BRIEF REPORT



Against the flow: unexpected migration movements over the open sea by inexperienced ospreys

Flavio Monti^{1,3} · Giampiero Sammuri² · Francesco Montillo³ · Olivier Duriez⁴ · Andrea Sforzi³

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Abstract

As part of a long-term monitoring program, more than 80 Mediterranean ospreys *Pandion haliaetus* (both adults and juveniles) were tagged with GPS-GSM transmitters and tracked to study their spatiotemporal behaviour. Here we document the peculiar and unexpected migration movements performed by three inexperienced (juvenile/immature) individuals, who crossed the open sea "*against the flow*", in the opposite direction to that foreseen for the given season. Using a combination of GPS tracking data and weather information, we found that such movements were linked to particular meteorological conditions occurring over the Mediterranean Sea during migration. Mean values of wind gust of approximately 20 km/h and moderate tailwinds seem to have mediated the onset of the movements, facilitating the flight of ospreys over water. Our findings suggest that both weather conditions (sidewinds) and the inexperience of the birds explain these long migration movements performed towards unexpected directions over the open sea. We conclude that migratory capabilities and the ability to cope with external conditions may lead inexperienced birds to perform extensive and tortuous dispersal/explotrative movements during both first autumn and spring migration.

Keywords Migration · Ecological barriers · Pandion haliaetus · Raptor · Sea · Wind

Introduction

During the migratory periods, birds can adjust the spatial and temporal schedules of their migratory journeys to minimize energy consumption and thus enhance their chances of survival. However, it requires the possessing of enhanced flight skills and knowledge, in order to cope with factors which may potentially have important effects on travelling performances (Sergio et al. 2014). Different possible proximate causes, both internal and external, can in fact affect flight performance and migratory components (Newton

Flavio Monti flaviomonti00@gmail.com

- ¹ Department of Physical Sciences, Earth and Environment, University of Siena, Via Mattioli 4, 53100 Siena, Italy
- ² Federparchi, Via Nazionale 230, 00184 Rome, Italy
- ³ Maremma Natural History Museum, Strada Corsini 5, 58100 Grosseto, Italy
- ⁴ CEFE, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry Montpellier 3, Montpellier, France

2010). Internal causes are mainly associated to the age of the bird and to its actual physiological state. Generally, adult birds are known to perform better than juveniles at selecting favourable winds and locating thermal currents (Hake et al. 2003; Harel et al. 2016; Chiatante et al. 2022), showing greater daily travel speeds and straightness of the tracks (Monti et al. 2018a). In contrast, juveniles are known to be less efficient foragers (hence carrying limited fat reserves) and less experienced flyers compared to adults (Harel et al. 2016; Rotics et al. 2016; Flack et al. 2018), often resulting in a greater variance of the migratory components.

Among external causes, weather is one of the main factors affecting the migratory behaviour of birds (e.g. Literák et al. 2021). Unclement weather conditions, such as fog and rain, have been demonstrated to reduce visibility and ultimately affect directional choices (e.g. Newton 2007; Pastorino et al. 2017; Becciu et al. 2021). In addition to that, adverse wind direction and speed can considerably impair migratory flights, making birds reluctant to proceed with the journey (e.g. Klaassen et al. 2011). In other cases, birds made long detours in order to bypass such unfavourable conditions. Before facing a risky flight stage, birds hence reorient their

migration flight in order to find suitable places to rest and refuel (Alerstam 1978, 1979). That way, birds reduced mortality risks associated with the unfavourable external conditions (Newton 2007; Klaassen et al. 2014). However, in case of unstable atmospheric conditions encountered en route, birds may risk to become at the mercy of unfavorable winds, and involuntarily to be dragged far from their normal route (e.g. Dinsmore and Farnworth 2006; Newton 2010). This is especially true for inexperienced birds commonly drifted by crosswinds, compared to adults who instead are able to more efficiently modulate their response at different places and times during their travels (e.g. compensation or overcompensation behaviour; Klaassen et al. 2011).

