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Migration path annotation: cross-continental study of migration-flight response to environmental conditions

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Abstract. Understanding the movements of animals is pivotal for understanding their ecology and predicting their survival in the face of rapid global changes to climate, land use, and habitats, thus facilitating more effective habitat management. Migration by flying animals is an extreme form of movement that may be especially influenced by weather. With satellite telemetry studies, and the growing availability of information about the Earth's weather and land surface conditions, many data are collected that can advance our understanding about the mechanisms that shape migrations. We present the track annotation approach for movement data analysis using information about weather from the North American Reanalysis data set, a publicly available, regional, high-resolution model–observation hybrid product, and about topography, from a publicly available high-resolution digital elevation model (DEM). As a case study, we present the analysis of the response to environmental conditions in three contrasting populations of Turkey Vultures (*Cathartes aura*) across North America, tracked with a three-dimensional GPS-based sensor. Two populations in the east and west coasts of the United States responded similarly to weather, indicating use of both slope and thermal soaring. Continental-interior, "Plains populations," exhibited a different migratory pattern primarily indicative of thermal soaring. These differences help us understand the constraints and behaviors of soaring migrants. The track annotation approach allowed large-scale comparative study of movement in an important migratory species, and will enable similar studies at local to global scales.

Key words: Cathartes aura; *flight; migration; movement ecology; navigation; soaring; Turkey Vulture; weather utilization.*

Introduction

Migration is one of the most conspicuous of animal movements in nature. Land use change, habitat loss, and climate change can and do disturb migration patterns at a risk to the conservation of migratory species (Wilcove and Wikelski 2008). Concerns about the responses of migrating species to climate change and other anthropogenic habitat disturbances have drawn attention to studies of current migration patterns and prompted attempts to forecast future patterns. To study animal movement from a mechanistic perspective, one needs to know both the path of the animal movement and the external and internal forcing in the migration landscape that affected that movement (Nathan et al. 2008). Path annotation is a data collection approach that meets these needs.

Borrowed from computer science, where it is used in web browsing, the term "path annotation" is used when additional data about important variables, encountered through a particular path, are added to the object whose path was recorded. In the context of animal movement, an annotated path would include the values of environmental and physiological variables, co-located in time and space with the moving organism. New tracking technologies that use global positioning system (GPS) sensors (Tomkiewicz et al. 2010), satellite, and radiotelemetry, and smart tracking sensors, allow extremely detailed observations of movement paths over large distances at high spatiotemporal resolution. We show how data obtained from satellite- or GPS-based tracking sensors mounted on a wild test subject can be annotated with the values of environmental variables at the times and places through which the animal moved. These annotated tracks can be used to understand the way in which environmental variables affect the movement of migrating organisms and to assess the degree to which these effects differ across a continental scale.

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Annotated track data recently have been used in studies of the ecological ranges of many species, including polar bears (Durner et al. 2009), seals (Austin et al. 2006), agoutis (Aliaga-Rossel et al. 2008), and monkeys (Crofoot et al. 2008), and a variety of birds. Smart sensors, which are incorporated in the tracking tag itself, collect data along the path, such as atmospheric pressure and temperature (Shannon et al. 2002*a*, *b*) or internal physiological variables such as heart rate (Bowlin and Wikelski 2008, Steiger et al. 2009). Nonetheless, tracking devices that only collect the bird location can be annotated post-flight. Publicly available environmental data sets, including large-scale remotely sensed data (e.g., Roshier et al. 2008, Durner et al. 2009), and atmospheric observations from meteorological stations (Beekman et al. 2002, Klaassen et al. 2004) provide additional data for track annotation.

Weather reanalysis data sets are the products of atmospheric models that are forced with a large number of satellite, meteorological ground stations, and weather balloon observations (for examples of path annotation using global reanalysis data, see Gill et al. 2009, Shamoun-Baranes et al. 2010). A major advantage of using these gridded data sets rather than direct observations from meteorological stations is that they have predictable error rates and a regular resolution across the entire continental- or global-scale domain of the movement track, which enables standardized comparisons over large spatial areas and time periods. The reanalysis data sets also provide variables that are not typically measured by weather stations, including turbulence kinetic energy (TKE), vertical air movement, and surface heat flux, which may be highly relevant to studies of flight. High spatial resolution regional reanalysis data sets are available across North America (North American Regional Reanalysis [NARR]; Mesinger et al. 2006), South America (Souto et al. 2007), and Europe (*available online*).[6] They provide data at a relatively high spatiotemporal resolution, typically every 1–4 hours, and at a length scale of 10–40 km. Data at these scales provide reasonable approximations for many atmospheric variables at levels of resolution relevant for assessing the variables that affect movement. Data set variables that are indicative of the vertical wind and turbulence are particularly important for the study of bird movement (Bowlin and Wikelski 2008), especially the migration of soaring birds (Mandel et al. 2008).

Here, we used annotated tracks of a large soaring migrant, the Turkey Vulture (*Cathartes aura*), from three populations in different parts of North America to explore regional differences in atmospheric conditions and modes of migration. We tagged birds in three areas: eastern Pennsylvania, USA; central Saskatchewan, Canada; and southern California, USA. Vultures from Saskatchewan migrate through the Great Plains. The two coastal populations often migrate along mountain ridges. Specifically, we used path annotation to combine position data from a novel three-dimensional GPS tracking device with meteorological conditions along the migratory paths from the NARR data set.

METHODS

We examined migratory movements in the context of the Movement Ecology Framework (Mandel et al., 2008, Nathan et al. 2008) by examining the role of external effects on movement, and navigation at a single spatial and temporal scale. We were interested primarily in the mechanics of migration and focused on the smallest temporal scale available to us, hourly. External effects were characterized by weather variables and by topography. For statistical analysis, we define movement as the straight-line distance between two observed location estimates separated by one-hour in consecutive GPS measurements. Navigation is defined according to angular deviations in hourly tracks from the overall linear bearing of the seven previous tracks (see Mandel et al. 2008).

