Migration by soaring or flapping: numerical atmospheric simulations reveal that turbulence kinetic energy dictates bee-eater flight mode

Nir Sapir[1],[*],[†], Nir Horvitz[1], Martin Wikelski[2],[3], Roni Avissar[4], Yitzhak Mahrer[5] and Ran Nathan[1]

[1]*Movement Ecology Laboratory, Department of Ecology, Evolution and Behavior, Alexander Silberman Institute of Life Sciences, Edmond J. Safra Campus, The Hebrew University of Jerusalem, Giv'at Ram, Jerusalem 91904, Israel*
[2]*Max Planck Institute for Ornithology, 'Vogelwarte Radolfzell', Schlossallee 2, 78315 Radolfzell, Germany*
[3]*Department of Biology, Konstanz University, 78315 Konstanz, Germany*
[4]*Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149-1098, USA*
[5]*The Seagram Center for Soil and Water Sciences, The Robert H. Smith Faculty of Agriculture, Food and Environment, The Hebrew University of Jerusalem, PO Box 12, Rehovoth 76100, Israel*

Aerial migrants commonly face atmospheric dynamics that may affect their movement and behaviour. Specifically, bird flight mode has been suggested to depend on convective updraught availability and tailwind assistance. However, this has not been tested thus far since both bird tracks and meteorological conditions are difficult to measure in detail throughout extended migratory flyways. Here, we applied, to our knowledge, the first comprehensive numerical atmospheric simulations by mean of the Regional Atmospheric Modeling System (RAMS) to study how meteorological processes affect the flight behaviour of migrating birds. We followed European bee-eaters (*Merops apiaster*) over southern Israel using radio telemetry and contrasted bird flight mode (flapping, soaring–gliding or mixed flight) against explanatory meteorological variables estimated by RAMS simulations at a spatial grid resolution of 250×250 m^2. We found that temperature and especially turbulence kinetic energy (TKE) determine bee-eater flight mode, whereas, unexpectedly, no effect of tailwind assistance was found. TKE during soaring–gliding was significantly higher and distinct from TKE during flapping. We propose that applying detailed atmospheric simulations over extended migratory flyways can elucidate the highly dynamic behaviour of air-borne organisms, help predict the abundance and distribution of migrating birds, and aid in mitigating hazardous implications of bird migration.

Keywords: biotelemetry; bird flight mode; cross-country flight; *Merops apiaster*; numerical atmospheric simulations; updraughts

1. INTRODUCTION

Atmospheric dynamics presumably shape various biological transport processes such as aerial migrations of insects and birds, the dispersal of air-borne seeds, pollen and invertebrates, as well as the spread of pathogens [1,2]. Yet, little is known about the role of atmospheric processes on aerial ecology because it is unfeasible to make atmospheric measurements for the entire trajectory of many transport processes. Also, moving organisms, especially small in size, are difficult to follow for long distances. Consequently, knowledge of atmospheric effects has thus far been limited to either coarse spatial and temporal resolution extending over large spatial and temporal domains [3–5], or to spatially restricted scales over which the influence of meteorological conditions on air-borne organisms has been assessed in detail (e.g. [6,7]). To overcome this trade-off between scale and resolution, we applied detailed numerical atmospheric simulations and portable radio telemetry to study how meteorological conditions affect the flight behaviour of a migratory bird.

Long-distance seasonal migration is abundant in numerous aerial organisms from diverse taxa around the world [8], including billions of birds [9]. Migrating birds are known to use two principal modes of flight when traversing land areas. During powered flapping flight, progress is made through continuous self-propulsion by the bird's wings [10], while during soaring–gliding, the wings are held in an outstretched position, and progress is obtained by exploiting energy available in the environment [11]. Soaring–gliding flight comprises two alternating phases, ascent soaring, usually achieved

* Author for correspondence (nir.sapir@mail.huji.ac.il).
† Present address: Department of Integrative Biology, University of California, Berkeley, 3060 Valley Life Sciences Building, Berkeley, CA 94720-3140, USA.

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by circling in convective updraughts during which the bird gains potential energy, and descent gliding, during which the bird uses its potential energy to move forward by sinking in the air.

