The interplay of wind and uplift facilitates over-water flight in facultative soaring birds

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Abstract

Flying over the open sea is energetically costly for terrestrial birds. Despite this, over-water journeys of many birds, sometimes hundreds of kilometers long, are uncovered by bio-logging technology. To understand how these birds afford their flights over the open sea, we investigated the role of atmospheric conditions, specifically wind and uplift, in subsidizing over-water flight at the global scale. We first established that ΔT, the temperature difference between sea surface and air, is a meaningful proxy for uplift over water. Using this proxy, we showed that the spatio-temporal patterns of sea-crossing in terrestrial migratory birds is associated with favorable uplift conditions. We then analyzed route selection over the open sea for five facultative soaring species, representing all major migratory flyways. The birds maximized wind support when selecting their sea-crossing routes and selected higher uplift when suitable wind support was available. They also preferred routes with low long-term uncertainty in wind conditions. Our findings suggest that, in addition to wind, uplift may play a key role in the energy seascape for bird migration that in turn determines strategies and associated costs for birds crossing ecological barriers such as the open sea.

Keywords: Energy landscape, migration, soaring, bio-logging, route selection, movement ecology.

Introduction

Dynamic atmospheric conditions largely define the energetic costs of flight for birds. Tail winds, for example, permit birds to reduce air speed while maintaining the speed of travel, helping them to save energy [1, 2]. Likewise, rising air as a consequence of warm air columns known as thermals and orographic uplift created by the interplay between wind and topography, can push flying animals upwards and reduce the energetic costs of remaining airborne [3–5]. However, the energy availability landscape [6] is interspersed with patches where energetic subsidies in the atmosphere are weak or absent, impeding efficient movement. Flight over these areas becomes energetically costly, yet some animals regularly engage in such seemingly risky flights, particularly during migration [7, 8]. How birds afford their flights across migratory barriers remains an open and important question for understanding the evolution of migratory routes and sea-crossing strategies.

The open sea is considered a major migratory barrier for all terrestrial species, and particularly for soaring birds [8, 9]. This is rooted in observational studies of birds gathering in large numbers at bottlenecks prior to setting out over even relatively short over-water passages [8, 10]. The existence of such large aggregations, together with the technological difficulty of observing birds over the open sea, led to a general understanding that sea-crossing poses a formidable challenge for birds that are unable to land or forage at sea [11]. Some early studies looked beyond the role of geography alone and suggested that the extent to which terrestrial birds aggregate through overland flyways vary greatly across space and time [12–14]. They further suggested that weather conditions play an important role in terrestrial birds' ability to embark on, and sustain, over-water flight [15]. Advances in bio-logging technology have since created a clearer picture of sea-crossing behavior in terrestrial birds.

Bio-logging has confirmed extremely long sea-crossings in terrestrial birds [16, 17]. It has provided evidence that the prevalence and extent of this behavior varies according to flyway [8, 11], season [18, 19], and morphology [20]. We now have ample evidence that, in most cases of sea-crossings, atmospheric support, mostly in the form of wind support (i.e. the length of the wind vector in a bird's flight direction) is an important facilitator [18, 21–24].

An emerging hypothesis is that uplift also plays a role in the energy seascape for soaring bird migration. Uplift can reduce the energetic costs of remaining airborne. Additionally, soaring birds can take advantage of strong uplift to soar. Past bio-logging studies measured flight altitude in soaring birds to provide indirect proof of thermal soaring behavior at sea [25, 26]. More recently, high resolution GPS tracking documented the circling flight pattern and vertical aerial climb of migrating ospreys over the Mediterranean Sea [27]. Duriez et al. [27] also confirmed the earlier suggestions that ΔT, defined as the difference in temperature between the sea surface and the air, can be used as a proxy for uplift potential over water [28]. Positive ΔT values correspond to upward moving air (warmer sea surface than air), while negative values can be interpreted as sinking air, termed subsidence. This proxy was consequently adopted to quantify the energy seascapes that enable juvenile European honey buzzards to survive longer sea-crossings compared to their earlier migrating adult conspecifics [19]. Yet, whether ΔT is a meaningful correlate of upward moving air has not been quantitatively tested.

In this study, we investigate sea-crossing behavior at the global scale to assess the role of uplift and wind in shaping the energy seascapes for terrestrial bird migration. To do this, we use bio-logging data collected for five raptor species that perform long sea-crossing journeys. These species differ in size, morphology, and stop-over strategies, and their overall dependence on soaring flight to cover long distances. However, they are all facultative soaring migrants and are expected to preferentially use soaring over flapping flight whenever possible, including flights over open water. This provides an opportunity to investigate sea-crossing behavior at all major migratory flyways at spatio-temporal scales equivalent to that of the publicly available global atmospheric information. Using these data, we set out to establish whether ΔT is a meaningful proxy for uplift potential over water, by testing its relationship with convective velocity (w^*; [29]). We further hypothesize that (i) sea-crossings are associated with temperature gradients that are indicative of uplift in all flyways and (ii) both wind and ΔT influence over-water route selection.

Methods

Bio-logging data set

We compiled a bio-logging data set containing migratory trajectories of birds that regularly perform sea-crossing during autumn. We did not include spring migration in this study, due to the limited amount of data for spring migration compared to autumn. Our data set was comprised of five species: the Oriental honey buzzard *Pernis ptilorhynchus* and the grey-faced buzzard *Butastur indicus* in the East Asian flyways, the osprey *Pandion haliaetus* and the peregrine falcon *Falco peregrinus*, in both the African-Eurasian and the American flyways, and the Eleonora's falcon *F. eleonorae* in the African-Eurasian flyway. These birds are all facultative soaring birds. Their dependence on uplift varies, with the falcons and the osprey being less dependent on uplift than the buzzards [11].

We focused only on sea-crossing behavior during migration to ensure a common flight purpose among all species and individuals in the analyses. We only included adults as they actively select their route based on experience, unlike juveniles that follow an innate direction of migration, likely without established route selection criteria [30, 31]. We limited our analysis to sea-crossing trips longer than 30 km, which corresponded to the spatial resolution of our environmental data (see Route selection analysis below).