Species

North American Turkey Vultures include two subspecies (Kirk and Mossman 1998). *Cathartes aura septentrionalis* occurs mainly east of the Mississippi River, and *C. a. meridionalis* occurs mainly west of the Mississippi River. The eastern subspecies includes individuals that do not migrate and birds that migrate from the northeastern USA and eastern Canada as far south as Florida, while the western subspecies migrates longer distances than the eastern populations, with large numbers of birds making an intercontinental migration into northern South America (Bildstein 2006). Vultures migrate using a combination of few basic processes: alternating soaring and gliding using isolated thermals for lift, slope soaring using winds deflected upwards by mountains for lift (Kirk and Mossman 1998), and, less often, flapping flight, which typically is used by migrants only during landings and takeoffs (cf. Ferland-Raymond et al. 2005).

Birds were tagged in eastern Pennsylvania ($n = 3$), central Saskatchewan ($n = 5$), and southern California ($n = 3$) in 2004–2008. In Pennsylvania, Turkey Vultures were captured in padded leg-hold traps baited with road-killed deer (*Odocoileus virginianus*) and groundhogs (*Marmota monax*). Traps were monitored from a blind, and birds were removed from traps immediately upon capture. In Saskatchewan, birds were hand-grabbed on their nests in abandoned farmhouses. In southern California, birds were trapped in a large box-trap baited with the carcasses of small mammals. All birds were fitted with a solar-powered GPS receiver and Argos satellite telemetry system transmitter unit (70 g; Microwave Telemetry, Columbia, Maryland, USA) using a "backpack"-style harness of Teflon ribbon.

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[6] ⟨http://www.euro4m.eu/⟩

TABLE 1. Listing of variables by category.

Category	Variables
Present state	bearing deviation† *or* (by model) distance†; latitude; speed; altitude
Landscape	terrain ruggedness; height of planetary boundary layer (HPBL)†
Winds	wind direction†; wind speed†
Turbulence	surface heat flux (SHF); vertical velocity of pressure levels; cloud top height; turbulent kinetic energy (TKE)†; convective available potential energy; cloud bottom height; W^*

Notes: Entries with a dagger (†) were used in statistical analysis. The height of the planetary boundary layer (HPBL), despite being an atmospheric variable, was strongly correlated with terrain ruggedness, and therefore was included in the analysis as a landscape variable. W^* is the free convection scaling velocity (Stull 1988), SHF is the sensible heat flux from the land surface. Both act as a potential indication of thermal uplift.

Harnesses were secured with unwaxed dental floss, which naturally rots after several seasons (E. Henkel, *personal communication*) and thereafter releases the harness from the bird. Captured birds were offered dead mice in captivity, and all were released within 24 h of capture. Birds preened vigorously immediately after release, but showed no noticeable effect after 2–3 days.

Assembly of database

Time series of movements were obtained from GPS receivers that had a spatial resolution of less than 10 m, recorded locations hourly, and uploaded the data to satellites (Mandel et al. 2008). For this analysis we used data from the fall migration (during October and November), the peak southbound migratory season. Migration movement was defined by latitudinal movements that exceeded those displayed during breeding and overwintering. Only hourly movements >4 km were included as migratory movements. We termed the collection of all movements for a bird in a given autumn migratory season as a "migration." Overall, the migratory data set included 11 individual birds followed during 15 different migrations.

We assembled hourly movement vectors coded in radial coordinates from the GPS movement data. In radial coordinates, it becomes necessary to establish a principal axis of movement and to measure angles (of wind direction and movement) in terms of deviations from that axis of migration. In addition, the interaction of wind speed and direction becomes a critical measure for interpreting the appropriate effects of wind.

For every movement vector, we used the bearings of the previous seven movement vectors to establish a direction of movement; we term this the "local axis" of migration. We chose a local axis and not a global axis (the direction between the start and end point of migration; see Thorup et al. 2003) because in such long migrations it is rather hard to define the exact point of migration start and end, and because many birds migrate along curved paths along coastlines, or between shelter, roost, and foraging grounds during the migration. For each local migration segment, we took the absolute value of the bearing of the movement vector minus the local axis of migration; we termed this calculated variable "the bearing deviation" (Thorup et al. 2007). Wind direction was calculated similarly, as a bearing minus the local axis of migration, which we termed "wind deviation." Thus, a wind deviation of zero would be considered a tailwind, whereas a wind deviation of 90 degrees would be a perpendicular crosswind. Following Oliveira et al. (1998), we used bearing and wind deviations to fit linear models. All angle calculations were done using the "Circular" package in R v. 2.3.1 (Ihaka and Gentleman 1996, Rao 2001).

Time series

We used the ARIMA technique (Box et al. 2008) to estimate the appropriate covariate structure, which was subsequently applied to all models. ARIMA diagnoses trends, autoregressivity, and sampling error in a time series, and then compensates for the presence of any of these using differencing, autoregressive correlation structures, and moving-window averaging, respectively. In all cases, a correlation matrix with a single autoregressive component (similar to a correlated random walk) was found to be most appropriate. An ARIMA transformation was applied to all dependent variables to remove the effects of the autoregressive dependency from the statistical analysis.

Predictive variables

We examined four classes of variables: (1) present state of the bird, (2) landscape, (3) wind (horizontal speed and direction), and (4) turbulence, which includes vertical motion of air (Table 1). These categories correspond roughly to what a soaring bird might perceive in flight: They know something about where they are, they can view the landscape below them, they can feel horizontal winds, and they have some knowledge of vertical air movement whether through feeling turbulence, seeing thermal-circling movements of other birds, or observing clouds. We used model-derived variables that approximate this information according to the four categories. For predictive variables that were highly correlated within categories, we used only one per category in statistical analyses.

1) Present state: The speed of travel and flight altitude measured at the start of the movement vector interval.