Bird flight mode may depend on bird size and the meteorological conditions encountered during flight. Flapping flight speed is higher than that of soaring–gliding flight regardless of body size and under a wide range of environmental conditions [12]. Nonetheless, for large bird species, overall progress by flapping averaged over the entire journey (including stopovers) is slower than that of soaring–gliding. This is because the metabolic demands of flapping flight increase disproportionately with body mass [10,12], and large flapping species must consequently obtain large fuel stores that their deposition necessitates lengthy stopover periods. The soaring–gliding flight mode is unfavourable to small migrating birds because gliding speed, and hence the speed of progression, declines with body mass [11]. Consequently, small birds are expected to migrate by flapping, while soaring–gliding is expected to prevail among large bird species [11,12].

Unlike flapping flight, which can be carried out regardless of the availability of convective updraughts, soaring flight depends on a minimal updraught intensity to support the bird's weight in the air [11,13]. We therefore hypothesize that soaring–gliding will be limited by convective updraught availability. Specifically, we predict that high turbulence kinetic energy (TKE) facilitates soaring–gliding because it is indicative of convective updraught intensity. TKE is the sum of the kinetic energy resulting from different turbulent atmospheric processes. High TKE is associated with intense atmospheric convection, specifically in the mid-section of the boundary layer [14,15] where it is exploited by soaring–gliding birds and glider pilots [11,16–18]. Other atmospheric processes may also create turbulence, but these are usually limited to other parts of the boundary layer. For example, both wind shear at the top of this layer and the friction from obstacles such as trees near the surface create turbulence. Since increased ground and air temperature facilitates atmospheric convection, we additionally hypothesize that soaring–gliding will be used when temperature is high.

The speed of cross-country flight during migration is considered an important component in the fitness of migrating birds [12,19]. Because bird ground speed is the sum of the bird's airspeed and the speed of the flow in the direction headed by the bird, tailwind increases bird ground speed, whereas headwind decreases it. The wind vector may thus strongly affect bird migratory performance (e.g. time of arrival to destination) and ultimately bird fitness [20]. Nevertheless, birds may be affected differently by similar wind vectors depending on their flight mode. Since bird airspeed during soaring–gliding is substantially slower than during flapping under most circumstances, the progression of soaring birds will be slower than that of flapping birds experiencing similar headwind conditions [12]. We consequently hypothesize that headwinds will promote flapping over soaring–gliding flight because ground speed in soaring–gliding may become unfavourably slow under headwinds.

In this study, we present the first application, to our knowledge, of comprehensive numerical atmospheric simulations to explore atmospheric effects on migrating birds. Specifically, we use the Regional Atmospheric Modeling System (RAMS; [21–23]) to simulate the meteorological conditions encountered by migrating birds in high spatial (250×250 m^2) and temporal (5 min) resolution, under a wide range of environmental conditions across large spatial and temporal domains. The application of RAMS was devised in order to circumvent the trade-off between resolution and extent that has characterized previous studies of biological transport processes in the atmosphere. Radio-telemetry tracking of migrating European bee-eaters (*Merops apiaster*) over southern Israel was used to determine bird position and flight mode along migratory routes. Our specific objectives were: (i) to measure the effects of TKE and temperature on bird flight mode, and (ii) to examine the role of tailwind assistance on bird flight mode selection.

2. METHODS

(a) *Study species and area*
The European bee-eater is an insectivorous long-distance migrant. Most of its populations breed in southern Europe and southwestern Asia, and over winter in sub-Saharan Africa [24,25]. This approximately 55 g bird is known to use both flapping and soaring–gliding flight during migration [24]. We trapped migrating bee-eaters during the springs of 2005 and 2006 at two sites: Eilat ($29°34'$ N, $34°58'$ E) and Grofit ($29°56'$ N, $34°04'$ E), located 40 km apart. The sites are found in the southern part of the Arava Valley in Israel, which is an extremely arid area. Following trapping and ringing, each bird was uniquely marked by white colouring the tip of several flight feathers to enable its visual identification during flight. Then, it was fitted with a 1 g (1.8% of the average body mass of the birds) transmitter (SP2000-HR, Sparrow Systems, Fisher, IL, USA), according to the procedure described in Cochran & Wikelski [26]. The continuously emitting transmitter at the 605 MHz band was frequency modulated by heart and flight muscle potentials [5,27], enabling the continuous recording of both heart beats and wing flaps by two vehicle-mounted radio-telemetry systems (for details, see [28,29]). A total of 11 birds were tracked over 30–230 km (figure 1) until their signals were lost. The experimental procedure was approved by the Animal Care and Use Committee of the Hebrew University of Jerusalem (permit NS−06−07−2).

