Sea-crossing along migratory flyways is limited more strongly by wind than by lack of uplift

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Abstract

The open sea is considered an ecological barrier to terrestrial bird movement. However, over-water journeys of many terrestrial birds, sometimes hundreds of kilometers long, are being uncovered by bio-logging technology. To understand how these birds afford their flights over the open sea, we investigated the role of atmospheric conditions in subsidizing sea-crossing behavior at the global scale. By analyzing forty years of temperature data, we show that the spatio-temporal patterns of sea-crossing in terrestrial migratory birds correspond to favorable uplift conditions. We then analyzed route selection over the open sea for four bird species with varying levels of dependence on soaring flight, representing all major migratory flyways worldwide. Our results showed that favorable uplift conditions, albeit not as common and powerful as over land, are not rare over the open seas and oceans. Moreover, wind, which is more variable than uplift in its spatio-temporal distribution, is the determining factor in the birds' route selection over the open sea. Our findings suggest a need for revisiting how ecological barriers are defined, to reflect what we know of animal movement in the era of bio-logging.

Keywords: Energy seascape, migration, soaring, energy landscape, 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 in thermal uplift or orographic uplift due to 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 (hereafter the energy landscape [6]) is interspersed with ecological barriers where energetic subsidies in the atmosphere are weak or absent, impeding efficient movement. Flight over ecological barriers becomes energetically costly, yet is unavoidable for some animals, particularly during migration [7, 8]. How birds afford their flights across such seemingly hostile environments remains an open and important question in movement ecology.

The open sea is considered a major ecological barrier for terrestrial bird migration, particularly for soaring birds [8]. This generally accepted assumption 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, 9]. Early studies of bird migration interpreted these large aggregations as a sign of a general unwillingness of the birds to fly over the open sea [10]. Advances in bio-logging technology have since uncovered the sea-crossing journeys of many terrestrial bird species in all major migratory flyways.

Atmospheric conditions, in particular wind, have been suggested to subsidize terrestrial birds' flight over the open sea, facilitating sea crossings [11–15]. However, some studies also show that wind support (i.e. the length of the wind vector in a bird's flight direction) is not imperative for sea-crossing [16–18]. In fact, high wind speeds can hinder movement by preventing migratory birds from initiating over-water flight [19], or causing birds to drift from their paths, resulting in death at sea [20]. Wind, therefore, seems to have a variable impact on both the propensity for and the energetics of sea-crossing, as it can both reduce and add to the costs of flight, depending on its speed and direction.

An emerging hypothesis is that uplift also plays a role in the energy seascape for terrestrial bird migration. This is particularly important for soaring birds, which specialize in extracting energy from the air to subsidize their metabolic costs of flight [4, 5]. Past bio-logging studies measured flight altitude in soaring birds to provide indirect proof of thermal soaring behavior at sea [21, 22]. More recently, high resolution GPS tracking documented the circling flight pattern and vertical aerial climb of migrating ospreys over the Mediterranean Sea [23]. These studies 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 [24] and predicts the occurrence of soaring flight over water. Positive ΔT values correspond to upward moving 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 cross the Mediterranean Sea successfully [17].

We successively come to the realisation that sea-crossing might not be a rare behavior and that it can be subsidized by atmospheric conditions. To reveal general patterns in the role of uplift and wind in the energy seascape for terrestrial bird migration, we investigate sea-crossing behavior at a global scale. We hypothesize that the spatio-temporal patterns of sea-crossing in soaring birds corresponds to positive values of ΔT. Consequently, we hypothesize that wind, which is more variable than ΔT in its spatio-temporal distribution, as well as its influence on sea-crossing, is the limiting factor in terrestrial birds' over-water route selection. We tested the first hypothesis by modeling the spatio-temporal distribution of ΔT in the main sea-crossing regions of the world. To test for the second hypothesis, we used bio-logging data to investigate route selection over the open sea.

Methods

Bio-logging data set

We compiled a bio-logging data set containing migratory trajectories of birds that regularly perform sea-crossings. Our data 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 *Falco eleonorae* in the African-Eurasian flyway. These birds are all capable of soaring flight, although their dependence on uplift varies, with the falcons and the osprey being less dependent on uplift than the buzzards [10].

