

Migration and wintering strategies in vulnerable Mediterranean Osprey populations

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A broad range of migration strategies exist in avian species, and different strategies can occur in different populations of the same species. For the breeding Osprey *Pandion haliaetus* populations of the Mediterranean, sporadic observations of ringed birds collected in the past suggested variations in migratory and wintering behaviour. We used GPS tracking data from 41 individuals from Corsica, the Balearic Islands and continental Italy to perform the first detailed analysis of the migratory and wintering strategies of these Osprey populations. Ospreys showed heterogeneous migratory behaviour, with 73% of the individuals migrating and the remaining 27% staying all year round at breeding sites. For migratory individuals, an extremely short duration of migration (5.2 ± 2.6 days) was recorded. Mediterranean Ospreys were able to perform long non-stop flights over the open sea, sometimes overnight. They also performed pre- and post-migratory trips to secondary sites, before or after crossing the sea during both autumn and spring migration. Ospreys spent the winter at temperate latitudes and showed high plasticity in habitat selection, using marine bays, coastal lagoons/marshland and inland freshwater sites along the coasts of different countries of the Mediterranean basin. Movements and home-range areas were restricted during the wintering season. The short duration of trips and high levels of variability in migratory routes and wintering grounds revealed high behavioural plasticity among individuals, probably promoted by the relatively low seasonal variability in ecological conditions throughout the year in the Mediterranean region, and weak competition for non-breeding sites. We stress the importance of considering the diversity in migration strategies and the particular ecology of these vulnerable populations, especially in relation to proactive management measures for the species at the scale of the Mediterranean region.

Keywords: barrier crossing, behavioural flexibility, GPS tracking, migration, *Pandion haliaetus*, wintering.

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Trade-offs between long-term costs and benefits associated with migration have promoted the development of diverse migration strategies among

and within avian populations (Shamoun-Baranes *et al.* 2017). Recent research on migration, supported by improvements in tracking technology, has revealed how heterogeneous such strategies can be, even within a single species or population (Sergio *et al.* 2014, Shamoun-Baranes *et al.* 2017). These differences may be related to a myriad of factors (endogenous and external processes). Among them, the external environment can play a key role in shaping migratory parameters, sometimes leading to particular movement strategies.

At a world scale, the Mediterranean basin is considered one of the most important biodiversity hot-spots for its richness of species and ecosystems (Médail & Quézel 1999, Mittermeier *et al.* 1999, Myers *et al.* 2000). Besides endemic species, the area supports populations of species common elsewhere in the Western Palaearctic but that differ in their ecology, habitat and behaviour (e.g. Pérez-Tris *et al.* 2004, Förschler & Kalko 2007). In this context, the case of the Western Osprey *Pandion haliaetus* (IOC World Bird List – hereafter referred to as Osprey) is of notable interest. In northern Europe, it is a relatively common species building tree-nests in forest habitats, and it is generally associated with freshwater lakes and rivers, or even saltwater habitats, for feeding during spring (but using mostly saltwater habitats on the wintering grounds; Poole 1989, Wahl & Barbraud 2014). Previous studies have revealed that Ospreys undertake long-distance migratory journeys carried out over *c.* 6000 km towards sub-Saharan wintering grounds (Hake *et al.* 2001, Alerstam *et al.* 2006, Strandberg & Alerstam 2007, Klaassen *et al.* 2008, Bai & Schmidt 2011). Despite important increases in population size recorded in the last 20 years for these northern populations (Saurola 2005), important threats remain at wintering grounds and migratory stopovers (Klaassen *et al.* 2014).

At lower latitudes, in the Mediterranean, the Osprey is a rare breeding species with a vulnerable conservation status (Muriel *et al.* 2010, Monti 2012). During the 19th and 20th centuries, Mediterranean Osprey populations suffered significant declines, and they are still vulnerable (Monti *et al.* 2014). Beside numerous threats on the breeding grounds (e.g. Monti *et al.* 2013), it is likely that other threats during the non-breeding season, including migration, may hinder the recovery of these populations, even after 30 years of legal protection (Monti 2012).

The ecology of Mediterranean Osprey populations differs from northern populations. Individuals

breed mostly on rocky pinnacles within a fragmented coastal habitat, and are closely linked to marine environments for fishing (Cramp & Simmons 1980, Monti 2012). Moreover, knowledge about their migration strategies and habitat use on the wintering grounds is scarce, consisting of only sporadic ring recoveries and anecdotal observations (Thibault & Patrimonio 1992, Thibault *et al.* 1996, 2001). Some Ospreys have been observed to stay on their breeding territories during winter (J.-M. Dominici and R. Triay unpubl. data), and others have been located several hundreds of kilometres from their nest-sites (Thibault & Patrimonio 1992, Thibault *et al.* 1996, 2001). Such fragmentary and contrasting data preclude a complete and comprehensive understanding of the year-round ecology of these populations, limiting the possibility of planning adequate conservation measures.

We studied migration and wintering strategies of Osprey populations from Corsica, the Balearic Islands and Italy via GPS tracking. We predicted that the peculiar environmental conditions of the Mediterranean region (e.g. high temperatures and relatively favourable sea conditions for feeding throughout the year) might promote the evolution of different strategies compared with populations exposed to stronger seasonality in continental and northern Europe. We therefore asked the following questions: (1) What proportion of the Osprey populations is migratory? (2) Where are the wintering destinations? (3) What is the timing of their migration and what are the routes taken by individuals to reach their destination (do they use stopovers)? (4) Do they use sites that differ from breeding and wintering sites (i.e. pre-migratory sites)? (5) Which habitats are Ospreys using in winter (e.g. seashores vs. inland marshes or lakes)? (6) What are the causes of mortality outside the breeding season? For all the questions listed above, we specifically investigated whether there was any difference in migratory and wintering behaviour between individuals of different origin and between sexes and age-classes (adults vs. juveniles).

