Erschienen in: CHILSON, Phillip B., ed., Winifred F. FRICK, ed. and others. Aeroecology. Cham: Springer, 2018, pp. 71-86. ISBN 978-3-319-68574-8
https://doi.org/10.1007/978-3-319-68576-2_4

Track Annotation: Determining the Environmental Context of Movement Through the Air

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Abstract

Volant organisms are adapted to atmospheric patterns and processes. Understanding the lives of animals that inhabit this aerial environment requires a detailed investigation of both the animal's behavior and its environmental context—i.e., the environment that it encounters at a range of spatial and temporal scales. For aerofauna, it has been relatively difficult to observe the environment they encounter while they move. Large international efforts using

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satellite and weather model reanalysis now provide some of the environmental data on atmospheric environments throughout the globe. Track annotation—the approach of merging the environmental data with the movement track measured via telemetry—can be conducted automatically using online tools such as Movebank-Env-DATA or RNCEP. New parameterization approaches can use environmentally annotated tracks to approximate specific atmospheric conditions, such as uplift and tail wind, which are not typically observed at the exact locations of the movement, but are critical to movement. Reducing the complexity of movement to single-dimensional characteristic (such as flight speed, elevation, etc.) and defining the temporal scope of the movement phenomenon in the focus of the analysis (seasonal, daily, minutely, etc.) makes it possible to construct empirical models that explain the movement characteristic as driven by the environmental conditions during flight, despite the highly dynamic, complex, and scale-dependent structures of both the flight path and atmospheric variables. This chapter will provide several examples for such empirical movement models from different species of birds and using several resources for atmospheric data.

1 Introduction

Aerial movement ecology is challenged by the ability of researchers to access environmental data at the appropriate scale, especially as many animals traverse remote environments that are difficult to measure (Bowlin et al. 2010). An additional challenge rises due to the high spatiotemporal variability of the atmospheric environment, coupled with the complex role that atmospheric conditions play in the movement. Furthermore, with any predictive movement model, it is difficult to determine which of the interdependent environmental variables is most probably affecting the migration pattern (Dodge et al. 2014).

As GPS and other tracking technologies have developed, collecting data about the migration route has gotten easier. Remote sensing and model reanalyses, which combine remote sensing and ground-based observations and modeling to generate gridded data products and are a common tool for weather forecast, now provide a wealth of information about environmental conditions worldwide. Capitalizing on advances in the collection of both animal tracking and environmental data, the track-annotation approach (Mandel et al. 2011) provides a surrogate for missing observations of environmental conditions en route by linking state-of-the-art environmental data with observed tracks of precise animal locations. An annotated track includes the original location coordinates (in space and time) of the observed movement and additional environmental variable values from external observations. These variables must be interpolated in space and time to the observed movement coordinates. Emerging tools for track annotation, such as Movebank's Environmental-Data Automated Track Annotation (Env-DATA) (Dodge et al. 2013) and RNCEP (Kemp et al. 2012), provide the means to automatically annotate large movement datasets with a large number of environmental variables from different datasets and data sources. Typical datasets that provide observations of variables that may affect aerial movement include wind speed and direction and other weather variables from global weather reanalyses, [such as the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA-Interim reanalysis], vegetation greenness and other land surface properties from the Moderate Resolution Imaging Spectro-radiometer Satellites (MODIS), and precipitation from the Tropical Rainfall Measuring Mission (TRMM) or the new global precipitation mission (GPM).

Provided this wealth of environmental data, analyzing the underlying biological and environmental effects that drive the movement as it is expressed in the observed movement tracks is getting easier. Approaches such as home-range analyses (Dodge et al. 2014; Bohrer et al. 2014), habitat selection (Cimino et al. 2013; Phillips and Dudík 2008), preferential use analysis (Bohrer et al. 2012), and individual-based models (McLaren et al. 2012; Bartlam-Brooks et al. 2013) can be conducted given movement tracks annotated with environmental variables.