ΔT and convective velocity

To determine whether ΔT is a meaningful measure of uplift velocity, we estimated the relationship between this variable and the convective velocity scale, w^* [29]. w^* is estimated on the basis that the buoyancy associated with surface heat flux produces uplift:

$$w^* = \left[gz \left(\frac{(w'T') + 0.61 T_{2m} (w'q')}{\theta} \right) \right]^{\frac{1}{3}}$$

where g [m/s^2] is the gravitational acceleration, z [m above reference sea level] is the depth of the atmospheric boundary layer, the term $(w'T' + 0.61\ T_{2m}(w'q'))$ approximates the surface virtual potential temperature flux, where $(w'T')$ [K m/s] is the surface temperature flux and $(w'q')$ [g_{water}/kg_{air} m/s] is the surface water vapor flux and T_{2m} [C] is the air temperature near the sea surface. θ [K] is the virtual potential temperature at the height of the boundary layer top (z), and was approximated using the wet adiabatic lapse rate (typical for oceanic boundary layers) as:

$$\theta = T_{2m} + 273.15 + 0.006\, z$$

We used data from the ERA-interim reanalysis database (Spatial and temporal resolution of 0.75 degrees and 3 hours, respectively) provided by the European Center for Medium-Range Weather Forecast (ECMWF; *https://www.ecmwf.int*). We accessed these data through the EnvDATA service [32] on Movebank (*www.movebank.org*), to get the values for z, T_{2m}, $w'T'$ and $w'q'$ (with some unit conversions). Overall, we closely followed Bohrer et al. [33] to calculate w^*, but including the contribution of the surface water vapor flux to the surface virtual potential temperature flux, and using the wet adiabatic laps rate to estimate the potential temperature at the height of the boundary layer top.

w^* represents uplift and can only be calculated for positive heat fluxes. Hence, we calculated w^* for all the sea-crossing points in our bio-logging data set where ΔT was positive and estimated the relationship between the two variables using a generalized additive model (GAM).

Spatio-temporal modeling of ΔT

To show the spatio-temporal variation in ΔT at the global scale, we used 40 years of temperature data. We focused on five regions where regular long-distance sea-crossing is performed by facultative soaring birds, namely South-East Asia, the Indian Ocean, the Mozambique Channel, Europe, and the Americas. We downloaded sea-surface temperature and temperature at 2 meters above the sea for these regions for 1981-2020 from the ECMWF ERA-interim reanalysis data set (Spatial and temporal resolution of 6 hours and 0.75°, respectively). We chose to use this data set instead of the higher resolution ERA5, to reduce the time and memory needed for the analysis. We spatially filtered the data to exclude lakes, as we were only

interested in the open seas and oceans. To include a proxy for the time of day, we calculated the solar elevation angle for each data point. We then created a categorical variable with three levels, night, low sun elevation, and high sun elevation, corresponding to sun elevation angles below -6, between -6 and 40 degrees, and over 40 degrees, respectively.

We loosely followed Nourani et al. [19] to construct energy seascapes. In brief, we modeled ΔT as a function of latitude, longitude, day of year, and time of day using the generalized additive mixed modeling (GAMM) approach. Five models were constructed in total, one per region. We extracted the timing and location of sea-crossings from our bio-logging data set. We did not have empirical data for migration over the Indian Ocean and therefore consulted the relevant literature to extract the spatio-temporal pattern of the Amur falcon's *Falco amurensis* sea-crossing over the region [34, 35]. Each model included two smoothers, one cyclic cubic regression splines smoother for the day of the year and a spline on the sphere for latitude and longitude. For both of these parameters, one smoothing curve was estimated for each level of time of day. Year was added as a random intercept in the models to control for annual variations in ΔT. We also included a variance structure in the models to account for the heteroscedasticity caused by higher ΔT variance in higher latitudes. Models were fitted using the mgcv package [36] in R ver. 4.0.2 [37].

We used each model to predict energy seascape maps for the autumn migration season (August-November). We spatially interpolated the prediction rasters to a 1 km resolution for visualization purposes.

Route selection analysis

We investigated route selection by fitting a step selection function [38] to relate the probability of presence over the sea with atmospheric conditions. Every two consecutive points along a track were considered a step. Atmospheric conditions were compared between the observed step and a set of alternative steps that were available to the birds in space and time. The grey-faced buzzard was excluded from this analysis because of the low resolution of the satellite-tracking data.

We filtered our data set to include only points over the open sea. Trajectories that intersected land, e.g. islands, were broken into sea-crossing segments. Segments shorter than 30 km, and those that included fewer than 3 tracking points, were removed. To ensure a uniform temporal resolution and to reduce spatio-temporal auto-correlation, we re-sampled all data to one-hourly intervals (with a tolerance of 15 minutes) using R package Move [39].

We prepared a stratified data set: along each sea-crossing segment, for each step, we generated 50 spatially alternative steps. based on the distribution of step lengths (gamma distribution) and turning angles (von Mises distribution) estimated using over-water tracking data, separately for each species-flyway combination. Diagnostics plots were used to assess the fit of the distributions. All data were then annotated using the ENV-data track annotation service [32] provided by Movebank. Each point was annotated with u (eastward) and v (northward) components of the wind, sea-surface temperature, and temperature at 2 m above the sea, all provided by ECMWF ERA5 reanalysis database (temporal and spatial resolution of 1 hour and 0.25°, respectively). We selected the bilinear and the nearest-neighbour methods of interpolation for the wind and temperature data, respectively. We then calculated wind support [40] and ΔT using the annotated data. Additionally, to investigate whether predictability of atmospheric conditions affected the sea-crossing

route choice, we annotated each point with long-term variances (over 40 years; 1981-2020) for wind support and ΔT.

We checked the annotated data set for multicollinearity and only used variables that were not highly correlated ($r < 0.6$). Prior to analysis, we converted all values of explanatory variables to z-scores (i.e. the distance of a raw value from the mean, measured in units of standard deviation) to ensure comparability among predictors.