METHODS

Study sites

Relict Osprey populations in the Mediterranean are restricted to four sites: Corsica (France – *c.* 30 pairs), the Balearic Islands (Spain – *c.* 20 pairs),

and the Mediterranean seashores of Algeria (< 10 pairs) and Morocco (< 15 pairs; Monti 2012, Monti *et al.* 2013). In addition, the species was reintroduced to Andalucía, Spain, in 2003 (13 pairs in 2013), Tuscany, Italy, in 2006 (three pairs in 2016) and Algarve, Portugal, in 2011 (one pair in 2015; Muriel *et al.* 2006, CIBIO 2011, Monti *et al.* 2012). We studied Ospreys belonging to three of these populations.

In Corsica, Ospreys breed on rocky pinnacles and cliffs along the west coast of the island, between Cape Corse in the north and Ajaccio in the south. A detailed monitoring of the breeding population has been ongoing since 1974, and most chicks are ringed at the nest each year (Bretagnolle *et al.* 2008). In the Balearic Islands, Ospreys also breed on rocky pinnacles and cliffs on the islands of Menorca, Mallorca and Cabrera. Monitoring of the breeding population has been ongoing since 1980 and chicks are ringed at the nest each year (Triay & Siverio 2008). In addition, captures of adults have been performed in marshes in winter for ringing. In Tuscany, Ospreys were reintroduced in 2006–2010, with chicks translocated from Corsica before fledging (Monti *et al.* 2014). A detailed monitoring programme has been set up for the entire population, with all chicks released or born in the wild being ringed, as well as some adults caught at the nest. The species has been breeding since 2011, nesting on trees or artificial structures. In the Mediterranean, Ospreys start breeding in March. In March–April females lay two to three eggs, which hatch in May. Chicks fledge at the end of June or early July (Triay & Siverio 2008, Monti 2012).

Capture and tracking techniques

Overall, 41 Ospreys were trapped and equipped with a GPS tag. We fitted 30-g Solar GPS/Argos PTT-100s (Platform Transmitter Terminal; Microwave Telemetry Inc., Columbia, MD, USA) to five adults and three juveniles from the Balearic Islands. PTT tags were programmed to record positions, altitude and instantaneous groundspeed at hourly intervals. All other birds from Corsica and Italy, and another six juveniles from the Balearic Islands were equipped with 24-g solar powered GPS/GSM devices (model Duck-4, Ecotone, Sopot, Poland). These tags were programmed to collect GPS fixes at hourly intervals, but only provided data on latitude and longitude (without altitude or speed).

In the Balearic Islands, five adults (three males, one female and one of undetermined sex) were trapped using a perch-trap in wetlands in the northeast of Mallorca in February and July of 2009 and 2010. Nine chicks were equipped with GPS tags at their nests, less than 10 days before fledging in June 2009 and 2013. In Corsica, seven adults (five females and two males) were caught before the onset of the breeding season in March–April 2013, using a noose carpet laid on the nest. Four chicks were equipped with GPS tags at their nests, less than 10 days before fledging in June–July 2013 and 2014. In Tuscany, four adult Ospreys (two males and two females, including one of Corsican origin) were trapped before the onset of the breeding season in March–April 2013, using a noose carpet laid on the nest. Twelve juveniles were fitted with GPS tags before or shortly after fledging in July between 2013 and 2016.

All birds were colour-ringed and measured. Bird handling (from capture to release) lasted in total 30–50 min. The sex of the birds was assessed based on size and plumage and/or using molecular sexing, following Griffiths *et al.* (1998). The combined mass of the tracking device and harness never exceeded 3% of the bird's body mass. All tags were attached as backpacks with a harness made of 7-mm-wide Teflon ribbon (Kenward *et al.* 2001).

Tracking data processing

Birds which remained in their breeding/natal areas all year round were classed as resident. Formally, for residents, home-ranges (HRs – see below) in the breeding season and winter overlapped (e.g. Cagnacci *et al.* 2016), and wintering HRs included the nest-site. Where there was no overlap in HRs (and therefore the nest-site was not in the wintering HR) birds were classed as migrants. Migratory Ospreys moved to a wintering area at least 240 km away (measured as the great-circle distance; see M05, Appendix S2).

We identified the beginning of each migratory journey by the clear shift, followed by a unidirectional and sharp variation, in latitude (e.g. Catry *et al.* 2011), of at least 1°. The departure date of autumn and spring migration was calculated as the last day during which the bird was present at the breeding/natal site or wintering site, respectively (Strandberg *et al.* 2008). The arrival date was calculated as the day when the bird arrived at its

destination (wintering site for autumn migration, and breeding/natal site for spring migration; Strandberg *et al.* 2008). A stopover site was defined as an area where a bird spent more than 24 h during the migration period (according to Strandberg *et al.* 2008, Limiñana *et al.* 2012). Pre- and post-migratory round trips were defined as movements towards a secondary site and back, carried out before and after migratory journeys from the breeding/natal or wintering site, respectively (Strandberg *et al.* 2008). These trips differed in both distance and duration from the foraging trips performed during both the breeding and the wintering seasons, which were generally < 10 km from nest/wintering site and lasted less than 1 h.