Here, we provide two different test cases to illustrate the possibilities of track-annotation driven analysis of aerial migration movement. We analyze flight data from two bird species—Swainson’s thrushes (*Catharus ustulatus*) and white storks (*Ciconia ciconia*). We particularly include a very coarse resolution dataset from a small migrant species (thrush) and a very high resolution dataset from a large migrant (stork) to contrast the challenges, limitations, and opportunities associated with each movement data type. For the both species, we hypothesize that the flight speed, which we consider one of the key characteristics of the movement, is dependent on environmental conditions. When analyzing migration data, it is important to consider the movement as the observable result of both internal and external factors (Nathan et al. 2008). Under this approach, environmental variables will directly interact with the internal capacity to move by governing the energetic cost of moving. For both species, certain environmental conditions will require larger energy expenditure to keep up a certain speed. Specifically, we demonstrate how to justify selection of a small number of environmental variables out of many available variables that could hypothetically affect the ground speed of flying bids.

2 Methods

2.1 Environmental Drivers of Swainson’s Thrush Flight Speed Crossing the Gulf of Mexico

The study species—Swainson’s thrush (*Catharus ustulatus*)—is a small Nearctic-Neotropical songbird species that breeds in Canada and the northern United States and migrates to Central and South America in the winter. There are two major populations of Swainson’s thrushes: the coastal population and the continental population. The coastal population migrates down the pacific coast to Mexico or Costa Rica and the continental population migrates along an eastern route to

Fig. 4.1 Swainson's thrush with radio transmitter attached to back Photo credit: William Cochran and Bill

Panama and South America. The migration of the continental population often involves a long, nonstop flight across the Gulf of Mexico (Cochran and Wikelski 2005). This trans-Gulf migration typically starts at dawn and continues throughout the night and next day for an average of about 20 h. The nature of this migration makes tracking and observing these birds difficult. The birds generally weigh between 23 and 45 g, and therefore any tracking device attached to a bird must be lighter than 2 g in order not to affect the bird's flight. GPS transmitters are larger than this size limit. This poses a strong limitation of the technology used for tracking these and similarly small sized birds. Radio telemetry provides the opportunity to locate the birds using a very small radio transmitter (Fig. 4.1). The observation, however, is limited to the locations of the telemetry antennas, and typically these types of observations provide very sparse information of the movement track (Cochran and Wikelski 2005; Bowlin and Wikelski 2008).

We studied the Swainson's thrush population that migrates from the Bon-Secour National Wildlife Refuge on the Fort Morgan Peninsula in Alabama in the USA (30°13′N, 88°00″W) to the northern coast of the Yucatan Peninsula in Mexico (21°31′N, 87°40″W) in the fall. The birds were captured using mist nets while flying through the wildlife refuge in Alabama. After capture, the birds were weighed, measured, and fitted with radio transmitters. These transmitters are glued to the back of the birds. The glue wears off in several days. This method allows the data to be collected automatically without having to recapture the birds in Mexico to recover the transmitter.

The study area included ten radio-telemetry towers: three in the Fort Morgan Peninsula in Alabama and seven in the Yucatan Peninsula (Fig. 4.2). Each tower in