2) Landscape: We used the GTOPO30 digital elevation model (DEM) available from the EROS database at the USGS, which has grid spacing of 30 arc seconds (~1 km). We created a map of terrain ruggedness based on the variance in altitude of adjacent grid cells using Manifold v. 2.1 (CDA International; *available online*).[7] Terrain ruggedness was calculated according to the formula provided by Riley et al. (1999) and provides a unit-less index of variance in elevation.

3, 4) Weather variables: Values were taken from the National Center for Environmental Prediction (NCEP) North American Regional Reanalysis (NARR) data set (*available online*).[8] NARR (Mesinger et al. 2006) 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, a vertical resolution defined along pressure levels, every 25 milibar (mb) near the surface, and a temporal resolution of two minutes. Snapshot and time-averaged data are saved every three hours and posted online.

Each migrant's longitude and latitude were matched with the nearest NARR grid cell center. NARR data for that cell were interpolated linearly in time to the time stamp of the bird GPS data point. For three-dimensional variables, we interpolated values vertically between the pressure levels above and below the GPS-determined altitude of the bird using the NARR pressure level height variable (HGT; geopotential height), except when the bird was in or below the lowest pressure-level height, in which case we used the model-interpolated surface variables. We included four groups of variables: (1) Wind speed (MagnitudeWind) and wind direction, processed from the NARR variables for latitudinal and longitudinal wind velocities (UGRD, VGRD, respectively). To analyze wind direction, horizontal winds were translated into polar coordinates, and the angle was translated into a deviation from the local mean axis of migration (WindDeviation). (2) Turbulent kinetic energy (TKE) is parameterized in NARR using empirical relationships between surface fluxes and the stability of the planetary boundary layer (Mellor and Yamada 1982). High TKE is typical for days with intermediate wind levels and strong convective heat flux from the ground (i.e., cloudless hot days) and indicates the presence of strong thermals; conversely, days with very strong winds, neutral boundary layer conditions, and strong mechanical shear can also produce high values of TKE (referred to here as "shear" TKE; Stull 1988). (3) Pressure vertical velocity is defined as the rate of change over time of the height of the pressure levels that make up the vertical dimension of the grid. The vertical movement of pressure surfaces is associated with the daily cycle of the growth and collapse of the planetary boundary layer with the daily dynamics of surface heat flux and mesoscale pressure fronts. (4) Cloud top height, and cloud bottom height and convective available potential energy are two-dimensional model fields that indicate different aspects of parameterized convective activity in the planetary boundary layer. In addition, we used sensible heat flux (SHF), which is a measure of energy transferred as heat flux from the land surface to the atmosphere, due to absorption of solar radiation by the earth's surface, and calculated W^*, the free convection scaling velocity (Stull 1988), as potential indications of uplift.

We specifically tested the correlation structure within the turbulence category (Fig. 1). Here, we used an array of variables, all produced from parameterization schemes within the NARR. Although a variable such as W^*, which would seem to directly capture vertical air movements at a scale appropriate to birds, is conceptually most appropriate, the high degree of parameterization involved in calculating this variable at the 32 × 32 km resolution of NARR ultimately yielded a poor fit to the data. It was also strongly correlated with SHF and other variables that were included in the analysis and therefore was omitted. Similarly, variables relating to cloud height seem appropriate perceptually, as they are something the migrant could see, but do not correlate well with available convection for flight. Turbulence kinetic energy (TKE), indicating the kinetic energy of the mixing of air within a bounded numerical cell of the model, yielded the best predictive power, and was used in our analysis. Height of the planetary boundary layer (HPBL) was correlated with TKE (Fig. 1), but represents a larger scale phenomenon, and also was included, as were wind direction and horizontal wind speed. Terrain ruggedness (TerrainRuggedness), which was highly correlated with TKE and HPBL, was omitted from the analysis (Fig. 1, Table 1).

Model simplification

Statistical analyses consisted of mixed-linear models created using the nonlinear and linear mixed-effects model (NLME) package in R (*available online*) with either the log of the distance or navigation bearing of each movement segment as the dependent variable and all other external and present location variables as independent variables.[9] For each mixed model, an a priori correlation structure from the ARIMA analysis was specified with a single degree of autocorrelation. All models began with the inclusion of all main effects and all potentially relevant interactions. Backward selection using maximum likelihood, and considering the effects of the interactions first, was performed to determine the final model. Final models were compared with initial models using ANOVA. The Akaike Information

