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Article

Migration distance affects stopover use but not travel speed: contrasting patterns between long- and short-distance migrating ospreys

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The development of migratory behaviour is a continuous process which is not only determined by genes, but also moulded by individual differences based on life-history variations occurring at each ontogenetic stage. Assessing consistency and plasticity in migratory traits between long distance (LDM) and short distance migratory (SDM) populations within the same species that may express dissimilarities in the leeway of annual schedules is essential to understand the evolution and ontogeny of migratory strategies.

We studied the migration strategies in autumn regarding flight speed and the use of stopovers (number and duration of stop-overs across the whole journey) at the intra-specific level, by tracking with GPS loggers the intercontinental migration of 43 adult and juvenile ospreys *Pandion haliaetus* from both LDM and SDM populations.

LDM ospreys travelled distances five times larger than SDM ospreys, but their total migration speed was 2.4 times slower. While daily distance travelled did not differ between populations, the reduced total migration speed by LDMs was due to higher stopover use compared to SDM birds. SDM birds used more direct routes, crossing open sea at higher flight speeds, even though both populations largely benefitted from wind assistance across their journey. Across populations, adult birds travelled longer distances per day and displayed less sinuous migratory paths than juveniles, suggesting that migratory capabilities improve with age and experience of the bird. Overall, the time constraint related to total migration distance was not the main driver of the total migration speed, and other factors such as physiological needs to rest and refuel at stopover sites may play an important role. Our study underlines the importance of investigating variability in migration strategies in partially migratory species, for a better understanding of avian migratory ecology.

Keywords: migratory strategy, raptor, GPS tracking



Introduction

A migration strategy is the product of a set of rules that determine the overall process of migration (Alerstam et al. 2006), resulting from the interaction of multiple factors. Major ‘primary’ migratory traits, such as timing (i.e. departures and arrivals) and routes (i.e. direction of main migration axes, distances covered and destinations), are thought to be mostly controlled genetically, and driven primarily by an endogenous clock-and-compass system (Berthold 1996, Thorup and Rabøl 2001). Conversely, ‘secondary resulting’ migratory traits such as daily travel speeds, flight performances and straightness of the tracks rather seem to be predominantly shaped by stochastic environmental factors (Cresswell 2014, Vansteelant et al. 2017a) and by the age/experience of the bird (Sergio et al. 2014). The development of migratory behaviour is hence a continuous process which is not only determined by genes, but also moulded by individual differences based on life-history variations occurring at each ontogenetic stage (Senner et al. 2015). In this sense, birds seem to adjust the spatial and temporal schedules of their migratory journeys (e.g. daily distance covered, time spent at stopovers) according to external and internal factors, to avoid detours triggered by adverse weather, to minimize energy consumption, to maximize speed of migration, and thus to enhance their chances of survival (Sergio et al. 2014, Vansteelant et al. 2015; but see, Lok et al. 2013, Goymann et al. 2017). Such modulation of migratory behaviours has been recorded in relation to windscares (Sinelschikova et al. 2007, Klaassen et al. 2010, Yamaguchi et al. 2011), food resources availability (van der Graaf et al. 2006, Duriez et al. 2009, Tøttrup et al. 2012), presence/absence of ecological barriers (Deppe et al. 2015) and exceptional weather events (Tøttrup et al. 2012, Vansteelant et al. 2015, 2016).

In many bird species, there are populations of long-distance migrating individuals (LDM) and others of short-distance migrating individuals (SDM) (Forchhammer et al. 2002, Limiñana et al. 2012, Shamoun-Baranes et al. 2017). The costs and benefits of long vs short distance migration in birds are still being debated (van Noordwijk et al. 2006, Pulido 2007). The cost of LDM (energy spent, various risks encountered en route) must be offset by benefits related to suitable climate or increased foraging opportunities at wintering grounds. Although the general picture emerging from studies on short and long-distance migrants is that LDMs achieve faster total migration speed compared to SDM, this picture is still blurred by many contradictory results. Most studies that investigated these questions used inter-specific comparisons, with the difficulty to separate differences due to morphology and due to motivation and migration strategies (La Sorte et al. 2013, Nilsson et al. 2014). Assessing consistency and plasticity in migratory traits between LDM and SDM populations within the same species that may express dissimilarities in the leeway of annual schedules therefore

seems essential to understand the evolution and ontogeny of migratory strategies.