We restricted the geographic extent of our study to the 0°- 60°latitudinal zone in the northern hemisphere. The majority of sea-crossing instances happen within this zone (but see for example [25]). Moreover, we only investigated autumn migrations, as spring migration data were scarce.

We focused only on sea-crossing behavior during migration to ensure a common flight purpose among all the

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 any route selection criteria (e.g.[26]). We limited our analysis to sea-crossing trips longer than 30 km. Shorter sea-crossings do not always represent individuals' decision-making over the sea. They can be accomplished, for example, by gaining height over land and gliding over the sea to the opposite shore [18]. In addition, due to the spatio-temporal coarseness of the atmospheric data used, we did not consider it informative to model sea-crossings at shorter distances.

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 30 minutes; see thinTrackTime in package Move [27]).

Spatio-temporal modeling of ΔT

To show the spatio-temporal variation in ΔT at the global scale, we used 40 years of global temperature data. We downloaded sea-surface temperature and temperature at 2 meters above the sea for the entire globe and for all the years that data was available (1979-2019) from the European Center for Medium-Range Weather Forecast (ECMWF; *https://www.ecmwf.int*) Era-Interim re-analysis database (temporal and spatial resolution of 6 hours and 0.7°, respectively). After downloading the data, we randomly sampled 50,000 data points for each year, in order to reduce computing requirements in further processing and analysis. We then spatially filtered the data to exclude lakes, as we were only interested in the open seas and oceans. To include a proxy for time of the 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. [17] to construct energy seascapes. In brief, we modeled ΔT as a function of latitude, longitude, day of the year, and time of the day using the generalized additive mixed modeling (GAMM) approach. We constructed four models in total, one for each region, where regular long-distance sea-crossing is performed by terrestrial birds, namely South-East Asia, the Indian Ocean, Europe, and the Americas. We extracted the timing and location of sea-crossings from our bio-logging data set. We did not have empirical data for bird 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 [28]. 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 [29] in R ver. 4.0.2 [30].

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 [31] 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 insufficiently low resolution of the satellite-tracking data.

Data preparation

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 and were analysed separately. Sea-crossing segments shorter than 30 km, and those that included fewer than 3 tracking points, were removed.

We prepared a stratified data set for analysis: along each sea-crossing segment, for each step, we generated 69 spatially alternative steps based on the step lengths and turning angles of the empirical data, so that each stratum had a total of 70 steps (1 used and 69 alternative). All data were then annotated using the ENV-data track annotation service [32] provided by Movebank (*www.movebank.org*). 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 (temporal and spatial resolution of 6 hours and 0.7°, respectively). We selected the bilinear and the nearest-neighbour methods of interpolation for the wind and temperature data, respectively. We then calculated wind support [33], wind speed, and ΔT (sea surface temperature minus overlaying air temperature) using the annotated