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[7] ⟨www.manifold.net⟩

[8] ⟨http://nomads.ncdc.noaa.gov/data.php⟩

[9] ⟨http://cran.r-project.org/web/packages/nlme/index.html⟩

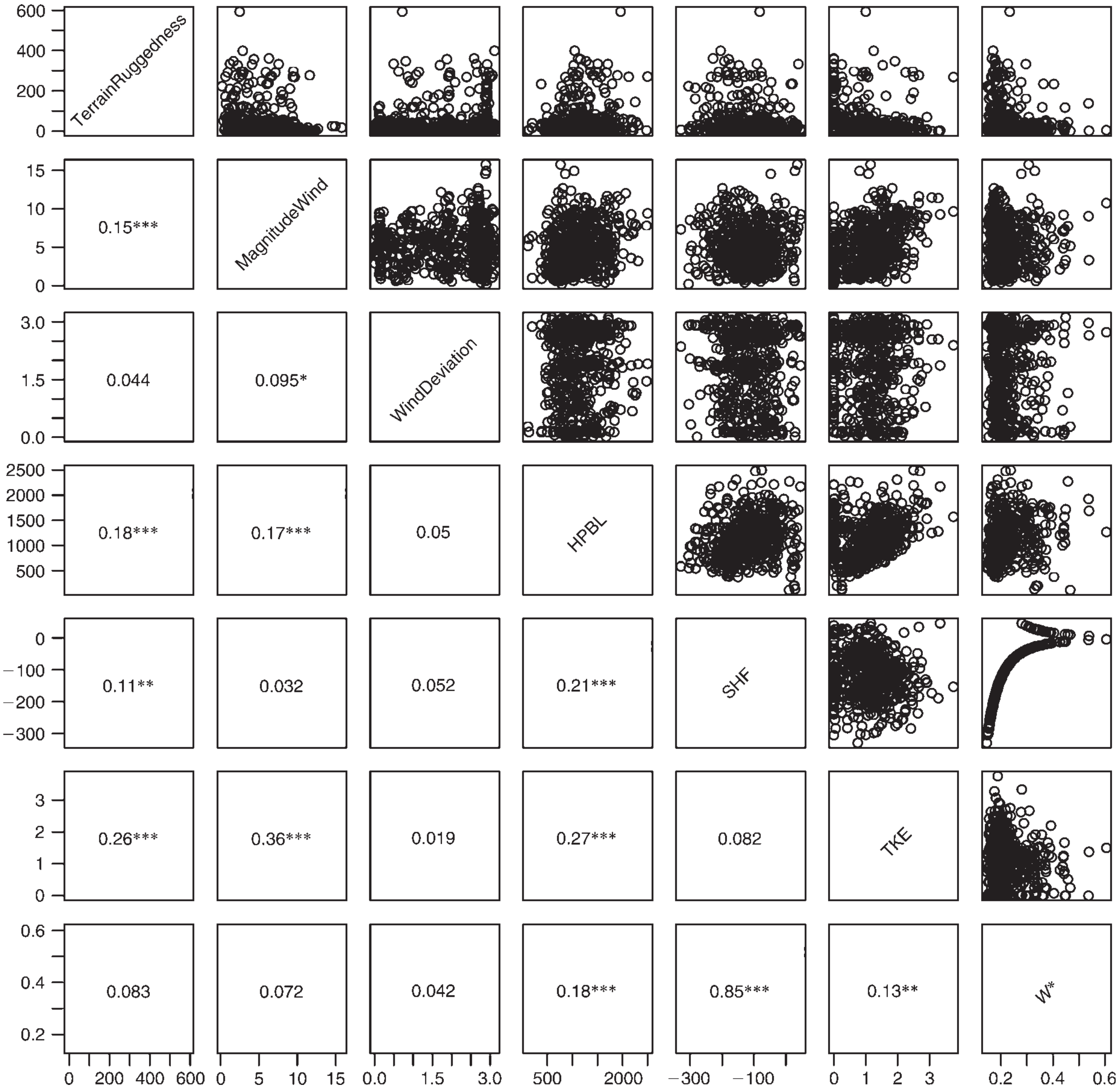

FIG. 1. Correlation matrix of major variables explored before statistical modeling. Variable names are listed on the diagonal. More details about the variables are listed in the section *Assembly of database*. The upper right diagonal contains scatterplots, while the lower right diagonal contains correlation coefficients (r values) and asterisks represent significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. These correlations provided the guidelines for variable elimination during model construction. For example, terrain ruggedness (TerrainRuggedness; first line, first column) was strongly ($r > 0.15$) and significantly ($P < 0.001$) correlated with turbulence kinetic energy (TKE; sixth line, first column) and height of the planetary boundary layer (HPBL; fourth line, first column), and therefore was omitted from the analysis. The scatter plots representing these correlations are in the first line, fourth (HPBL) and sixth (TKE) columns. MagnitudeWind is wind speed, and WindDeviation wind direction. W* is the free convection scaling velocity (Stull 1988), SHF is the sensible heat flux from the land surface. Both act as a potential indication of thermal uplift. Units are as follows: Terrain Ruggedness, m; Magnitude Wind, m/s; Wind Deviation, radians, HPBL, m; SHF, W/m^2; TKE, m^2/s^2; and W*, m/s.

Criterion (AIC) was observed to decrease throughout model selection in all models. Parameter values in the final models were then estimated using restricted maximum likelihood. The models were compared to identical models without random effects to determine if the random effects significantly changed the model. This was done by comparing the difference of −2(ln-likelihood) with a chi-square table and one degree of freedom.

RESULTS

Three east-coast vultures flying from the northeastern United States to Florida traveled along a route that included both coastal lowlands and the Appalachian

