Age-specific migration timing affects the energy seascape over an ecological barrier

Nourani, E.[1,2]*, Vansteelant, W. M. G. [3], Byholm P.[4], and Safi, K. [1,2]

[1] Department of Migration, Max Planck Institute of Animal Behavior, Radolfzell, Germany.

[2] Department of Biology, University of Konstanz, Germany.

[3] Theoretical and computational Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, The Netherlands.

[4] Novia University of Applied Sciences, Ekenäs, Finland.

*corresponding author. E-mail: enourani@ab.mpg.de; mahle68@gmail.com

Abstract

Background: Soaring birds extract energy from the atmosphere to achieve energetically low-cost movement. Species that fly over ecological barriers, such as open seas, need to adjust the spatio-temporal patterns of their passage to extract the highest possible energy from the atmosphere over the barrier. We introduce the concept of "energy seascapes" in migration of terrestrial birds and test its application in autumn migration of European honey buzzards *Pernis apivorus* over the Mediterranean Sea.

Methods: We used GPS-tracking data to identify the most important environmental variables affecting the sea-crossing length in adult and juvenile honey buzzards. Then, considering this variable as a proxy for available energy over the sea, using forty years of temperature data, we constructed energy seascapes for two periods in autumn, corresponding to adult and juvenile migration periods.

Results: We found temperature gradient over the sea to be an important determinant of sea-crossing length and therefore constructed energy seascapes based on this variable. Our results revealed a temporal variation in the energy seascapes, with higher energy available over the sea when juveniles migrate.

Conclusions: This finding helps to explain how juvenile honey buzzards achieve a high survival rate on their first autumn migration, even though they make much longer flights over the sea than adults. Our approach to constructing energy seascapes was successful in showing that dynamics of energy availability over ecological barriers affect the strategy that soaring birds adopt to tackle them.

Keywords

Energy landscape, water-crossing, thermal uplift, soaring, sea surface temperature, temperature gradient

Background

Flying animals have evolved to interact with and negotiate their highly dynamic atmospheric environments and are selected for energetic efficiency. Almost all species extract energy from the atmosphere by flying in suitable winds [1] or at least reduce energy expenditure by avoiding headwind and adverse weather conditions [2]. Thermal soaring birds (hereafter soaring birds) are the masters of extracting energy for flight by relying on uplifts [3], which are vertically rising air currents that subsidize or entirely pay for their energetically inexpensive soaring flights [4, 5]. To understand the energetic costs of moving through the environment for soaring birds, "energy landscapes" [6, 7] can be defined as a function of uplift potential and wind conditions. Optimal migration routes would therefore minimize the cost of transport by maximizing the availability of energetic subsidies over the landscape, where wind is supportive [8, 9] and topography, vegetation, and the general atmospheric conditions, allow for strong uplift formation [3, 10, 11].

Assuming that migratory birds follow an energy-minimizing movement strategy, they should circumnavigate areas of high cost of transport, or exploit conditions when having to cross them, that allow maximum energy saving. Open seas and oceans are energetically costly to cross for soaring birds, and are therefore ecological barriers [12-14]. Landing over sea surface is not

possible for these birds. Moreover, water surfaces, being generally colder than the air above them during the day, produce subsidence that can drag down the birds. Such low, or negative, uplift potential requires the birds to sustain long bouts of flapping flight over open water. While their large wing areas compared to body mass makes soaring birds perfectly adapted to extract energy from uplifts, flapping flight, precisely because of the large wings, represents an overly expensive task for these species [15, 16]. Consequently, the ability to undertake considerable water-crossing, for instance in the Eleonora's flacon *Falco eleonorae* or the Osprey *Pandion haliaetus*, is reflected in morphological adaptations [13, 17]. That is, as so called facultative soaring birds, these species boast less wing area for their weight, making them less reliant on uplifts and allowing for flapping flight to be less energetically expensive. In addition to morphology, most cases of water-crossing by soaring birds are associated with suitable atmospheric support, mostly in the form of supportive wind [8, 14, 18, 19], but more recently has been shown to be also in the form of updrafts [17, 20].

In some species, different demographic groups have varying propensities to cross the open sea. European honey buzzards *Pernis apivorus* are an extreme case of age-dependent migratory behaviour among soaring birds. Adults almost exclusively migrate over land, while subadults regularly and very widely cross the Mediterranean Sea. The two age groups have little morphological differences that cannot account for the performance differences. In addition, the sea-crossing does not lead to higher mortality in subadults [21] and it seems that this age-specific behaviour is characteristic for the species [14, 22]. The two age groups also migrate at different times. Juveniles on their first autumn migration from northern European breeding

grounds to sub-Saharan African wintering grounds start migration about two weeks later than adults, with no access to social information to learn the optimal migration routes.

