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Animal behaviour

Migrating ospreys use thermal uplift over the open sea

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Most large raptors on migration avoid crossing the sea because of the lack of atmospheric convection over temperate seas. The osprey *Pandion haliaetus* is an exception among raptors, since it can fly over several hundred kilometres of open water. We equipped five juvenile ospreys with GPS-Accelerometer–Magnetometer loggers. All birds were able to find and use thermal uplift while crossing the Mediterranean Sea, on average 7.5 times per 100 km, and could reach altitudes of 900 m above the sea surface. Their climb rate was 1.6 times slower than over land, and birds kept flapping most of the time while circling in the thermals, indicating that convections cells were weaker than over land. The frequency of thermal soaring was correlated with the difference between the sea surface and air temperature, indicating that atmospheric convection occurred when surface waters were warmer than the overlaying air. These observations help explain the transoceanic cosmopolitan distribution of osprey, and question the widely held assumption that water bodies represent strict barriers for large raptors.

1. Introduction

Many large bird species have evolved a specialized morphology to optimize soaring–gliding flight, i.e. the use of ascending air currents to gain potential energy at a low cost, and then conversion of this potential energy into horizontal movement. Over land, ascending air currents are generated either by orographic uplift, when horizontal wind is deviated upwards by relief, or by atmospheric convection, when heterogeneities in the Earth's surface temperature generate rising hot air bubbles, called thermals [1]. At sea, orographic currents are totally absent and thermal currents are reportedly rare and weak [2]. This lack of ascending air currents at sea is often invoked to explain why large raptors (as defined by Newton [2]) perform long detours during their migratory trips, instead of crossing seas [2]. Larger raptors indeed quickly get exhausted when they have to sustain wing-flapping flight for a long time, and therefore run the risk of drowning when crossing sea [3]. However, there is evidence that atmospheric convection does occur over warm water [4], and evidence that this source of uplift is routinely used by some specialized tropical seabirds like frigatebirds [5], and, albeit less frequently, by temperate seabirds like gulls [4,6].

Among large raptors, the osprey *Pandion haliaetus* is an exception, in terms of phylogeny (family Pandionidae), morphology (slender wing-shape with

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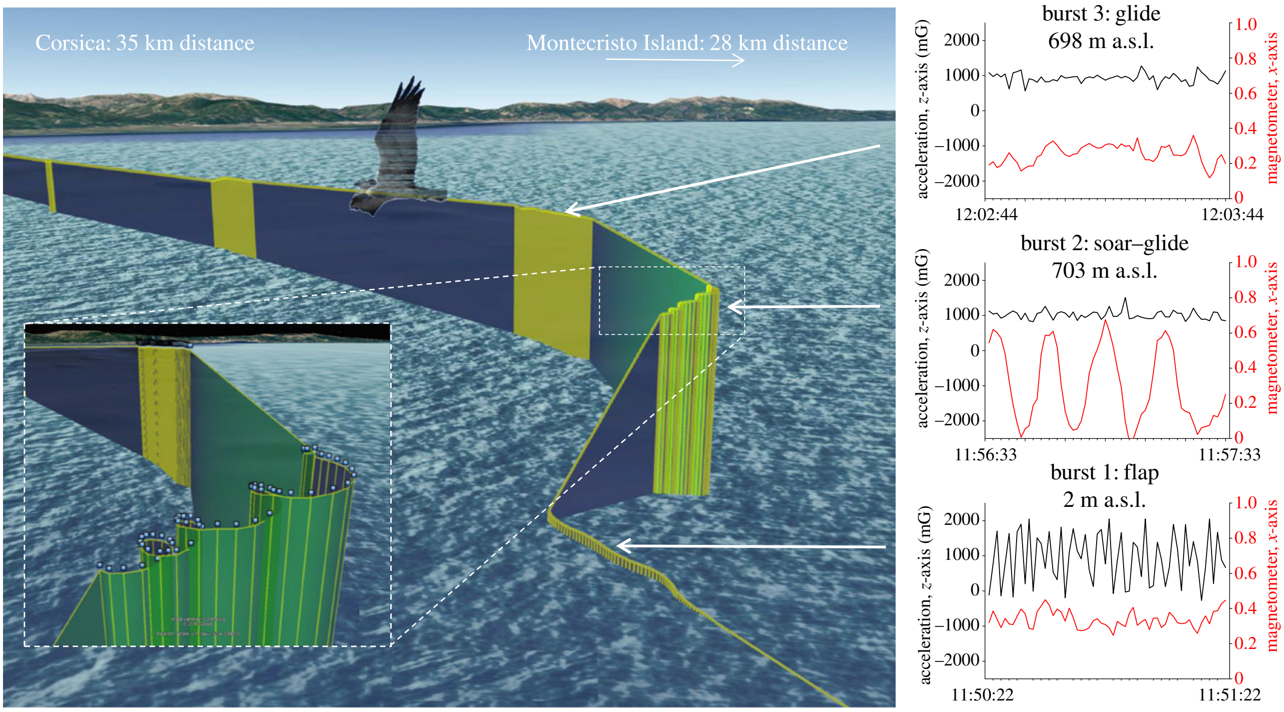