(b) *Bird flight-mode determination*
We divided the migration routes of all the birds into (mean ± s.d.) 2.4 ± 3.4 km long segments that are the most detailed approximation of the birds' actual flight path as recorded by the tracking system. In each segment, bird flight mode was identified as either flapping, soaring–gliding or mixed flight, based on the recorded audio. Flapping was characterized by a series of rapid wing flaps interspersed by pauses. Soaring–gliding was identified by a lack of wing flaps and a characteristic sinusoidal pattern of decibel level during soaring in a circling path within convective thermals. This pattern was created when the receiving antenna was on and off phased with the transmitter's antenna [28]. Gliding without wing flaps followed soaring. Mixed flight was determined by the sinusoidal decibel pattern during soaring, which usually did not include wing flapping, followed by gliding with frequent wing flaps. Audio decibel patterns were verified by direct observations of marked birds during tracking, and
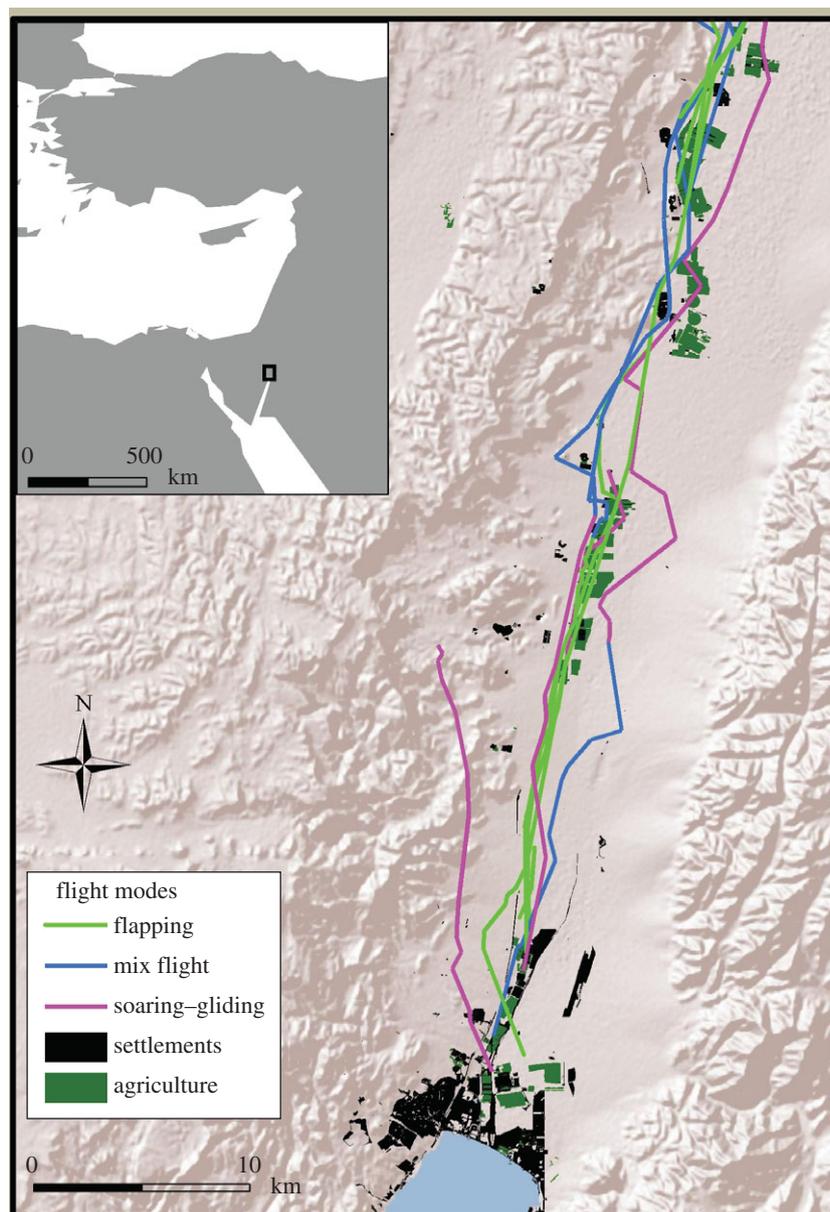
Figure 1. Flight tracks of migrating European bee-eaters recorded by vehicle-mounted radio-telemetry systems over the southern section of the Arava Valley in Israel.