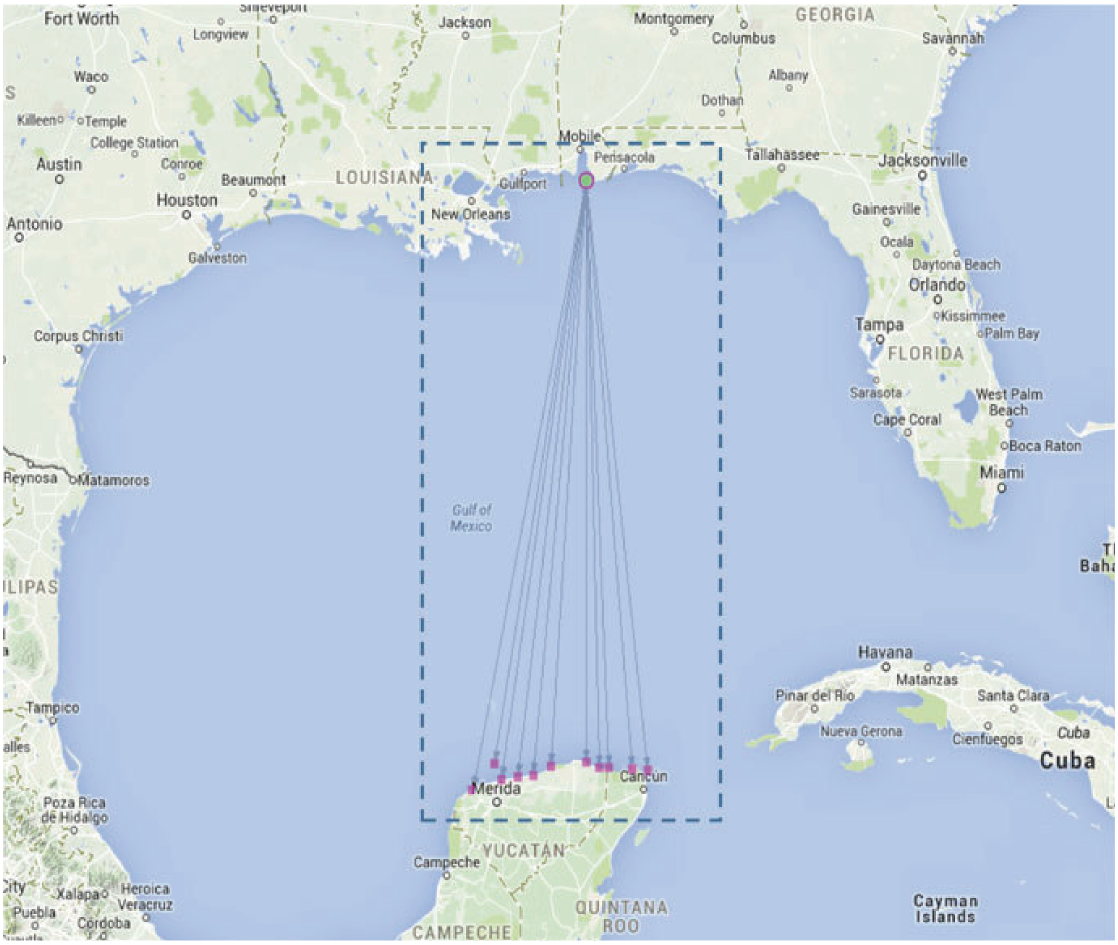

Fig. 4.2 Assumed tracks of Swainson's Thrushes recorded in the Yucatan Peninsula from Movebank.org. Dashed box illustrates the area that was annotated with gridded environmental information

Alabama had an Automated Receiving Unit (ARU, Sparrow systems, Inc.) attached to six antennas (Kays et al. 2011). The towers in Alabama recorded when the birds departed on their flight across the Gulf of Mexico. The towers in the Yucatan each consisted of an ARU with two antennas and recorded when the birds arrived on the continent after the flight across the Gulf of Mexico. The Yucatan towers were located in Sisal, Chicxulub, Dzilam de Bravo, Rio Lagartos Field Station, El Cuyo Field Station, Holbox, and Isla Contoy, creating a "fence" of receivers.

For each bird that was detected on at least one receiver in Alabama and one in Yucatan, we determined the crossing time by calculating the time difference between the last detection in Alabama and first detection in Yucatan. In cases where the bird was observed by more than one tower in Yucatan, we assigned an average between-towers location to the arrival detection location. We defined the migration-track bearing over the entire trans-Gulf migration section (following a similar approach to Thorup et al. 2007), as the exact path was unknown, assuming a straight flight path between the departure and arrival locations (Fig. 4.2). The mean flight speed could then be calculated as the distance between the two detection locations divided by the crossing time.

There were 145 birds tagged from September 26, 2009 to October 21, 2014. Of these, 42 (29%) were redetected in the Yucatan Peninsula; however, 19 (45% of arrivals) took longer than expected to arrive at the Yucatan via a direct flight (<35 h), suggesting that they took circuitous routes around the Gulf or left Ft. Morgan and stopped over elsewhere before making direct flights. The remaining 23 successful arrivals (55% of arrivals) were recorded crossing within a reasonable time for a direct flight. Of these 23 birds, six were documented in 2009, eight in 2010, four in 2012, two in 2013, and three in 2014. Direct flights ranged in duration from 14.85 to 34.55 h, with a mean of 21.77 h (Deppe et al. 2015).