Step selection functions were then estimated using the Integrated Nested Laplace Approximation (INLA) method using the INLA package [41] in R ver. 4.0.2 [37]. We constructed a multilevel model with fixed effects for ΔT, wind support, long-term variance of wind support, and an interaction term for wind support and ΔT. Species and individual IDs (nested within species) were included as random effects on the slopes. Following Muff et al. [42], we set $N(0, 10^4)$ as the prior for fixed slope parameters and Penalized Complexity priors $PC(3, 0.05)$ to the precisions of the random slopes. The model converged after 50 minutes on an Intel Core i7-8700 12 x 3.20 GHz processor (running on 10 cores in parallel).

Results

We found a positive relationship between the convective velocity scale, w^*, and ΔT (Fig. 1; r^2 *(adj.)* = 0.31; $p < 0.05$). The sea-crossing data from all species showed overnight flights (Fig.1, Electronic supplementary material Fig. S4). There was no clear difference between the pattern of correlation between w^* and ΔT in different times of the day or for different species (Fig.1).

The spatio-temporal pattern of sea-crossing in the six terrestrial bird species (the five species in our bio-logging data set plus the Amur falcon) corresponded with positive uplift potential over the open sea (Fig. 2; see subplots for within-year and within-day variations in each region; see electronic supplementary material Table S2 for detailed GAMM outputs). The osprey was the only species flying over the open sea when the sea surface was colder than the air (i.e. negative ΔT). This pattern occurred over both the Mediterranean and the Caribbean Seas (Fig. 2). The Eleonora's falcons flying over the Mozambique Channel also experienced relatively low and sometimes negative ΔT (Fig. 2). However, over-water flight in the absence of uplift did not set the two species apart from the other species in route selection regarding ΔT.

We analyzed over-water route selection in 112 sea-crossing tracks of 65 individuals (Electronic supplementary material Table S1 and Fig. S3). We did not include the long-term variance of ΔT in the model, as it was correlated with the long-term variance of wind support ($r = 0.61$; $p < 0.05$). The most important variable determining over-water route selection was wind support, with a positive effect. The interaction between ΔT and wind support also showed a positive, yet smaller, effect (Fig. 3). ΔT and the long-term variance of wind support had negative impacts on route selection. We found a significant effect of species-level random effects for wind support in the Eleonora's falcon with a higher preference and the osprey, which showed a weaker preference (Electronic supplementary material Fig. S1).

Discussion

We found that, in all flyways that we studied, facultative soaring birds were more selective for wind

support than uplift when flying over the open sea. This confirms previous findings that birds aim at maximizing wind support, probably to reduce the time and energy required to complete their journeys [18, 21–24, 44–46]. Our model also showed a positive effect of the interaction between wind support and ΔT. This indicates that when wind support is favorable, the birds also select high values of ΔT to gain better advantage of uplift (Fig. 4).

Selection of suitable wind support went beyond the individuals' instantaneous response to wind conditions. The birds avoided areas with high long-term variability in wind support when flying over water (Fig. 3). The 40-year conditions that we considered here are beyond one individual's experiences, but point to population-level preferences, which might be socially transmitted across generations to achieve efficient movement [47, 48]. Reducing uncertainty in the energetic costs of migration in this way can be a mechanism for formation of efficient migratory routes within populations.

Contrary to our expectations, after accounting for the other variables, higher ΔT values alone had a lower probability of being chosen on route selection. This suggests that in the absence of suitable wind support, the birds did not choose stronger uplifts to fuel their flights (Fig, 4). Still, we show that uplift conditions over the sea were generally favorable during the autumn migration season (Fig. 2) as well as at the start of sea-crossing (Electronic supplementary material Fig. S4). We speculate that the birds may avoid turbulent conditions by avoiding high ΔT. The fact that the birds mostly encountered positive ΔT along their over-water routes (Electronic supplementary material Fig. S2 and S3) indicates that even when selecting low values of ΔT, they were still likely to experience some amount of uplift regardless, and would not prefer higher uplift for forgoing better wind support.

The sea surface tends to be warmer than the air in autumn, creating upward heat flux. This is reflected in our global energy seascape map (Fig. 2). The mostly positive values of ΔT on this map indicates that the spatio-temporal patterns of sea-crossing in autumn is associated with favorable uplift conditions, supporting our first hypothesis. Moreover, the range and mean of ΔT values were similar between the observed and alternative steps in our step selection function estimation (Electronic supplementary material Fig. S2). The birds thus faced more variability in wind conditions than in uplift, which can further explain why wind support was the most important criterion for route selection (Fig. 3). We further showed that ΔT has a relatively low seasonal variation, except in Europe (subplots in Fig. 2). As a result, birds flying along these flyways in spring could potentially benefit from uplift. However, we cannot make generalizations about sea-crossing patterns in spring based on ΔT alone. As our route selection analysis showed, wind support plays a more important role in over-water flight than uplift. Even in similar uplift conditions between the two seasons, variations in wind support can lead to loop migration patterns [49, 50] and even avoidance of sea-crossing in one season [18]. Moreover, species may differ in their energy- or time-saving strategies between seasons. Uncovering the role of atmospheric subsidies in shaping sea-crossing patterns in spring requires multi-species bio-logging data, which were not available to our study.