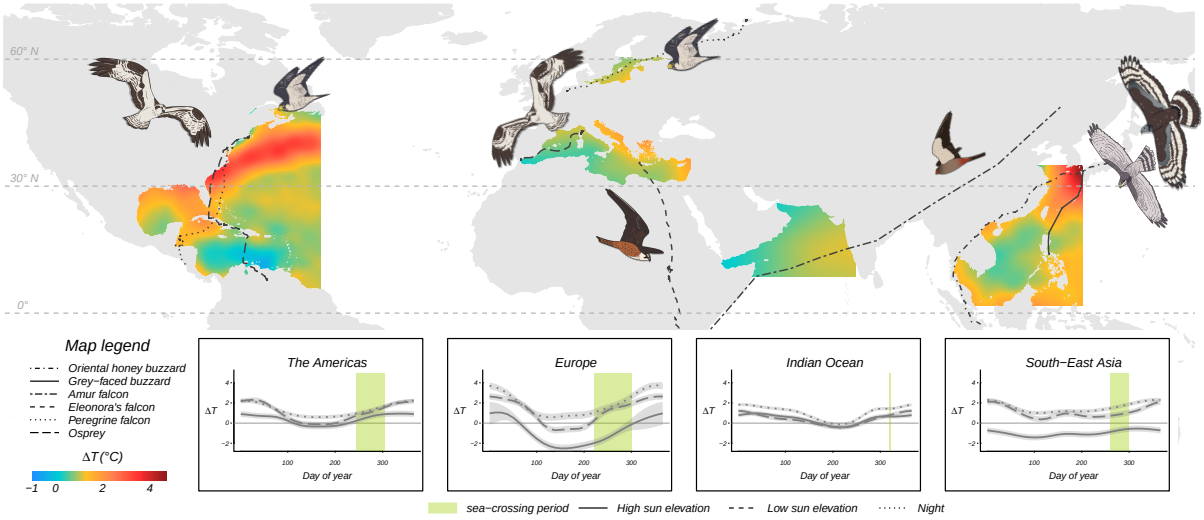

Figure 1: Energy seascapes for soaring bird migration in autumn. The map shows the energy seascapes for August-November derived from 40 years of temperature data. Tracks correspond to sample migratory trajectories. All tracks are based on empirical data, except for the Amur falcon, which is based on the available literature [28]. Subplots show the distribution of ΔT throughout the year in each region, for each time of the 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.

data. Additionally, to investigate whether predictability of atmospheric conditions affected the sea-crossing route choice, we annotated each point with long-term variances (over the 40 years that data was available from ECMWF Era-Interim database) for wind support and ΔT.

Data analysis

We checked the annotated data set for multicollinearity and only considered 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 [34] in R ver. 4.0.2 [30]. Model fitting procedure and priors were based on Muff et al. [35]. We constructed a multilevel model with fixed effects for ΔT, wind support, wind speed, long-term variances of ΔT and wind support, as well as an interaction term for wind speed and ΔT. Species and individual IDs (nested within species) were included as random effects on the slopes. To construct alternative models, in a step-wise manner, we removed explanatory variables with insignificant coefficients (i.e. with credible intervals including zero). We then compared the alternative models using the Widely Applicable Information Criterion (WAIC) and the log marginal likelihood (MLik) scores ([36]). The model with the lowest WIAC and MLik scores was considered the best.

Results

The spatio-temporal pattern of sea-crossing in the six terrestrial bird species corresponded with positive uplift potential over the open sea (Fig. 1; see subplots for within-year and within-day variations in each region). 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 occurs over both the Mediterranean and the Caribbean Seas (Fig. 1). However, this behavior did not set the osprey apart from the other species in route selection criteria, as we did not find species-specific differences in route selection in our step selection function analysis (Supplementary Fig. 1).

We analyzed route selection in 210 sea-crossing segments of 46 individuals (Supplementary Table 1). The most important variable determining over-water route selection was wind support, with a positive effect. The interaction between ΔT and wind speed also showed a positive, yet smaller, effect (Fig. 2). ΔT had a small and non-significant impact on route selection (Fig. 2). Neither of the long-term variances were retained in the best model (i.e. model 3; Table 1; see Supplementary Table 2 for detailed GAMM outputs).

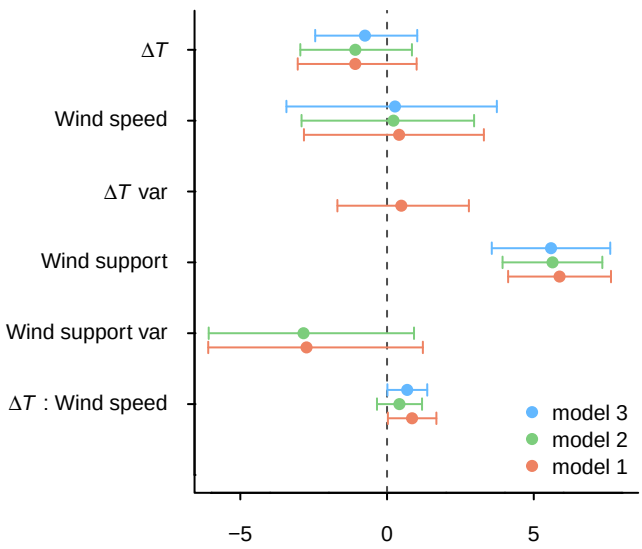

Figure 2: Posterior means (z-scores) and 95 % credible intervals for the fixed effects in the INLA models. Models corresponds to those in Table 1.