Figure 1. Three-dimensional view of a portion of migratory track of bird #A, crossing the Mediterranean between Italy (via Montecristo Island) and Corsica on 11 August 2017. The GPS tag was recording a GPS burst of 60 s at 1 Hz, followed by a pause of 5 min. The vertical yellow lines show the projection of the 3D track over the 2D plan. The inset shows the detail of a thermal soaring behaviour bout, revealed by a GPS burst where the position (dots) was recorded once per second. The spiral indicates that the thermal drifted to the north on the southerly wind. The panels on the right show the acceleration (*z*-axis, in black) and the magnetometer (*x*-axis, in red) signals for three GPS bursts, allowing the flight behaviour (strong oscillation on accelerometer indicates flapping flight for burst 1; oscillation for magnetometer and constant acceleration indicate soaring flight without flap for burst 2; constant signal on both sensors indicates gliding flight for burst 3) to be determined.

high aspect ratio between 8 and 9 similar to that of a seagull), piscivorous diet, migratory habit (can fly hundreds of kilometres over open sea [7–10]) and cosmopolitan transoceanic distribution [11]. As ospreys cannot land or float on the water, it is currently assumed that they wing-flap continuously during these sea crossings, and therefore require strong tail winds to help them perform long sea crossings [12]. Here we test the hypothesis that osprey may find and use thermal uplift at sea, which may explain their ability to perform these long sea crossings during migration, and ultimately how they were able to attain their remarkable cosmopolitan geographical distribution. We tracked the three-dimensional movements of five juvenile ospreys during their first autumn migration, with combined high-resolution GPS-accelerometer–magnetometer loggers, allowing us to clearly identify the different flight modes across the Mediterranean Sea [13,14].

2. Methods

We equipped five fledgling ospreys from Tuscany (Italy; 42°39′ N, 11°05′ E) [15]. Birds were caught in their nest one week before fledging (mean age of 52.3 days) and fitted with rings and backpack-mounted Ornitrack 25 units (Ornitela) [8].

In 2017, each unit was set to record GPS positions in 3D from dawn to dusk, with a burst of GPS positions at 1 Hz (1 fix per second) during 60 s, followed by a pause of 5 min (to limit excessive battery drain). During GPS bursts, the tracks are pre-processed by the GPS service, allowing high-accuracy positioning (Ornitrack manufacturer factsheet). The magnetometer and accelerometer sensors were set to record data at 1 Hz in synchrony with the GPS record during burst, and at 20 Hz during 20 s after each GPS burst. All data were remotely transmitted via the GSM network. In order to better understand the peculiarities of sea crossing, for each bird in 2017, we also used the same GPS and sensor settings during 1 or 2 full days of migratory flights over land, as a control.

In 2018, owing to battery problems, the same units were set in economy mode by recording GPS positions at 10 min fixed interval without sensor data, except when entering into 10 geofences pre-defined over the Mediterranean Sea, within which they used the same GPS and sensor high-resolution settings as in 2017, without time restriction, allowing recording also at night in case of nocturnal sea crossing. Therefore, in 2018, only portions of several hundred kilometres of the migratory tracks over sea were recorded, and no track over land.