Movement data analyses

Migratory tracks were examined in ARCGIS 9.3, distinguishing segments travelled over sea and over land. In the analyses, we only considered hourly segments to avoid possible effects of variation in segment lengths (Tanferna *et al.* 2012). On land, we first removed movements at stopovers and considered only genuine migration segments. We defined a migratory movement only when hourly locations were spaced by a minimum of 10 km (Sergio *et al.* 2014), to exclude local movements between nocturnal roosts, and possible prospecting for feeding places along the way (which differed from stopovers because they were < 24 h). Hereafter, we refer to these hourly track distances as 'cumulative'.

During winter, we estimated adult HRs (95% UD = utilization distributions) and core areas (50% UD) for every wintering season with fixed kernel density contours and least-square cross-validation factors (*sensu* Worton 1989), using the Hawth's tool Extension (Hooge & Eichenlaub 2000). We collected 26 wintering events from 16 adults. However, because some birds were tracked for consecutive years, to avoid any pseudo-replication bias we systematically selected only the last wintering event. This approach was the most conservative because it limited the risk of using an immature during its first winter (the birds' exact age at ringing was not known for all tagged adult birds). Our dataset was hence composed of 16 wintering events for adults.

Juveniles, once their first migration was achieved, generally stayed at wintering grounds for approximately 18 months (thus skipping the spring migration of their second calendar year)

before returning to their natal area for breeding (when sexual maturity is reached; Poole 1989). The juveniles' wintering period is thus not ecologically comparable with the wintering period of adults. For this reason, we did not consider this period in the analyses of timing of wintering for juvenile birds.

As Ospreys need aquatic habitats to catch fish, we qualified wintering habitat type composition within the home-range only according to aquatic environments: sites were classified as saltwater, brackish or freshwater. This was achieved using satellite-images from Google EARTH as a source, together with local surveys, when feasible. All GPS data can be consulted in the Movebank database (www.movebank.org; project study name: Osprey in Mediterranean).

Mortality

Mortality was assumed when the bird did not move for more than 2 days according to its GPS position. Mortality could be assessed directly (when a dead bird was recovered) or indirectly when detailed examination of satellite photos revealed dangerous elements (e.g. power lines, wind farms) or proximity to a human settlement (direct persecution). However, these cases of indirect mortality sometimes cannot be distinguished from tag failure or tag loss, and hence must be viewed with caution.

Statistical analyses

We evaluated the effects of age, sex and country of origin on migratory components of autumn migration through general linear mixed effects models (Crawley 2007). Response variables are explained in Table 1. We included 'individual' and 'year' as random effects, and 'age', 'sex' and 'country of origin' as fixed effects. Model selection used the Akaike's information criterion corrected for small sample sizes (AICc). Models were retained for inference if they had $\Delta AICc \leq 2$ units, and if their AICc value was lower than that of any simpler, nested alternative (Richards 2008, Richards *et al.* 2011). We selected among all combinations of models using the 'dredge' function in the R package 'MuMIn' (Bartoń 2012). Model coefficients were estimated using the 'confint' function, after averaging across the top models (using the model.avg function in R; Bartoń 2012). All

Table 1. Summary of response variables used to study migratory components. Sample size $n = 23$.

Response variable	Abbreviation	Units and explanation
Departure date	Departure date	
Arrival date	Arrival date	
Duration of the migratory journey	Duration	In days; transformed as log function to meet normality assumptions
Total distances travelled during migration	Migration distance	In km; calculated as the sum of total daily distances during travel days, excluding movements at stopover sites and both pre- and post-migratory movements (following Strandberg <i>et al.</i> 2008)
Direct distance between nest and wintering ground	Distance nest stop	In km; the direct (great circle) distance between nest and wintering site
Maximum distance covered in a day during the migratory journey	Maximum distance	In km; maximum distance travelled in a day
Daily distance	Daily distance	In km per day
Straightness index of the migration path	Straight index	Calculated as the ratio of the total distance covered to the great circle distance between the nest and the wintering site

statistical analyses were conducted in R 2.15.0 (R Core Development Team).

Fisher's exact test was used to assess absolute frequencies of resident vs. migratory individuals in our populations. For the winter period, due to the limited sample size, differences in daily distances, home-range and core areas between migratory and resident adults were tested using non-parametric tests.

For spring migration, we had 11 tracks of seven birds. To avoid pseudoreplication related to repeated journeys by the same individual, we arbitrarily selected the first migratory track per individual and only considered adults. Data are reported as mean \pm standard deviations.

RESULTS

Overall, GPS tracking data were available for 41 individuals (16 adults and 25 juveniles: 12 from Corsica, 14 from the Balearic Islands and 15 from mainland Italy). Details are provided in Appendix S1.

Occurrence of migratory behaviour

Mediterranean Ospreys showed heterogeneous migratory patterns (Fig. 1). Of 16 tagged adults, nine adults (56.3%) never migrated. This behaviour was observed in adults from all three Mediterranean populations. The remaining seven adults (43.7%) migrated from the breeding area. For the 25 juveniles, only two individuals (8%)

were residents; all others (92%) departed on migration (Fig. 1; Appendix S1). Overall, proportions of resident vs. migratory individuals per population were significantly different (Fisher's exact test: $P = 0.025$), with 16.6% and 83.4% for Corsica, 33.3% and 66.7% for Italy, and 28.6% and 71.4% for the Balearic Islands, respectively.