Discussion

Our global-scale analysis of sea-crossing behavior showed that soaring birds were more selective for wind than uplift while flying over water. We found that uplift conditions are mostly favorable, particularly in autumn (Fig. 1). Wind conditions however were more variable at small spatio-temporal scales than uplift (Supplementary Fig. 2). Thus, birds were more responsive to instantaneous wind conditions, particularly wind support, when selecting their sea-crossing routes.

We used 40 years of temperature data to model ΔT as a function of space and time. This allowed us to make energy seascape maps that corresponded to when and where major sea-crossing events regularly take place. The mostly positive values of ΔT on these maps indicate that soaring birds are not facing strong subsidence when flying over water. We further observed that, during autumn migration, the range and mean of ΔT values were similar between the observed and alternative steps in our step selection function estimation (Supplementary Fig. 2). The birds thus face more variability in wind conditions than in uplift, which can explain why wind support was the most important criteria for route selection (Table 1).

ΔT has a generally low seasonal variation (subplots in Fig. 1). This suggests that birds could benefit from uplift during spring migration as well as in autumn. However, we caution against making generalizations about sea-crossing patterns in spring based on ΔT alone. As we show, wind support plays a more important role in sea-crossing than uplift. Thus, even in similar uplift conditions between the two seasons, variations in wind support can lead to loop migration patterns ([37]; e.g. [38]) and even avoidance of sea-crossing in one season (e.g. [13]). 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.

We found a small positive effect of the interaction between ΔT and wind speed in sea-crossing route selection (Fig. 2). On the one hand, at moderate wind speeds, even small values of positive ΔT are enough for supporting over-water soaring flight [39]. On the other hand, strong winds can destroy thermals and impede soaring flight. Therefore, the energy seascape is formed by a complex interplay of uplift and wind conditions. To understand the energetics of terrestrial birds' flight over the open sea, future studies can employ theoretical modeling as well as

Table 1: Model specifications for the step selection function analysis using INLA. Fixed effects included ΔT, wind speed (wspd), wind support (wspt), long-term variance of ΔT (ΔT var) and long-term variance of wind support (wspt var). The model with the lowest WAIC and MLik values (model 3) was selected as the best model.

Model	Fixed effects	Random effects	WAIC	MLik
1	ΔT * wspd + wspt + ΔT var + wspt var	species, ID	$1.552\,614 \times 10^{204}$	-13217.56
2	ΔT * wspd + wspt + wspt var	species, ID	8.0517×10^{148}	-13234.67
3	ΔT * wspd + wspt	species, ID	$6.673\,001 \times 10^{134}$	-13785.91

high-resolution bio-logging to quantify the birds' response to different combinations of wind and uplift conditions during over-water flight.

In the literature, sea-crossing behavior is commonly associated with the morphological capability of sustaining long bouts of flapping flight, aided by favorable wind conditions. Although evidence for soaring flight over the sea has accumulated for at least a decade now, many studies still overlook uplift potential when explaining sea-crossing behavior. Studies that try to include uplift do so by using a variety of proxies, including air temperature [16], air temperature gradient [13], vertical air velocity [13], boundary layer height [40], and solar irradiance [18]. These studies rarely find the uplift proxy as the most important determinant of sea-crossing. The reason for this could be that, similar to our step-selection analysis, the naturally low variance in uplift conditions (Fig. S2) make it an insignificant criterion for route selection, despite its positive effects. Another explanation could relate to the meaningfulness of the proxies themselves. These proxies are all related to upward movement of air in the atmosphere, but have not been shown to correlate with soaring flight in birds. ΔT however, has been proven, both by direct observations [39] and bio-logging technology [23], to be related to soaring flight. We encourage future studies to take advantage of this proxy, not least because widespread use of ΔT makes comparisons among studies possible. Yet, there remains a strong need for quantifying the amount of energy, or the realized uplift, that a bird can gain from ΔT. Theoretical studies could investigate realized uplift across different morphological characteristics, as well as wind and other environmental conditions.