Because the migration period combines the migratory journey with stopovers, the total migration speed (defined as the total distance covered divided by the total duration of travel, including time spent at stopovers; Nilsson et al. 2013) is not only determined by the flight speed but also largely by the time spent at stopover sites (Piersma and Baker 2000, Nilsson et al. 2013). This was clearly demonstrated in greater white-fronted geese *Anser albifrons* migrating between western Europe and Russia, where seasonal differences in migration speed are dictated mainly by different decision rules on the use of stopovers rather than flight speed that remained fairly constant (Kölzsch et al. 2016). Adjustments in stop-over schedules seem to act as a major determinant of seasonal difference in total migration speed, representing a primary mechanism for ensuring timely arrival (Schmaljohann 2018).

When a certain species, population or individual must travel longer distances, we expect more stringent constraints on the migratory distance to be covered (Shamoun-Baranes et al. 2017). However, for some versatile flyers like gulls, able to exploit atmospheric updrafts as well as to migrate through adverse weather in active flight, the distance might not necessarily represent a major constraint (Shamoun-Baranes et al. 2017). On the other hand, a journey of several thousand km requires stamina and a fine management of energy reserves (Drent et al. 2003). A solution for migrants to increase flight speed and/or reduce costs of flight and save fuel, is to get assistance from wind by selecting tailwinds and avoiding headwinds (Vansteelant et al. 2017b).

But how are LDMs most likely to deal with the challenge of travelling longer distances than SDMs? As the distance to be covered is larger, LDM are supposed to suffer stronger constraints than SDM, having limited leeway in their annual schedules to linger. Therefore, LDM are hypothesized to increase their total migration speed, to reach their destination as fast as possible, particularly in pre-nuptial migration (La Sorte et al. 2013, Nilsson et al. 2013, Dodge et al. 2014). Because of their time constraint, most LDM birds do not have the possibility to wait for favourable wind conditions, but rather have no other choice than to travel even when conditions are relatively poor (Thorup et al. 2006). While some LDM species may be able to advance their departure to arrive on time at destination, others like geese or waders must wait for specific environmental features (e.g. food resources to fuel or wind assistance) only available at specific seasons to time their departure (Piersma et al. 2005, Duriez et al. 2009). On the other hand, if SDM are more flexible in their timing, they may be more prone to travel slowly and to minimize energy expenditure and risks, by using several stopovers, particularly in adverse weather conditions when they can stop and wait for the most favourable conditions. The little data available on SDM seems to confirm this pattern (e.g. common buzzard *Buteo buteo*; Strandberg et al. 2009a, lesser black-backed gull *Larus fuscus*; Klaassen et al. 2011). The

ability of SDMs to quickly react to local weather conditions has been demonstrated also for raptor species: for example, a rapid phenological response in the postnuptial migration timing has been recorded in relation to the thermal regime (Jaffré et al. 2013). Overall, SDMs are expected to reduce the various risks encountered during migration by choosing the safest route under the safest conditions (e.g. avoiding ecological barriers and/or adverse weather), whereas LDM should take more risks to travel fast (Harel et al. 2016a).

We studied the migration strategies in autumn regarding flight speed and the use of stopovers in a migratory raptor, the osprey *Pandion haliaetus*, in two latitudinally separated breeding populations in the Western Palearctic. Osprey populations from northern Europe typically perform long-distance migratory journeys towards sub-Saharan wintering grounds, using a combined strategy made up by fly-and-forage bouts and stop-overs (Hake et al. 2001, Alerstam et al. 2006, Strandberg and Alerstam 2007, Klaassen et al. 2008, Bai and Schmidt 2011). In contrast, osprey populations living in southern Europe, around the Mediterranean basin, are mostly resident or short distance migrants, departing from islands such as Corsica or Balearics, towards wintering grounds along Mediterranean shores (Monti et al. 2014, 2018).

Because of the likely difference in time restriction (see above) between Mediterranean birds (SDM) compared to northern birds (LDM), we tested three predictions regarding their migration strategy.

Our primary prediction concerns the use of stopovers and migration routes. Because ospreys cannot perch when crossing the sea (feathers are only partly waterproof, and do not allow to remain floating in the water for a long time), individuals that breed on islands might have limited possibilities to use stopovers. Thus, we expected SDM birds to use fewer stopovers than LDM and fly larger distances between stopovers, including large sea-tracts. However, the time spent at stopovers may differ between populations, and the total time spent at stopovers may consist of long stays at few stopovers or short stays at numerous stopovers. If SDM birds are more selective in their choice of wind assistance, we predict that they may use more stopovers per unit distance, or stay longer at each stopover, to wait for the optimal weather conditions.