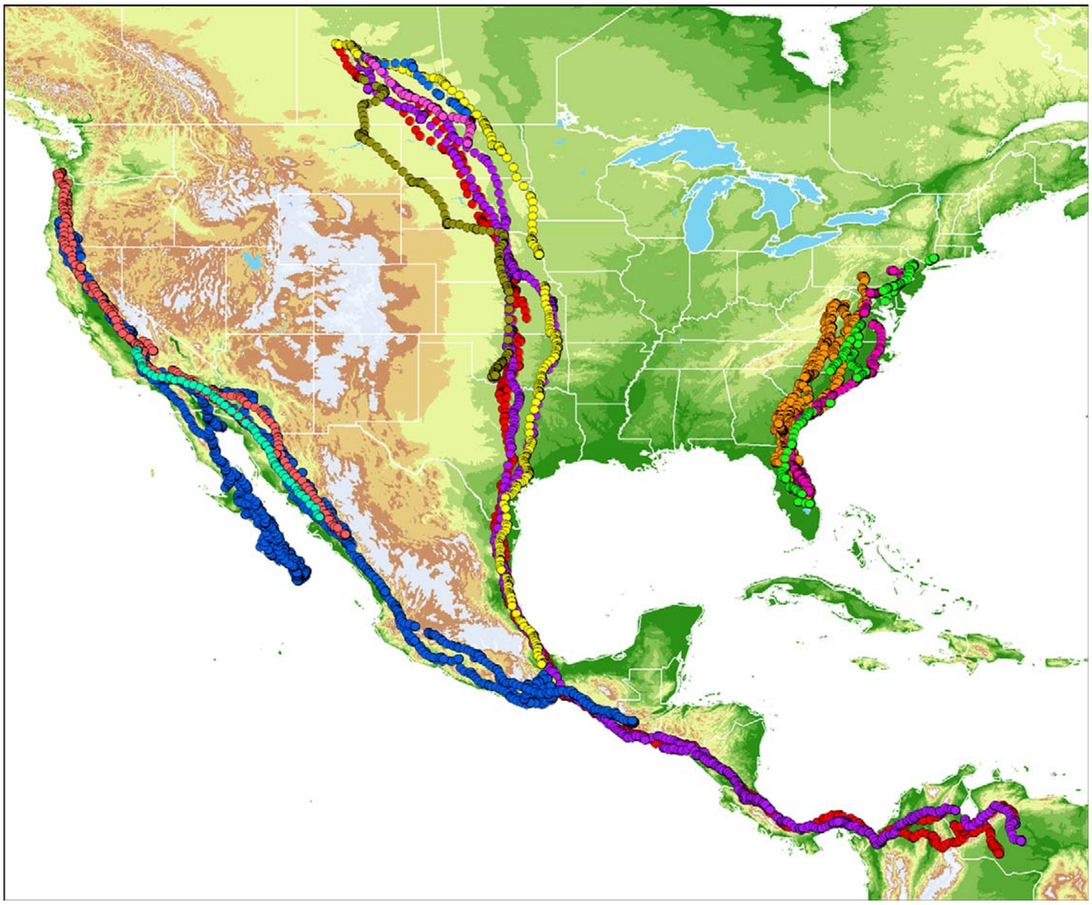

FIG. 2. A topographic map of North America with the complete Turkey Vulture (*Cathartes aura*) movements that were used in this study. One position per hour was plotted. Nearby migrations (by different birds or the same birds in different years) are plotted in different colors.

Mountains. Five continental-interior vultures, flying south from Saskatchewan, traveled through the central plains of southern Canada and the central United States and did not encounter mountain ranges until reaching southern Mexico, where they joined the migratory route of the western population along the central Cordillera of that country. Three west-coast vultures traveled along Pacific Coast mountain ranges while flying south through California, Mexico, and Central America (Fig. 2). From the perspective of terrain encountered, it is possible to view the east- and west-coast migrants, both of which traveled along mountain ranges, as more topographically similar than mid-continental migrants, which did not fly along mountains, at least during the large migration segment through the United States and Canada.

TKE was most strongly correlated with movement in all populations (Table 2). However, it also is clear that the movements of east- and west-coast birds, which fly over and along mountains, are influenced by the height of the planetary boundary layer (Table 2). In both populations, a higher planetary boundary layer reduces the positive effect of TKE (Fig. 3). For mid-continental birds, which are primarily flatland migrants, the height of the planetary boundary layer did not affect movement. For these migrants only, winds that deviated from the primary axis of movement were correlated with shorter daily flights (Table 2).

Navigation models revealed different patterns among the three populations. In all populations, horizontal wind speed (either as a direct effect or through its interactions with bearing deviation) played the largest role in determining the extent of deviations from the local axes of migration (Table 2B). However, the way in which winds interacted with navigation varied among populations. For continental interior migrants, the pattern was simple. High-velocity crosswinds led to course deviations (as apparent in Table 2B by the negative effect between wind magnitude and bearing deviation), and this effect was stronger with higher winds (positive interaction between wind magnitude and deviation). No other factors influenced flight direction in this population. For the west-coast birds, high winds were positively correlated with long-distance movement regardless of their direction. The positive role of winds in this population likely indicates the use of slope

TABLE 2. Summary of model effects (correlation coefficient,*r* and significance *P* value) for the (A) distance model and (B) navigation model.

	East-coast population		Mid-continent population		West-coast population	
Model effect	*r*	*P*	*r*	*P*	*r*	*P*
A) Effects on distance						
TKE	0.518	<0.001	0.137	<0.001	0.712	<0.001
HPBL		NS		NS		NS
WindDeviation		NS	−0.091	0.008		NS
TKE × HPBL	−0.0002	0.002		NS	−0.0003	0.002
df	525		507		185	
B) Effects on navigation						
WindDeviation		NS		NS		NS
MagnitudeWind		NS	−0.107	0.046	0.084	<0.001
HPBL		NS		NS	−0.0002	0.022
WindDeviation × MagnitudeWind	−0.026	0.049	0.036	0.024		NS
df	527		508		186	

Notes: Relationships were considered nonsignificant (NS) when $P > 0.05$. These variables were removed from the model. Navigation is measured as bearing deviation. An interaction is shown by ×. Degrees of freedom (df) of the test for the variables in each model are also given. See Table 1 for abbreviations.

soaring along mountain ridges, a method that is dependent on strong, steady coastal winds. In the NARR model, over the large scale, the boundary layer height is strongly correlated with topography and gets higher over mountain ranges because the land surface increases in height and boundary layer heights are known to increase in the presence of mountains (Lieman and Alpert 1993). We found that bearing deviation was negatively correlated with the height of the planetary boundary layer. This can be explained by slope soaring: When the birds find themselves over a mountain range, typically with a high boundary layer, they slope soar and