Uplift reduces the energetic costs of remaining airborne, not only for obligate soaring birds that depend on this resource for crossing the sea, but also for flapping flyers. We show that different species of raptors, with different morphological characteristics and soaring flight dependencies, all potentially benefit from the positive uplift conditions when flying over water, while maximizing wind support. In fact, we found no significant species-specific differences in route selection among the four species (Fig. S1). Our results can further shed light on the energy seascapes for other animals flying over the open sea. The relatively high uplift during the night compared to daytime (Fig. 1) means less drag and could lead to energetically cheaper flight in nocturnal migrants, for example over the Mediterranean [41, 42] and the Caribbean [43, 44] Seas. Moreover, dragonflies [45] and cuckoos (*Cuculus* spp.; *https://birdingbeijing.com/the-mongolia-cuckoo-project/*) migrate within the same time window as the Amur falcon over the Indian Ocean (Fig. 1), perhaps also taking advantage of the energetic subsidy that the atmosphere provides.

Conclusion

The common narrative of many papers reporting sea-crossing behavior in terrestrial birds is based on the premise that flying over the open sea, particularly by soaring, is an exceptional behavior. We show that this is not the case, because favorable uplift conditions, albeit not as common and as powerful as over land, are not rare over the open seas and oceans. The spatio-temporal pattern of sea-crossing in many terrestrial animals coincides with favorable uplift conditions. We further show that wind support is the main limiting factor for route selection over the open sea. Our findings suggest a need for revisiting how ecological barriers are defined, to reflect what we know of animal movement in the era of bio-logging.

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Authors' contributions

EN conceived the study and designed the analyses with input from KS and PB. EN carried out the analyses and wrote the paper. ROB, OD, SG, HH, CK, OK, NL, FM, IP, AS, JFT, NT, NMY, and MW contributed data. All authors commented on and edited the manuscript drafts.