Second, because of the limited leeway in time schedules, we predict that LDM birds who cover greater daily distances would yield faster total migration speed compared to SDM birds that are less affected by time restriction. Furthermore, individual experience may also affect migration strategy (Senner et al. 2015, Vansteelant et al. 2017a). Because ospreys are highly faithful to their wintering site (Poole 1989), adult birds who know their final destination have a clear goal in mind, while juvenile birds are naïve and may try several stopover sites before deciding where to spend the winter. Experienced adults should also possess enhanced flight skills, especially when meteorological conditions are challenging (Hake et al. 2003, Thorup et al. 2003, Harel et al. 2016b,

Vansteelant et al. 2017a). Hence, we expected the total migration speed to be higher in adult birds than in juveniles. Finally, our third prediction concerned variation in flight speed between populations. As wind is known to be the most important factor affecting flight performance (Kemp et al. 2012b, Mellone et al. 2012, Shepard et al. 2016, Vansteelant et al. 2016), we hypothesized that ospreys from both populations would try to take advantage of wind assistance, but for different reasons. SDM birds, not constrained by time but by the necessity to cross large sea tracts, would select the best wind conditions for their migratory flight. On the other hand, LDM birds, more constrained by time and distance to cover should be less selective than SDM with respect to wind conditions. Furthermore, within each population, we expect experienced adults to perform better than juveniles at selecting favourable winds and thermal currents (Harel et al. 2016b), thereby flying at greater cross-country speeds.

Material and methods

Birds and tracking technologies

Overall, our dataset included 43 migratory ospreys from the Western Palearctic (Supplementary material Appendix 1). In Sweden, adult and juvenile birds were fitted with 45-g Solar Argos/GPS PTT-100s (Microwave Telemetry, Columbia, USA) at their breeding sites (Grimsö or Ivosjön region). All birds were trapped with a clap net or a noose-carpet mounted on the nest. Tracking devices were attached with a harness as backpacks; further details on trapping and tagging methods are available in Hake et al. (2001) and Klaassen et al. (2008). For our study, we re-analysed tracks from 3 adult ospreys previously published by Klaassen et al. (2008) and added new data for 3 other adults and 12 juvenile individuals tagged between 2006 and 2011. The complete Swedish dataset included 18 birds, 6 adults (3 males, 3 females) and 12 juveniles (undetermined sex).

In the Mediterranean, the dataset included 7 adults and 18 juveniles that behaved as SDMs. The 7 adult ospreys were caught between 2009 and 2013 in two regions. In Mallorca (Balearic Islands, Spain), one adult was trapped using a perch-trap in July 2009 and fitted with 30-g Solar Argos/GPS PTT-100s. In Corsica (France), six adults (5 females and 1 male) were caught in March–April 2013, using a noose carpet laid on the nest before egg laying. Eighteen juvenile ospreys (9 from Balearics islands, 8 from Corsica and 5 from Italy) were fitted with GPS tags during ringing actions before or shortly after fledging at their nesting sites in June–July 2013 and 2014. Except 3 juveniles from Balearics in 2000 that were equipped with Argos PTT-100s (Supplementary material Appendix 1), all other juveniles from Mediterranean were equipped with a 24-g solar powered GPS/GSM tag (model Duck-4, Ecotone, Poland). All birds from Mediterranean had their tag attached as

backpack with a harness made of 7-mm-wide Teflon ribbon (Kenward et al. 2001).

All devices were programmed to record positions at hourly intervals. Argos/GPS PTT tags provided data on latitude, longitude, altitude, instantaneous groundspeed. GPS-GSM tags only contained data of latitude and longitude. In all cases, the mass of the equipment never exceeded 3% of bird body masses. All birds were color ringed, measured, and adults only were sexed based on size and plumage and/or using molecular sexing (Griffiths et al. 1998).

Tracking data processing for migration speed and stopover use

For each bird, the onset of autumn migration was defined as the last GPS position at the breeding site and the end of migration as the first GPS position at destination (for details see Monti et al. 2018). We defined a migratory bout only when hourly locations were spaced by a minimum of 10 km (Sergio et al. 2014), to avoid the inclusion of local movements between nocturnal roosts, and to exclude possible prospections for feeding places along the way. A stopover site was defined as an area where a bird spent more than 24 h during the migration journey (following Strandberg et al. 2008 and Limiñana et al. 2012).