We believe that there might be a hitherto overlooked facet to energy extraction from the atmosphere over open seas that can be explained by taking into account the temporal dynamics in energy availability. We introduce the concept of "energy seascapes" in migration of terrestrial birds, which we define as energy availability over the sea, and test its application in understanding the causes of the age-specific sea-crossing strategies adopted by the European honey buzzard.

Methods

Tracking data

We used GPS-tracking data collected for autumn migration of honey buzzards breeding in Finland. Data included complete autumn journeys for 22 juveniles [21] on their first autumn migration over 2011-2013 and nine adult birds of unknown age over 2011-2016 (Additional file 1). We had data over 2-5 years for the adults, totalling 29 complete tracks (Fig. S1). The amount and type of data varied among tags depending on the devices and programming schedule (see [21] and Additional file 1), but all data was resampled to hourly or larger intervals due to gaps in data or lower measurement resolution (e.g. at night and in the tropical forest).

For the purpose of this study, we extracted sections of the tracks that overlapped with the Mediterranean Sea. To prevent over-dispersion in our analyses, we removed tracks with shorter

water-crossing lengths than the 10% quantile of the lengths of all water-crossing tracks (415.18 km). These tracks (Figs. 1 & Additional file 2) corresponded to journeys of adult birds that clearly avoided the Mediterranean Sea by flying through the strait of Gibraltar (n = 2) or the eastern flyway (n = 3).

Track annotation

Each sea-crossing track was annotated with temporal and environmental variables. We calculated the length of the sea-crossing track (including islands) and the Julian date of first encountering the Mediterranean Sea (hereafter date of arrival at sea). Every sea-crossing track (excluding islands) was interpolated with regular points 500 m apart and annotated using the Env-Data track annotation service of Movebank [23]. For each point, eastward (u) and northward (v) components of the wind (m/s) at 925 hPa pressure level, sea surface temperature (K), and temperature at 2-m above ground (K) were obtained with 0.7° resolution (all from European Centre for Medium-Range Weather Forecast; ECMWF). We selected bilinear and nearest-neighbour interpolation methods for wind and temperature, respectively. For each sea-crossing track, we calculated wind support (wind parallel to flight direction) and crosswind (wind perpendicular to flight direction) from one point to the next and calculated averages for each track. Average crosswind was calculated as the mean of absolute values along each track, as we were not interested in the direction of crosswind, but its overall strength. For each point, we calculated temperature gradient (ΔT) as the difference between sea surface temperature and temperature at 2 m above ground and averaged all ΔT values along each track. We did not convert the unit of temperature variables from K to °C, because the two units have the same magnitude. Hence, ΔT values that we calculated can be interpreted in either unit. We used ΔT

as an indicator of uplift potential over water. Positive values of ΔT (i.e. warmer sea than air) indicate upward moving air and correspond to higher uplift potential (see [17]), while negative values indicate subsidence.

Statistical analysis

To understand whether atmospheric conditions facilitate sea-crossing, we investigated the distance of sea-crossing (i.e. length of the sea-crossing tracks) as a function of wind support, cross-wind, and ΔT along the track, as well as date of arrival at sea. The data was analysed using a linear model with a random effect for year. We did not include a random effect of individuals, because we did not have repeated tracks for most of them. Age group was also not included, because of its high correlation with date of arrival at sea (i.e. all adults arrived at sea earlier than juveniles). All fixed effects were checked for multi-collinearity and were z-transformed to ensure comparability of effect sizes. Due to the small sample size (n = 46), we kept the model simple by estimating a small number of parameters using the data and including no interaction terms. We built separate models for wind (Model A) and ΔT (Model B), and a model combining the variables with highest effect sizes in the previous two models (Model C). Models were compared based on the amount of variation that they explained.