Resident birds regularly travelled between nesting areas and feeding sites located < 20 km away (straight-line distance). In the Balearics, the wetlands of Albufera and Ses Salines represented the main feeding areas. Only two exceptional exploratory movements (of 65 and 77 km, respectively) to Menorca were recorded for two males during spring. In Corsica, an adult female stayed all year round along the coast, fishing in marine coves. In Italy, three adults and two juveniles stayed all year round along the coast, fishing in the wetland system of southern Tuscany.

Migratory destination

Migrant Osprey wintering areas at least 240 km straight-line distance from their breeding site were spread out within the Mediterranean basin, between 16°N and 43°N latitude (latitude width = 27°) and 17°W and 16°E longitude (longitude width = 33°). These wintering grounds were mostly located in southern continental Spain, Morocco, Algeria, Sardinia, Corsica, the Balearic Islands and continental Italy (Fig. 1). Only five birds (16.6%) crossed at least a part of the Sahara: two adults (one from Corsica and one from the the

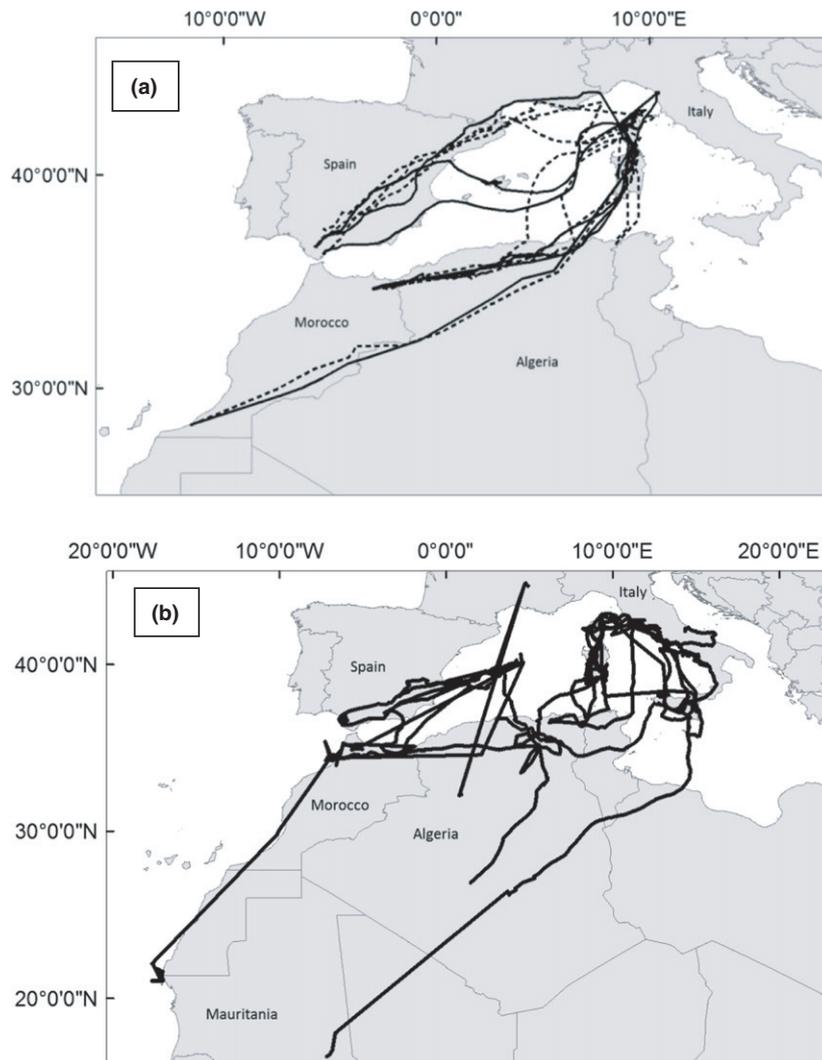


Figure 1. Migratory journeys of Mediterranean Ospreys (excluding resident birds): (a) Corsican adults crossing the Mediterranean Sea and reaching the wintering grounds in Sardinia, Spain, Morocco and Algeria; black lines for autumn migration ($n = 11$ tracks) and dotted lines for spring migration ($n = 11$ tracks); (b) juveniles originating from Italy, Corsica and the Balearics and wintering in Spain, Morocco, Algeria and Italy ($n = 24$ tracks). Three juveniles that disappeared during the Sahara Desert crossing are also included.

Balearic Islands wintered respectively in southern Morocco and Mauritania) and three juveniles (two from the Balearic Islands and one from Italy; Fig. 1b). To reach the wintering areas, Ospreys were able to conduct non-stop flight bouts over the open sea (range 86.8–1023.5 km; $n = 15$ tracks).

Migratory routes, timing of migration and use of stopovers

After excluding resident birds, 49 migratory tracks were analysed (85.7% of which were complete),

38 tracks in autumn and 11 in spring, carried out by 30 individuals (Appendix S2). Tracks from multiple migratory journeys were available for seven individuals (six adults and one immature). In seven cases, transmission stopped due to device failure, resulting in incomplete migratory datasets, for which we could only integrate response variables such as date of departure or daily distances (Appendix S2).