Migratory tracks were imported into ArcGis 9.3. We calculated: a) the total duration of migration (as days elapsed between the first and the last fix of the migratory journey); b) the daily distance travelled during migration days (as cumulative distances between fixes expressed in km); c) the total cumulative distance of migration (km), as the sum of total daily distances during travel days (cumulative distances), excluding movements at stopover sites and both pre- and post-migratory movements (following Strandberg et al. 2008; see definitions in next paragraph and also Monti et al. 2018); d) the total migration speed (in km d^{-1}) as total cumulative distance of migration divided by total duration of migration, including stopovers; e) the direct migration distance (km) between nest and wintering site (great circle); f) the straightness of the migration path (hereafter 'path straightness index'), calculated as the ratio of the total cumulative distance of migration to the direct migration distance; g) the total stopover duration (duration of stay, in days); h) the number of stopover sites used; and i) the mean distance between each stopover site (km).

Pre- and post-migratory movements through a secondary site are different in timing and distance compared to migratory movements (Monti et al. 2018) and have been described also for other raptor species (e.g. marsh harrier *Circus aeruginosus*; Strandberg et al. 2008). In the present study for most adults, we considered that migration started from this secondary site instead as from the nest. Because a few failed breeders joined this site just after failure, sometimes 2–3 months before the migration period, we preferred to consider this site as part of the home range in the breeding ground rather than a stopover site.

Flight data analyses

To compare flight performance of individuals from both populations across the same habitat matrix and wind conditions, we selected a geographic area between 25°N and 45°N of latitude and 25°W and 20°E of longitude, including the Mediterranean area from southern France to northern Sahara in Morocco.

We only considered hourly segments to avoid possible effects of variation in segment lengths (Tanferna et al. 2012), separating hourly segments travelled over sea to those over land (and excluding the few segments containing both land and sea). We computed average cross-country speeds (calculated as the number of km between two sequential points divided by the time between two consecutive fixes) for adults and juveniles for tracks over land and at sea. On land, we excluded local movements at stopovers to consider only genuine migration segments.

We estimated wind-assistance by interpolating tracks with the package 'RNCEP' (Kemp et al. 2012a) using weather data from the NCEP/NCAR Reanalysis project (Kalnay et al. 1996) and the NCEP/DOE reanalysis II dataset (Kanamitsu et al. 2002; <www.cdc.noaa.gov>). For each point of the track we downloaded the -u (west-east) and -v (south-north) wind components, which were combined in a single wind vector incorporating the strength and the direction of the wind, from which we obtained a tailwind component (following Kemp et al. 2012b). For tracks over land, wind data were extracted for a pressure level of 925 hPa, which corresponds to an altitude of ca 750 m a.s.l., i.e. the altitude at which ospreys have usually been measured to migrate (Klaassen et al. 2011). For locations over the sea a pressure level of 1000 hPa (corresponding to 110 m a.s.l.) was set, corresponding to mean flight altitudes that were recorded using PTT-100s. We computed flight airspeed, which is the speed realized by birds relative to the air when in flight (taking account to the effect of winds). Airspeed was calculated by subtraction of the wind vector from the track vector (track direction, cross-country speed) of the bird (following Kemp et al. 2012b and Nilsson et al. 2014).

Statistical analyses

We evaluated the effects of population (SDM vs LDM) and age on migratory components of autumn migration through GLMMs (using the 'lme4' package: Crawley 2007). We included 'individual' and 'year' as random effects; 'population', 'age' and their interaction were included as fixed effects.

To compare flight performances, differences in cross-country speeds, tailwinds and airspeeds were tested with GLMMs, with 'individual' and 'year' included as random effects, and 'population', 'age', and 'habitat' (sea vs land) as fixed effects.

We initially computed global models, including all considered predictors. We selected among all models using the 'dredge' function in the R package 'MuMIn' (Bartoń 2012), fitting all possible models and using the maximum likelihood

estimator (Zuur et al. 2009). Model selection used the Akaike's information criterion corrected for small sample sizes (AICc) to fit for each response variable. Models were retained for inference if they had $\Delta\text{AICc} \leq 2$ units, and if their AICc value was lower than that of any simpler, nested alternative (Richards 2008, Richards et al. 2011). Model coefficients were estimated using the 'confint' function, after averaging across the top models (using the model.avg function in R; Bartoń 2012). All statistical analyses were conducted in R (R Core Development Team). Other results are reported as mean \pm standard deviations.