We then constructed energy seascapes using the most influential variable in our linear model. To further investigate the temporal and spatial dynamics of energy seascapes, we predicted this variable as a function of latitude, longitude, and time, in a generalized additive model (GAM; [24]). To do this, we obtained the relevant atmospheric data for the Mediterranean Sea for autumn (August- October) from ECMWF ERA-Interim reanalysis archive

(*https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era-interim*) for all the years for which data was available (1979-2018). We included a two-dimensional smoothing term for latitude and longitude and a one-dimensional smoothing term for Julian date using penalized regression splines. ERA-Interim data are provided for every six hours. We therefore included time of the day (00:00, 06:00, 12:00, and 18:00 UTC) as a factor variable to investigate sub-daily patterns of variation in uplift potential. We used the mgcv package [25] for building the GAM and used a generalized cross validation criterion to estimate the best smoothing parameter. To produce energy seascape maps, we used the model to make predictions for two time periods corresponding to juvenile (Sep. 25-Oct. 23) and adult (Aug 30-Oct. 4) migration over the sea. This data was a subset of the 40-year dataset that was used to build the model. To create smooth maps, we spatially interpolated the output raster layers to 1-km resolution.

Results

We identified temperature gradient (i.e. a proxy for uplift potential) as the most important atmospheric variable contributing to sea-crossing. Our best model (i.e. with the highest deviance explained; model C) showed that increasing temperature gradient (warmer sea surface temperature than air) can explain higher sea-crossing distance in migrating honey buzzards. We also found a considerable effect of crosswind and date of arrival at sea (Table 1).

Temperature gradient was then used in a GAM to construct energy seascapes. The importance of timing and temperature gradient over the sea during the migration of juveniles was confirmed by the results of this analysis (Table 2; Fig. 3). These results showed that as the

autumn migration season progresses, temperature gradient over the sea rises (Figs. 1 & 2). Energy seascape maps over the Mediterranean Sea showed that, earlier in autumn, when adults encounter the sea, sea surface is colder than the air above it, causing subsidence (Fig. 1a). Later in the season, however, warmer sea surface compared to the air above it produces more uplift potential (Fig. 1b). For both time periods, the spatial pattern of temperature gradient over the sea shows higher subsidence in the Alboran Sea (i.e. between the Iberian Peninsula and north-western Africa) and parts of the Aegean Sea (i.e. the eastern coast of the Anatolian Peninsula), while the Adriatic Sea (separating the Balkan and Italian Peninsulas) and the Balearic Sea (separating north-eastern coast of Spain and the Balearic Islands) have higher uplift potential than other regions.

The model also showed a difference in temperature gradient at different times of the day (Table 2), with midnight having the highest temperature gradient, followed by 6:00 and 18:00. The only time of day with a negative average temperature gradient was noon.

Discussion

We found that intra-specific differences in the propensity to cross the open sea in honey buzzards is related to the temporal dynamics in the energy seascape. We derived the energy seascapes using temperature gradient, a proxy for uplift potential [17], which represented the most important source of variation in the length of migration trajectories over the sea. Observations of adult European honey buzzards that cross the Mediterranean Sea at long stretches suggest that they do so in favourable wind [26], particularly when soaring flight over

187 land is hampered by unsuitable conditions [14]. Our results did not show a high importance of
188 wind support, however. This can be due to the fact that both age groups crossed the sea with
189 moderate wind support (Fig. 3).

190 Dynamic energy seascapes that we constructed showed an increase in uplift potential over the
191 Mediterranean Sea as autumn progresses. This translates into higher uplift potential later in the
192 season when juveniles are migrating, indicating that following a migration route with long sea-
193 crossing might not be energetically expensive for them. The consistency of this pattern, at least
194 over the forty years of data that we analysed, suggests that this could be a contributing factor
195 to the high survival of juvenile honey buzzards flying over the Mediterranean Sea on their first
196 autumn journey [21]. We do not interpret these findings as the reason for later departure in
197 juveniles. In fact, later migration onset is likely be related to the time required for the
198 development of juveniles to become capable of migration.

199 Considering that uplift potential is lower earlier in autumn when adults migrate, a question that
200 arises is why do adults not migrate later to save energy over the sea too. One potential answer
201 could be related to carry-over effects that a delay in autumn migration could have on the later
202 stages of their life-cycle, as reproductively active part of the population, and requires further
203 research. Moreover, being more experienced at soaring flight and orientation [21, 27], adults
204 are likely to be better able to track routes that maximize the availability of energetic subsidies
205 over the landscape, for example by detouring the sea or crossing at narrower stretches of water.
206 Schmid [28] (cited in [22]) proposed that adult European honey buzzards start migration early
207 to benefit from soaring conditions along overland routes. They argue that by the time juveniles

208 migrate, soaring conditions overland are already too poor to make a detour energetically
209 beneficial for juveniles [28].