2.2 Environmental Drivers of Stork Flight Speed

White storks (*Ciconia ciconia)* breed from Europe to Northwest Africa and Western Asia. Western European birds migrate southwest via France and Western Spain to Gibraltar, where they cross the Strait of Gibraltar to overwinter in West Africa. Storks from the eastern European population leave their colonies in Central Europe along a south-eastern route. They fly through the Middle East to their overwintering areas in East and South Africa (Hagemeijer and Blair 1997; Watson et al. 1978).

During migration, white storks congregate in large flocks, a tendency which may allow faster thermal detection (Shamoun-Baranes et al. 2003). In order to stay in a flock, however, individuals need to respond appropriately to their neighbor's movements. With the goal of studying group behavior, the juveniles of a small stork colony in the South of Germany (47° 45′ 10.8″N, 8° 56′ 2.4″E) which consists of 22 nests was followed during migration. All birds belong to the western subpopulation that migrates through Western Europe to the northwestern parts of Africa.

Storks are large enough to carry a transmitting GPS with a relatively large battery that can obtain and report location and instantaneous speed and compass heading measurements at high frequency. In total, 61 juveniles, the colony's entire offspring, were equipped with high-resolution, solar GSM-GPS-ACC loggers (E-Obs GmbH; Munich, Germany) one week prior to fledging. The transmitters (weight 43 g) were attached using a Teflon-nylon harness (weight ~12 g). The total weight of transmitter and harness was 65 g, corresponding to approximately 2% of the mean body mass of white storks. The GPS is set to provide every 15 min high frequency (1 s) observations for 5 min.

We used one 5-min set of high-frequency data from 10 tagged birds, flying in the same area (within several km) during noontime of August 14, 2014. We calculated the flight speed using the incremental observations between two consecutive GPS locations. We did not calculate wind support as the wind dataset is much coarser in space and time than the secondly movements of the storks and the turbulent eddies that affect their direction. We averaged flight speed and all other annotated environmental variables over all the observations within the 4-min period, per bird.

2.3 Environmental Annotation: The Movebank Env-DATA System

Movebank is an online database of animal tracking data, which provides users with a place to store, manage, analyze, and share animal movement data (Kranstauber et al. 2011). The Env-DATA system is an extension of Movebank that automatically annotates tracks with environmental data (Dodge et al. 2013) (see full list of annotation variables the system enables in: https://www.movebank.org/node/7471).

There are two types of annotation interfaces available through Env-DATA: (1) a set trajectory, which uses the Env-DATA online graphic user interface (GUI) and the movement track stored in Movebank to annotate the observed movement coordinates and (2) a gridded geographical area that corresponds to a given movement track, but includes a gridded set of locations around the observed track and is annotated using an R program function. The thrush data only contained two locations for each bird, the last radio-telemetry identification upon departure and the first detection upon arrival. The actual path, between these two points, was unknown. We, therefore, used the gridded area annotation method to get an estimate of the mean environmental conditions the birds would experience during the flight in the approximate area of the migration (Fig. 4.2). The storks, on the other hand, had exact locations of each bird at 1-Hz resolution during the section of flight that we analyzed. We, therefore, used the trajectory annotation method for this dataset.

Env-DATA provides several interpolation methods. The bi-linear approach fits best with regularly gridded data of continuous variables and was used for all variables in this study. For variables that are provided on a 3-D mesh that includes a vertical coordinate (e.g., wind speed from reanalysis), bi-linear interpolation include eight points at the two heights above and below the reported elevation of the movement observation. In both bi-linear and weighted distance interpolations, data are first interpolated in space and then two spatially interpolated values from the last available environmental data before and the first after the movement observation time are further interpolated in time to match the spatiotemporal coordinate of the movement point (Dodge et al. 2013).