Data accessibility

All GPS data analysed in this study can be consulted in the Movebank database (<www.movebank.org>). Project study names are: 1) osprey (A), southern Sweden; 2) osprey (B), southern Sweden; 3) osprey in Mediterranean (Corsica, Italy, Balearics).

Results

Forty-three ospreys were GPS-tracked, among which 7 individuals have been tracked over multiple (2–4) seasons (Fig. 1a–b; Supplementary material Appendix 1). Thus, the entire dataset included 54 migratory tracks in autumn, whereby 88.8% were complete (Supplementary material Appendix 1). All seven adult birds tracked for more than one year returned to the same breeding ground, stop-overs and wintering ground during successive years. In six cases transmission stopped due to devices' malfunctioning and/or data transmitting failures, resulting in migratory data being partially available. According to the available data these incomplete tracks were only partially included in the analyses.

Migratory components

Total cumulative migration distances of Swedish ospreys (all LDMs) were about five times greater than those covered by Mediterranean ospreys (SDMs) (Fig. 2a; Table 1; Supplementary material Appendix 3). The mean direct migration distance was 1.2 and 1.8 times higher in adults than in juveniles for LDM and SDM birds, respectively (Table 1; Supplementary material Appendix 3). Despite this, the mean cumulative distance (the real distance covered during the migratory journey) differed only by ca 300 km between adults and juveniles, for both populations (Fig. 2a). Path straightness index was highest in adults (especially in LDMs, but also in SDMs) and significantly lower for juveniles (Fig. 2e; Table 1; Supplementary material Appendix 3). Duration of migration lasted 61.0 ± 17.8 d for LDMs and only 5.1 ± 2.5 d for SDM birds (Fig. 2b). The duration of migration was slightly longer in juveniles than adults in both populations (Table 1; Supplementary material Appendix 3).

The total migration speed of LDM birds was 2.4 times slower than that of SDMs (107.85 ± 26.47 km d⁻¹ vs 259.48

± 144.0 km d⁻¹ respectively) and this difference was more pronounced when comparing adults (3.2 times slower in LDM). Adults migrated faster than juveniles in SDMs but not in LDMs (Fig. 2c; Table 1; Supplementary material Appendix 3).

Daily distances travelled did not significantly differ between populations (LDM = 202.4 ± 41.1 km d⁻¹; SDM = 211.4 ± 87.7 km d⁻¹). Adults travelled 33% faster than juveniles (adults = 226.7 ± 78.1 km d⁻¹ vs juveniles = 184.9 ± 50.8 km d⁻¹): this difference in age was prominent especially for SDM, but not for LDM birds (Fig. 2d; Table 1; Supplementary material Appendix 3).

Stopovers and route chosen

During autumn migration, LDM ospreys stopped 30 d longer than SDM ospreys (Fig. 1c–d). Time spent at stop-over sites accounted for the 50% of the migration duration in LDM (31.5 ± 13.3 d; Fig. 1c; Fig. 2f). Juveniles stopped for 6 d more than adults (Fig. 2b). LDMs used on average 2.3 ± 1.04 stopovers (range: 1–5) (Fig. 1c; Fig. 2g; Table 1; Supplementary material Appendix 2). Stopovers were mainly located in central Europe (e.g. France and Germany for the first stopover – STP1) and south of the Mediterranean region (southern Spain or north Africa for the second stopover – STP2). Direct distance between the breeding site and the STP1 was 791.02 ± 521.3 km, whereas the average distance between STP1 and STP2 was of 943.08 ± 841.3 km (Supplementary material Appendix 2).

Migratory paths of adult LDM ospreys in the Mediterranean region were mainly drawn over land, whereas sea-crossing was reduced by funnelling through the shortest passage at Gibraltar Strait (Fig. 1a). Juveniles LDM showed a broader migration front compared to adults (Fig. 1a): three individuals travelled south-west along the same routes of adults (via Gibraltar), whilst four others travelled south via the central Mediterranean (e.g. passing through Italy).

Among Mediterranean ospreys, 80% of SDM migrated without stopover, while the 20% remaining stopped on average for 2 ± 0.7 d at one stopover (Fig. 1d; Fig. 2f; Supplementary material Appendix 1, 2). Mediterranean ospreys were able to cover long distances over open sea (mean = 430.37 ± 269.3 km, range: 86.84–1023.51 km; n = 15 tracks), performing non-stop movements lasting 10.4 ± 7.6 h (range: 3–25 h), sometimes continued overnight.

