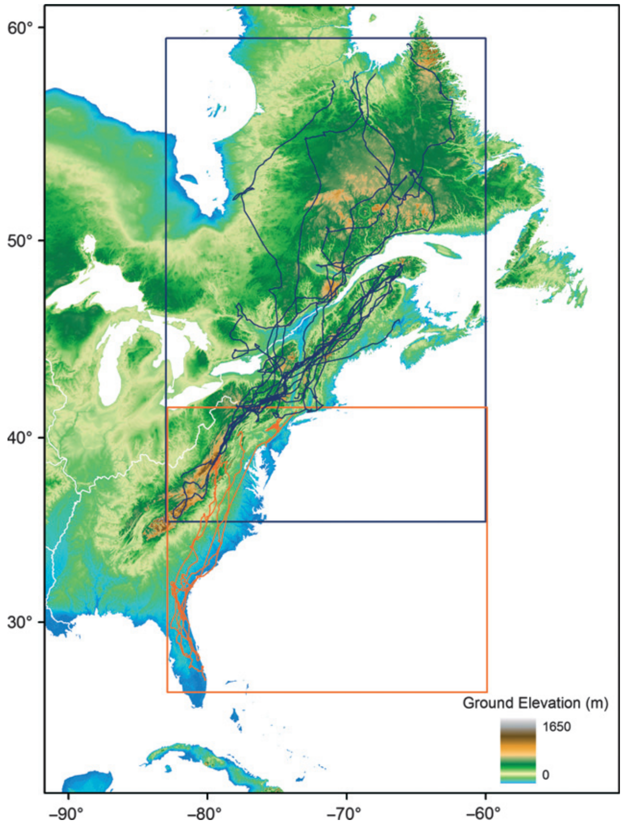

Figure 1 Topographical map of eastern North America, illustrating the bird tracks used (turkey vulture in orange; golden eagle in blue). Areas in the NARR models that are covered by water (from the NARR surface variable LAND) are white. The geographical extent of the background domains for turkey vultures and golden eagles are illustrated by boxes (orange and blue, respectively).

low energy expenditure. Higher wind loading implies that stronger uplift is needed to maintain or gain flight altitude. Therefore, we hypothesise that golden eagles specialise in soaring in stronger orographic uplift. In a previous study (Mandel *et al.* 2011) have indicated that turkey vultures of the US east-coast population use both orographic and thermal uplift and we therefore hypothesise that they will show a preferential use pattern for both uplift modes. The autumn migration routes and timing of the two species also differ in North America with golden eagles typically moving south from higher latitude breeding areas and later in the season (Brodeur *et al.* 1996; McIntyre *et al.* 2008; Miller *et al.* 2010) when solar radiative input and thus thermal lift is likely to be weaker. Thus, the two species provide a model case to test the generality of updraft preferences. We set out to test the hypothesis that golden eagles and turkey vultures gain different benefits from particular uplift modes and, therefore, choose locations and times where their 'preferred' uplift mode is stronger.

MATERIALS AND METHODS

Estimation and upscaling of orographic uplift

Deflection of horizontal wind by topography produces orographic uplift velocity, w_o. The value of w_o was initially estimated based on the 30 arc-sec (c. 1-km resolution) global GTOPO30 digital elevation model (DEM) (USGS 1996) following the formulation of Brandes & Ombalski (2004). This dataset consists of 33 non-overlapping tiles, two of which (100W90N and 100W40N) were used in the application described in this article. Because the results must be aggregated to the spatial scale of the meteorological dataset (NARR, 32×32 km^2, see meteorological data section) and we are interested in developing a general method applicable to any region of the world, the km-scale GTOPO30 data are appropriate for our purposes. The value of w_o can be determined based on wind speed and direction, and terrain slope and aspect (Brandes & Ombalski 2004):

$$w_o = vC_\alpha \tag{1}$$

$$C_\alpha = Sin(\theta)Cos(\alpha - \beta) \tag{2}$$

where v is the horizontal ground wind speed, C_α is an updraft coefficient that depends on the constant slope angle, θ (degrees, level = 0), and terrain aspect, β and the dynamic wind direction, α (both in degrees, North = 0). In this simplified formulation we do not consider updrafts that are associated with turbulent eddies or lee waves, and all resulting negative values for w_o (i.e. on the leeward side of terrain) are set to 0. Values of θ and β were calculated using Zevenbergen & Thorne (1987):

$$\theta = \arctan\left[\left(\frac{dz}{dx}\right)^2 + \left(\frac{dz}{dy}\right)^2\right]^{1/2} \tag{3}$$

$$asp(\beta) = \arctan\left[\frac{(dz/dx)}{(dz/dy)}\right] \tag{4}$$

where $dz/\mathrm{d}x$ and $dz/\mathrm{d}y$ are the eastward and northward terrain slope components.