Similarly, the presence of physical barriers (e.g. desert and open water) can make birds reluctant to cross or cause side effects during the crossing (e.g. Strandberg et al. 2010; Mellone et al. 2015). For example, raptors migrating over the Sahara desert have shown a high percentage of aberrant behaviours including abrupt course changes, interruptions, failed or aborted crossings followed by retreats (Strandberg et al. 2010). Similarly, flying over the open sea is energetically costly for land birds (Nourani et al. 2021). Having such an ecological barrier ahead could promote movements in other directions, in order to search for a better spot for crossing the barrier or for bypassing it. In the case of large soaring birds like raptors and storks, the success of migration relies on their ability to exploit thermal and orographic updrafts, to reduce energy expenditure during protracted flights (Pennycuick 1975). The morphology and body mass of these birds prevent them to use a constant flapping (powered) flight for long distances (Newton 2008; Agostini et al. 2015), especially over the open water, where thermal updrafts are generally much weaker than over land (Duriez et al. 2018; Nourani et al. 2021). This is the reason for which heavier and broad winged raptors are obligate soarers congregating at strategic points (bottlenecks) to reduce the distance to be covered over water (Agostini et al. 2016, 2022; Panuccio et al. 2016; Premuda et al. 2015). For instance, short-toed snake eagles Circaetus gallicus breeding in southern Italy and Greece have evolved a peculiar migration strategy which entails long detours across southern Europe for crossing the Mediterranean Sea at its narrower points (ca 14 km), the Strait of Gibraltar and the Bosphorus, respectively (Panuccio et al. 2012).

The osprey *Pandion haliaetus* is a peculiar raptor that feeds exclusively on fishes. Thanks to its morphological characteristics that limit the energetic cost of flapping flight (Agostini et al. 2015; Monti 2021) the species usually migrate on a broad front, undertaking sea crossings of hundreds of kilometres. In addition, the osprey is also able to exploit the weak thermals that form over water further limiting the energetic cost during long sea-crossings (Duriez et al. 2018). Ospreys breeding at temperate latitudes, such as those of the Mediterranean region, are mostly sedentary or short-distance migrants and show a higher variability in migratory strategies compared to Central-Northern European conspecifics, both in terms of route choice and main direction followed (Hake et al. 2001; Monti et al. 2018a, b; Monti 2021), including large migratory bouts over the open sea. Previous studies have investigated daily movements of migrating Mediterranean ospreys and their sea-crossing performances in relation to wind data (e.g. speed, altitudes; Monti et al. 2018a; Duriez et al. 2018).

Here we document for the first time unexpected cases of migration movements over the open sea performed "against the flow" (i.e. in the opposite direction to that foreseen for the given season) by three juvenile/immature Mediterranean ospreys. By coupling GPS tracking data with weather information, we describe the characteristics and likely causes of these long unexpected migration movements. These specific cases are of considerable interest and inform on the relative importance of individual's behavioural determinants for crossing ecological barriers and coping with atmospheric conditions during migration.

Methods

As part of a long-term monitoring program applied to the conservation of the species in the Mediterranean region, 88 both adult and juvenile ospreys were trapped at their nests in mainland Italy; Corsica and Balearic islands. They were measured, marked with both a metal ring and a coloured darvic ring with an alpha-numeric code and sexed through DNA analyses on samples extracted from the feathers (Griffiths et al. 1998). In this study, we refer only to the tracks of 3 juvenile/ immature individuals who performed peculiar migratory movements. Two individuals carried 24 g solar powered GPS/ GSM devices (model Duck-4, Ecotone, Poland) that provided latitude and longitude data at hourly interval (without altitude or speed). The third individual (#IBH) carried 25 g solar powered GPS/GSM devices (model Ornitrack-25, Ornitela, Lithuania) that provided data at a 5-min interval, including additional data (altitude, groundspeed, accelerometer and magnetometer; see sampling protocol described in Duriez et al. (2018)). The dataset from this latter bird was sub-sampled at 1 fix per hour, to be compared with the other two individuals for the purposes of this work (Appendix). Both types of tags were programmed to collect GPS fixes between 05:00 and 21:00, the time range in which most large soaring raptors migrate (Mellone et al. 2012). The tag was attached by mean of backpacks with a harness made of 7-mm-wide Teflon ribbon (Kenward et al. 2001; Anderson et al. 2020). The combined mass of the tracking device and harness was under the 1.5% of the birds' body mass.