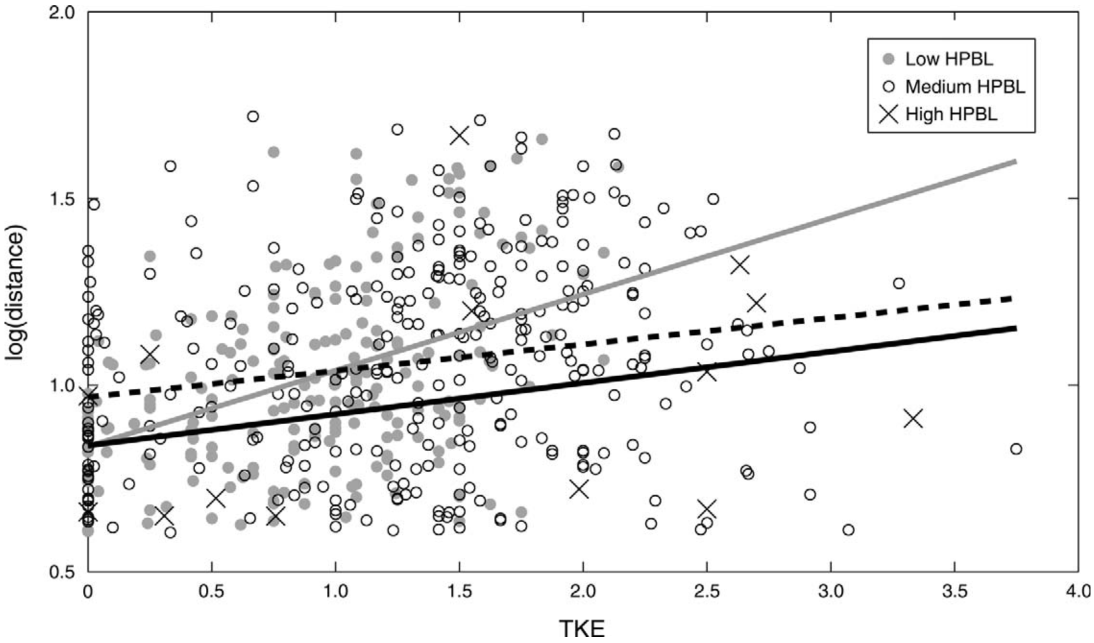

FIG. 3. Illustration of the interaction between movement segment distance and TKE in the eastern Turkey Vulture population. Each line corresponds to a linear regression between a scatterplot of data, representing the log-transformed movement segment distance and TKE at a range of planetary boundary layer heights (HPBL). Low HPBL values (gray circles; gray regression line) were below 1 km, medium values (open circles, dashed regression line) were between 1 km and 2 km, and high values (×'s, solid regression line) were higher than 2 km (the maximal recorded value was 2.5 km). The relationship is similar for the west-coast population and shows that TKE promotes movement (steeper positive slope) at low levels of HPBL, but matters less when the planetary boundary layer is high. In the North American Regional Reanalysis (NARR) model, over the large scale, HPBL is strongly affected by topography and gets higher over mountain ranges. This suggests that, at high levels of HPBL, i.e., over mountains, other movement options, such as slope soaring that do not depend on TKE the way it is parameterized in the model, are being used.

change direction off the principal axis of migration to follow and gain lift from updrafts along mountain ridges. In east-coast birds, the significant negative interaction between wind magnitude and deviation may also suggest slope soaring. In low winds, regardless of direction, birds maintained course. In high winds, however, bearing deviation was lowest as winds approached a perpendicular angle to the birds' direction. Given the geography of the region, with migration paths and the Appalachian range aligned largely on a north–south axis and sea breezes providing a strong and regular easterly wind, this pattern suggests slope soaring. High winds in the direction of movement caused course deviations, which is likely a result of disrupting the spatial structure of TKE (Mandel et al. 2008).

Discussion

The combination of GPS locations and regional-scale meteorological data enables a detailed comparative analysis of animal movement, in general, and large-scale continental movement, such as bird migration, in particular. Movement track annotation with environmental data opens new possibilities in studies of habitat utilization and home range in migrating organisms. It also allows measuring the response patterns of moving organisms to their external environment in situ, even in species whose movement tracks are extremely long, and where direct, continuous observations of the organisms and the conditions around them are impossible. With particular relevance to migrating birds, future changes to regional weather patterns may shift leading wind directions and patterns of rainfall, both of which could have important implications for the energy economics of migration in this and other species. Land use changes, such as the expansion of irrigated-field areas, could affect the strength of thermal uplift (e.g., Ozdogan et al. 2010) and, thus, modify migration patterns. By understanding how weather conditions along the migration track affect the energy expenditure and viability of the migrating organism, it will be possible to better predict their response to rapid changes to climate, land use, and habitats, thus facilitating more effective habitat management.

In this study, we have demonstrated how meteorological data from a regional reanalysis data set can be used to study the flight and navigation decisions of Turkey Vultures from different populations across North America. The analysis of one of the longest soaring migrations in the world, and the only long-distance migration by a scavenging raptor (Bildstein 2006), shows a remarkable similarity in response to landscape and weather among geographically and behaviorally (in terms of overall length of migration) distinct populations. In all three populations, turbulence, represented here by the parameterized NARR variable TKE, is the dominant correlate of movement. This pattern is consistent with a flight that is dominated by thermal soaring.

We also found an important slope-soaring component in migration among the two coastal populations. In these populations, at low boundary layer heights, which typically occur over flatter terrain, movement is driven primarily by TKE, but over mountains, this effect disappears. We attribute this effect to a transition from thermal soaring to slope soaring when the birds are traveling along mountain ridges. This transition does not occur in the interior, where migrants do not encounter mountains. Interior migrants also are constrained by horizontal winds, whereas the coastal birds can use slope soaring to minimize these effects.

Our models suggest that each of the three populations has its own suite of navigational responses to weather. With respect to winds, several key differences emerge. Continental interior migrants flying over relatively flat terrain tend to deviate from the migratory direction only in response to the mean wind direction. Because of this, we attribute the changes in response to wind from the two coastal populations to the presence of mountains. West-coast birds show larger deviations in high winds and are not affected by wind direction. Instead, they migrate along the straightest path when the planetary boundary layer is high. East-coast birds fly their straightest migration paths either when winds are low or when winds are high but orthogonal to the axis of movement, suggesting a greater alternation between slope soaring and thermal soaring than occurs in west-coast birds.

Based on our model, the two coastal populations use slope soaring and thermal soaring, and therefore have a more complex relationship with external conditions than do the continental interior migrants, which depend almost entirely on thermal soaring. Why the Plains migrants do not follow a more direct route over the Rocky Mountains, but move southeast out of Canada before turning more southerly remains unstudied. Each of the Plains vulture migrants followed a remarkably consistent route, roughly 45 degrees east of south for the first 1000 km. This corresponds with prevailing northwesterly winds across the northern Great Plains and the path of other bird species from Saskatchewan (for example, Swainson's Hawk and Osprey; Houston and Fung 1999, Houston and Martell 2002, Houston 2004), all keeping east of the Rocky Mountains. The most likely explanation is that the leading westerly wind in the northern United States results in wind directed downslope on the eastern face of the Rocky Mountains, which is not conducive to slope soaring.