For each GTOPO30 grid-point we calculate eight C_α coefficients (one for each of eight 45° directional sections). Since the wind data we use are provided by the 32×32 km NARR dataset there are approximately 1089 such C_α coefficients for each wind direction within each NARR grid-cell. Two important questions now arise: (1) how does one choose a single C_α value that is representative of a whole 32-km NARR grid-cell? And (2) how can the effect of updrafts generated by sub 1-km scale terrain variability be represented in the coefficients?

Regarding the first question, we require a method that will identify or highlight rather than average-out the presence of terrain features conducive to migration. Movement of migrating raptors in a preferred direction along terrain features is an example of an oriented or directed walk (Nams 2006). To sample updraft-coefficient values within a NARR grid-cell likely to be experienced by migrating raptors, we developed an averaging method based on directed walks through each 32×32 matrix of updraft coefficients. The walks were started at equally spaced points along the north boundary of each NARR cell and move southward, preferentially selecting the adjacent grid-point with the highest C_α value. We then calculated the mean value of C_α along 1600 of these walks in each NARR cell. See Appendix S1 for detailed explanation of the upscaling approach.

To assess the second question, we repeated the calculations of C_α with 3 arc-sec (or c. 100 m) SRTM DEM data (Farr *et al.* 2007) as well as the GTOPO30 data (1 km). This higher resolution terrain data better resolves the terrain features (ridges, mountains) used by migrating raptors (Brandes & Ombalski 2004). We made the calculations on selected regions of varying topography corresponding to portions of western Colorado, Iowa and Pennsylvania, to represent a wide range of terrain ruggedness. As expected, use of the higher resolution DEM data consistently resulted in higher terrain slope and updraft estimates. The 32 km aggregated coefficients derived from the 3 arc-sec SRTM were strongly correlated with the 30 arc-sec GTOPO30-derived uplift coefficients for identical 32-km square regions corresponding to NARR grid-cells (regression test, $y = 1.82x + 0.01$, $R^2 = 0.88$, Significance $P < 0.001$) (Appendix S1). This linear regression equation was used as an empirical correction that we used to scale up the GTOPO30-based C_α for sub-km scale terrain features. Thus, the final matrix of C_α values used at the NARR scale includes both directed path averaging and an empirical scaling factor to account for fine scale terrain features.

Estimation of thermal uplift velocity

The diurnal solar heating of the surface produces strong heat flux. The buoyancy associated with this flux drives thermals. Estimation of thermal uplift velocity is provided through a scaling coefficient, known as the convective velocity scale, w^* (Stull 1988):

$$w^* = [gzH/T]^{1/3} \tag{5}$$

where g is the gravitational acceleration, z is the flight height, which is assumed to be within the atmospheric boundary layer, ABL and T is the potential temperature in Kelvin and H is the surface sensible heat flux and w^* is proportional to the mean uplift at any particular height at the ABL. In classical formulations of w^*, the virtual potential temperature and flux are used rather than the potential temperature. The difference is the buoyant effect of water vapour. However, this effect tends to cancel out from w^* as virtual potential heat flux is divided by virtual temperature, especially in well mixed ABLs (typically during daytime). Convective velocity scale, w^* is used commonly in boundary layer meteorology as a parameter for estimation of vertical transport and the structure of the ABL (Holtslag & Moeng 1991;

Raupach 1991; Kristensen *et al.* 2010) and was used to analyse soaring birds flight data (Shannon *et al.* 2002a,b). A negative w^* occurs when the surface is cooling the atmosphere, typically at night, after rain events or when the surface is covered with snow. This state represents conditions that are unsupportive of flight using thermal soaring.