In autumn, migration distances (mean cumulative distances) were 1347.8 ± 837.6 km (mean straight-line distances from nest: 948.6 ± 709.8 km). We

did not detect strong differences between age and sex classes on the response variables tested, except for daily distances travelled, which were shorter in juveniles than in adults (Appendix S3; Fig. 2). Ospreys travelled on average for only 5.2 ± 2.6 days and stopped occasionally (mean stopover duration: 2.0 ± 0.7 days; $n = 5$ birds that actually did make a stopover; Appendix S2). Exceptionally for two birds, the duration of the migratory journey was > 50 days (Appendix S2). Autumn migration was concentrated in time, with mean departure date from breeding sites and mean arrival dates to wintering sites occurring on around 12 and 22 August, respectively (range for departures: adults = 24 June to 9 November; juveniles = 29 July to 28 August; range for arrivals: adults = 25 June to 17 November; juveniles = 3 August to 2 September). Combining

sexes, there was a tendency for the straightness index to differ between age classes (adults = 0.85 ± 0.1 vs. juveniles = 0.64 ± 0.1).

In spring, migratory tracks were only available for adults. Adult Ospreys left their wintering grounds in mid-February (mean departure date = 21 February \pm 16.4 days; range 6 February to 25 March) and arrived at breeding sites 5.8 ± 4.3 days later (mean arrival date 27 February; range 6 February to 4 April). Only one bird used a stopover site. Other parameters are reported in Appendix S2.

Two of six migratory adults from Corsica performed a loop-migration, taking different routes in autumn (crossing the Mediterranean Sea directly from Corsica to reach Spain) and spring (crossing Spain over land until the Pyrenees, then reaching

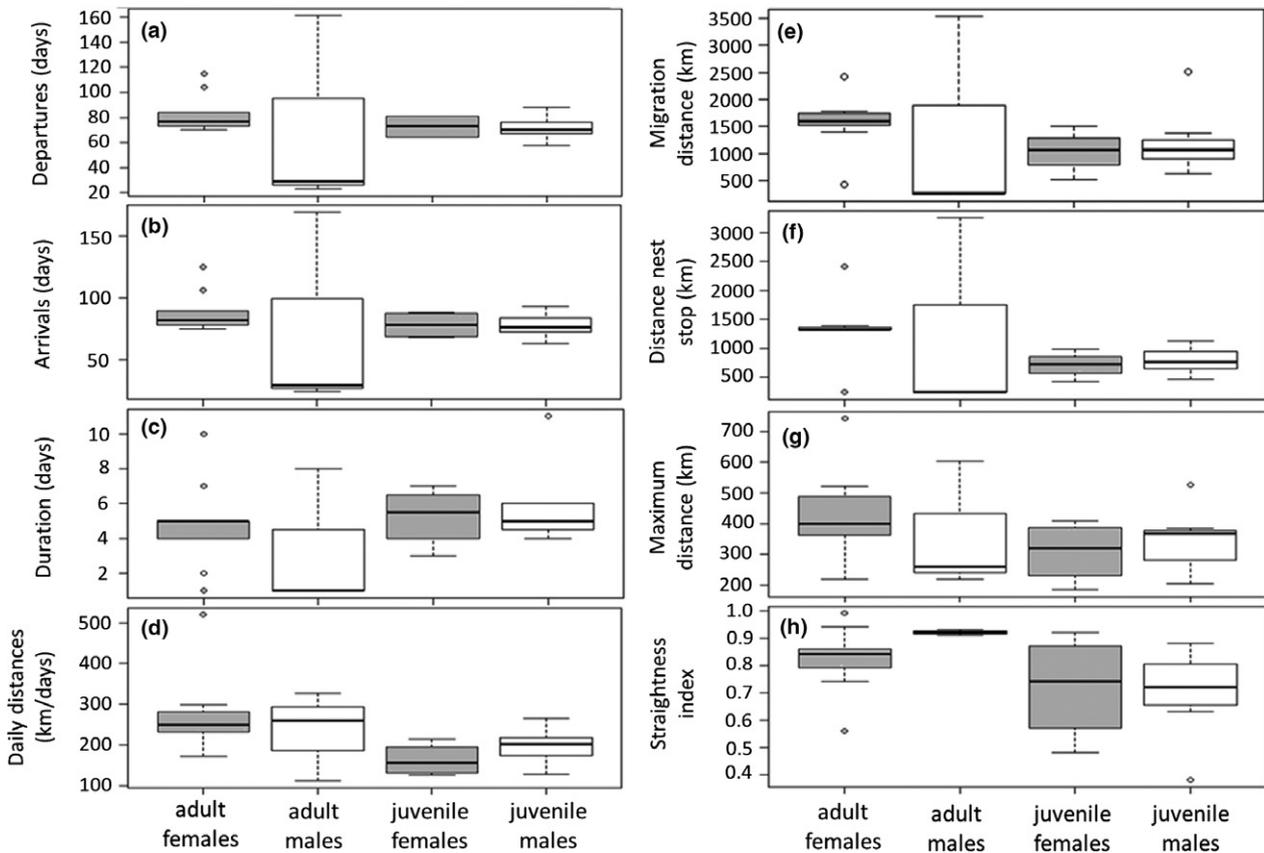


Figure 2. The main response variables for migratory Ospreys, during autumn migration. Number of days after 1 June (a) for departures and (b) for arrivals; (c) duration of migration; (d) daily distances; (e) migration distance; (f) direct distance between nest and wintering ground ('distance nest stop'); (g) maximum distance covered in a day during the migratory journey; and (h) straightness index of the migration path, calculated as the ratio of the total distance covered to the great circle distance between the nest and the wintering site. Females and males are represented by grey and white boxplots, respectively. Age (adult vs. juveniles) is also reported (adult females $n = 5$; adult males $n = 2$; juvenile females $n = 7$; juvenile males $n = 8$; migratory parameters for individual birds are reported in Appendix S2).