For each track, we annotated all the 60 s GPS burst segments with one of five behavioural classes: perched, (linear) flapping, (linear) gliding, (thermal) soaring–gliding (i.e. soaring in circles without flapping wings), (thermal) soaring-flapping (i.e. soaring in circles with flapping wings) (figure 1, details in electronic supplementary material S1). We regressed the rate of thermal soaring against the difference between sea surface and air temperatures (ΔT) in a piecewise binomial linear model (details in electronic supplementary material S2).

3. Results

All five individuals performed a migratory trip above the Mediterranean Sea (range 184–712 km; figure 2*a–e*). 3D-GPS tracks revealed unambiguous evidence of thermal soaring over sea (figure 1). Birds used an average of 7.5 ± 4.9 (s.d.) thermals per 100 km of sea crossing, compared with 18.8 ± 5.5 thermals per 100 km over land (table 1), i.e. one thermal every 20.3 km at sea and every 6.4 km over land. Overall they spent 55% of time soaring over land and

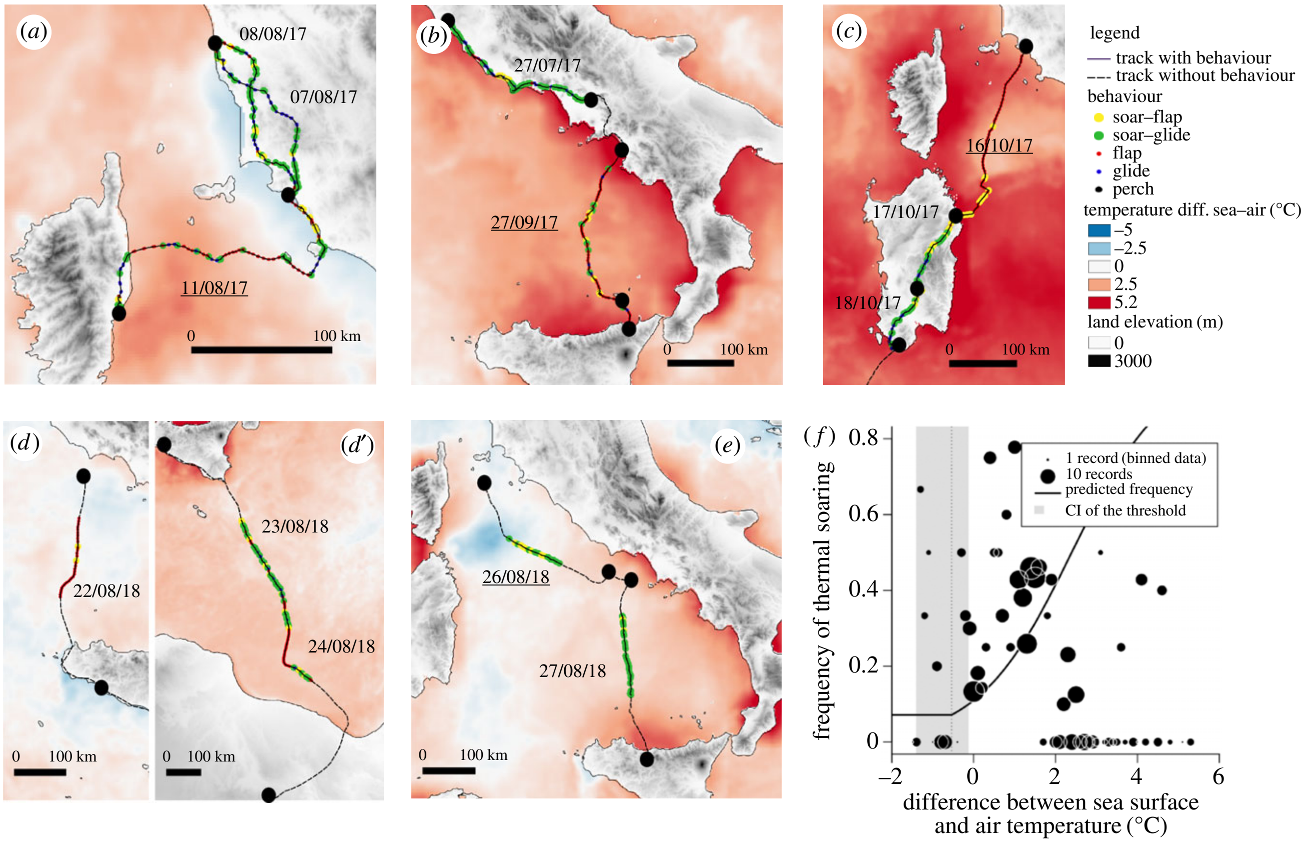

Figure 2. (*a–e*) The migration of five juvenile ospreys. The letter label of each panel corresponds to an individual described in table 1 (e.g., panel (*a*) shows the migration of bird #A). The solid and dashed lines indicate respectively parts of tracks recorded with behaviours (with GPS burst) and without behaviour (no GPS burst). Coloured dots indicate flight behaviour along the track. The background colour indicates the difference between sea surface and air temperatures (approximately at the time the middle of the journey at sea on the date underlined; the other dates correspond to other parts of the tracks described in table 1 without temperature map shown). Note that (*d*)′ shows a nocturnal journey (started at 17.00 in Sicily, with arrival in Libya at 12.00 on the following day). (*f*) Threshold binomial linear mode of the relationship between the frequency of thermal soaring and the difference between the sea surface and air temperature (dots correspond to 0.1°C bins, with the dot size representing the sample size in that bin).

32% at sea (30% by day and 39% at night). Interestingly, bird #D flew by night and still used thermal soaring–gliding flight over the sea, reaching an altitude of 183 ± 83 s.d. m on average (figure 2*d*′).