2.4 Annotation Variables

Remote-Sensing data and data from global weather reanalyses were used to generate information about specific environmental conditions during the flight. Weather reanalysis datasets are the products of atmospheric models that are forced with a large number of satellite, meteorological station, and weather balloon observations. For annotating the gridded area used for the thrush study, we used data from the NCEP North American Regional Reanalysis [NARR, at a spatial resolution of ~32 × 32 km, and at 3-hourly time resolution (Mesinger et al. 2006)): the U (East-West) and V (North-South) components of wind speed at 10 m above sea level, air temperature and humidity at 2 m above sea level, and the height of the planetary boundary layer (HPBL). Additionally, we used the cumulative daily precipitation from TRMM [with a spatial resolution of 0.25° and a temporal resolution of 3-hourly (Kummerow et al. 1998)]. Though the birds fly high above the sea surface, humidity and temperature tend to be well correlated within the atmospheric boundary layer. However, and particularly at nighttime, narrow wind jets can develop above the thin nightly boundary layer. Nonetheless, because the flight height of the thrushes was unknown, we were limited to choosing an arbitrary elevation. We chose the surface values of the atmospheric variables, as representatives to the values throughout the atmospheric column, rather than the values at any particular height. Unlike Deppe et al. (2015), which provide a more conclusive analysis to an expanded version of the same dataset, we did not include any internal variables, such as sex, age, and fat reserves in the analysis of the effects of environmental variables we conduct here.

Variables were interpolated to a gridded array of location, covering the region of interest (dashed box in Fig. 4.2). The coordinates of four corners of the annotated grid were: 91°W 31°N; 91°W 20°N; 85°W 20°N; and 85°W 31°N, with time varying between birds. We gridded that region at a resolution of 25 × 25 km. This resolution was chosen somewhat arbitrarily, to provide fine and uniform coverage across all the source datasets (each with a different grid and resolution). We define the flight time as the period between the departure time and arrival time. Depending on the dataset, data was available at temporal sampling intervals of 6, 4, or 3 h. We used all the data observation times that were available during the flight time. For each bird, data for all the locations within the region were averaged in each data time step, and then the regional mean was averaged in time over the Gulf-crossing event period per bird. The storks' tracks were annotated using the set trajectory approach, with U and V components of wind speed from ECMWF at the observed height of their flight and with thermal uplift, derived from ECMWF variables.

Wind-speed components data were further processed into three wind characteristics: wind speed, direction, and support defined as:

$$w_{\mathrm{s}} \quad \sqrt{U^2 + V^2} \tag{4.1}$$

$$w_{\mathrm{d}} \quad \tan^{-1}(U, V) \tag{4.2}$$

$$w_{\mathrm{p}} \quad w_{\mathrm{s}} \cos\left(w_{\mathrm{d}} \quad h_{\mathrm{d}}\right) \tag{4.3}$$

where w_{s} is wind speed in m/s, w_{d} is wind direction in degrees, w_{p} is wind support in m/s, and h_{d} is the movement bearing. Wind support is defined as the component of the wind speed at the direction of movement.

2.5 Hierarchal Modeling

We tested the pairwise correlation between each environmental variable and the flight speed. We only used environmental variables for which we had a hypothesis of how they may affect flight speed. A list of the variables we tested appears in Tables 4.1 and 4.2. We assume that wind support (as defined above, Eq. 4.3) assists the bird to fly faster with lower energy expenditure, uplift assists the bird in saving energy while maintaining or gaining elevation, and temperature and humidity affect the physiological state of the birds at flight. Additionally, some variables can provide indirect indications for conditions that are supportive of fast flight; for example, the high planetary boundary layers (PBLs) are typical of conditions with stronger uplift than during times of low PBLs, and a certain combination of temperature and humidity over the Gulf of Mexico is associated with the movement of weather fronts that provide preferable wind direction (as found for our study area, Deppe et al. 2015). We then discarded the variables that did not have a significant pairwise correlation with flight speed. We used all the variables that significantly correlated with the total Gulf-crossing flight time to construct an empirical model using a step-wise hierarchal approach. We built a set of

Table 4.1 Summary of correlation data (coefficient of determination, R^2 and significance, P) between listed variables and the flight speed of the thrushes

Model	R^2	*AICc*	P
HPBL	**0.4676**	**104.07**	**<0.001**
Wind speed	**0.4574**	**104.05**	**<0.001**
Temperature	0.3526	107.40	0.0028
Humidity	0.2227	107.44	0.0230
Precipitation			NS
Wind support			NS

NS marks nonsignificant results ($P > 0.05$). The Akaike information criterion, *AICc*, for the whole model indicates the justification for adding each incremental variable. Variables were added in the order of their pairwise R^2 if they had a significant correlation with flight speed. Variables that had a significant and justified effect on the overall model and were included in the final model are marked in bold type

Table 4.2 Summary of correlation data (R^2 and significance, P) between listed variables and the flight speed of the storks