It is important to note that w^* calculated from NARR data is a statistical indication, providing a proportional estimate to the mean thermal uplift strength that a bird will experience over a 3-hours time period of the model output and at the 32×32 km^2 of the model grid-cell. However, uplift is a small-scale turbulent phenomenon and the actual uplift at the exact bird location and time vary around the estimate provided by w^*. Because the actual high-resolution values of turbulence cannot be produced by a model, even at very high resolution due to the chaotic nature of turbulence, we assume that the mean uplift, as approximated by w^*, will provide an effective descriptor of the actual conditions incurred by the migrating bird.

Meteorological data

Weather variables values were taken from the North American Regional Reanalysis (NARR) model-observation hybrid dataset (Mesinger *et al.* 2006), available on-line through the National Oceanic and Atmospheric Administration's and the National Climatic Data Center's National Environmental Satellite, Data, and Information Services (NESDIS) (NOAA 2010). NARR is a product of the ETA regional model (Janjić 1994) forced with a large set of satellite, surface and balloon observations. It consists of a three-dimensional grid that covers North America with a horizontal resolution of 32×32 km^2, a vertical resolution defined along pressure levels, every 25 milibar near the surface (roughly 250 m) and a temporal resolution of 2 min. Snapshot and time-averaged data are saved every 3 h and posted on-line.

Each migrant's location was matched with the nearest NARR grid-cell centre. The NARR data for that cell were interpolated linearly in time to the timestamp of the bird GPS data point. Wind speed and wind direction were processed from the NARR variables for latitudinal and longitudinal wind velocities. To determine w_o, the ground wind direction was rounded to the nearest one of 8 sectors, for which w_o coefficients were calculated, and the horizontal surface wind speed (at 30 m above ground) was multiplied by the coefficients for that wind direction sector (eq. 1). Value of w^* was evaluated from the variables provided by NARR, assuming z and the height at which T is taken are at the geopotential height of the highest pressure level below the top of the ABL. This assumption is equivalent to assuming that the bird is able to optimise its height within the ABL. The variables for temperature and pressure can be used to calculate the potential temperature, T, while surface sensible heat flux, H and ABL height, z, are provided directly by NARR. See Appendix S2 for definition of meteorological terms and NARR variable codes.

Raptor-track data

Data were obtained from 70 g solar-powered GPS Argos satellite telemetry transmitter units (Microwave Telemetry, Inc., Columbia, MD, USA) that had a spatial resolution of < 10 m, using either 1-h or 3-h duty cycles. Some of the birds were tracked continuously for more than a year, however, we only used autumn migration tracks. We used data from six individual turkey vultures over 10 migration tracks (2008; 2011); and seven individual golden eagles over 15 migration tracks (Miller *et al.* 2010) during partially overlapping periods of 3 years for each species (Fig. 1). Movement speed was calculated using the Haversine formula for any two consequent (1 h apart) location observations in each bird track.

Data analysis – Comparison with background domains

For each GPS observation we assigned w_o and w^* calculated at the nearest neighbour grid-cell from the NARR dataset, and interpolated the data in time, to the timestamp of the GPS observation. We calculated the distribution of the different uplift components among the observed track points. We hypothesise that the birds prefer specific conditions of uplift. During the day, when wind speed is larger than 0 and solar radiation heats the ground, both uplift modes are available at almost all track points. They also tend to be inter-correlated as both show a strong diurnal pattern and wind speed dependency. It is therefore not possible to simply test which of the uplift modes is stronger within the observed tracks. To correctly test our hypothesis, we determined the background (prior, null) distribution of each of the uplift modes that each of the species would encounter if they would have chosen their paths without any information about uplift (i.e. at random with respect to uplift modes). A bias towards high or low values in the distribution of a particular uplift mode in the observations in comparison to the random background distribution of the same uplift mode will indicate that the flight path and time were not selected at random but were the result of targeted selection for (or against) that particular uplift mode.