All GPS data analysed in this study have been uploaded in the Movebank database (www.movebank.org), under the project study named "Osprey in Mediterranean (Corsica, Italy, Balearics) — movement study ID: 20,039,459". To define migratory periods (autumn and spring), natal and breeding areas as well as wintering areas, we referred to Monti et al. (2018a, b), as these 3 individuals belong to the same Mediterranean population whose migratory and wintering strategies have been already described in detail. All GPS locations were imported into QGIS (v. 3.6.1) and projected to the Universal Transverse Mercator (UTM) coordinate system for all spatial analyses and for generating maps and figures.

For these birds, annotated dataset of atmospheric conditions at 0.25° resolution were gathered from the Environmental Data Automated Track Annotation System (Env-DATA; Dodge et al. 2013) in Movebank (movebank.org). Since we were mainly interested in obtaining information on the factors that favoured the initiation of these movements, we selected the following variables: (i) ECMWF ERA5 SL 10 Metre Wind Gust, representing the maximum wind gust at a height of 10 m above the surface of the Earth; wind gust is defined as the maximum value of the 3-s running average wind speed, then deduced by the ECMWF Integrated Forecasting System (IFS) (for details see Env-DATA; Dodge et al. 2013); (ii) ECMWF ERA5 SL Wind (10 m above Ground U Component), representing the velocity of the east-west (zonal) component of wind at 10 m above the surface of the Earth. Positive values indicate flow from west to east; (iii) ECMWF ERA5 SL Wind (10 m above Ground V Component), representing the velocity of the north-south (meridional) component of wind at 10 m above the surface of the Earth. Positive values indicate flow from south to north; (iv-v) U and V components were estimated at 100 m above ground (ECMWF ERA5 SL Wind 100 m above Ground U and V Components). The two parameters (U and V components) were combined to obtain the speed and direction of the horizontal wind, both at 10 m and 100 m a.g.l. Speed was expressed in km/h and the direction (in degrees) with respect to true north (0 = north,90 = east, 180 = south, 270 = west) that the wind is coming from. Extracted wind data, despite not encompassing the full range of altitudes covered by migrating ospreys over water (Kerlinger 1989; Duriez et al. 2018), are informative and describe the external conditions encountered especially at the onset of these movements.

Results

Three juvenile/immature ospreys performed long migration movements over the open sea, in the opposite direction to that foreseen for the given season (Figs. 1, 2 and 3). The first one concerns a first calendar-year individual belonging to the Italian population during the 2020 autumn migration. The other two have been carried out during the first spring migration in 2022 and 2015 by second calendar-year individuals, respectively belonging to the Italian and the Balearic population. Such "*against the flow*" movements were linked to particular meteorological conditions over the Mediterranean Sea occurring during migration. Results gathered by coupling metereological information and GPS tracking data are reported for each bird (Appendix).