Model	Coefficient	R^2	*AICc*	P
Thermal uplift	**−1534**	**0.90**	**−7.50**	**<0.001**
HPBL	**4.38**	**0.88**	**−11.11**	**<0.001**
Orographic uplift		0.84	−10.01	<0.001
Topographic elevation		0.63	−9.58	0.006
Wind speed	**1.53**	**0.44**	**−13.13**	**0.036**

Variables that had a significant and justified effect on the overall model (according to the decrease in whole-model *AICc* compared to the simpler model) were included in the final model and are marked in bold type. The final model coefficient for each variable is also listed increasingly complex models using the aforementioned variables. For each new model, a comparison of the goodness-of-fit, significance, and the information criterion were used to determine if the last variable that was incrementally added provided a justified improvement to the model. A typical concern with environmental variables is cross-correlation. Most variables have similar diurnal, seasonal, and spatial variation that creates a strong cross-correlation between them. We use Akaike's information criterion to determine the most parsimonious model. For example, in a case where two environmental variables are strongly correlated, including both correlated variables, will create a less parsimonious model compared to an alternative one that only includes one of these correlated variables, because both variables include the same information. We used the Akaike information criterion (*AICc*) to reconcile the goodness of the fit with the number of parameters used in the model to determine the most justified model (Akaike 1974). Regressions and stepwise model statistics were calculated with the JMP.11 software (SAS Corporation, Cary, NC).

3 Results

3.1 Swainson's Thrushes

For the thrushes crossing the Gulf of Mexico, the height of the PBL (NARR variable—HPBL) was the variable most strongly correlated with the flight speed of the birds (Table 4.1). As the height of the boundary layer increases the birds tend to fly faster, as shown in Fig. 4.3b. In addition to the boundary layer height, the wind speed was also significantly correlated with flight speed (Table 4.1). Finally, both humidity and temperature were also correlated with flight speed (Table 4.1). In both cases, the flight speed decreases as the temperature and humidity increase (Fig. 4.3). Precipitation and wind support were not significantly correlated with mean flight speed (Table 4.1). The final model included HPBL and wind speed and did not include temperature, humidity, wind support, or precipitation.

3.2 White Storks

For storks flying over central Europe in their southern migration, we found that thermal uplift and wind speed were the major drivers of flight speed. While orographic uplift, boundary layer height, and ground elevation also had significant pairwise correlation with flight speed, they did not add significant information to the model, probably because they are strongly cross-correlated with wind speed and thermal uplift.