Evidence for soaring flight over the sea has accumulated for at least a decade. Yet, many studies overlook uplift potential when explaining sea-crossing behavior. This could be due to the presumption that thermals do not form over the sea, as well as a lack of a reliable and easy to compute proxy for uplift over water. Studies that try to investigate uplift do so by using a variety of proxies, including air temperature [51], air temperature gradient [18], vertical air velocity [18], boundary layer height [52], and solar irradiance [53], which makes interpretation of the results and comparisons among studies difficult. ΔT is shown, by direct

observations [54] and bio-logging technology [27], to be related to soaring flight. Our results confirming the correlation of ΔT with w^*, a widely accepted measure of uplift by the movement ecology community (so far mostly used to estimate uplift over land [33]), further point to the potential of this proxy as a measure of uplift over the open sea. Duriez et al. [27] showed that ospreys predictably engaged in thermal soaring over the Mediterranean Sea when ΔT values were higher than 3° C. Although we provide a range of w^* values (m/s) for each value of ΔT in our data, the resolution of our data did not allow us to directly investigate whether and in what ΔT conditions the birds engaged in soaring flight. In fact, there remains a strong need for quantifying the amount of energy, or the realized uplift, that a bird can gain from ΔT. Theoretical and high-resolution multi-sensor bio-logging studies can investigate this for birds with different morphological characteristics and under different wind conditions.

Although we show that it is possible to estimate w^* using publicly available weather data, it is not an ideal proxy for measuring uplift under all circumstances over the open sea. Firstly, w^* can only be estimated for upward moving air. This means that there will be no values estimated for subsidence. ΔT does not have this limit, as it provides positive values for uplift and negative values for subsidence. Secondly, calculating w^* requires at least a basic knowledge of meteorological concepts and units. Different reanalysis data sets provide different variables for potential and water vapor fluxes, making our method of calculating w^* difficult to adapt for other studies. This is while ΔT can be calculated only using two simple variables, sea-surface and air temperature, and yields the same result whether temperature data is obtained in units of Kelvin or Celsius. It is therefore a more approachable and possibly reliable measure than w^*. Lastly, although it is ideal to be able to calculate uplift in meters per second, w^* has not been ground-truthed. We cannot be sure whether our estimated w^* values are a precise representation of the strength of uplift over water. Although ΔT does not provide realized uplift, it is an intuitively interpretable measure of uplift potential.

Uplift reduces the energetic costs of remaining airborne, for both soaring and flapping flyers. We used facultative soaring species as our model system. These species varied in morphological characteristics and soaring flight dependencies. Apart from minor differences in responding to wind support between ospreys and Eleonora's falcons, we found no significant species-specific variation in the impact of wind support and uplift on sea-crossing behavior (Electronic supplementary material Fig. S1). This indicates that the patterns that we found can be true for sea-crossing in other species as well. Moreover, our study included all major bird migration flyways. As a result, our findings can further shed light on the energy seascapes other animals flying over these flyways would encounter. For example, the relatively high uplift during the night compared to daytime (Fig. 2) means less drag and could lead to energetically cheaper flight in nocturnal migrants over the Mediterranean [55, 56] and the Caribbean [57, 58] Seas (but see [59] for a suggestion that songbirds prefer non-turbulent air for sea-crossing). Moreover, dragonflies [60] and cuckoos (*Cuculus* spp.; [61]) migrate within the same time window as the Amur falcon over the Indian Ocean (Fig. 2), perhaps taking advantage of the energetic subsidy that the atmosphere provides.

Conclusion

The literature on migratory behavior is increasingly recognizing that atmospheric conditions can reduce the risks associated with sea-crossing in terrestrial birds. Evidence of the role of wind support as a facilitator of this behavior for many species is mounting. Yet, not much is known about the role of uplift. Our findings confirm

the role of wind support as the main facilitator of over-water flight, but also provide evidence for widespread uplift potential over the open sea, at least in autumn. We provide quantitative evidence that ΔT is a meaningful proxy for uplift over the open sea and encourage future studies to take advantage of this proxy, not least because widespread use of ΔT will make comparisons among studies possible. Our findings suggest that the energetic costs of sea-crossing for soaring birds could be at least partially alleviated by overseas uplift. This may have important consequences for shaping routes, timing, and strategies of birds crossing ecological barriers.

Ethics

Capture and tagging of ospreys in Europe were authorized by Istituto Nazionale per la Protezione e la Ricerca Ambientale (ISPRA) and the National authority in Italy for Environmental Research and Protection. The Ministry of Environment and Energy (Greece) granted permission for capturing and tagging Eleonora's fal- cons (License numbers: 6ΧΨΑ0-ΟΚΤ, Ψ9Θ24653Π8-ΡΤ3). The capture and tagging of Eleonora's falcons from Spain were authorized by the Regional Government of the Canary Islands (Permit numbers: ES-000844/2012, ES-000642/2013, 2014/2224, 2015/3835, 2017/6829). Oriental honey buzzards were tracked under permits no.1705311 (Ministry of the Environment, Japan) and no.6 (Aomori Prefecture). Capture and tagging of ospreys in North America were authorized by the USGS permit no. 20096 (USA) and scientific collecting permit 10907 (Canada). The work was approved by the University of North Carolina at Charlotte's IACUC, protocol 08-024, and by the IACUC of Drexel University, protocol 20632. The peregrine falcons in North America were captured under USGS permit no. 22749 and the state of New Jersey no. SC 2016120. Work on Peregrine falcons in Russian was done under permit No. 77-18/0854/4388 from The General Radio Frequency Centre, permit No. RU/2018/406 from Federal Service for Supervision of Communications, Information Technology and Mass Media (Roskomnadzor), and permit No. RU0000045099 from Federal Security Service. No specific permissions were required from Federal Service for Supervision of Natural Resources (Rosprirodnadzor) according to §44 and §6 of the Federal Law of the Russian Federation No. 52 from 24.04.1995 (last up- date 24.04.2020) "On Wildlife", and from Federal Service for Technical and Export Control (FSTEC/FSTEK) according to Russian Federation government decree No. 633 from 29.08.2001 and Letter from FSTEK No. 240/33/1373 from 06.04.2015.

Data accessibility

All data used in this study can be accessed via *https://doi.org/10.5061/dryad.r4xgxd2cthttps://datadryad.org/stash/share/ fzD3TQdw6XMltpP51m_73Pvh4BXrGlyd_dIiToKvByE*. R codes are available at *https://github.com/mahle68/global_seascape_public*.