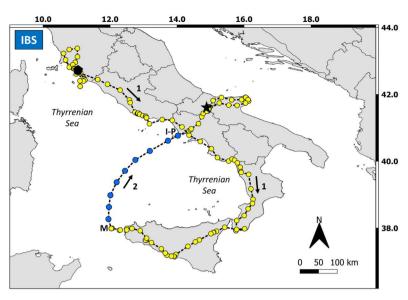
#IBS

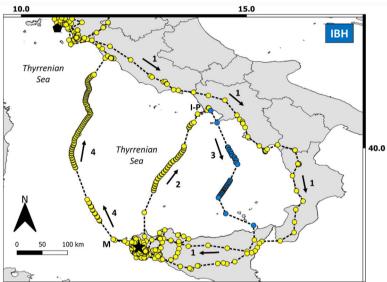
The bird was ringed and equipped with a GPS device on the 12/06/2020 at its nest in the Maremma Regional Park (Tuscany, Central Italy). The autumn migration started on the 07/08/2020 at 10:00. (Fig. 1). The bird left the natal area and followed a coastal route southward, along the Italian peninsula up to Calabria. Then, it reached Sicily by crossing the Strait of Messina. Once in Sicily, the bird moved first to Lake Arancio, an inland freshwater water body, where it spent the day on the 13th of August. On the morning of the 14th, it moved to the coastal area of Trapani and from here to the islands of Favignana first and then Marettimo, where it spent the night. At the early morning (7:04) of the 15th of August, the bird resumed its migration by crossing the open sea towards North. The onset of such "against the flow" migration movement was mediated by a wind gust (i.e. the maximum of the wind averaged over 3-s intervals) of up to 20 km/h and by moderate south-westerly winds (16.08 km/h wind at 10 m a.g.l and 18.68 km/h wind at 100 m a.g.l) that facilitated the osprey moving northward, far away from the Marettimo island. Wind conditions encountered en route during sea crossing show that the bird was slightly drifted by moderate western winds (Figs. 2 and 3), which strengthened since 12:00. That way, the bird flew continuously for nine hours over the open sea, until it reached Ischia and Procida islands (Campania region) at around 16:00. The sea-crossing was 414.5 km long and was covered at an average speed of 46.05 km/h. From Ischia and Procida islands, it headed mainland Italy and continued its migration until it reached Lake Occhito, in the Molise region, on the 17/08/2020 (Fig. 1). Here it spent its first winter months, from September to mid-January.

#IBH

The bird was ringed and equipped with a GPS device on the 12/06/2020 at its nest in Diaccia Botrona Nature Reserve (Tuscany, Central Italy). After some brief explorations in the surroundings of the nest, it left the natal area for the autumn migration on the 09/08/2020, following a Southward route along the Italian west coast, and it reached Sicily on the 13/09/2020, where it spent the wintering period at the Trinity Lake. The bird started its first spring migration at the

Fig. 1 Movements of Mediterranean ospreys are indicated by dotted lines and coloured circles. Blue circles indicate unexpected migration movements over the open sea, while yellow ones includes all other movements. The black hexagon is for the nesting area from which the birds departed. The black star indicates the wintering ground. Black arrows and numbers suggest the direction and sequence of movements. IBS: first calendar year osprey migrating during summer 2020 with unexpected migration movement conducted on the 15/08/2020 (M is for Marettimo island, while I-P is for Ischia and Procida islands). IBH: second calendar year osprey at first spring migration during April 2022 and unexpected migration movement conducted on the 10/04/2015. H7: second calendar year osprey at first spring migration during April 2015 and unexpected migration movement conducted on the 08/04/2015-09/04/2015. Movement details are reported in the text