Untangling different modes of flight and the conditions under which they are used should be a topic of future research. Our approach successfully identified the relationships between migration paths and weather variables. Our approach is limited somewhat by the differences in scales between particular behavioral patterns and conditions during flight (at the very local scales), the resolution of the observations of movement (intermediate scale), and the broader regional scale at which spatially and temporally continuous meteorological data are available.

With a full hour between readings, slope soaring and thermal soaring can take place within a single flight leg. In addition, at a three-hourly timescale and multi-kilometer spatial resolution, the model-derived meteorological variables, which are assumed as the driving forces of these behaviors, are less precise than would be ideal. Parameterized variables, such as TKE and HPBL, are indicative of a tendency to produce thermals in the planetary boundary layer, but, at these resolutions, the models cannot directly resolve thermals or determine their exact location and time of occurrence. At greater resolutions, large eddy simulations can provide explicit details about turbulent airflow and its interactions with the surface energy (thermals), topography, and land cover (e.g., Poggi and Katul 2007, Bohrer et al. 2009). Unfortunately, with current computational capabilities it remains impossible to simulate even a single flight path (several days, hundreds of kilometers) at the extremely high resolutions (few meters) needed by such simulations, even on a large supercomputer. Nonetheless, the use of observation-forced regional atmospheric reanalysis models to derive data on environmental conditions provided advantages not available with other approaches. With no other available data could we compare in a standardized way the physical environment of a bird in tropical Mexico with one in northeastern Pennsylvania. It also allowed us to look beyond standard sparse measurements of mean wind and temperature, to incorporate three-dimensional GPS data on the bird altitude and begin to understand the role of turbulence regimes, heat fluxes, and weather–landscape interactions in migratory movement.

The length and heading deviation of flight segments in three different North American populations of vultures are correlated to different environmental variables describing the topography and wind conditions they encountered during flight. We also showed that these correlations are different between the three populations. We cannot determine whether these observed differences in response to the environment are driven by selection and represent evolutionary optimization of these populations to their different environments or are the results of behavioral responses that any vulture could "select" in a given wind and landscape conditions.

We provided an example showing that track annotation with remote sensing, topographic, and weather reanalysis data sets can be used to generate an empirical model of movement responses to environmental variables. Similar use of data can allow expanding more predictive and mechanistic models of movement and home range. For example, Brownian-bridge models (BBM; e.g., Horne et al. 2007) generate hypotheses for the probability of animal presence at a location based only on the statistical characteristics of the observed locations. A shortcoming of the BBM approach is the assumption that the characteristic variance of the movement is only a function of the trajectory and not dependent on the interaction between the movement parameter and the external environment (Nathan et al. 2008). Annotation with environmental variables will facilitate a more complex random movement model that incorporates the covariance of the location with those environmental data. Similarly, location data annotated with environmental variables can be used to determine with home ranges and preferred paths, which can be calculated using a utilization distribution approach (e.g., Schaefer et al. 2007) or a niche model (Hirzel et al. 2002). The data annotation, in this case, allows quantifying the specialization and marginality of environmental factors in the likelihood of occurrence, where specialization defines how important specific environmental conditions are, and marginality defines how tolerant the species is to deviances from the optimum. Using these models, it is possible to derive habitat suitability models providing hypotheses as to which variables and at what threshold values a restriction on occurrence and movement range of a population might arise.

Data repository, management and analysis tools, such as Movebank (*available online*) facilitate similar studies.[10] The Movebank provides a secure online archive to store movement data and tools to process it. Users maintain control over the rights to their tracking data in Movebank and share them as widely or narrowly as they like. There are presently more than four million data points from 134 species archived by 273 registered users of Movebank, including many hundreds of tracks of migrating raptors and water birds. The latest development in Movebank will include automated data annotation of uploaded movement tracks by land use and topography data and with global meteorological data from NCEP/NCAR Reanalysis-II. The potential benefits from expanding our approach to multispecies, global-scale, comparative analysis of the effect of weather, climate, and land cover patterns on animal movement will soon be just a few mouse clicks away.

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[10] ⟨www.movebank.org⟩

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LITERATURE CITED

Aliaga-Rossel, E., R. W. Kays, and J. M. V. Fragoso. 2008. Home-range use by the Central American agouti (*Dasyprocta punctata*) on Barro Colorado Island, Panama. Journal of Tropical Ecology 24:367–374.

Austin, D., W. D. Bowen, J. I. McMillan, and S. J. Iverson. 2006. Linking movement, diving, and habitat to foraging success in a large marine predator. Ecology 87:3095–3108.

Beekman, J. H., B. A. Nolet, and M. Klaassen. 2002. Skipping swans: Fuelling rates and wind conditions determine differential use of migratory stopover sites of Bewick's Swans *Cygnus bewickii*. Ardea 90:437–460.

Bildstein, K. L. 2006. Migrating raptors of the world: their ecology and conservation. Cornell University Press, Ithaca, New York, USA.

Bohrer, G., G. G. Katul, R. L. Walko, and R. Avissar. 2009. Exploring the effects of microscale structural heterogeneity of forest canopies using large-eddy simulations. Boundary-Layer Meteorology 132:351–382.

Bowlin, M. S., and M. Wikelski. 2008. Pointed wings, low wingloading and calm air reduce migratory flight costs in songbirds. PLoS ONE 3: e2154.

Box, G. E. P., M. Gwilyn, G. Jenkins, and C. Reinsel. 2008. Time series analysis: forecasting and control. Fourth edition. John Wiley and Sons, Hoboken, New Jersey, USA.

Crofoot, M. C., I. C. Gilby, M. C. Wikelski, and R. W. Kays. 2008. Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. Proceedings of the National Academy of Sciences USA 105:577–581.