210 Our results also indicated that energy availability over the sea is highest at midnight and early
211 hours of the day. This is the opposite of what is observed over land, where thermals are
212 stronger during the day, and emphasizes how radically different the atmosphere functions
213 between these environments. Honey buzzards usually migrate at mid-day to benefit from
214 strong thermals over land, as our tracking data also show (Fig. 4). Regardless of the time of day,
215 the relationship between temperature gradient and Julian date is positive. This suggests that
216 birds crossing the sea at any time during the day still benefit from less subsidence and higher
217 potential uplift later in the season. Moreover, this finding contributes to our understanding of
218 why facultative soaring raptors can engage in sea-crossing at night (e.g. [17, 29]).

219 The energy seascapes that we constructed can be informative for gaining insight into the
220 energetic subsidies available over an ecological barrier. Our results showed that tackling an
221 ecological barrier, such as the Mediterranean Sea, is not only dependent on the morphological
222 characteristics of the birds [13], but also on the specific environmental conditions that
223 determine energy availability when the birds encounter these regions. The importance of the
224 atmospheric environment in sea-crossing behaviour of soaring birds is also shown by Nourani,
225 Yamaguchi [18]. They used high-resolution horizontal and vertical wind data to investigate the
226 suitability of migration over the East China Sea region for Oriental honey buzzards *P.*
227 *ptilorhynchus*. They showed that by migrating over the sea in autumn, birds can subsidize their
228 migration with wind support, while in the absence of supporting wind in spring, detouring the
229 ecological barrier and following a route over land is more suitable [18]. Seasonal detours are

also observed over the Sahara Desert, an ecological barrier for Afro-Palearctic migrants. This has been related to the seasonality of wind conditions [30], but to our knowledge, previous studies have not constructed energy landscapes to investigate the energetic costs of adopting alternative routes.

To better understand how different strategies of tackling ecological barriers contribute to the total costs of migration, it would be necessary to investigate the energy landscapes of migration over both land and sea. It is difficult to construct such energy landscapes using atmospheric variables, as these are not consistent over both land and sea. For example, although it is possible to calculate temperature gradient over land, it would not be a suitable proxy for uplift formation as variations in topography and other substrate and superstrate conditions affect uplift formation. Variables such as thermal and orographic uplift [3] can be calculated for land surfaces but not for the sea.

An alternative approach to constructing energy landscapes that would be consistent over both land and sea is to use a proxy for activity-related metabolic rate of the birds to quantify energy expenditure [7]. Such information can be collected using heart-rate loggers or tri-axial accelerometers [31] and would also provide means of making inter- and intra-specific comparisons in energy extraction from the atmosphere over open seas and oceans.

We suggest future studies quantify energy landscapes over ecological barriers and over alternative routes detouring them. This will lead to a better understanding of the energetic trade-offs associated with different strategies of responding to the barrier. In the case of the European honey buzzard, for example, constructing energy landscapes before arrival at sea as

well as over the sea would lead to better understanding of the decision-making process that each individual goes through in selecting a strategy to respond to this ecological barrier.

Conclusions

Our findings showed that the dynamics of energy seascape encountered by soaring birds affect their propensity to cross the sea. Energy seascapes constructed for the two time periods corresponding to adult and juvenile honey buzzard migration suggested that temporal variation in the energy seascapes makes oversea flight less energetically costly for juveniles than adults. This finding helps to explain how juvenile honey buzzards achieve a high survival rate on their first autumn migration, even though they make much longer flights over the sea than adults.

Declarations

Ethics approval and consent to participate

Capturing of the birds was done under a ringing permit (permit 2604) issued by the Finnish Museum of Natural History. Attachment of tracking devices was permitted under the following licences issued by Finnish authorities: EPOELY/135/07.01.2013, ESAVI/2195/04.10.07/2014, PIRELY/49/07.01/2013, VARELY/73/07.01/2013, VARELY/215/2015.

Consent for publication

Not applicable

Availability of data and materials

The datasets supporting the conclusions of this article are available in [21] (for juvenile birds) and Movebank repository (*movebank.org*) under study name "*Pernis_apivorus_Byholm _Finland*" (for adult birds).

Competing interests

The authors have no competing interests.

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Authors' contributions

EN conceived the study, analysed the data, and drafted the manuscript. KS and WMGV provided input and discussion on data analysis, interpretation of results, and manuscript preparation. PB collected the data and provided comments on the manuscript. All authors revised the manuscript and gave final approval for publication and agree to be held accountable for the work performed therein.

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Additional files

Additional file 1. Metadata of bio-logging data for adult honey buzzards *Pernis apivorus* breeding in Finland.