are also known from radio-telemetry tracking of birds elsewhere [30,31].

(c) Application of the Regional Atmospheric Modeling System

We used RAMS to simulate the atmospheric conditions of the bee-eaters' migratory flyways with a horizontal grid mesh of $250 \times 250 \, \text{m}^2$. The vertical resolution of the model varied by altitude, starting with a 50 m resolution from the surface, and increasing by a factor of 1.1 with altitude (e.g. the second vertical grid was 55 m high, from 50 to 105 m above-ground). Bird altitude determined by telemetry and direct observations was 234 ± 198 m above-ground (range 10–700 m, $n = 31$ accounting for about 10% of tracking data, see [32]). We note that bird altitude could not usually be determined when the tracked bird flew at relatively high altitude in the proximity of the tracking vehicles owing to technical difficulties in positioning the antennas correctly towards the bird for elevation angels greater than $30°$. We report the

findings of the analysis made on the segments that their altitude was determined by the tracking systems. We additionally analysed all segments by using atmospheric data from two fixed altitudes of 500 and 100 m. TKE is usually relatively high during thermal convection at an altitude of 500 m above-ground [14]. We also analysed data from a fixed altitude of 1000 m above-ground, but these results are not reported because they were similar to those of 500 m altitude. RAMS input included National Centers for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) reanalysis data [33], sea temperature, radiation, land-use and topographic data of the study area [21–23]. Output variables included temperature, TKE and the u (west–east), and v (south–north) components of wind velocity. We calculated bird tailwind speed in each segment by calculating the projection of u and v components in the direction the bird was moving. Positive values of tailwind speed indicate that wind blew from the tail of the bird and negative values indicate that the bird encountered headwinds.

(d) Statistical analysis

To test for the effects of TKE, temperature and tailwind speed (independent factors) on bird flight mode (dependent factor), we used multi-nominal logistic regression, and selected between different statistical models using the Akaike Information Criteria (AIC; [34]). We first ran the analysis using all the data without weights and then repeated the analysis using weights to correct for potential bias owing to variation in sample size among individuals. To include data from different individuals equally, the data from each bird were weighted based on the inverse proportion of the bird's sample size from the total data from all the birds [35,36]. For example, since an equal contribution for a bird is achieved when it contributed 9.1 per cent (100% divided by 11, the number of birds) of the data, if a certain bird contributed 15 per cent of all data points, this bird's data were weighted by a factor of $9.1/15 = 0.6067$. Similarly, if a bird contributed only 5 per cent of all the data, its data were weighted by a factor of $9.1/5 = 1.82$. Lastly, we ran an analysis using data consisting of actual bird altitude as registered during tracking, with meteorological variables matching bird altitude.

All tests were two-tailed tested using SPSS v. 15.0 [37] and all tests and confidence intervals were calculated using $\alpha = 0.05$. Data are reported as mean $\pm$ s.d.