Flight speed and wind assistance

Within the Mediterranean region (between 25°N–45°N of latitude and 25°W–20°E of longitude), the average cross-country speed of migrating ospreys was similar between populations (mean: 30.7 ± 11.7 km h⁻¹), but significantly different between marine vs terrestrial ecosystems. Cross-country speed was in average 10 km h⁻¹ higher during sea-crossing than over land (Fig. 3a: sea = 38.2 ± 11.3 km h⁻¹ vs land = 29.8 ± 11.5 km h⁻¹). Both LDM and SDM birds benefitted from favourable tailwinds over both habitats,

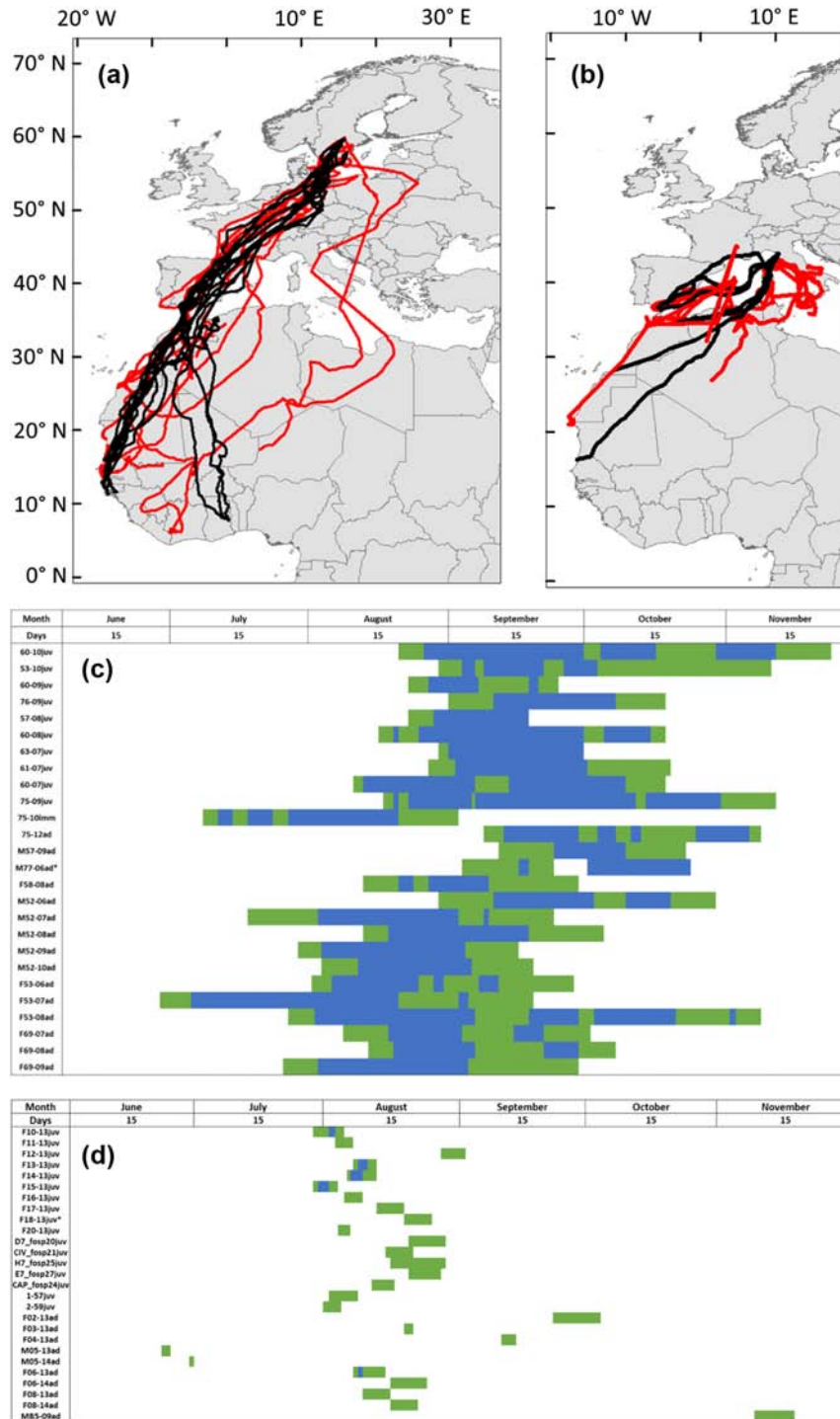


Figure 1. Spatial and temporal migratory patterns of individual ospreys. Maps show autumn migration of (a) LDM ospreys from Sweden, and of (b) SDM ospreys from Mediterranean (adults in black and juveniles in red). Timelines during autumn migration of (c) LDM ospreys and (d) SDM ospreys (green and blue colours indicate travel and stopover days, respectively; each individual track is specified in rows by its ring, year of tracking and age).