Corsica from the continental French shores; Figs 1 & 3). The detour in spring, probably due to bad weather conditions across the Mediterranean Sea, added 93 km and a 2-day delay for one bird, and 299 km and a 5-day delay for the second bird. On its one migration to Mauritania in 2009–2010, the Balearic bird BAL5M also carried out a loop-migration across the Sahara Desert.

Only five juveniles survived more than 2 years and returned to their natal areas. Four of them spent their second calendar year entirely at their wintering area and came back to their natal area in their third calendar year, after 18 months. The fifth bird (bird CIV_fosp21 from Corsica) spent its first winter in Algeria, went back to its nest and to a secondary site in Corsica in its second year (after 9 months, arriving in June and departing in November), and then again in its third year (in March and August). After their return to their natal areas, all these five birds performed extended trips further north (e.g. France, Italy, Germany).

Pre- and post-migratory movements

Before autumn migration, 90% of migratory adults performed pre-migratory trips to a secondary site, on average 103.0 ± 65.4 km from their nest, located at the seashore or inland near a lake or river. Most birds spent on average 23.2 ± 22.6 days (range: 5–60 days) at these

secondary sites (Fig. 3). However, in three cases, autumn migration started from these secondary sites, which could then be considered as stopover sites.

Similarly, for three Corsican adults, we observed repeated post-migratory round trips performed after spring migration and before the onset of the breeding season. Only one male performed two round trips during the winter season: from its wintering site in Sardinia, it flew 239 km to visit its nest in Corsica. A Corsican Osprey (failed breeder) first moved north to a site in Tuscany (Massaciuccoli Lake; where it remained between May and July) before travelling south to its wintering ground in Sardinia.

Movements and habitat use in winter

Migratory adult Ospreys spent about 6 months (mean: 172.7 ± 25.2 days, $n = 6$; Appendix S4) on their wintering grounds and generally used a single area throughout the whole winter. Daily movements were restricted (mean cumulative distance = 11.7 ± 6.8 km/day) and did not differ between resident and migratory birds (Mann–Whitney U -test: daily distance: $U = 72.5$, $P = 0.41$, $n = 14$). Exploratory movements were made only occasionally during winter (e.g. F03 covered 140 km, coming back to its main wintering site on the same day). Home-range sizes were

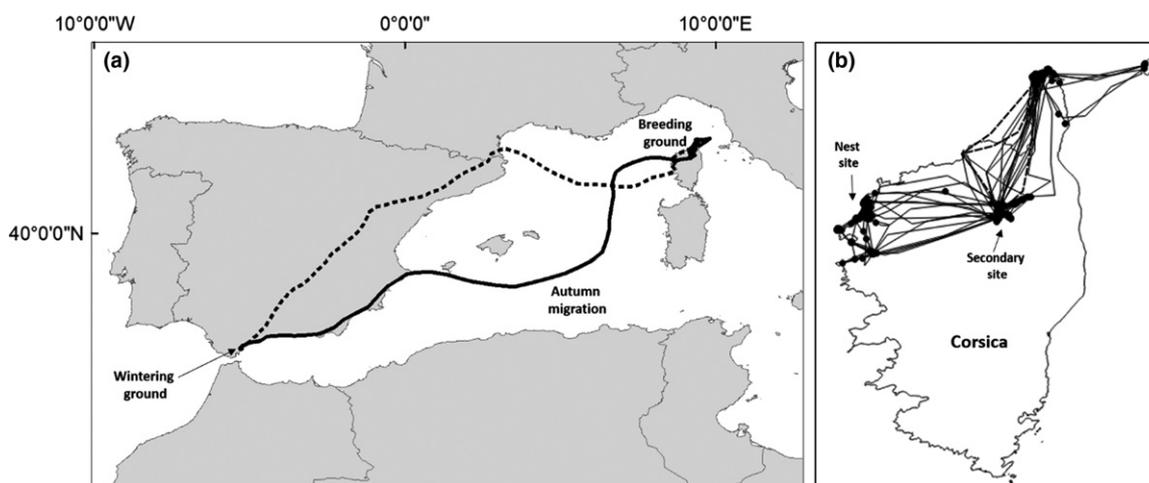


Figure 3. (a) Example of loop-migration of a Mediterranean adult (F04) during a complete migratory cycle: solid line for autumn migration, dotted line for spring migration; location of both breeding and wintering ground are shown. (b) F04's movements in Corsica: movements during the breeding season represented by solid and dotted lines for pre-migratory (autumn) and post-migratory (spring) movements, respectively; circles are for staging points. The location of both the nest and the secondary site are shown.

very small during the wintering period (home-range = $70.0 \pm 83.7 \text{ km}^2$; core area = $8.0 \pm 6.9 \text{ km}^2$; Appendix S4) and did not differ between resident and migratory birds (Mann–Whitney *U*-test: home-range: $U = 124$, $P = 0.95$, $n = 16$; core areas: $U = 114.5$, $P = 0.67$, $n = 16$).