3. RESULTS

We followed migrating bee-eaters over southern Israel for a total distance of 810 km (figure 1) and divided their migratory routes into a total of 334 segments. Segment length depended on bird position sampling frequency by the portable telemetry systems. In eight segments, flight mode was ambiguous and these segments were excluded from the analysis. Seven out of the 11 birds employed flapping flight, seven birds used mixed flight modes, and six birds soar–glided. One soaring–gliding bird was found to soar and glide only during two segments and these data were excluded from the analysis; therefore, soaring–gliding data were analysed from a total of five birds. Altogether, the data from the 324 segments used consisted of 8–45 segments per flight behaviour per bird, with a total of 91 segments of flapping birds (13.0 ± 5.1 segments per bird), 92 segments of soaring–gliding birds (18.4 ± 14.3 segments per bird) and 141 segments of mixed flight (20.1 ± 12.3 segments per bird).

(a) The effects of turbulence kinetic energy, temperature and tailwind speed on bird flight mode

We report the results of RAMS validation analysis in the electronic supplementary material (including figure S1). We found that TKE was the single factor explaining the flight mode of European bee-eaters during their passage over southern Israel for the 500 m altitude (table 1). Flapping flight was used under extremely low TKE whereas soaring–gliding flight took place under much higher TKE. Mixed flight was employed under a broad range of TKE values (figure 2). Similarly, soaring–gliding took place under higher ambient temperature compared with flapping flight. The addition of temperature and tailwind speed to the model containing TKE did not improve its AIC, possibly owing to a positive correlation between TKE and temperature (electronic supplementary

Table 1. Results of multi-nominal logistic regressions at 500 m altitude with comparisons between flight modes for each variable. TKE, turbulence kinetic energy; temp., temperature; TWS, tailwind speed; F, flapping; M, mixed flight; S, soaring–gliding; n.s., not significance ($p > 0.05$).

factor	AIC	ΔAIC	Nagelkerke pseudo-r²	p F–M TKE	p F–S TKE	p M–S TKE	p F–M temp.	p F–S temp.	p M–S temp.	p F–M TWS	p F–S TWS	p M–S TWS	p overall model
TKE	431.6	0	0.543	***	***	**							***
TKE, temp.	485.9	54.3	0.570	***	***	n.s.	**	n.s.	**				***
TKE, temp., TWS	486.6	55.0	0.576	***	***	n.s.	**	n.s.	**	n.s.	n.s.	n.s.	***
TKE, TWS	495.9	64.3	0.552	***	***	**				n.s.	*	n.s.	***
temp.	637.0	205.4	0.228				***	***	***				***
temp., TWS	639.9	208.3	0.231				***	***	***	***	n.s.	n.s.	***
TWS	694.1	262.5	0.055							n.s.	***	*	***

*$0.05 > p > 0.01$.
**$0.01 > p > 0.001$.
***$p < 0.001$.
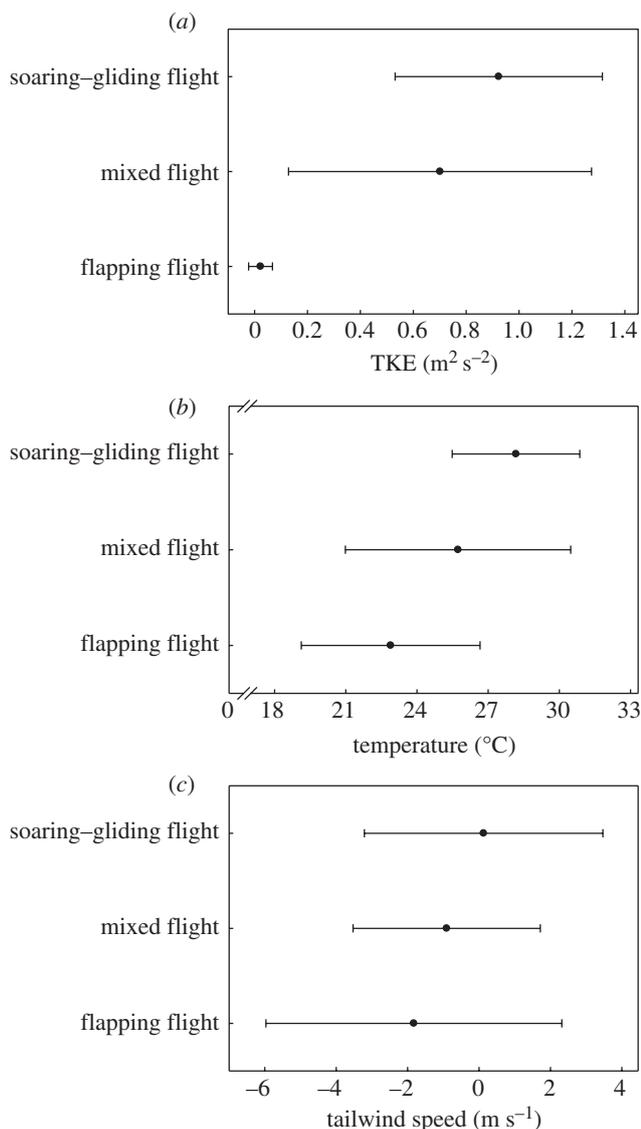
Figure 2. The relationships between meteorological variables simulated at 500 m above-ground and bird flight mode. (*a*) TKE, (*b*) temperature and (*c*) tailwind. For statistical details see table 1.