Durner, G. M., et al. 2009. Predicting 21st-century polar bear habitat distribution from global climate models. Ecological Monographs 79:25–58.

Ferland-Raymond, B., M. Bachand, D. Thomas, and K. L. Bildstein. 2005. Flapping rates of migrating and foraging Turkey Vultures *Cathartes aura* in Costa Rica. Vulture News 53:4–9.

Gill, R. E., T. L. Tibbitts, D. C. Douglas, C. M. Handel, D. M. Mulcahy, J. C. Gottschalck, N. Warnock, B. J. McCaffery, P. F. Battley, and T. Piersma. 2009. Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? Proceedings of the Royal Society B 276:447–458.

Hirzel, A. H., J. Hausser, D. Chessel, and N. Perrin. 2002. Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? Ecology 83:2027–2036.

Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges. Ecology 88:2354–2363.

Houston, C. S. 2004. Osprey's second trip to Costa Rica. Blue Jay 62:214–215.

Houston, C. S., and K. I. Fung. 1999. Saskatchewan's first Swainson's Hawk with satellite radio. Blue Jay 57:69–72.

Houston, C. S., and M. Martell. 2002. Speedy migration: Saskatchewan's first Osprey satellite transmitter. Blue Jay 60:74–79.

Ihaka, R., and R. Gentleman. 1996. R: a language for data analysis and graphics. Journal of Computational and Graphical Statistics 5:299–314.

Janjić, Z. I. 1994. The step-mountain ETA coordinate model: further developments of the convection, viscous Sublayer, and turbulence closure Schemes. Monthly Weather Review 122:927–945.

Kirk, D. A., and M. J. Mossman. 1998. Turkey Vulture (*Cathartes aura*). Number 339 *in* A. Poole and F. Gill, editors. The birds of North America. The Birds of North America, Philadelphia, Pennsylvania, USA.

Klaassen, M., J. H. Beekman, J. Kontiokorpi, R. J. W. Mulder, and B. A. Nolet. 2004. Migrating swans profit from favourable changes in wind conditions at low altitude. Journal of Ornithology 145:142–151.

Lieman, R., and P. Alpert. 1993. Investigation of the planetary boundary-layer height variations over complex terrain. Boundary-Layer Meteorology 62:129–142.

Mandel, J. T., K. L. Bildstein, G. Bohrer, and D. W. Winkler. 2008. The movement ecology of migration in turkey vultures. Proceedings of the National Academy of Sciences USA 105:19102–19107.

Mellor, G. L., and T. Yamada. 1982. Development of a turbulence closure-model for geophysical fluid problems. Reviews of Geophysics 20:851–875.

Mesinger, F., et al. 2006. North American regional reanalysis. Bulletin of the American Meteorological Society 87:343–360.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences USA 105:19052–19059.

Oliveira, E. G., R. B. Srygley, and R. Dudley. 1998. Do neotropical migrant butterflies navigate using a solar compass? Journal of Experimental Biology 201:3317–3331.

Ozdogan, M., M. Rodell, H. K. Beaudoing, and D. L. Toll. 2010. Simulating the effects of irrigation over the United States in a land surface model based on satellite-derived agricultural data. Journal of Hydrometeorology 11:171–184.

Poggi, D., and G. G. Katul. 2007. Turbulent flows on forested hilly terrain: the recirculation region. Quarterly Journal of the Royal Meteorological Society 133:1027–1039.

Rao, J. S. 2001. Topics in circular statistics. World Scientific Publishing, Republic of Singapore.

Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Science 5(1–4):23–27.

Roshier, D., M. Asmus, and M. Klaassen. 2008. What drives long-distance movements in the nomadic Grey Teal *Anas gracilis* in Australia? Ibis 150:474–484.

Schaefer, K. M., D. W. Fuller, and B. A. Block. 2007. Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the northeastern Pacific Ocean, ascertained through archival tag data. Marine Biology 152:503–525.

Shamoun-Baranes, J., J. Leyrer, E. van Loon, P. Bocher, F. Robin, F. Meunier, and T. Piersma. 2010. Stochastic atmospheric assistance and the use of emergency staging sites by migrants. Proceedings of the Royal Society B 277:1505–1511.

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

Shannon, H. D., G. S. Young, M. A. Yates, M. R. Fuller, and W. S. Seegar. 2002*b*. Measurements of thermal updraft intensity over complex terrain using American white pelicans and a simple boundary-layer forecast model. Boundary-Layer Meteorology 104:167–199.

Souto, R. P., et al. 2007. Processing mesoscale climatology in a grid environment. IEEE Computer Society, Los Alamito, California, USA.

Steiger, S. S., J. P. Kelley, W. W. Cochran, and M. Wikelski. 2009. Low metabolism and inactive lifestyle of a tropical rain forest bird investigated via heart-rate telemetry. Physiological and Biochemical Zoology 82:580–589.

Stull, R. B. 1988. An introduction to boundary layer meteorology. Kluwer Academic, Dordrecht, The Nederlands.

Thorup, K., T. Alerstam, M. Hake, and N. Kjellen. 2003. Bird orientation: compensation for wind drift in migrating raptors is age dependent. Proceedings of the Royal Society of London Series B 270:S8–S11.

Thorup, K., I. A. Bisson, M. S. Bowlin, R. A. Holland, J. C. Wingfield, M. Ramenofsky, and M. Wikelski. 2007. Evidence for a navigational map stretching across the continental US in a migratory songbird. Proceedings of the National Academy of Sciences USA 104:18115–18119.

Tomkiewicz, S. M., M. R. Fuller, J. G. Kie, and K. K. Bates. 2010. Global positioning system and associated technologies in animal behaviour and ecological research. Philosophical Transactions of the Royal Society B 365:2163–2176.

Wilcove, D. S., and M. Wikelski. 2008. Going, going, gone: Is animal migration disappearing? PLoS Biology 6:1361–1364.