In winter, individuals used marine (19.73%) and coastal brackish water (58.92%) habitats as well as freshwater sites (21.35%) in both coastal and inland areas (e.g. bays and coastal waters, river mouths, marshes, dams and artificial ponds). Inter-individual plasticity in habitat choice (calculated on 95% home-ranges) was high, as 6.25% of the birds used only freshwater sites and 25% used exclusively brackish habitats such as marshland or coastal lagoons. The remaining 68.75% were opportunistic and frequented different habitats during the same season. No bird had a home-range fully associated with the marine environment (Appendix S4).

Causes of mortality

The end of GPS tracking was uncertain for 28 (68.3%) of the 41 Ospreys. In 23 cases, it was not possible to assess whether the bird died or not, but in five cases the bird was later observed alive and identified by ring re-sighting (Appendix S1). Death was ascertained in seven cases and was usually directly or indirectly associated with human activities: illegal shooting (three ascertained cases), electrocution at a power line (one case), collision with wind turbines (one case), trapped and drowned in a net in a fish pond (one case), and burnt at a petroleum plant (one case). Overall, we recorded a high mortality rate for juveniles, of which 65.4% died or disappeared within the first year of life and during winter. For further details, see Appendix S2.

DISCUSSION

Migratory strategies

This is the first study of the migratory and wintering strategies of the vulnerable Osprey populations breeding in the Mediterranean. Mediterranean birds showed inter-individual heterogeneous migratory behaviour, typical of partially migratory populations (e.g. Chapman *et al.* 2011, Shaw & Levin 2011). The short duration of trips together with high levels of variability in migratory routes

(and direction of movements), timing and wintering grounds revealed a ‘relaxed system’ and consequently a high plasticity in behaviour, probably promoted by a relatively low seasonal variability in ecological conditions throughout the year in the Mediterranean region and possibly by weak competition for non-breeding sites (given that the regional population is small).

Mediterranean Ospreys were able to perform long non-stop flights over open sea, sometimes carried out overnight. Across much of their range, Ospreys are known to be capable of engaging in such flights, including nocturnal flight (Martell *et al.* 2001, DeCandido *et al.* 2006, Horton *et al.* 2014, Väli & Sellis 2016), thus without the benefit of land-based thermals. This is probably related to the aerodynamics of flight (e.g. Ospreys have relatively narrow wings), which are quite different from most raptor species. Mediterranean Ospreys rarely performed long detours following the coasts, as observed in other raptor species relying on land-based thermals (e.g. Griffon Vulture *Gyps fulvus*, Bildstein *et al.* 2009; Short-toed Snake Eagle *Circus aeruginosus*, Mellone *et al.* 2011, Panuccio *et al.* 2012; European Honey Buzzard *Pernis apivorus*, Vansteelant *et al.* 2017). The duration of flights over sea ranged between 3 and 25 h, suggesting that these birds are able to store sufficient body reserves before departure.

Before departing on migration, most individuals performed pre-migratory movements to a secondary site. This behaviour has also been observed in other birds (e.g. Western Marsh Harrier *Circus aeruginosus*, Strandberg *et al.* 2008; Lesser Black-backed Gull *Larus fuscus*, Klaassen *et al.* 2012). Time spent at these sites ranged from a few days to several weeks and visits were repeated several times before the onset of migration. The function of such movements might be related to the necessity to build fat reserves before crossing the barrier. In this sense, it would be worthwhile to collect higher resolution tracking data or accelerometer data to document fishing events (of very short duration) to test whether energy acquisition is more efficient at secondary sites than at the nesting area.

In autumn, Ospreys generally crossed the sea, but in spring two individuals preferred to travel over land, reducing oversea passages. Such loop-migrations were probably shaped by northerly winds that facilitated sea-crossing in autumn but hindered sea-crossings in spring (as described for

Crested Honey Buzzard *Pernis ptilorhyncus*, Yamaguchi *et al.* 2011).

Our results showed that the migratory behaviour of Mediterranean Ospreys was highly flexible and could be adapted to local circumstances. As distances to reach wintering sites were relatively short and little time was required, individuals could choose to invest part of their energy to cross the sea when there were favourable winds, otherwise selecting a safer but longer route over land (F. Monti unpubl. data). For a short migration, they may concentrate their efforts on flying at sea for a limited time, even if it is energetically more demanding. We recorded only a few cases of trans-Saharan migration, indicating that at least some individuals from the Mediterranean region do winter in sub-Saharan Africa, as their conspecifics from northern Europe commonly do. However, the great majority of Mediterranean Ospreys wintered within the Mediterranean basin.

Finally, it is worth highlighting the specific case of the Corsican juvenile Osprey CIV_fosp21, which returned to its natal site after only 9 months. This is very unusual for juvenile/immature individuals, which tend to stay about 18 months at wintering sites before returning to their natal area for the first time (Poole 1989). As far as we know, there are two instances of Ospreys returning to Great Britain in their second calendar year (T. MacKrill pers. comm.). The case of bird CIV_fosp21 represents the first documented record for the Mediterranean.