material, table S1), which is expected because high temperatures facilitate the atmospheric convection characterized by high TKE. Overall, tailwind speed was the factor explaining the least, if any, variation in bird flight mode (table 1). Repeating this analysis using weighted data according to the relative contribution of each bird to the overall dataset did not change these conclusions (electronic supplementary material, table S2).

The results of the analysis at 100 m altitude were somewhat different from those at 500 m altitude. At 100 m, TKE explained the most variation among the three single-variable models. Yet, the model with the lowest (best) AIC included all three meteorological variables examined (electronic supplementary material, table S3). At this altitude, TKE during flapping was significantly lower than TKE during soaring–gliding (electronic supplementary material, table S3 and figure S2).

The analysis using only data with altitudinal information in which RAMS-simulated data in each segment corresponded to the actual altitude of the bird above-ground found that the model with the lowest AIC value

included TKE and tailwind speed (electronic supplementary material, table S4 and figure S3). While TKE significantly differed between flapping and soaring–gliding segments, no such difference was found in tailwind speed. A significance difference in tailwind speed was found only between flapping and mixed flight segments. Therefore, bee-eater flight mode, specifically flapping versus soaring–gliding, primarily varied according to TKE, while headwind did not influence the propensity to use flapping over soaring–gliding.

4. DISCUSSION

We found that TKE dictated the flight mode of migrating European bee-eaters: flapping flight was carried out when TKE was very low, while mixed flight and especially soaring–gliding flights took place under much higher TKE. Temperature variation related to bird flight mode in a similar manner, with soaring–gliding flight made under high ambient temperatures and flapping flight carried out under low ambient temperatures. These findings strongly support our first prediction that updraught-related meteorological variables primarily determine bird flight mode. Yet, contrary to our second prediction, tailwind assistance did not have any important effect in flight mode selection. Migrating European bee-eaters thus consider the availability of updraughts when selecting their mode of flight en route and disregard the assistance or hindrance of the wind.

(a) *Effects of turbulence kinetic energy on the flight of migrating birds*

Our findings (figure 2) suggest that birds may soar and glide only when thermal intensity is higher than a certain threshold allowing the birds to remain airborne while soaring. Taking a TKE threshold of $0.21 \ \mathrm{m^2 \ s^{-2}}$ (the minimal TKE value found in soaring–gliding segments at 500 m altitude), we found that TKE in all flapping flight segments but one (98.9% of all segments) was below this threshold. Thus, soaring–gliding and flapping are characterized by distinctly different TKE ranges. Updraught availability was also found to affect bird flight mode in migrating common cranes (*Grus grus*) tracked by radar and motorized glider over southern Sweden [38,39]. This species alternates between flight modes in a similar manner to the bee-eaters reported in the present study. Cranes used flapping flight where thermals were lacking (over the sea), whereas soaring was employed only over land where thermals developed [38]. Crane soaring depended on local weather conditions, which affected the intensity of thermals, and pure soaring–gliding flight was restricted to extremely intense thermals. Otherwise, cranes commonly used mixed flight behaviour [39]. Despite the similar response of cranes and bee-eaters to updraught availability, it is unknown whether the minimal TKE allowing bee-eaters to soar and glide would also allow cranes to do so, or whether cranes necessitate stronger thermals owing to their higher wing loading [40]. Another soaring–gliding species, the American white pelican (*Pelecanus erythrorhynchos*), was also found to soar only above a certain threshold of thermal intensity. This species is adapted only for sustained soaring and cannot flap for long periods of time; therefore, the birds

did not fly when updraught intensity was below this threshold [13].