Additional file 2. Autumn migration tracks for honey buzzards *Pernis apivorus* breeding in Finland. Dotted lines represent tracks that were not included in the linear model (see Methods for more information).

370 **Figure legends**

371 Figure 1. Energy seascapes constructed by predicting temperature gradient (delta T; °C) over
372 the Mediterranean Sea for the period of honey buzzard autumn migration for a) adults (Aug 30-
373 Oct. 4) and b) juveniles (Sep. 25-Oct. 23) over the sea. The dashed lines in each figure show
374 autumn migration tracks for the corresponding age group. The dotted lines in (a) correspond to
375 migration tracks removed from the linear model analysis (For complete migration tracks within
376 the flyway, see Additional file 2).

377 Figure 2. Smooth term showing the relationship between temperature gradient (delta T) and
378 Julian Date over the Mediterranean Sea. The pink and blue shaded areas corresponds to the
379 periods of adult and juvenile migration over the sea, respectively.

380 Figure 3. Density distribution of average wind support (m/s), crosswind (m/s), and temperature
381 gradient (delta T; °C) along the sea-crossing tracks of juvenile and adult European honey
382 buzzards *Pernis apivorus*. Average values are calculated for interpolated tracks (500 m intervals;
383 see Methods for more information).

384 Figure 4. Hourly distribution of autumn migration tracking points of European honey buzzards
385 *Pernis apivorus* over the Mediterranean Sea. Tracks that do not show considerable water-
386 crossing are not included (see Methods for more information).

387

388

Tables

Table 1. Results of linear modelling with a random effect for year. Distance of sea-crossing over the Mediterranean Sea was investigated as a function of wind support, crosswind, temperature gradient, and date of arrival at sea.

Model	Coefficients (SE)					Random effects	AIC	Adjusted R^2
	Intercept	Wind support	Crosswind	ΔT	Julian date			
A	805.69 (33.69)	2.21 (26.88)	58.82 (26.01)	-	51.04 (26.81)	Year[1]	576.21	0.20
B	806.36 (31.96)	-	-	71.61 (26.39)	30.17 (27.32)	Year[2]	580.98	0.23
C	803.58 (28.66)	-	56.77 (23.30)	69.22 (25.01)	20.44 (25.96)	Year[3]	569.20	0.33

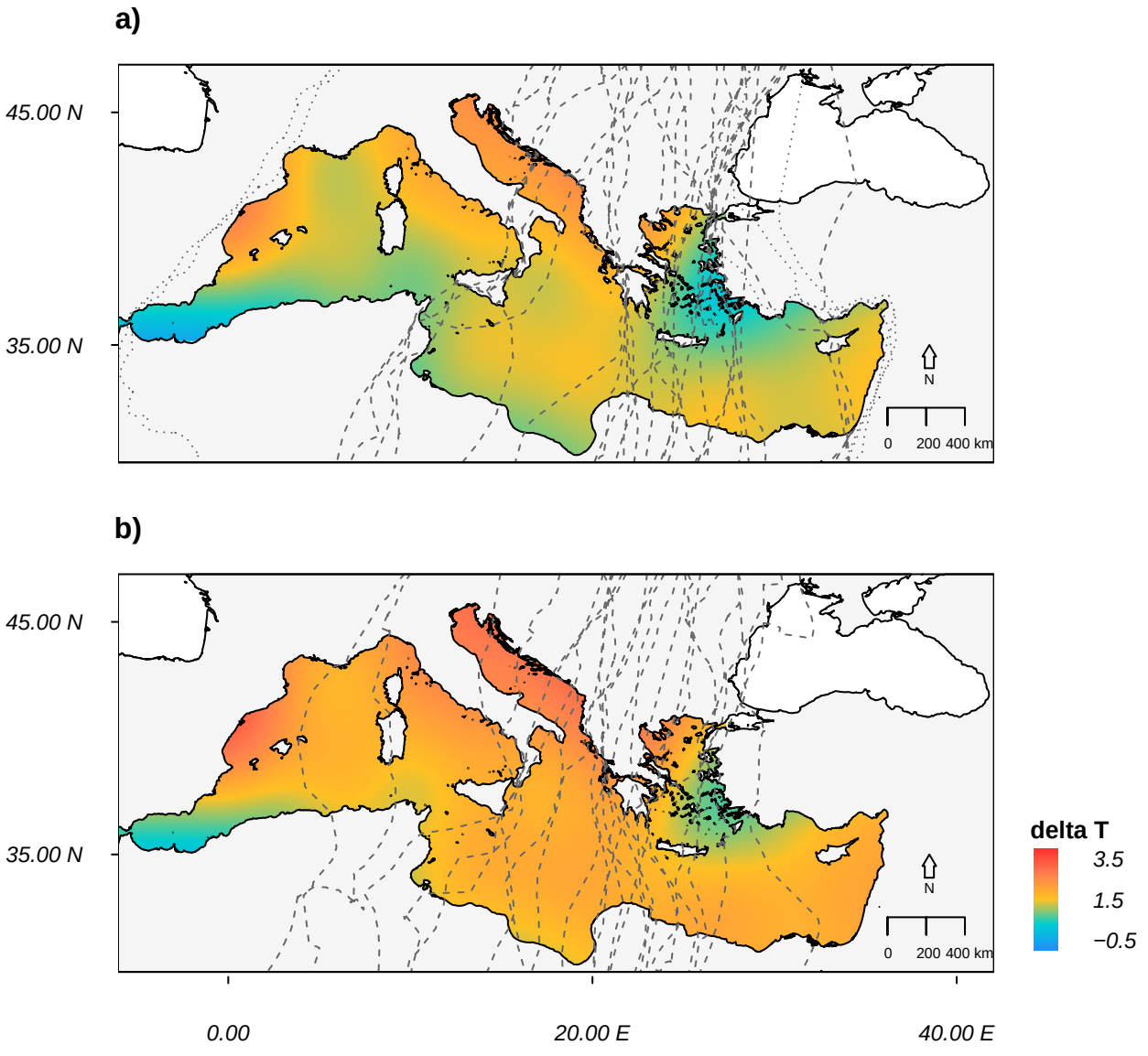
[1]Between-year standard deviation: 49.82; residual standard deviation: 162.90