Ospreys kept flapping their wings 42% of the time when using thermal uplift at sea, versus only 24% when using thermal uplift over land (table 1). The average climb rate was 1.6 times lower in thermals over sea than over land (table 1). Mean flight height was 200 m lower at sea than over land (table 1). In thermals, ospreys reached on average altitudes of 237 m at sea (maximum 899 m) and 333 m over land (maximum 1974 m) (table 1). The frequency of thermal soaring increased as soon as the sea became warmer than the air (figure 2*f*). The frequency of thermal soaring reached a predicted 46% when the sea was 3°C warmer than the air (prediction standard error: 44%).

4. Discussion

This study is the first to directly demonstrate the use of thermal uplift at sea by a raptor. All five juvenile ospreys used thermal uplift at sea when the conditions of temperature were suitable. We recorded the same behaviour in two different years, confirming that thermal soaring at sea is not an anecdotal behaviour. Our results complement previous studies that showed ospreys exploiting tailwinds whenever available, but also efficiently migrating in their absence [9,16], which overall showcases the osprey as a versatile flyer, able to take advantage of a range of available resources when flying over sea.

Our results should indeed not be interpreted as evidence that osprey need thermal uplift to successfully migrate over sea. Indeed, in 2017, with and without thermals, ospreys flapped almost constantly while at sea, i.e. they kept expending muscular energy even in thermals. We therefore suggest that the function of thermal soaring might be to gain altitude for safety, rather than for energy. However the 2018 data showed that birds could in some conditions stop flapping for extended periods of time, at least in the context of strong crosswinds (as evidenced by strongly drifted thermals, see electronic supplementary material S3). Crosswinds may increase the efficiency of soaring–gliding flight like for dynamic soaring seabirds [17].

Beyond raptors, Woodcock [4] observed gulls performing thermal soaring above temperate seas, but only if sea surface temperature exceeded air temperature by at least 2°C. Our results confirm and further formalize this observation, with a threshold analysis indicating that atmospheric convection may occur for even smaller air/water temperature gradients. The unexpected use of thermals at night by bird #D can then be explained by the different dynamics of air and sea temperatures after sunset, thus favouring a positive sea–air temperature difference.