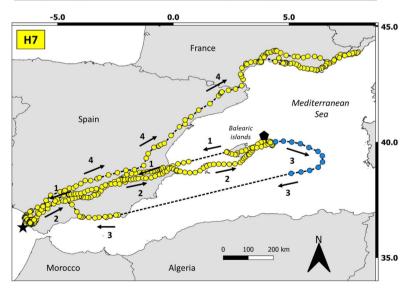
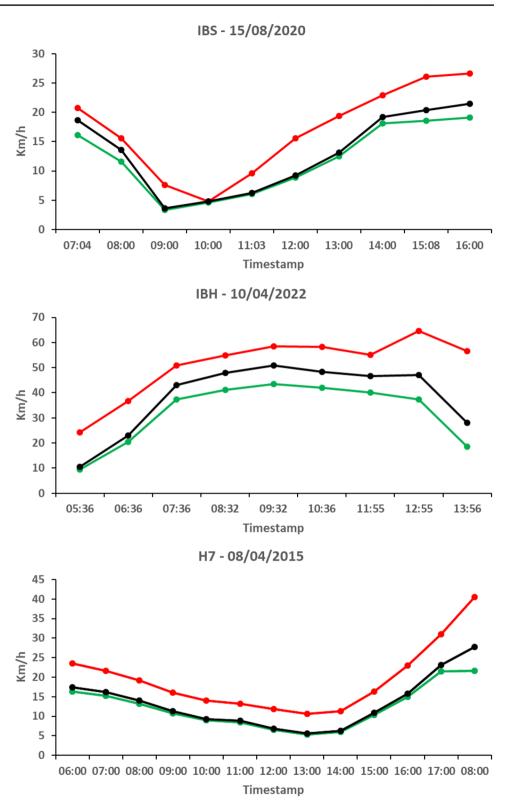
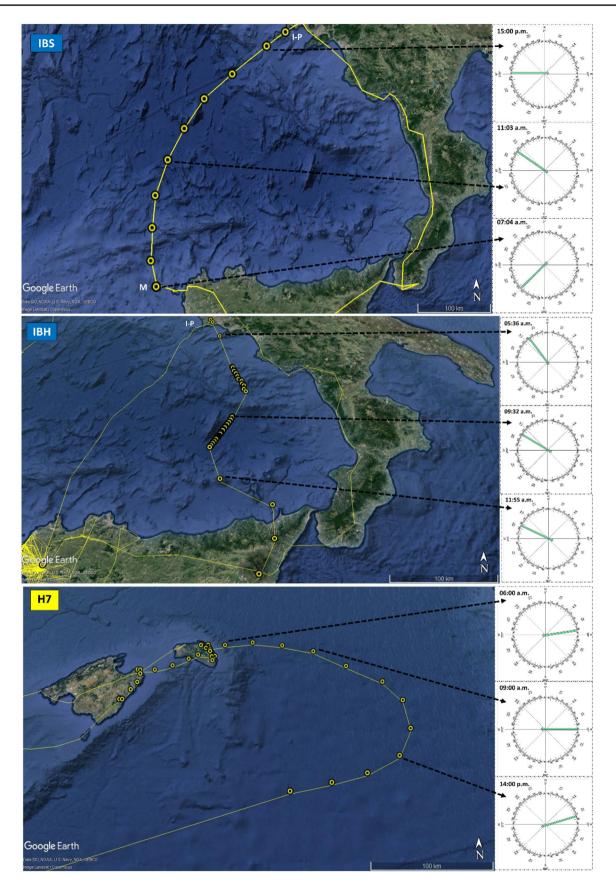


Fig. 2 Wind conditions during the unexpected migration movements over the open water by migrating Mediterranean ospreys. Bird ID and date are reported on the title of each graph. Timestamp (hour:minutes) on the x-axis and speed expressed in km/h on the y-axis. In red the wind gust at a height of ten metres above the surface of the Earth and speed of the horizontal 10 m and 100 m wind, in green and black respectively



age of two, on the 09/04/2022 at 07:47. It left Sicily on the same day at around 9:00 at San Vito Lo Capo promontory, and crossed the open sea performing a 6 h non-stop flight, eventually reaching Ischia and Procida islands at around

15:00 (Fig. 1). It continued its journey toward inland Italy, until it settled for the night in the surroundings of Naples. A migration movement in the opposite direction to that expected for the season started on the subsequent day at



◄Fig. 3 Unexpected migration movements over the open water carried out by three juvenile/immature ospreys (IBS, IBH and H7; referring to Fig. 2) and direction of the horizontal 10 m wind over a wind rose diagram provided for three different timings during the crossing. Full details are provided in the Appendix. M is for Marettimo island, while I-P is for Ischia and Procida islands

5:36, when the bird flew over the open water again, but in a Southerly direction (Figs. 2 and 3). Atmospheric conditions at the onset of such movement were characterized by a wind gust of 24.2 km/h and by a north-westerly breeze (9.51 km/h wind at 10 m a.g.l and 10.60 km/h wind at 100 m a.g.l) that likely promoted a flight towards South. The crossing was approximately 350 km long and lasted about 8 h (average speed: 43.7 km/h). The bird did not make use of thermals, as indicated by a straight flight during GPS-burst data of the track (i.e. no circling at sea was observed - the tag of this bird provided also additional data at higher frequency). The bird reached the Sicilian coasts on the 10/04/2022 at 13:56 and the day after returned to the previously used wintering site at 15:37. There, it spent 9 days before leaving again for a second spring migration that started on the 20/04/2022at 07:31 and was carried out over the open sea up to the coasts of Lazio region (touching land at 17:57 p.m.). It then resumed North, reaching its natal area on the 22/04/2022.