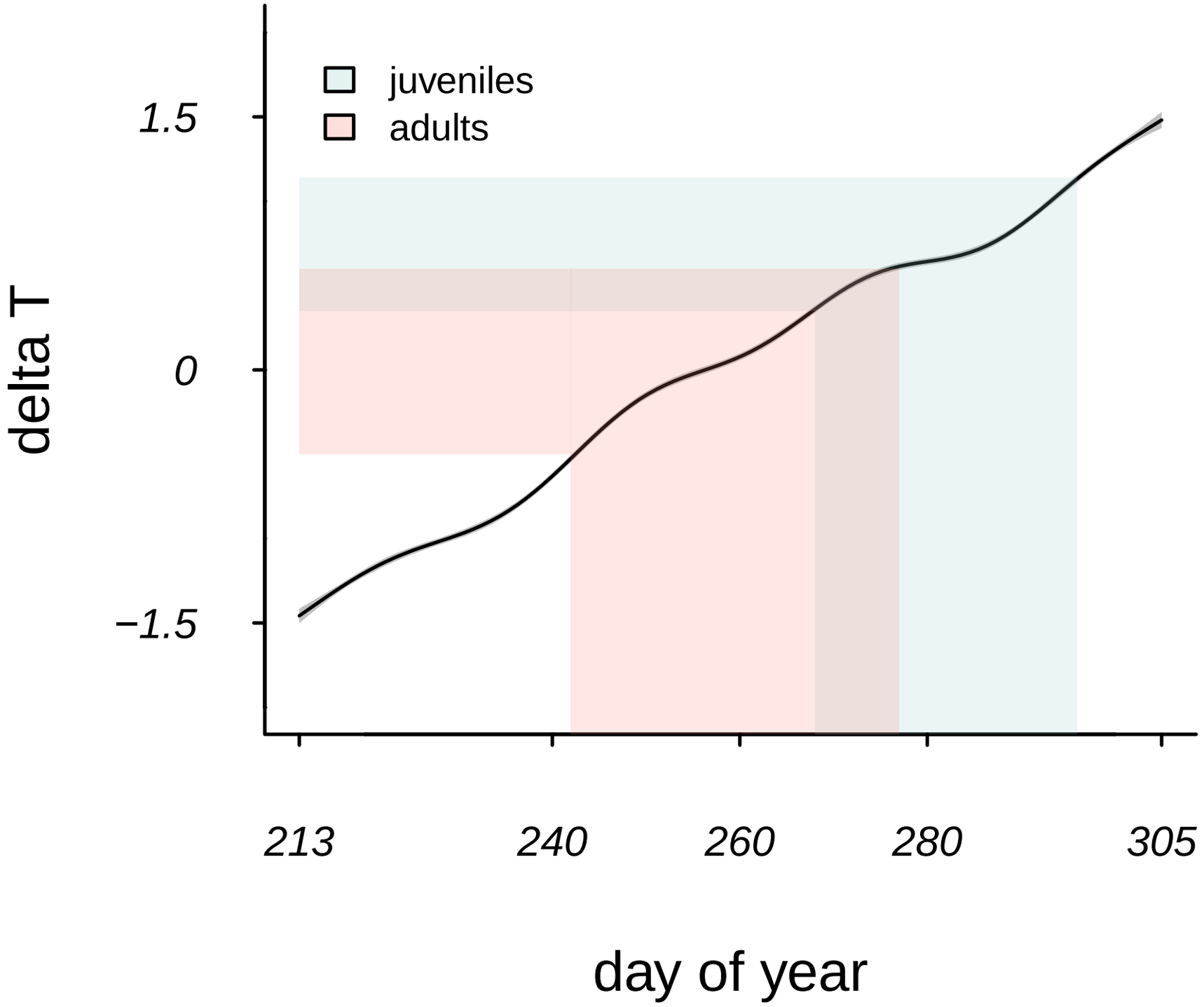
[2]Between-year standard deviation: 46.15; residual standard deviation: 158.50