In conclusion, these exciting new observations help explain how the osprey was able to expand into a cosmopolitan

Table 1. Comparisons between flight metrics during successful sea crossings and when flying over land. Chi-square and Mann–Whitney *U*-tests of the difference between behaviours at sea and over land were performed on the pooled data from all birds. Means are presented ± s.d., with range in parentheses.

	successful migration at sea						migration over land				
	#A	#B	#C	#D	#E	mean ± s.d.	#A	#B	#C	mean ± s.d.	test
date	11 Aug 2017	27 Sep 2017	16 Oct 2017	22, 23, 24 Aug 2018	26, 27 Aug 2018		7, 8 Aug 2017	27 July 2017	17, 18 Oct 2017		
total distance covered (km)	183.5	261.9	284.1	712.8	277.9		407.9	294.3	307.5		
total time in flight (h:min)	05:14	07:21	07:09	17:06	06:20		16:18	08:28	12:08		
sample size (no. GPS burst segments)	60	71	69	170	64		119	85	122		
total no. thermals	11	13	13	58	45		72	46	61		
no. thermals per 100 km	4.9	4.9	4.6	7.0	16.2	7.53 ± 4.95[a]	22.6	11.8	19.6	18.8 ± 5.5[a]	
% time in thermals	18.3	18.3	18.8	29.1	77.7	32.4 ± 25.7[b]	60.5	54.1	50.0	54.9 ± 5.3[b]	$\chi^2_1 = 39.2$, $p < 0.001$
% time in flapping bouts (linear + thermals)	68.3	85.9	100	68.4	28.7	70.3 ± 26.7[b]	26.1	18.8	31.1	25.3 ± 6.2[b]	$\chi^2_1 = 122.3$, $p < 0.001$
(thermals only)	18.2	46.1	100	22.4	22.2	41.8 ± 34.4[c]	26.4	15.2	27.9	23.4 ± 6.9[c]	$\chi^2_1 = 2.17$, $p = 0.141$
mean flight height (m a.s.l.)	244 ± 252 (−2–899)	168 ± 137 (−7–592)	91 ± 68 (−9–256)	136 ± 123 (−7–536)	322 ± 180 (92–868)	176 ± 169[b]	459 ± 485 (−16–1974)	198 ± 163 (−45–915)	384 ± 316 (17–1694)	363 ± 375[b]	$U = 46472$, $p < 0.001$
mean flight height in thermals (m a.s.l.)	308 ± 261 (68–899)	185 ± 93 (89–592)	117 ± 60 (24–256)	213 ± 101 (47–536)	301 ± 161 (92–868)	237 ± 148[c]	398 ± 450 (68–1974)	214 ± 180 (−45–915)	346 ± 266 (35–1694)	333 ± 344[c]	$U = 11526.0$, $p = 0.219$
mean climb rate in thermals (m min^{-1})	63.9 ± 48.4 (8–157)	48.3 ± 29.9 (14–97)	31.9 ± 17.8 (9–59)	55.5 ± 42.6 (10–178)	46.0 ± 36.1 (7–157)	47.9 ± 11.3[c]	79.5 ± 66.8 (0–250)	74.9 ± 50.4 (0–228)	67.7 ± 40.7 (5–181)	74.3 ± 54.8[c]	$U = 8962.0$, $p < 0.001$

[a]Mean over individuals ($N = 3$ over land and $N = 5$ at sea). [b]Mean over total number of GPS bursts ($N = 434$ at sea and $N = 326$ over land; total = 760 bursts). [c]Mean over total number of thermals ($N = 140$ at sea and $N = 179$ over land; total = 319 bursts).

transoceanic distribution and question the relative importance of physiological and behavioural determinants for ecological barriers to animal migration.

Ethics. Captures were carried out by Istituto Nazionale per la Protezione e la Ricerca Ambientale (ISPRA) under the authorization of Law 157/1992 [Art. 4 (1) and Art. 7 (5)] and under authorization no. 2502 05.05.2016 and no. 4254 27.03.2018 issued by Regione Toscana.

Data accessibility. All GPS tracks are available at www.movebank.org (study 'Osprey in the Mediterranean').

Authors' contributions. O.D. and D.G. initiated the study; F.M. and A.S. did the fieldwork; O.D. and G.P. analysed the data; all authors wrote the paper. All authors approve the final version of the manuscript and they agree to be held accountable for the work performed.

Competing interests. We declare we have no competing interests.