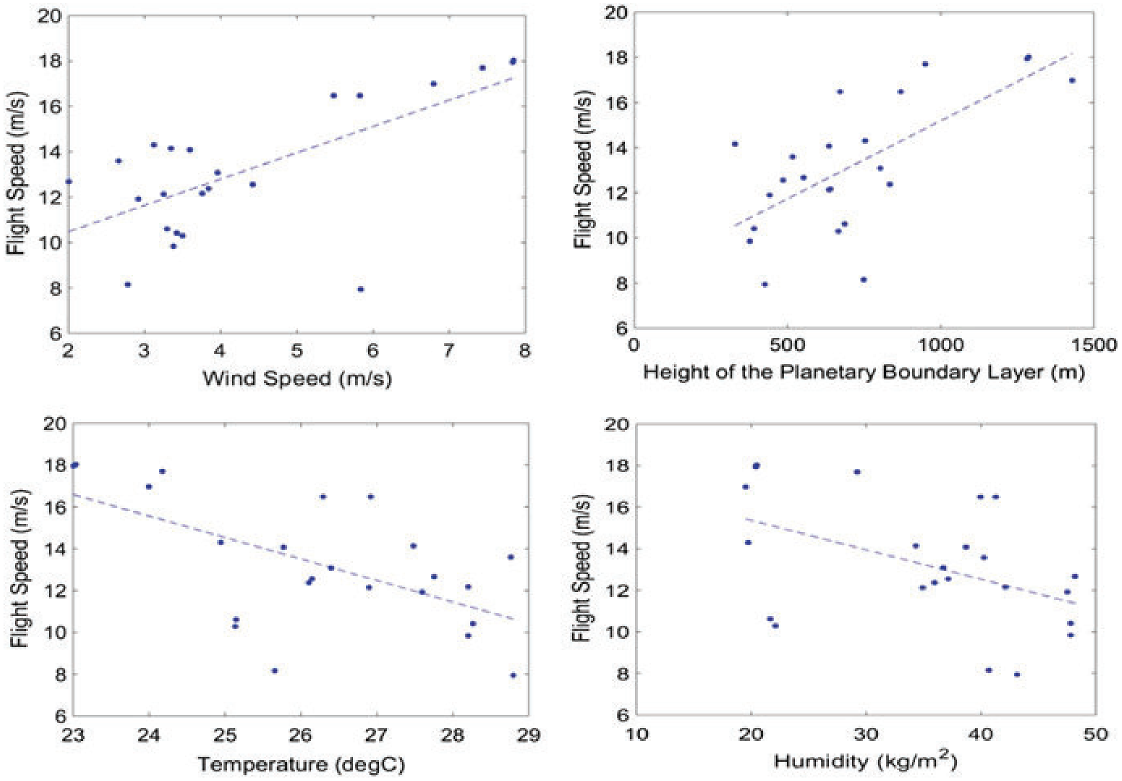

Fig. 4.3 Correlations between thrush flight speed and (**a**) wind speed, (**b**) height of the PBL, (**c**) temperature, and (**d**) Humidity

4 Discussion

The final model for the thrushes included boundary layer height and wind speed. As shown in Fig. 4.3b, the flight speed increases with increasing boundary layer height. The planetary boundary layer is the atmospheric layer that is directly influenced by the planetary surface. Over the ocean, the height of this layer is mostly affected by the ocean-surface temperature (von Engeln and Teixeira 2013). A warmer ocean relative to the atmosphere creates strong sensible heat flux that drives thermal uplift and increases the height of the boundary layer. Conditions such as these would be beneficial to the thrushes as they fly across the Gulf of Mexico. Although the thrushes aren't soaring birds, like the storks, the thermals could still help them conserve energy by gliding through the buoyant eddies instead of flapping their wings. This may be particularly true over the ocean at nighttime where thermals in general are particularly weak. A slightly thermally conductive boundary layer may make a big difference than a shallower stable boundary layer that suppresses thermal uplift. The algorithm used in Movebank to determine thermal uplift is only applied on land. The NARR-based PBL height is, therefore, the only environmental variable available over the Gulf of Mexico that can indirectly infer the availability of thermal uplift. PBL height may also be indicative of flight height, as often, and particularly at nighttime, strong wind jets which may be preferable for flight develop just above the PBL.

We found that wind speed reduces the Gulf-crossing time regardless of wind direction. Surprisingly, the wind support, which incorporates both wind speed and direction and the migration heading, did not have a significant effect on the mean flight speed over the Gulf. This could potentially be explained by the fact that most birds timed their departure to periods when the winds were generally oriented towards the bearing of the Gulf crossing. Deppe et al. (2015), who accounted for internal variables that significantly affected the departure decision, and included more individuals and more species of passerines, did find a significant effect of wind support. It is also possible that small wind direction fluctuations, during times when birds did cross the Gulf, did not have a strong effect and the thrushes were able to navigate with the wind while still, eventually, getting to their destination, regardless of the exact wind direction within the general south-western direction.

Finally, it is possible that the mean wind direction over the entire Gulf at 10 m above ground was not a good representative of the wind direction the birds actually flew with, at a particular elevation and path across the Gulf. A strong limitation of this analysis for the thrushes, which stems from the availability of thrush movement data, is the assumption that the flight path of the thrushes is straight. The method used to track the thrushes allowed for only two recorded timestamps—departure from Alabama and arrival in Mexico, everything in between these points is unknown. A 3D movement model (Rachel T. Bolus, personal communication) for the thrushes indicates that selection of flight elevation may provide additional wind support, compared to the conditions near sea the surface, that is used by the birds but cannot be estimated by the 10-m wind data. The small size of these birds does not permit GPS sensors, and information on the track is not available beyond the departure and arrival times. The area that we annotated was relatively small and the time span matched each bird's flight time, and therefore the averaged values of that sub-domain provided a reasonable, though limited, representation of the conditions met by the bird. In future studies, individual-based movement models (as done for soaring birds by van Loon et al. 2011) could provide predictions for hypothetical routs for the observed Gulf-crossing events, and these could be used to improve the time and space resolution of the environmental data used.