But why did European bee-eaters prefer soaring and gliding over flapping when updraughts were available? We propose that the propensity of bee-eaters to soar and glide whenever possible is driven by the substantially lower energetic demands associated with this mode of flight [28]. A potentially important cost of using soaring–gliding flight, especially for small birds, concerns the lower gliding, and hence progress, speed associated with this mode of flight compared with flapping [12]. Yet, in practice, when the birds' ground speeds were compared between soaring–gliding and flapping segments, no significance difference in ground speed was detected, suggesting that the cost of slower migration during soaring–gliding is probably small, if exists at all [28]. Moreover, it has been recently proposed that metabolic demands during flapping flight increase under atmospheric instabilities [5], and this may potentially deter bee-eaters and other facultative soarer–gliders from using flapping flight when convective thermals are intense and the air is turbulent.

(b) Promises and limitations in applications of numerical atmospheric modelling

Several previous studies that investigated flight behaviour of birds over long migration flyways used atmospheric model output data (e.g. NCEP/NCAR reanalysis) with low spatial (tens to hundreds of kilometres) and temporal (several hours) resolution (e.g. [3–5]). Local conditions within a single cell of such models may vary to a considerable degree, and variation within a single time step may be relatively large; this lack of resolution inevitably results in substantial differences between the conditions experienced by an organism and those provided by the model. A different approach is to record the atmospheric conditions using detailed, local measurements [6,7,29]; however, this does not permit estimating the conditions encountered by the animals when moving away from the area. Application of local and regional atmospheric models was used in two cases to predict the flight behaviour of soaring birds [13,41], providing important information on atmospheric processes affecting flight initiation, speed and altitude. These models were, nevertheless, limited in the processes they simulated and in their ability to incorporate both synoptic-, meso- and small-scale processes.

Our approach aims to simulate the conditions experienced by air-borne organisms at high spatial and temporal resolution, while providing a benchmark from which future improvement can be sought. Applying higher model grid resolution may reduce the deviation between RAMS-simulated and measured data because the model may be able to better represent processes that are not well represented in the $250 \times 250 \, m^2$ grid resolution. Moreover, application of the new ocean–land–air model (OLAM) may further improve model prediction [42,43]. We note that previous studies exploring the effects of atmospheric conditions on migrating organisms, especially those applying coarse-scale models such as NCEP/NCAR reanalysis, did not quantify the deviation of model products from data measured in the field. We suggest that estimating these differences should be a common practice in studies of biological transport

processes that apply environmental modelling. In the present study, the deviation between RAMS-simulated data and field measurements might limit inferences regarding the effects of wind on bird flight owing to differences between model products and field measurements. Despite this deviation, RAMS was able to correctly simulate general trends of wind direction and wind speed throughout the daily cycle (electronic supplementary material, figure S1). Although measured wind speed was, on average, higher than RAMS-simulated wind speed, the difference between the two datasets rarely exceeded $3 \, m \, s^{-1}$. The majority of simulated data (76.8%) was within $90°$ of measured wind direction, indicating that the model can predict the general direction of the wind encountered by birds throughout their cross-country flight.

Predicting animal behaviour during migration using simulations of atmospheric conditions is important for understanding the abundance and distribution of aerial migrants on multiple temporal and spatial scales, and for mitigating hazardous implications of animal migration, such as bird–aircraft collisions [44]. The present findings demonstrate that an integrated research framework coupling animal movement data with atmospheric modelling may prove useful for a wide range of aero-ecological studies by overcoming the practical limitation of estimating the meteorological conditions aloft [1,2].

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