though wind assistance increased by 4 km h^{-1} at sea compared to land (Fig. 3b). Airspeeds were generally 5 km h^{-1} higher during sea-crossing compared to land in both populations (Fig. 3c).

Lower cross-country speeds values were associated to SDM juveniles (Fig. 3a; Table 2; Supplementary material Appendix 4). SDM juveniles experienced worse tailwinds, while LDM juveniles benefitted from better wind assistance (Table 2;

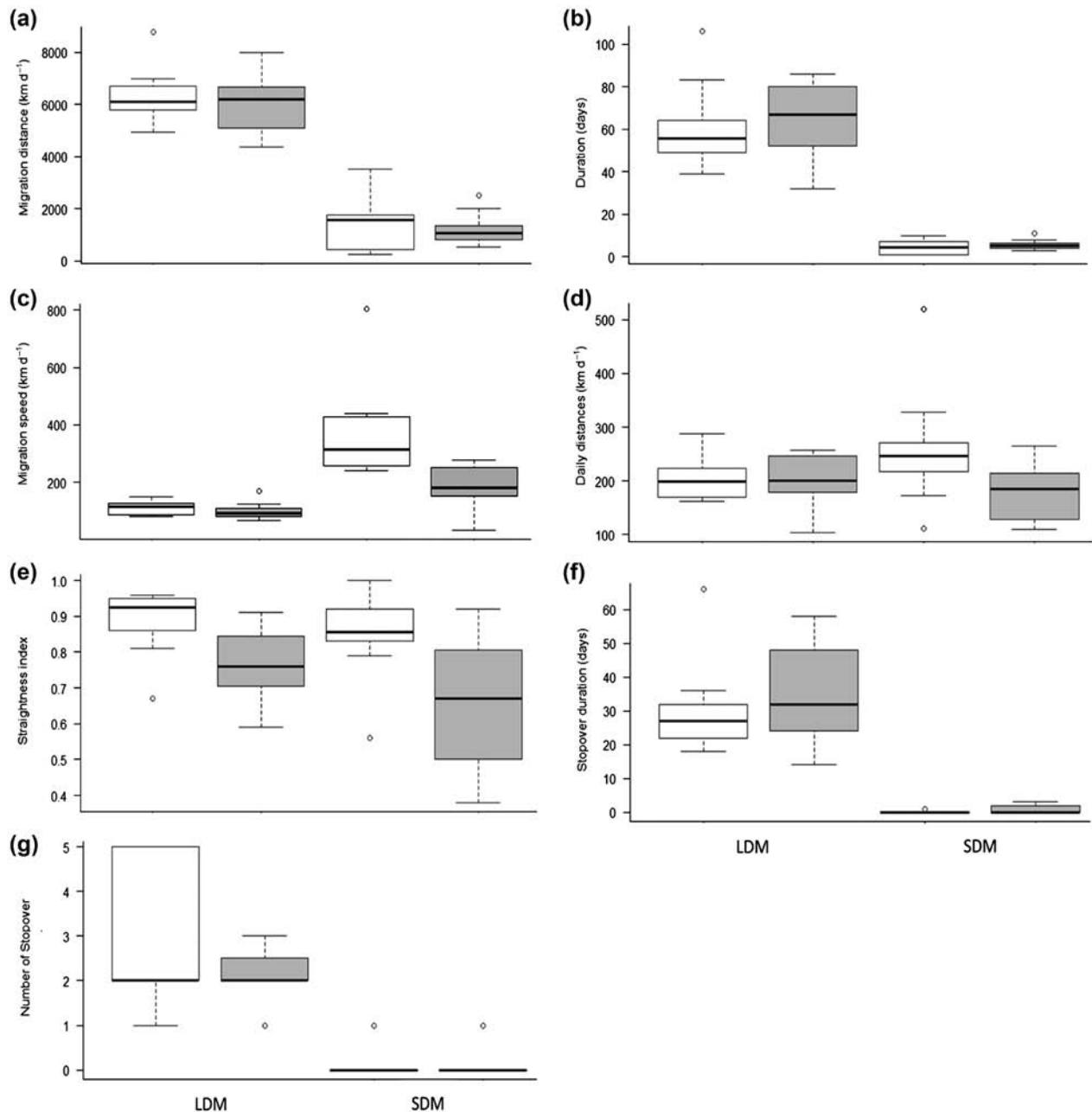


Figure 2. Main migration components in autumn for ospreys originating from Sweden (long-distance migrants – LDM) and Mediterranean (short distance migrants – SDM): (a) cumulative migration distance, (b) duration of migration, (c) total migration speed, (d) daily distances travelled, (e) path straightness index, (f) stopover duration and (g) number of stopovers. Adult and juvenile birds are represented by white and grey boxplots, respectively (refer also to Supplementary material Appendix 1).

Supplementary material Appendix 4) and had lower airspeeds at sea (Table 2; Supplementary material Appendix 4).

Discussion

Ospreys breeding at different latitudes in the Western Palearctic used different migration strategies, probably evolved as a response to different ecological conditions encountered en route. Osprey display a leap-frog migration

system, with populations breeding at higher latitudes overpassing the latitudes where southern populations live, as described also for other raptor species in the Western Palearctic (such as in the kestrel (Wallin et al. 1987) and in the marsh harrier (Panuccio et al. 2013)). Interestingly, this implies that northern birds have to cross the Sahara Desert, a major ecological barrier that the Mediterranean ospreys do not have to confront, as already postulated in other species (Drent and Piersma 1990).

Table 1. Results of model selection of GLMM on the effects of population and age on components of autumn migration of Swedish (LDM) and Mediterranean (SDM) ospreys. Selected models are shown in bold and the sample size is the number of migratory tracks.