#H7

The bird was ringed and equipped with a GPS device on the 15/06/2013 at its nest in Minorca island (Balearics, Spain). It departed for autumn migration on the 04/08/2013 and wintered in southern Spain (Andalucia region). At the age of two, on the 02/04/2015 at 8:00, it departed for its first spring migration attempt. It crossed continental Spain and reached Minorca island on the 06/04/2015 at 10:30. The contrary migration movement started on the 08/04/2015 at 05:00 (Fig. 1). The bird flew over the open sea and, after an initial movement in an easterly direction towards Sardinia, it was probably pushed in the opposite direction by the winds that forced it to fly over the sea all night long, arriving on land the morning of the 09/04/2015 (first fix received at 08:00 close to the city of Almeria). Atmospheric conditions at the onset of such movement were characterized by a wind gust of 23.5 km/h and by a moderate easterly wind (16.3 km/h wind at 10 m a.g.l and 17.4 km/h wind at 100 m a.g.l; Figs. 2 and 3). Since the GPS did not record locations during the night, the crossing was estimated to be approximately 1000 km and lasted ca 27 h (average speed: 37 km/h). From here, the bird returned to the previously used wintering site (10/04/2015) and, 10 days later, undertook a second spring migration attempt. This time,

it pointed North and crossed continental Spain, up to the southern coast of France.

Discussion

We documented unexpected migration movements over the open sea by migrating ospreys, using a combination of GPS tracking data and weather information. As mentioned above, the selective pressure of water barriers can vary according to species-specific morphological traits. Some species are more adapted than other to fly over the open water. For example, both wing's morphology (e.g. aspect ratio) and body mass, by affecting the energy consumption of flapping flight, play an important role in predicting which species of raptors are more efficient when crossing this ecological barrier (Agostini et al. 2015). Moreover, recent studies highlighted how the interplay between wind and uplift can facilitate over-water flight in facultative soaring raptors (Nourani et al. 2021). In this sense, the osprey is capable of repeating soaring-gliding flights, exploiting the weak marine thermal uplifts (Duriez et al. 2018). The species has a body mass of about 1.4-1.8 kg, but high aspect ratio (relatively long wings; average value of 8.18; Agostini et al. 2015), which contains the energy consumption of flapping flight when the bird performs long sea-crossings. However, in the migration process, the experience plays a key role. Juveniles are naïve and, at first migration, do not have yet a precise final destination. In particular, it has been documented that juvenile ospreys display more sinuous migratory paths than adults, and that experienced adults perform better than juveniles at selecting favourable winds (Monti et al. 2018a). The same study showed how migratory ospreys generally benefitted from favourable tailwinds over the Mediterranean Sea, with cross-country speed in average 10 km h-1 higher than over land (mean 38.2 km h-1). However, when comparing different age classes, juveniles showed reduced speeds and experiencing reduced tailwinds' support compared to adults (Monti et al. 2018a). Adults, in fact, can rely on their experience from previous years for getting wind assistance across their journey and reach a precise goal (Alerstam et al. 2006), while inexperienced juveniles are usually strongly influenced by sidewinds and tend to carry out extensive explorative/dispersal movements.

The three inexperienced birds tracked in this study, flew in similar wind conditions at the onset of their unexpected flight (towards north in autumn and towards south in spring) over the open sea, by exploiting winds with a tail component and with similar values of wind gust (approximately 20 km/h).

The above can indicate how migratory capabilities and the ability to cope with external conditions (hence interacting with landscape characteristics) can especially influence inexperienced birds during their explorative/ dispersal movements at their both first autumn and spring migration. Beyond environmental factors, a further consideration can be made to explain these unusual migratory movements: being less constrained in their migratory schedules than long-distance migrants, short-distance migrants (as the majoirty of Mediterranean ospreys are) can move without facing a real ecological barrier (e.g. the Mediterranean Sea) in search of suitable wintering areas relatively close to their natal site, while immatures can spend time in explorative flights during spring.

Appendix

Wind conditions during the unexpected migration movements over the open water by migrating Mediterranean ospreys. Bird ID, Timestamp, latitude, longitude, wind gust at a height of ten metres above the surface of the Earth (km/h) and speed and direction of the horizontal 10 m and 100 m wind, respectively. Speed is expressed in km/h and direction, the direction with respect to true north (0=north, 90=east, 180=south, 270=west) that the wind is coming from, in degrees. Wind conditions at the onset of movements are reported in bold.