The choice of a domain, over which to sample the background distributions, is not without assumptions. There is a continuum of the levels of details that can be included in the selection of such domain. In this study we chose a background with an intermediate level of complexity – we assume that a linear box, bounded by the most extreme points (east, west north and south) for which we have observations to provide a general, yet realistic, background domain (Fig. 1). We incorporated one assumed interaction with the environment – both species do not fly over large water surfaces – by including only land points. We also generalised the timeframe by testing data only from the migration season of each species, defined as the time of year that includes 95% of the observations of southward migration, during years for which we have observations of each species, and include only daytime hours (NARR timesteps 12, 15, 18 and 21 GMT, i.e. 7 AM–4 PM eastern standard time), as we assumed neither species migrates at night. With these defined background domains for each species we calculated the null distributions for w_o and w^* using each NARR grid-cell and timestep within the background domain for each species.

Statistical analysis

We used the Kolmogorov-Smirnov (KS) test (MATLAB 7.9.0, Statistics toolbox) to test the significance of the overall differences between pairs of distributions of either w_o or w^* in the background vs. in the observed tracks. To prevent pseudo-replication due to the arbitrary observation timestep (one hour), we calculated the critical value of the D statistic of the KS test, D_{ks}, for a degree of freedom based on a one sided test with a sample size equal to the number of migration events we observed (15 in eagles, 10 in vultures). A migration event is the entire track (thousands of observations) collected from a single bird during a single fall migration season.

Because of the small sample sizes considered, we assume significance at $0.05 < P \leq 0.10$ as marginally significant.

RESULTS

The distributions of observed w_o and w^* in golden eagle and turkey vulture tracks differed significantly ($D_{ks} = 0.339$; 0.434; $P = 0.049$; 0.01, respectively). Of course, this may be a result of sample bias due to the small partial overlap between the sampling domain in space and time. As a hypothetical example, it is possible (though not the case) that 2008 – for which we have only eagle data – had exceptionally strong orographic uplift, and thus, the observed difference may be in part a result of sample bias and not a difference in weather preference. It is also hypothetically possible that turkey vulture routes, for example, are over the coastal plain and therefore encounter far less orographic uplift. To properly test the differences in preference, we therefore tested the observed uplift distribution in each species tracks compared to the background distribution for that uplift mode in the corresponding species domains.

The value of w_o in golden eagle tracks was significantly different and w^* in turkey vulture tracks was marginally significantly different than their distributions in the background domains ($D_{ks} = 0.318$; 0.347; $P = 0.040$; 0.073, respectively) (Fig. 2). In contrast, there were no significant differences between observed and background w^* in golden eagle tracks and observed and background w_o in turkey vulture tracks ($D_{ks} = 0.125$; 0.238, respectively, $P > 0.1$ in both cases) and Fig. 2 shows that in these cases the observed distribution of the uplift modes is strikingly similar to the background 'null' distribution. This indicates that the two species exhibit contrasting patterns of use of the different uplift components (thermal or orographic) during migration.

For both species the null distribution of orographic updrafts showed that strong uplift was rare in the landscape and the distribution of w_o was skewed towards low values, but had a thicker high-value tail, with the maximal values exceeding 12 m s^{-1}. The background distribution in the golden eagle domain was less skewed with a thicker tail than the one for turkey vulture, indicating a greater background probability of strong orographic uplift in the former's domain. The distribution of w^* is bimodal, becoming negative when surface heat flux is negative and conditions do not support thermal-aided flight; and positive in sunny days when the surface heat flux is positive. As indicated by the distributions of w^* and w_o, uplift stronger than 1 m s^{-1} was more prevalent as thermals for both species, but the greatest lift (larger than 3 m s^{-1}), though rare, was generated by orographic wind deflection.

To further study differences in golden eagle and turkey vulture flight tactics, we determined the threshold uplift velocity for each case as the velocity value where the observed distribution crossed the background distribution. In the case of the orographic uplift, this threshold happened at 0.4 m s^{-1} (Fig. 2). However, the trends between golden eagles and turkey vultures tracks were in opposite directions. The observed distribution of w_o in golden eagle tracks is skewed towards higher values relative to the background distribution and the probability of observing high w_o values (above the threshold of 0.4 m s^{-1}) is higher than in the background distribution. In turkey vulture tracks the probability of observing values higher than 0.4 is lower than its corresponding background distribution. Notably, this opposing trend is apparent for thermal uplift. The probability to observe stronger w^* than 1.2 in turkey vulture tracks is higher than the background probability, whereas in golden eagle tracks the probability of observing thermal uplift stronger than 0.6 is lower than the background probability for eagles domains. This implies a bias against good flight conditions of the 'wrong' updraft mode.