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Electronic Supplementary Material: Migrating ospreys use thermal uplift over the open sea

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ESM 1: details of behaviour classification methods

For each 60-second GPS burst, we first inspected the data visually on 3D maps proposed by the Google Earth program. The high accuracy and high resolution of the burst datasets made it easy to detect, with the naked eye, any circling and ascending behaviour (indicating thermal soaring). For a more formal and systematic behavioural state assignation, we then used the sensor analysis software Framework4, available from http://www.framework4.co.uk [1]. From the groundspeed variable, we identified flight vs perched behaviour. From the height above mean-sea-level, we identified ascending flight, level flight, or descending flight. From the 3-axis accelerometer data, we identified flapping bouts (strong oscillations in vertical z-axis), gliding bouts (smooth in vertical z-axis), and perched bouts (no movement detected on any axis) (Fig. 1). The full detail of this procedure is provided by Williams et al [2]. From the 3-axis magnetometer data, we identified linear movement (no change in any axis), and circling movement (strong oscillations in the horizontal plane indicating that heading took all directions on a 360° trigonometric circle) [3] (Fig. 1).

We then further simplified the output of the above procedure, by manually annotating all the segments of each track with just one of 5 behavioural classes: perched, (linear) flapping, (linear) gliding, (thermal) soaring-gliding (i.e. soaring in circles without flapping wings), (thermal) soaring-flapping (i.e. soaring in circles with flapping wings). Each behaviour annotated by Framework was visually cross-checked with Q-GIS v.2.18. There were never more than two behaviours per segment. For the sake of simplicity in the subsequent analyses, we annotated only one behaviour for each segment, taking the behaviour that lasted longer (>30 s) as reference (e.g. of the 60 s segment was composed 20 s of glide and 40 s of soaring-flapping, we retained the second behaviour). Only in case of segment encompassing perched and flight behaviour we split the segment in two parts and did not considered the segment in the analyses.

For each segment, we also calculated the average flight height by subtracting the altitude recorded by the logger and the ground or sea altitude given by a reference Digital Elevation Model (ASTER DEM, 1 arc-second spatial resolution) obtained via the Movebank Env-DATA track annotation service

[4]. We calculated the climb rate as the difference between the maximal and minimal heights above sea level of the segment.