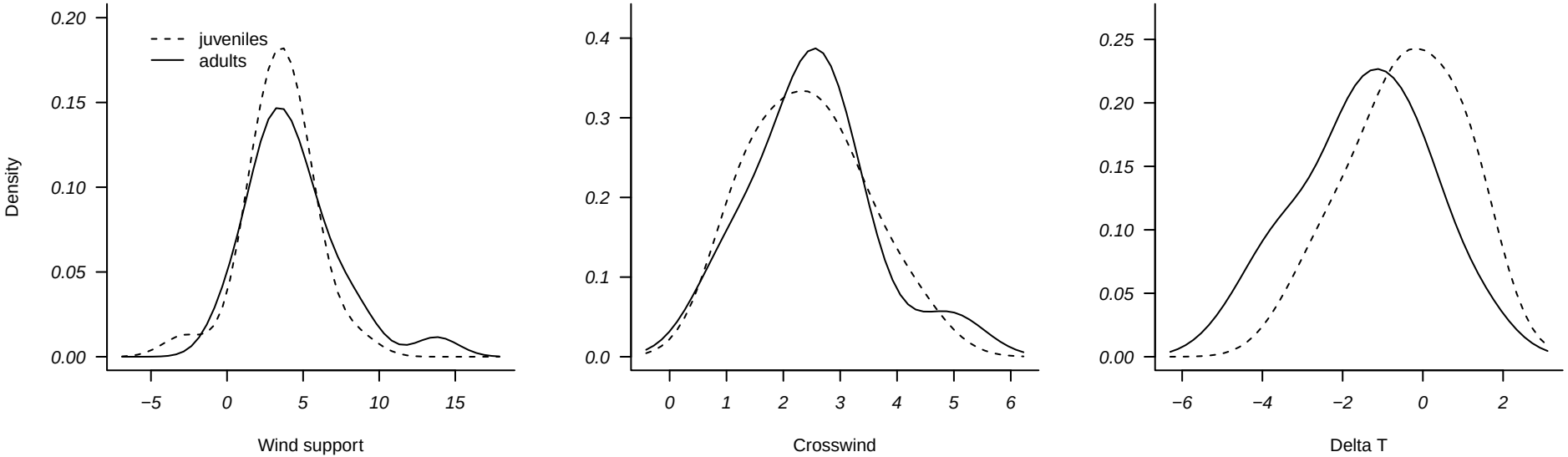
[3]Between-year standard deviation: 37.75; residual standard deviation: 150.93