We tested a multivariate model for movement speed, including tailwind and both uplift modes (Fig. 3). All pair-wise regressions were significant, but the R^2 were low (0.07 and 0.13 for the combined model in turkey vultures and golden eagles, respectively). The correlations between movement speed and each uplift mode showed that thermal uplift was highly beneficial for both species. Tailwind, calculated here

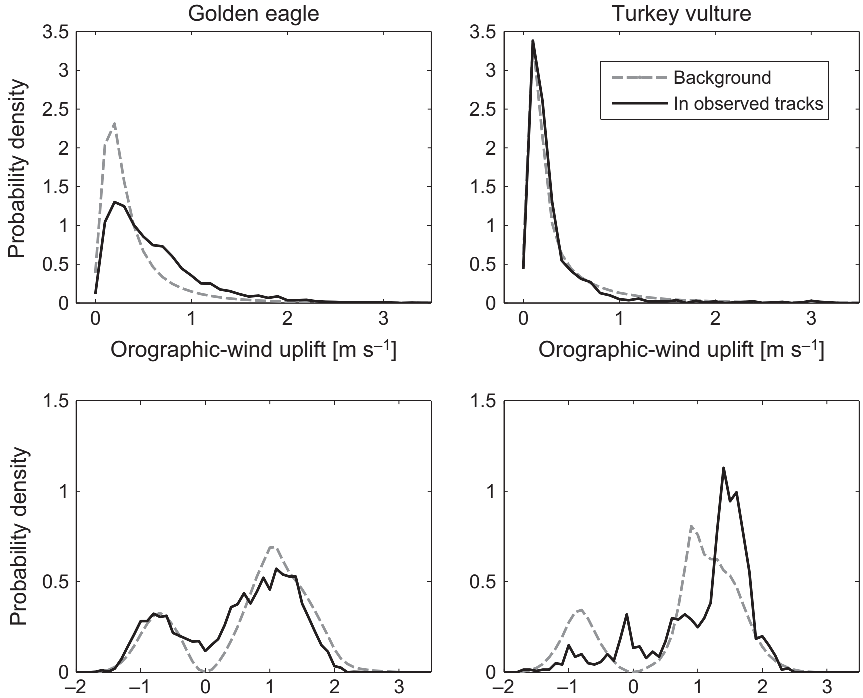

Figure 2 The distributions of orographic uplift (top panels) and thermal uplift (bottom panels) for golden eagles (left panels) and turkey vultures (right panels) within the background domain (shaded dashed lines) and observed tracks (solid lines). Golden eagles and turkey vultures display opposing preferences to uplift mode. Golden eagles have a strong bias to strong orographic uplift above the threshold value of 0.4 m s^{-1} (top left panel) and a slight bias against strong thermal uplift above 0.6 m s^{-1} (bottom left panel), while turkey vultures have strong bias for strong thermal uplift above 1.2 m s^{-1} (bottom right) and a slight bias against strong orographic uplift above 0.4 m s^{-1} (top right).