Authors' contributions

EN conceived the study and designed the analyses with input from KS and PB. EN conducted the analyses and wrote the paper. GB provided guidance for estimation of *w**. ROB, OD, JF, LG, SG, HH, CK, OK, NL, FM, IP, AS, JFT, NT, WMGV, DSV, NMY, and MW contributed data. All authors commented on and

edited the manuscript drafts.

Competing interests

We declare we have no competing interests.

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Figures

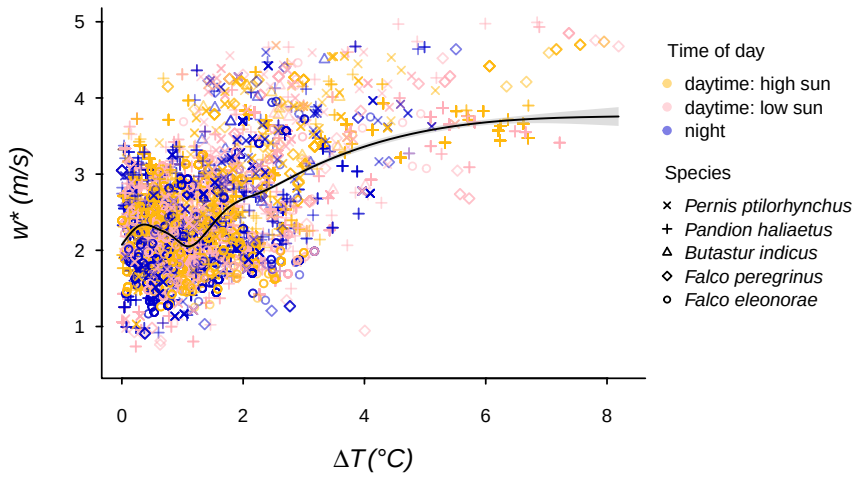

Figure 1: Relationship between ΔT and the convective velocity, w^* (for all points with positive ΔT). The sea-crossing bio-logging data (pooled for all five species) were annotated with values of ΔT and w^*. The smooth curve shows cubic regression splines fitted to the data predicting w^* as a function of ΔT (with the 95% confidence interval). Colors and shapes represent different times of day and species, respectively.

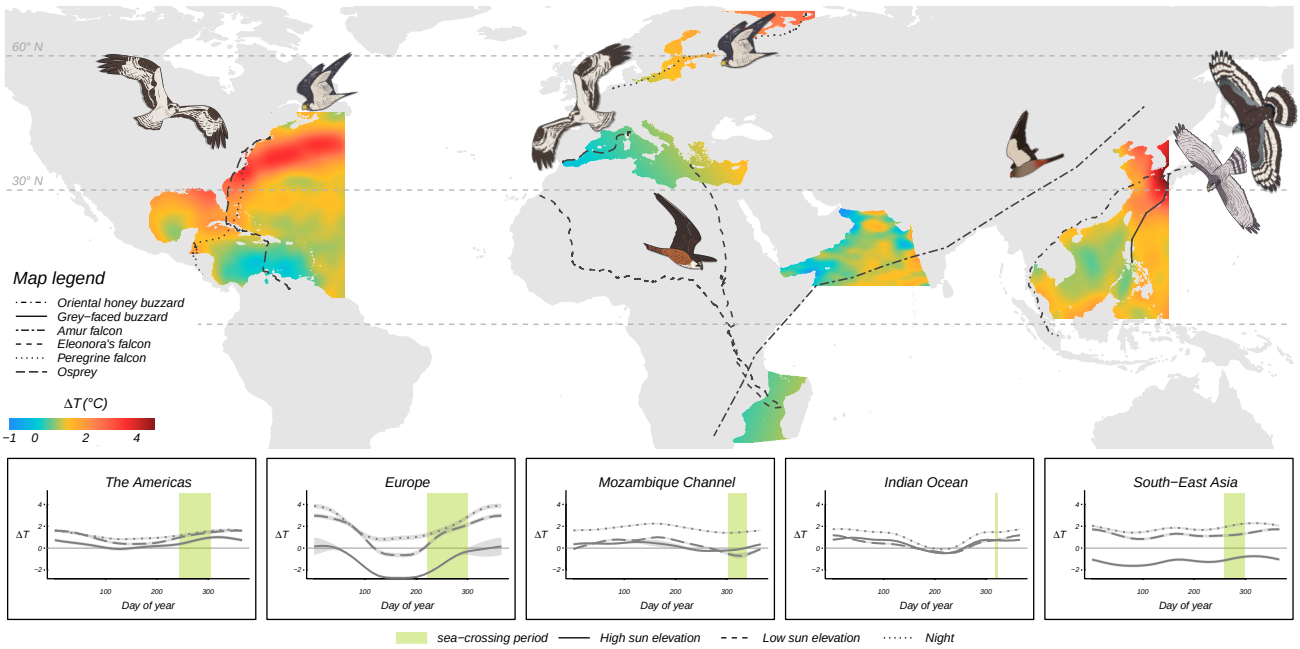

Figure 2: Energy seascapes for soaring bird migration in autumn. The map shows the energy seascapes for August-November derived from 40 years of temperature data. Tracks correspond to sample migratory trajectories. All tracks are based on empirical data, except for the Amur falcon, which is based on the available literature [35]. Subplots show the distribution of ΔT throughout the year in each region, for each time of day (based on summed effects from the GAMMs with 95% confidence intervals). Green shaded areas in the subplots show the timing of sea-crossing in the species flying over the corresponding region.