The final model for the storks included thermal uplift, boundary layer height, and wind speed. Two of these variables are closely related, as the thermal uplift directly affects the boundary layer height. The storks are soaring birds, and it was expected that the thermal uplift would be a large factor that affected flight speed (Kemp et al. 2010; Shamoun-Baranes et al. 2003; van Loon et al. 2011; Flack et al. 2016). However, it is interesting to note that the stronger thermals actually led to a slower flight speed (negative coefficient, Table 4.2). Over long time periods, storks will typically spend less time in updrafts when thermal uplift is strong and produces strong thermals, than when thermal uplift is weak, because they gain height faster. However, the very short time period sampled here represents a typical period of rising within a single thermal. Therefore, for this limited dataset and high temporal resolution but very short period, we hypothesize to see the opposite relationship.

Over just a few minutes (i.e., during a single thermal and at a very small domain), individuals in locations with stronger uplift were probably engaged in thermal soaring within that thermal. At the same time, individuals over areas with lower thermal uplift were probably gliding in a straight line on their way from one thermal, which they used a short time before the observation period, to the next one they will use after the observation period. Because we used the horizontal distance covered by the birds over the 5-min period to calculate the flight speed, birds that were riding thermals mostly moved in circles and their overall speed would not be as large as the birds that were gliding in a straight line. As mentioned above, higher boundary layer is associated with stronger uplift. However, over land the boundary layer height is also associated with topographic elevation. This explains the fact that after including HPBL in the model, the topographic elevation did not contribute new information to the model and was not included in the final model, despite having a very high pairwise correlation with flight speed.

Contrary to the thrushes study, there was an abundance of location observation data for the storks—but it was all during a very short period (4 min) and over a small domain. The limiting factor here was the available resolution of the environmental data. The dataset we used is at roughly 75 × 75 km. Therefore, it included very small variation over the area where the 10 storks' flights took place.

5 Conclusions

Track-annotation tools provide information that helps us understand movement ecology more fully and particularly help quantify the interactions between internal and external states of migrating birds and other animals. This type of analysis can identify the environmental drivers of migration paths, including variables that were impossible to observe directly at the time and place the bird flew. These data have numerous applications, each working to increase the general understanding of aerial migrants and the factors that affect them.

It is important to point out that track annotation only provides information about the location and time of the observed track. As such, it is strongly dependent on the resolution of the movement locations and the resolution of the environmental data sources. As the two test cases analyzed here show, our conclusions may have been different if the thrush movement data was at higher spatiotemporal resolution and included elevation information and more observed locations during the Gulf crossing. Similarly the stork flight analysis could have been improved with wind and uplift data at much higher resolution than possibly available from global reanalyses models. New tag technology and approaches to estimate wind speed, direction, and uplift from the high resolution GPS measurements provided by the bird-borne tags (Treep et al. 2016) may offer a future solution to this need. The limited scope of track-annotation analysis precludes it from being directly used for analysis of habitat selection, flight strategy, and migration departure decisions. These analyses are intrinsically dependent on comparing the conditions along the observed track locations, with conditions when the birds were and were not present. In such cases, the statistics and distribution of selected environmental conditions in a prescribed reference area or a set virtual null observations or simulated tracks can be compared with the distributions of the same environmental variables that were annotated to the tracks to draw conclusions about the location, flight, or habitat preferences of migrating birds (e.g., Bohrer et al. 2012).

An increased understanding of the interactions between the environment and aerial migratory movement will be increasingly important as our planet's climate continues to change. A change in climate will likely affect weather patterns in the areas that these birds migrate.

Acknowledgements The authors would like to acknowledge advice and comments from Rachel Bolus. The studies described here were supported by the National Science Foundation (IOS Award #1146832, 1147096, 1145952, and 1147022) and NASA (grant #NNX11AP61G). Additional support for the thrush study was provided by the National Geographic Society Committee on Research and Exploration (Award # 8971-11), Eastern Illinois University (Research and Creative Activity Awards to J.L.D.), University of Illinois Urbana-Champaign, the Max-Planck Institute for Ornithology, and The University of Southern Mississippi. The data on the white storks was collected with the help of Wolfgang Fiedler.

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