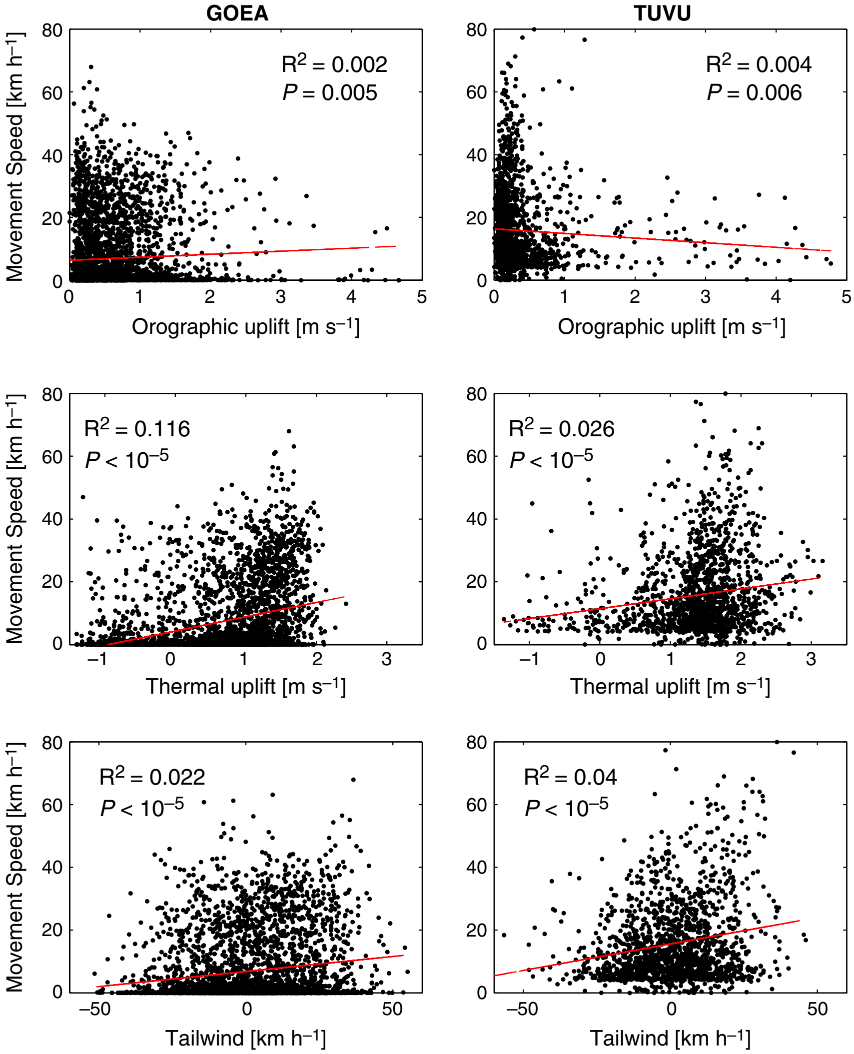

Figure 3 The relationships between orographic uplift (top panels), thermal uplift (middle panels) and tailwind (bottom panels) and movement speed for golden eagles (left panels) and turkey vultures (right panels). Points are observations; dashed line marks a linear regression curve. R^2 and significance P-values are indicated on the plots.

as the wind-speed component at the bird flight-segment direction, was the most effective driver of movement speed in turkey vultures. Orographic uplift had very low correlation with movement speed in both species. It significantly increases segment-movement speed for eagles but was negatively correlated with it in vulture tracks. To explain this fact, we calculated the distribution of orographic uplift relative to thermal uplift in the background domains (Fig. 4). We observed a negative correlation between strong orographic (above 0.6) and thermal uplift and between strong thermal (> 2.1 m s^{-1}) and orographic uplift, which could explain the appearance of slight biases against high orographic uplift in observed turkey vulture tracks and against strong thermal uplift in golden eagle tracks.

DISCUSSION

Our results provide insight into the flight preference and behavioural responses to weather of migrating birds. By comparing two, primarily soaring, raptors from similar areas, we found that migrating golden eagles and turkey vultures differ in patterns of updraft use. We observed a bias by migrating golden eagles towards use of strong orographic uplift (Fig. 2), suggesting a preference for this uplift mode. Observations of migration behaviour suggest that this choice is primarily achieved by selecting flight paths over the windward side of

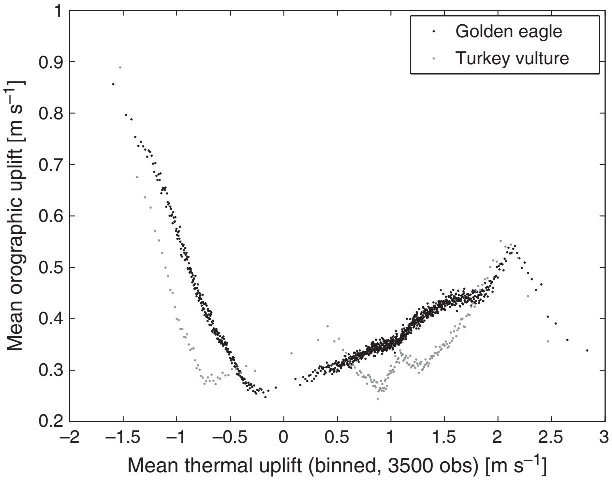

Figure 4 The relationships between orographic uplift and thermal uplift. This relationship is plotted by binning thermal uplift into bins of 3500 data-points and calculating the mean orographic uplift in each of these thermal uplift bins. The patterns between the turkey vulture and golden eagle domains are rather similar. Overall, the strongest orographic uplift is associated with strong negative thermal uplift. Orographic and thermal uplift are negatively correlated in the negative range of thermal uplift.