ID_bird	Date	Time	Latitude	Longitude	10 m Wind Gust	Wind 10 m Speed	Wind 10 m Direction	Wind 100 m Speed	Wind 100 m Direction
IBS	15/08/2020	07:04	37.987699	12.036866	20.746	16.081	225.091	18.687	221.169
	15/08/2020	08:00	38.269116	11.951066	15.610	11.571	242.633	13.582	238.806
	15/08/2020	09:00	38.630032	11.966083	7.597	3.347	277.493	3.643	273.329
	15/08/2020	10:00	38.9822	12.00915	4.784	4.594	381.383	4.852	383.098
	15/08/2020	11:03	39.371849	12.196166	9.623	6.051	306.434	6.239	307.048
	15/08/2020	12:00	39.71365	12.446549	15.614	8.878	280.831	9.243	281.083
	15/08/2020	13:00	40.038166	12.753866	19.382	12.532	270.757	13.095	271.055
	15/08/2020	14:00	40.308733	13.187849	22.936	18.157	260.466	19.240	260.744
	15/08/2020	15:08	40.613316	13.728183	26.116	18.578	272.525	20.422	272.354
	15/08/2020	16:00	40.76595	14.024949	26.665	19.094	280.312	21.456	280.768
IBH	10/04/2022	05:36	40.83232498	14.20354843	24.196	9.517	322.132	10.614	326.492
	10/04/2022	06:36	40.5615654	14.34564018	36.813	20.465	318.406	22.978	318.814
	10/04/2022	07:36	40.01963043	14.58057499	50.986	37.271	310.937	43.033	310.987
	10/04/2022	08:32	39.64250183	14.80019855	54.988	41.236	309.114	47.991	309.469
	10/04/2022	09:32	39.28489304	14.63619041	58.489	43.390	304.503	50.862	305.172
	10/04/2022	10:36	38.9738121	14.43015003	58.271	41.915	301.655	48.390	302.259
	10/04/2022	11:55	38.54481506	14.53693485	55.176	40.169	296.015	46.754	296.418
	10/04/2022	12:55	38.28282928	15.15558624	64.554	37.275	289.045	47.009	289.210
	10/04/2022	13:56	37.95940399	15.17361164	56.596	18.591	307.146	28.011	303.700
H7	08/04/2015	06:00	40.018016	4.420099	23.520	16.366	82.994	17.436	83.022
	08/04/2015	07:00	40.044266	4.758416	21.573	15.304	81.791	16.258	81.875
	08/04/2015	08:00	40.0058	5.118382	19.120	13.242	85.234	13.995	85.393
	08/04/2015	09:00	39.933816	5.490816	16.023	10.771	89.612	11.335	89.664
	08/04/2015	10:00	39.767583	5.858366	14.022	9.039	78.947	9.321	78.531
	08/04/2015	11:00	39.598333	6.252683	13.142	8.426	69.280	8.889	69.045
	08/04/2015	12:00	39.410066	6.437616	11.791	6.519	61.239	6.879	61.253
	08/04/2015	13:00	39.145266	6.447549	10.628	5.380	62.233	5.619	61.936
	08/04/2015	14:00	38.912	6.260766	11.310	6.020	76.350	6.226	76.492
	08/04/2015	15:00	38.77605	5.891683	16.339	10.405	89.557	10.834	89.719
	08/04/2015	16:00	38.7086	5.517466	22.920	14.965	92.245	15.835	92.397
	08/04/2015	17:00	38.649666	5.094583	31.038	21.473	90.635	23.115	90.782
	09/04/2015	08:00	36.843533	-2.373882	40.484	21.688	38.454	27.722	37.444

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Author contribution FM (corresponding author) conceived the idea, collected data, did the analyses and wrote the manuscript; GS, OD and AS collected data and helped in conceiving the manuscript; FM helped with fieldwork and writing. All authors contributed critically to the manuscript and gave final approval for publication.

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Data availability All GPS data analysed can be consulted in the Movebank repository at www.movebank.org under the project study "Osprey in Mediterranean (Corsica, Italy, Balearics) - movement study ID: 20039459".

Declarations

Conflict of interest The authors declare no competing interests.

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