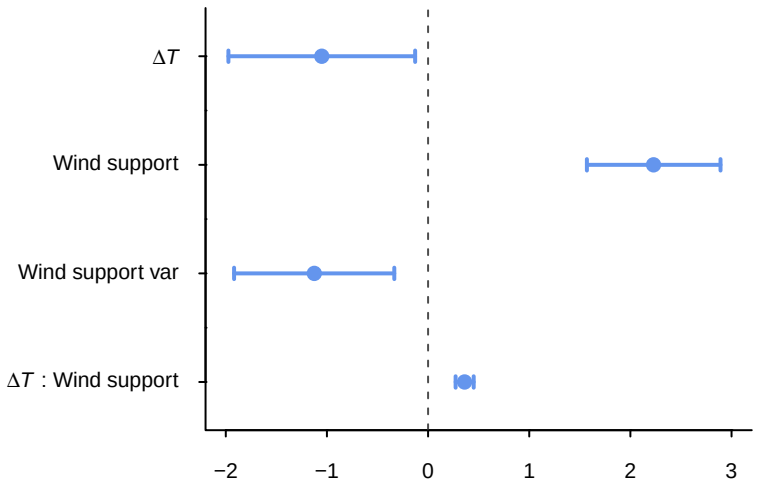

Figure 3: Posterior means (z-scores) and 95 % credible intervals for the fixed effects in the INLA model.

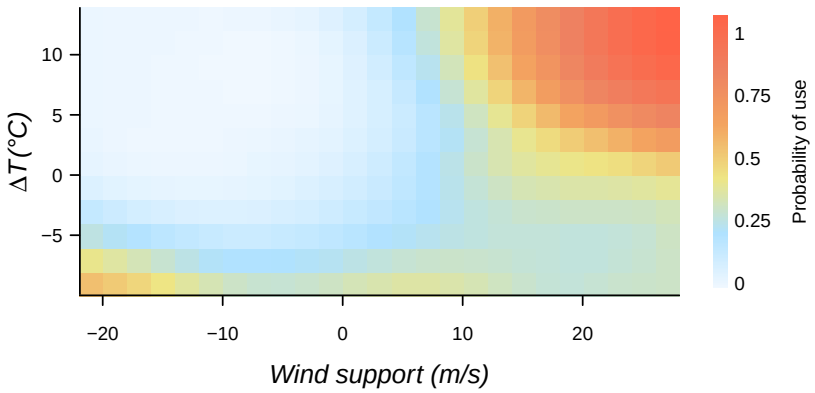

Figure 4: Probability of use under varying wind support and uplift conditions, based on INLA model predictions.

The interplay of wind and uplift facilitates over-water flight in facultative soaring birds

Abstract

Flying over the open sea is energetically costly for terrestrial birds. Despite this, over-water journeys of many birds, sometimes hundreds of kilometers long, are uncovered by bio-logging technology. To understand how these birds afford their flights over the open sea, we investigated the role of atmospheric conditions, specifically wind and uplift, in subsidizing over-water flight at the global scale. We first established that ΔT, the temperature difference between sea surface and air, is a meaningful proxy for uplift over water. Using this proxy, we showed that the spatio-temporal patterns of sea-crossing in terrestrial migratory birds is associated with favorable uplift conditions. We then analyzed route selection over the open sea for five facultative soaring species, representing all major migratory flyways. The birds maximized wind support when selecting their sea-crossing routes and selected higher uplift when suitable wind support was available. They also preferred routes with low long-term uncertainty in wind conditions. Our findings suggest that, in addition to wind, uplift may play a key role in the energy seascape for bird migration that in turn determines strategies and associated costs for birds crossing ecological barriers such as the open sea.

Supplementary material

Supplementary Figure 1

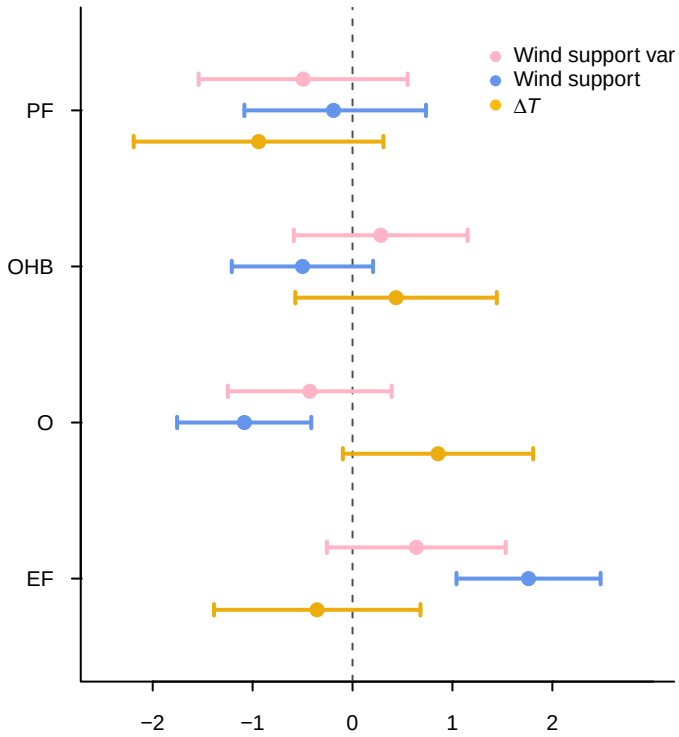

Figure S1: Species-specific variation in route selection. Posterior means and 95 % credible intervals are shown for the species-level random effects of the best INLA model.