the crests of the Appalachian Mountains and ridges (Allen *et al.* 1996; Brodeur *et al.* 1996). Turkey vultures use thermal uplift more than randomly available in the background and, contrary to our hypothesis, show a slight bias against high values of orographic uplift (Figs 2 and 3). This is consistent with observations that vultures are able to find and use small sources of thermal uplift (Mandel & Bildstein 2007).

The correlations between uplift modes and flight speed further support these findings. These correlations were very weak, likely because uplift does not necessarily translate to higher flight speed. Uplift may be used to save energy by gaining height while circling in thermals, or lead to jagged tracks among ridges. Additional variation is due to the fact that flight speed is not simply defined. It can be measured instantaneously, over an arbitrarily short segment (1 h in our case), over the course of a single behaviour, and over the course of a specified distance. Over a long distance vultures may move faster, as they likely travel longer without stopping to forage for food. We expect that eagles, with their higher wing loading, will move faster than vultures in single behavioural legs of their journeys, but that over a course of complete migration events, many other factors will come into play. That said, if the study focus is on the time spent in a particular flight behaviour (thermal vs. ridgetop gliding), a method to differentiate these flight modes from the data must be devised. The next generation of tags with 3D accelerometers (Weimerskirch *et al.* 2005) or with high-frequency GPS data collection (Lanzone, M.J., Katzner, T. and C. Halverson, unpublished data) could provide such information.

Another peculiar fact apparent in the observed distributions of w^* in turkey vultures and golden eagles is that whereas vultures avoid flying when and where w^* is negative, as one would expect for soaring flight, eagles do not. This is due to the correlation structure between orographic and thermal updrafts. The strongest orographic uplift is associated with strongly negative thermal uplift. This is because strong winds, which are required for orographic uplift, produce shear that tends to break apart thermal formation. Golden eagles, therefore, do not avoid negative thermal uplift because it occurs coincidentally with strong orographic uplift. In fact, golden eagles are often observed in the study area migrating in late autumn on days with high winds and heavy overcast, conditions that immediately follow the passage of regional cold fronts.

We refer to 'preference' and preferential use of a particular uplift mode in a broad sense. Our data cannot directly determine whether the bias towards high values of a particular uplift mode is a result of long evolutionary and genetic processes, learned behaviour, or 'on-the-fly' responses to changing weather conditions. Further tests and observations, particularly inter-population comparisons and long-term multi-year tracking of individuals will help identify the extent to which, if any, each of the three processes contribute to the use patterns we observed.

Understanding how weather conditions affect the migration path of birds is critical to both to avian conservation in general, and to predicting the demographic responses of avian populations to on-going and future climate and land-use change (Shamoun-Baranes *et al.* 2010a). We have shown that golden eagles and turkey vultures use weather differently during their migratory flights. A change in land cover, such as addition of road cuts along ridges, or climatic fluctuations along the migration path that may change uplift conditions may change the energetic costs of migration and may alter the selective environment for migratory species. We suggest that golden eagles, which use orographic uplift heavily, will be more sensitive to land-use changes that will affect or interact with uplift on mountain ranges. This includes mountaintop removal mining that will decrease uplift and disturb habitat directly under the flight paths, and power-lines, wind turbines or other obstruction at the ridge tops that may lead to increased collision rates or avoidance of terrain conducive to orographic lift. On the other hand, turkey vultures may be more sensitive to land-use changes that affect thermal uplift, including irrigation or development.

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AUTHORSHIP

GB and DB wrote the manuscript with comments and additional contributions by all co-authors. They also developed the formulation for the uplift components. GB conducted the weather data annotation, data analysis and Figs 2 and 3. JM and KB conducted the turkey vulture tracking and provided the data. TM, TK, CM, ML and JT conducted the golden eagle tracking and provided the data. TM produced Fig. 1.

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Appendix S1 Extended methods description.
Appendix S2 Meteorological glossary.

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