Wintering

We recorded a weak migratory connectivity (*sensu* Cresswell 2014) between breeding and non-breeding areas for Mediterranean Ospreys, as already predicted on the basis of ring-re-sightings of Corsican birds (Thibault *et al.* 1996), and as has been found to be common among different species of migrant landbirds (e.g. Finch *et al.* 2017). Mediterranean Ospreys tracked in winter mostly used temperate areas characterized by different habitat types (from marine bays to marshlands or freshwater sites). On the one hand, a high inter-individual plasticity was detected within the Mediterranean populations, but each adult individual generally used only one site (rarely two) during winter. This general lack of mobility in winter is in accord with the strictly piscivorous feeding habits of the species and also with the limited movement recorded

during the breeding period (F. Monti unpubl. data). Having arrived at the wintering ground, adult Ospreys rarely moved, but rather exploited a small area associated with a specific water body. This behaviour suggested a strategy aimed at reducing energy expenditure by minimizing efforts in movements and fishing activities during this season. This tendency for birds to invest little energy in foraging during winter seems to be a common feature of various species of migrant landbirds (Schlaich *et al.* 2016). In tropical Africa, Ospreys generally spent little time (3–5% of daylight hours) fishing and eating, resting for most of the day (Zwarts *et al.* 2009). It is likely that Mediterranean Osprey had a similar time-budget in winter. In our opinion, the choice of the wintering ground for adult birds was more related to individuals' early-life experiences (adults returning to secure locations with good fishing opportunities that allowed their survival during previous winters), as most evidence suggests that non-breeding sites of migrant birds are not set genetically (Cresswell 2014, Vansteelant *et al.* 2017).

Washburn *et al.* (2014) recorded that North American Ospreys spent *c.* 5–6 months wintering at tropical latitudes, using a diversity of aquatic habitats, and foraging on a large variety of fishes. During winter, North American Ospreys also moved infrequently, showing limited home-ranges and core areas (12.7 and 1.4 km², respectively; Washburn *et al.* 2014). These results show how some aspects of the wintering ecology of this raptor may be similar across different continents. Ospreys tend to be opportunistic, adapting their behaviour to the location and water bodies available, with fishing opportunities probably being the most important requirement.

Implications for conservation

Recent studies have demonstrated how hazardous long-distance migratory journeys in different raptor species may be (Klaassen *et al.* 2014, Oppel *et al.* 2015). Long-distance migration is energetically demanding and exposes migrants to unfavourable conditions (e.g. poor resource availability at stopovers, harsh weather events, hazards) that increase the risk of mortality. In addition, human-related hazards might also occur on the sub-Saharan wintering grounds, where poaching and illegal shooting are common. Such threats have an important role in controlling the demographic trends of

populations, in turn affecting the health of the populations and their fate (Klaassen *et al.* 2014, Oppel *et al.* 2015).

In this sense, the strategy adopted by Ospreys of staying in the Mediterranean basin provides several advantages in terms of energy saving and risk reduction, compared with their northern European conspecifics. By migrating over limited distances, Mediterranean Ospreys probably reduce energy expenditures, which should increase survival. Despite this, there are still risks, e.g. illegal shooting and killing of protected migratory species is still commonplace (Brochet *et al.* 2016). Populations such as those of the Mediterranean Osprey, which are isolated, small or both, are especially at risk. These populations live in a fragmented coastal habitat and on islands that are highly exploited by humans, and where available nest-sites are more limited than in northern Europe, where continuous forests provide potentially unlimited opportunities for nesting (Saurola 2005).

In the Mediterranean, reintroduction programmes have been carried out to promote the recolonization of the species' historical range. However, in most of these, individuals from north and central Europe have been used as source populations for translocated young (Muriel *et al.* 2010, CIBIO (Centro de Investigação em Biodiversidade e Recursos Genéticos) 2011), except in Italy (Monti *et al.* 2014). Ospreys from north and central Europe are known to perform long-distance migrations, a migratory strategy very different from that observed for Mediterranean birds. Translocating migratory birds from source populations in areas where different migratory strategies have been detected might have ecological consequences and promote new behaviours in newly established populations, as described in other birds (e.g. Little Bustard *Tetrax tetrax*, Villers *et al.* 2010; Macqueen's Bustard *Chlamydotis macqueenii*, Burnside *et al.* 2017). In this sense, it would be extremely interesting to investigate whether Ospreys which originated in northern Europe (e.g. long-distance migrants) and were translocated to the Mediterranean as fledglings adhere to the long-distance migration strategies of their source population, or whether they are able to adopt short-distance migration strategies of the target population. For these reasons, understanding variation in population and individual levels of migratory patterns is of fundamental importance for developing management actions and appropriate conservation

strategies in migratory bird populations (e.g. Nathan *et al.* 2008, Burnside *et al.* 2017, Meyburg *et al.* 2017). We stress the importance of carefully considering source populations for future translocations in the Mediterranean area, taking into account the particular migratory behaviour and ecology of these populations. Finally, it is important to note that the low migratory connectivity of this Mediterranean Osprey population (i.e. high variability in migratory routes and wintering grounds) can have important conservation implications, requiring adequate protection from illegal hunting across a regional network of high-quality habitats, including areas that do not have formal protected status (Cresswell 2014).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Year of tagging, age, sex, population of origin, migratory category (MIG, migrant; RES, resident) and location of both pre-migratory sites and wintering grounds of Mediterranean Ospreys.

Appendix S2. Mean values of migratory parameters for Mediterranean Ospreys (excluding resident individuals), reported for both seasons and age classes.

Appendix S3. Model selection.

Appendix S4. Winter home-ranges (fixed kernel

95%), core areas (fixed kernel 50%) and mean cumulative distances of daily movements of Mediterranean adult Ospreys.