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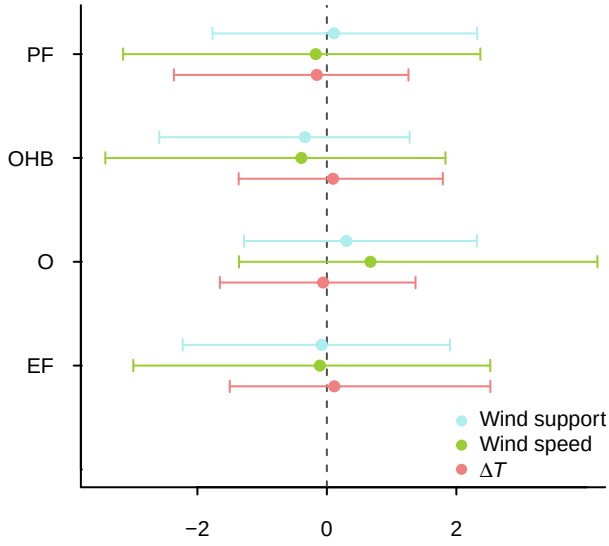
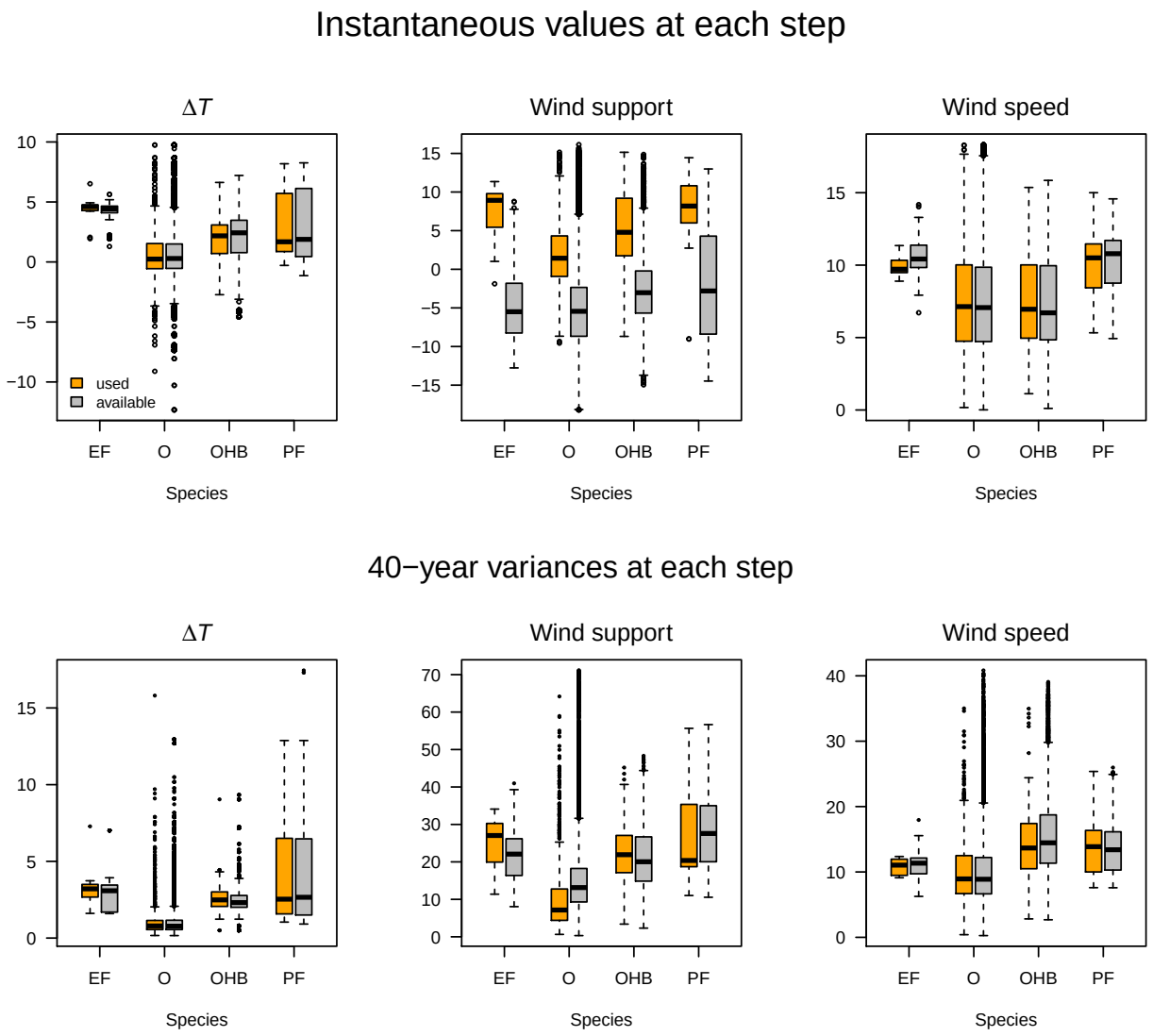
Supplementary material

Supplementary Figure 1



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

Supplementary Figure 2



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 Table 1

Summary of biologging data used in the step-selection function analysis. The number of individuals (Individuals), number of migratory tracks (Tracks), and number of sea-crossing segments (Segments) correspond to the data that were retained after filtering the raw data set (see methods). The corresponding Movebank study names can be found in the footnotes.

Species	Tagging_location	Device	Years	Individuals	Tracks	Segments
Eleonora's falcon	Greece	GPS	2015	3	3	4
Oriental honey buzzard	Japan	GPS	2017-2018	8	14	32
Osprey [a]	South Europe	GPS	2013	3	4	6
Osprey [b]	North America	GPS	2009-2018	28	48	157
Peregrine falcon [c]	North Europe	GPS	2018	1	1	1
Peregrine falcon [c]	North America	GPS	2016	3	3	10
Totals				46	73	210

[a] Osprey in Mediterranean (Corsica, Italy, Balearics)
[b] Osprey Bierregaard North and South America
[c] LifeTrack Peregrine falcon

Supplementary Table 2

Results of regional GAMMs built using forty years of global temperature data. These models were used for constructing energy seascapes (Fig. 1).