Supplementary Figure 2

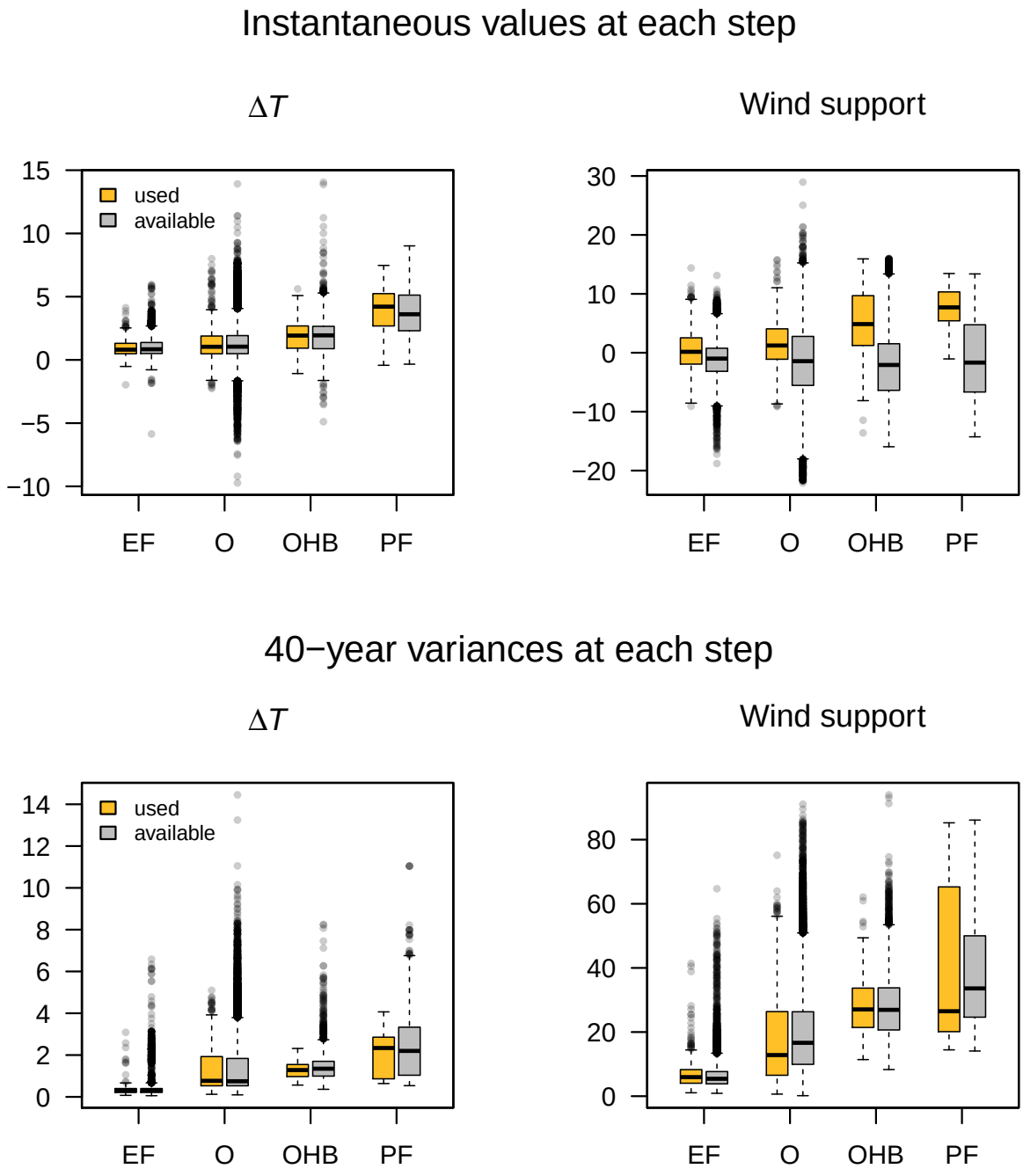

Figure S2: Distribution of values over the used and available steps. These were used for building the step-selection functions. The top row shows the instantaneous values and the bottom row the long-term variances. In the top row, it can be seen that wind support has more variability than ΔT and higher values of wind support are selected by the birds.

Supplementary Figure 3

Figure S3: Bio-logging data for sea-crossing tracks annotated with wind support and ΔT. Data is pooled for sea-crossing segments during autumn migration of the Oriental honey buzzard *Pernis ptilorhynchus* and the grey-faced buzzard *Butastur indicus* in the East Asian flyways, the osprey *Pandion haliaetus* and the peregrine falcon *Falco peregrinus*, in both the African-Eurasian and the American flyways, and the Eleonora's falcon *Falco eleonorae* in the African-Eurasian flyway. For samples of complete tracks, see Fig. **??**.

Supplementary Figure 4

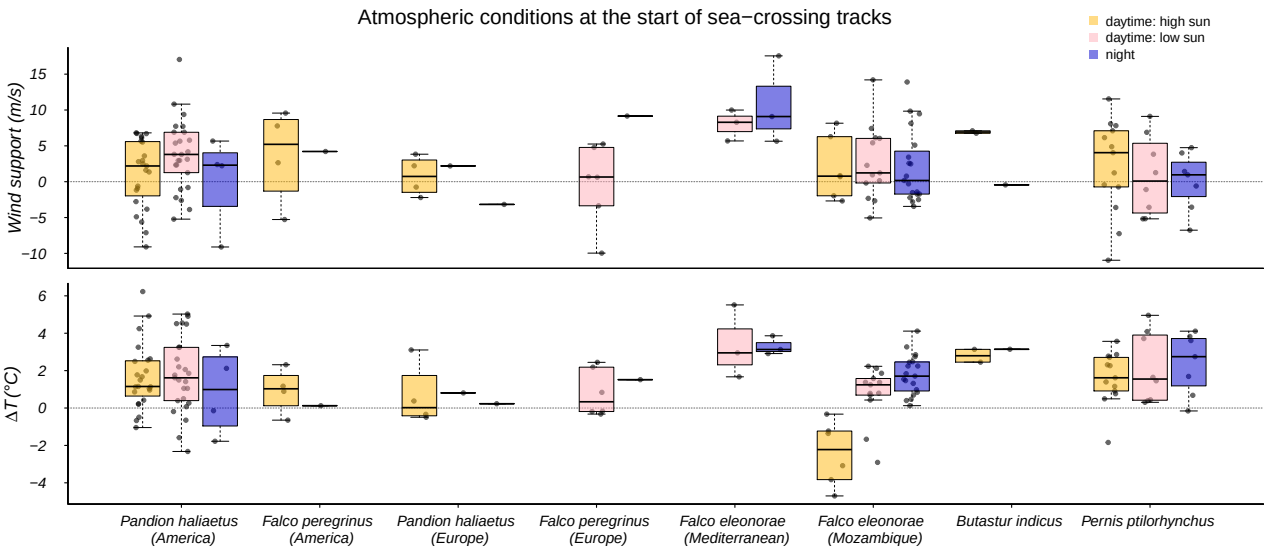

Figure S4: Wind support and ΔT values at the start of each sea-crossing track, grouped by time of day. Most species initiated sea-crossing with positive ΔT and tailwind. An overview of wind support and ΔT along the sea-crossing tracks is presented in Fig. S3.