ESM 2: details of environmental covariates analyses

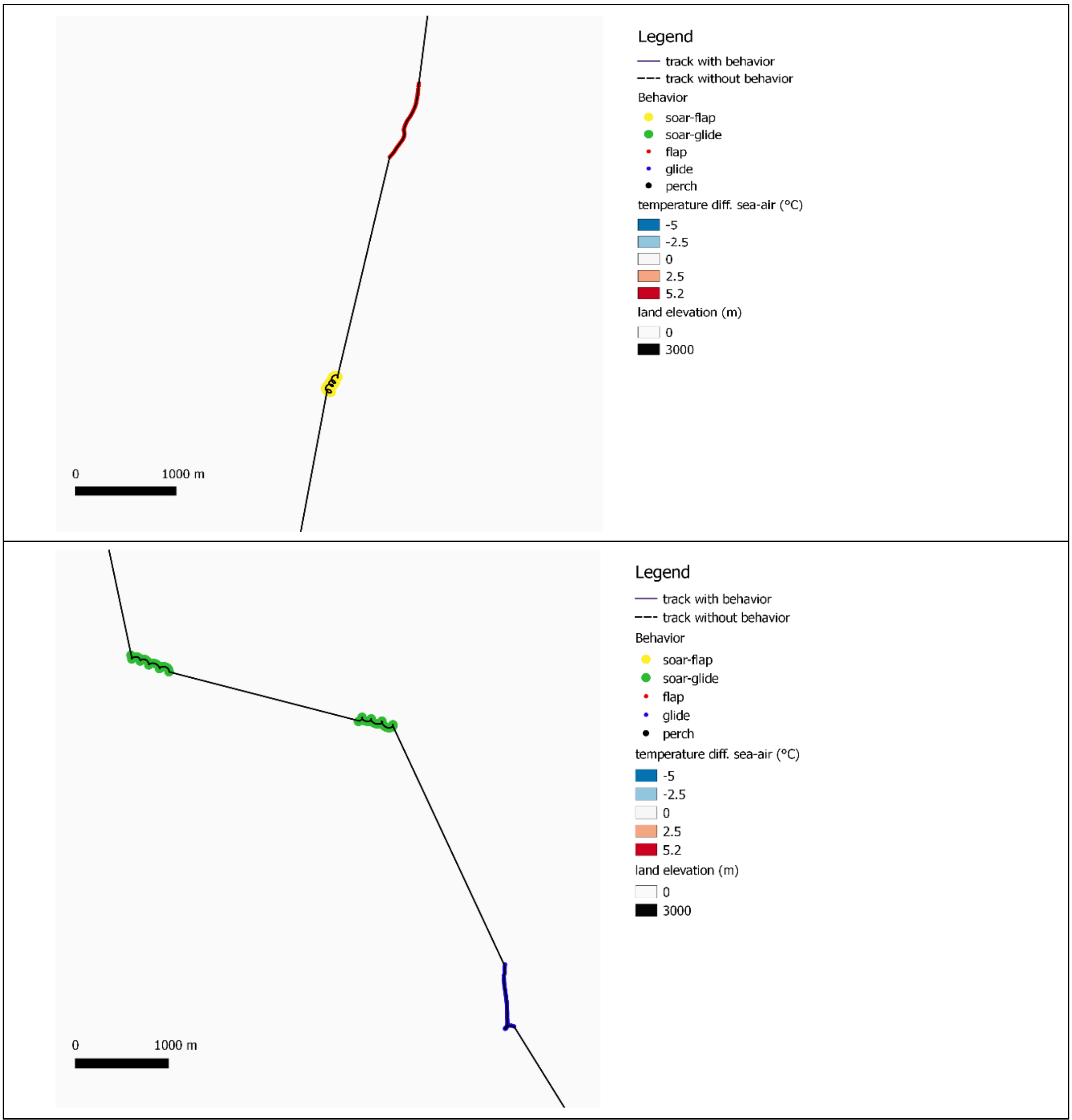
We used remote-sensed sea-surface temperature data for the Mediterranean Sea, generated daily at a 0.02° resolution, from http://cersat.ifremer.fr/thematic-portals/projects/medspiration. We choose these data, rather than the global forecasts that are available via the Movebank Env-DATA service, because their spatial resolution was much finer. We also downloaded forecasted air temperatures for the 2 m layer above the sea from http://apps.ecmwf.int/datasets/data/tigge/levtype=sfc/type=cf/ [5]. These forecasts are generated from a global network of weather stations, four times daily at a 0.5° resolution.

We regressed the rate of thermal soaring against the difference between sea surface and air temperatures (ΔT) in a binomial linear model. We allowed the relationship to adopt a piecewise shape by successively fitting models with incremental 0.2°C increases in threshold value, thereby obtaining the maximum-likelihood threshold value and its model-averaged confidence interval. We also compared the fit of models without threshold or without effect of ΔT.

As a side note, we could not apply the same approach to study the link between wind and the frequency of thermal soaring because of major inconsistencies between different datasets of wind speed and direction. At many instances, the true wind direction evidenced by obvious wind drift in thermals (as shown in fig 1 and ESM 3) did not match with the wind direction forecasted by large-scale maps of wind directions and strength by ECMWF and interpolated by Movebank Env-Data. Therefore it was not possible to estimate reliable wind assistance in the Mediterranean sea context (perhaps because winds change direction very quickly, typically within an hour while weather maps provide wind estimates for 6-h time windows). In addition, although we could have estimate wind speed and direction using bird drift in thermals [6], such estimate was not possible for migration bouts where birds were only using linear flapping flight.

ESM 3: effects of strong winds on thermal soaring behaviour.

Two extracts of GPS-burst segments of 60 seconds (separated by 5 min intervals without recording) of the flight of bird D. On the top panel, on 22 Aug 2018 in the morning, under moderate tailwind, the bird traveling south first performs a flapping bout (in red) and then a soaring-flapping bout (in yellow) with regular circles. This sequence was repeated several times during the monitored time period. In the bottom panel, on 23 Aug 2018 at night, under strong crosswind (orientated eastward), the bird traveling south alternates between soaring-gliding bouts (in green) with distorted circles, and gliding bouts (in blue). This suggests that crosswinds either suppressed the benefit of flapping while in thermal, or could be used by the bird to increase its uplift thereby making flapping unnecessary.



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