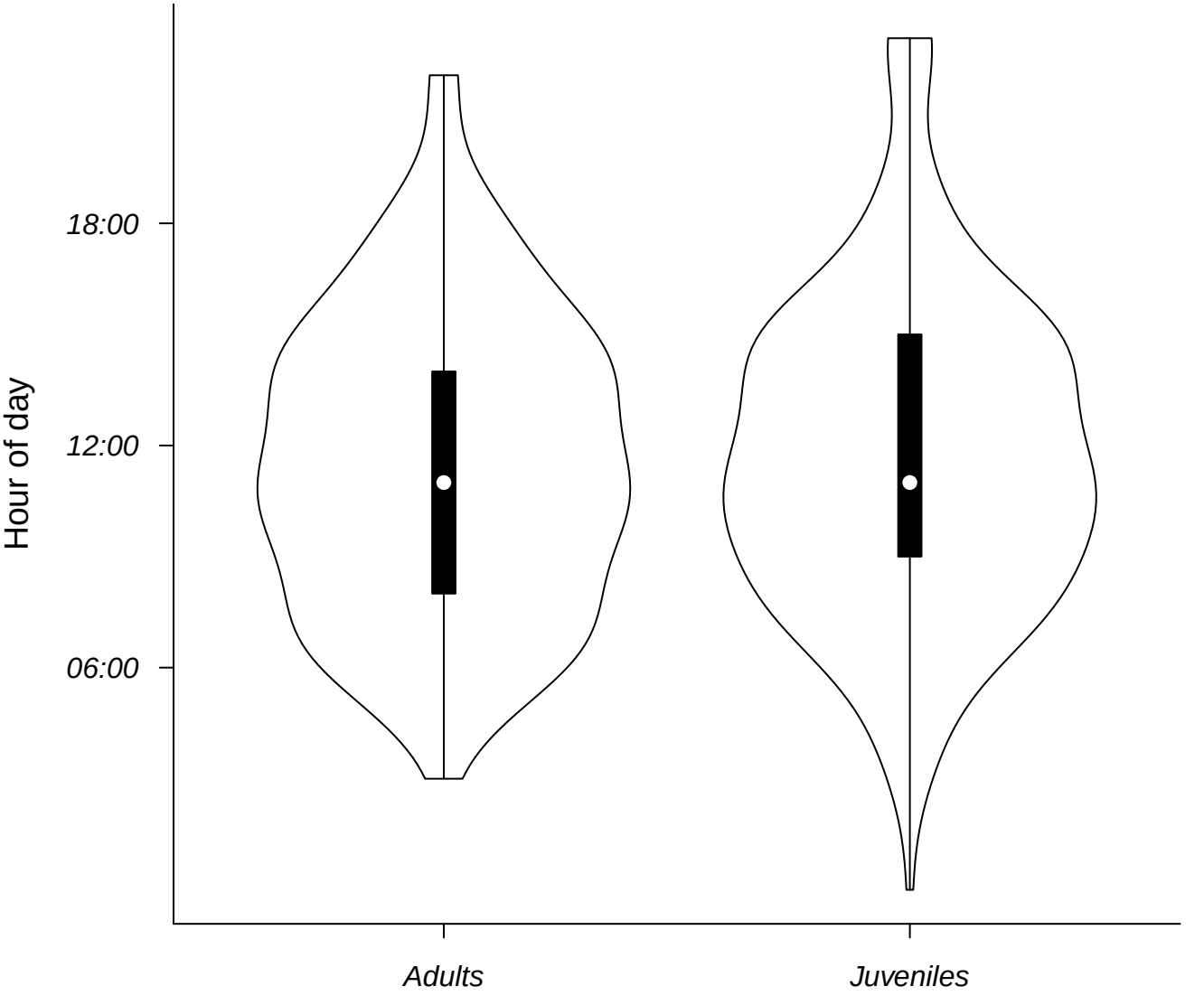
Table 2. Results of generalized additive model predicting temperature gradient as a function of longitude, latitude, Julian date, and hour. The model includes a 2-dimensional smooth term for longitude and latitude, a smooth term for Julian date, and a parametric term for hour as a factor.

Intercept (SE)	Parametric terms		Smooth terms				Adjusted R^2
	Term	Coefficient (SE)	Term	Effective df	F	*P*-value	
2.10 (0.001)	Hour 6	-0.40 (0.002)	S(lon,lat)	29.00	20841	< 0.001	0.50
	Hour 12	-3.43 (0.002)	S(Julian date)	9.00	197352	< 0.001	
	Hour 18	-1.43 (0.002)					


a)
45.00 N
35.00 N
N
0 200 400 km
b)
45.00 N
35.00 N
N
0 200 400 km
delta T
3.5
1.5
−0.5
0.00
20.00 E
40.00 E


juveniles
adults
1.5
0
−1.5
delta T
213
240
260
280
305
day of year


juveniles
adults
Density
0.20
0.15
0.10
0.05
0.00
−5
0
5
10
15
Wind support
0.4
0.3
0.2
0.1
0.0
0
1
2
3
4
5
6
Crosswind
0.25
0.20
0.15
0.10
0.05
0.00
−6
−4
−2
0
2
Delta T


Hour of day
18:00
12:00
06:00
Adults
Juveniles