Supplementary Table 1

Table S1: Summary of bio-logging data used in the step-selection function analysis. The number of individuals and migratory tracks correspond to the data that were retained after filtering the raw data set (see methods). The corresponding Movebank study names are shown in the footnotes.

Species	Tagging_location	Device	Years	Individuals	Tracks
Eleonora's falcon	Greece	GPS	2015	3	3
Eleonora's falcon	Spain	GPS	2012-2018	10	19
Oriental honey buzzard	Japan	GPS	2017-2019	8	17
Osprey [a]	South Europe	GPS	2013-2019	4	4
Osprey [b]	North America	GPS	2010-2019	10	15
Peregrine falcon [c]	North Europe	GPS	2018-2020	4	5
Peregrine falcon [c]	North America	GPS	2016	3	3
Totals				42	66

[a] Osprey in Mediterranean (Corsica, Italy, Balearics)

[b] Osprey Bierregaard North and South America

[c] LifeTrack Peregrine falcon

Supplementary Table 2

Table S2: Results of regional GAMMs built using forty years of global temperature data. These models were used for constructing energy seascapes (Fig. 2).

East Asia

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	-0.5051	0.0092	-54.9250	< 0.0001
sun_elev_flow	2.1566	0.0114	189.5042	< 0.0001
sun_elev_fnight	2.3400	0.0103	227.6074	< 0.0001
B. smooth terms	edf	Ref.df	F-value	p-value
s(lat,lon):sun_elev_fhigh	88.4643	88.4643	97.8487	< 0.0001
s(lat,lon):sun_elev_flow	91.2851	91.2851	196.2278	< 0.0001
s(lat,lon):sun_elev_fnight	92.7295	92.7295	190.2838	< 0.0001
s(yday):sun_elev_fhigh	7.6664	8.0000	231.6346	< 0.0001
s(yday):sun_elev_flow	7.7456	8.0000	228.6311	< 0.0001
s(yday):sun_elev_fnight	7.7940	8.0000	471.8103	< 0.0001
s(year)	0.0000	1.0000	0.0018	< 0.0001

The Americas

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	0.0296	0.0108	2.7394	0.0062
sun_elev_flow	1.3794	0.0129	106.6076	< 0.0001
sun_elev_fnight	1.6410	0.0126	130.5864	< 0.0001
B. smooth terms	edf	Ref.df	F-value	p-value
s(lat,lon):sun_elev_fhigh	90.0437	90.0437	169.5629	< 0.0001
s(lat,lon):sun_elev_flow	94.5179	94.5179	141.5539	< 0.0001
s(lat,lon):sun_elev_fnight	95.7668	95.7668	197.9859	< 0.0001
s(yday):sun_elev_fhigh	7.4179	8.0000	326.2731	< 0.0001
s(yday):sun_elev_flow	7.4498	8.0000	787.2890	< 0.0001
s(yday):sun_elev_fnight	7.2856	8.0000	524.7097	< 0.0001
s(year)	0.0000	1.0000	0.0000	0.8275

Indian Ocean

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	-0.1858	0.0051	-36.2476	< 0.0001
sun_elev_flow	0.0578	0.0065	8.8270	< 0.0001
sun_elev_fnight	1.2402	0.0057	216.8062	< 0.0001
B. smooth terms	edf	Ref.df	F-value	p-value
s(lat,lon):sun_elev_fhigh	94.7248	94.7248	231.4795	< 0.0001
s(lat,lon):sun_elev_flow	96.0323	96.0323	170.5800	< 0.0001
s(lat,lon):sun_elev_fnight	95.7945	95.7945	151.6102	< 0.0001
s(yday):sun_elev_fhigh	7.9279	8.0000	1455.4752	< 0.0001
s(yday):sun_elev_flow	7.9261	8.0000	1537.6625	< 0.0001
s(yday):sun_elev_fnight	7.9736	8.0000	5190.4193	< 0.0001
s(year)	0.0000	1.0000	0.0000	0.8801

Europe

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	-1.3977	0.0943	-14.8277	< 0.0001
sun_elev_flow	2.3936	0.0953	25.1193	< 0.0001
sun_elev_fnight	3.4697	0.0955	36.3168	< 0.0001
B. smooth terms	edf	Ref.df	F-value	p-value
s(lat,lon):sun_elev_fhigh	2.0000	2.0000	56.3685	< 0.0001
s(lat,lon):sun_elev_flow	75.6502	75.6502	14.5510	< 0.0001
s(lat,lon):sun_elev_fnight	82.6352	82.6352	40.0598	< 0.0001
s(yday):sun_elev_fhigh	6.0995	8.0000	210.8682	< 0.0001
s(yday):sun_elev_flow	7.8303	8.0000	1434.8943	< 0.0001
s(yday):sun_elev_fnight	7.6710	8.0000	1046.5831	< 0.0001
s(year)	0.0000	1.0000	0.0000	0.0634

Mozambique Channel

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	0.1469	0.0279	5.2605	< 0.0001
sun_elev_flow	0.2450	0.0334	7.3248	< 0.0001
sun_elev_fnight	1.7059	0.0280	61.0334	< 0.0001
B. smooth terms	**edf**	**Ref.df**	**F-value**	**p-value**
s(lat,lon):sun_elev_fhigh	89.1660	89.1660	30.6120	< 0.0001
s(lat,lon):sun_elev_flow	71.4595	71.4595	165.7619	< 0.0001
s(lat,lon):sun_elev_fnight	95.5807	95.5807	83.2314	< 0.0001
s(yday):sun_elev_fhigh	6.5492	8.0000	362.2948	< 0.0001
s(yday):sun_elev_flow	7.5523	8.0000	299.7936	< 0.0001
s(yday):sun_elev_fnight	7.5972	8.0000	608.8270	< 0.0001
s(year)	0.0001	1.0000	0.0002	0.0780