East Asia

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	-0.3737	0.0226	-16.5284	< 0.0001
sun_elev_flow	1.9447	0.0243	79.9753	< 0.0001
sun_elev_fnight	2.1579	0.0215	100.2584	< 0.0001
B. smooth terms	edf	Ref.df	F-value	p-value
s(lat,lon):sun_elev_fhigh	64.5741	81.3019	13.7932	< 0.0001
s(lat,lon):sun_elev_flow	69.7417	85.7923	37.3508	< 0.0001
s(lat,lon):sun_elev_fnight	65.9621	82.6007	38.8957	< 0.0001
s(yday):sun_elev_fhigh	6.1590	8.0000	27.3294	< 0.0001
s(yday):sun_elev_flow	7.4983	8.0000	145.0565	< 0.0001
s(yday):sun_elev_fnight	7.1658	8.0000	187.9675	< 0.0001
s(year)	0.0001	1.0000	0.0008	0.0030

The Americas

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	0.0463	0.0191	2.4236	0.0154
sun_elev_flow	1.3822	0.0217	63.5896	< 0.0001
sun_elev_fnight	1.5836	0.0208	76.2830	< 0.0001
B. smooth terms	edf	Ref.df	F-value	p-value
s(lat,lon):sun_elev_fhigh	78.8271	92.2667	34.9271	< 0.0001
s(lat,lon):sun_elev_flow	85.4616	95.8348	45.2217	< 0.0001
s(lat,lon):sun_elev_fnight	88.8377	97.1879	59.2249	< 0.0001
s(yday):sun_elev_fhigh	6.7925	8.0000	97.9569	< 0.0001
s(yday):sun_elev_flow	7.6164	8.0000	614.0085	< 0.0001
s(yday):sun_elev_fnight	7.0471	8.0000	377.0264	< 0.0001
s(year)	0.0000	1.0000	0.0005	0.0002

Indian Ocean

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	-0.1403	0.0156	-8.9865	< 0.0001
sun_elev_flow	0.0443	0.0197	2.2493	0.0245
sun_elev_fnight	1.1822	0.0170	69.3469	< 0.0001
B. smooth terms	edf	Ref.df	F-value	p-value
s(lat,lon):sun_elev_fhigh	58.8983	75.9306	23.4275	< 0.0001
s(lat,lon):sun_elev_flow	68.5374	84.8222	18.4597	< 0.0001
s(lat,lon):sun_elev_fnight	67.8403	84.2877	12.8269	< 0.0001
s(yday):sun_elev_fhigh	7.2166	8.0000	131.6948	< 0.0001
s(yday):sun_elev_flow	7.0067	8.0000	178.1643	< 0.0001
s(yday):sun_elev_fnight	7.7796	8.0000	561.3510	< 0.0001
s(year)	0.0000	1.0000	0.0000	0.4452

Europe

A. parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	-0.9691	0.1379	-7.0264	< 0.0001
sun_elev_flow	1.9372	0.1393	13.9061	< 0.0001
sun_elev_fnight	2.7871	0.1393	20.0115	< 0.0001
B. smooth terms	edf	Ref.df	F-value	p-value
s(lat,lon):sun_elev_fhigh	22.8483	31.9256	2.4926	< 0.0001
s(lat,lon):sun_elev_flow	48.0279	63.7198	5.8838	< 0.0001
s(lat,lon):sun_elev_fnight	56.9228	73.5363	10.1998	< 0.0001
s(yday):sun_elev_fhigh	5.2234	8.0000	44.5510	< 0.0001
s(yday):sun_elev_flow	7.5201	8.0000	301.3130	< 0.0001
s(yday):sun_elev_fnight	7.0936	8.0000	270.2968	< 0.0001
s(year)	0.0000	1.0000	0.0001	0.0673