Response variable (sample size)	Model	Variables retained	K	logLik	AICc	Δ AICc	Weight
Migration duration (47)	1	Population	5	-182.182	375.800	0.00	0.687
	2	Population + Age	6	-181.900	377.90	2.07	0.244
	3	Population + Age + Population \times Age	7	-181.763	380.4	4.57	0.070
	4	Null	4	-203.086	415.1	39.30	0.00
	5	Age	5	-202.564	416.6	40.76	0.00
Cumulative migration distance (47)	1	Population	5	-381.259	774.000	0.00	0.662
	2	Population + Age	6	-380.888	775.900	0.18	0.257
	3	Population + Age + Population \times Age	7	-380.651	778.2	4.19	0.081
	4	Null	4	-397.567	804.1	30.10	0.00
	5	Age	5	-397.508	806.5	32.50	0.00
Total migration speed (47)	1	Population + Age + Population \times Age	7	-265.710	548.300	0.00	0.995
	2	Population + Age	6	-272.859	559.8	11.52	0.003
	3	Population	5	-274.783	561.0	12.74	0.002
	4	Null	4	-278.888	566.7	18.43	0.00
	5	Age	5	-278.141	567.7	19.45	0.00
Direct migration distance (47)	1	Population + Age + Population \times Age	7	-346.769	710.300	0.00	0.665
	2	Population	5	-350.381	712.200	1.85	0.263
	3	Population + Age	6	-350.365	714.8	4.44	0.072
	4	Age	5	-371.290	754.0	43.67	0.00
	5	Null	4	374.348	757.6	47.29	0.00
Path straightness index (47)	1	Population + Age	6	34.684	-55.300	0.00	0.463
	2	Age	5	33.043	-54.600	0.65	0.335
	3	Population + Age + Population \times Age	7	35.154	-53.400	0.18	0.185
	4	Population	5	29.689	-47.90	7.35	0.012
	5	Null	4	27.666	-46.40	8.89	0.005
Daily distance travelled (45)	1	Population + Age + Population \times Age	7	-248.799	514.600	0.00	0.592
	2	Age	5	-251.912	515.400	0.74	0.408
	3	Population + Age	6	-251.376	517.0	2.34	0.131
	4	Null	4	-254.098	517.2	2.57	0.117
	5	Population	5	-254.001	519.5	4.92	0.036
Stopover duration (45)	1	Population	5	-162.299	336.100	0.00	0.695
	2	Population + Age	6	-161.790	337.800	1.66	0.305
	3	Population + Age + Population \times Age	7	-161.354	339.7	3.60	0.103
	4	Null	4	-177.868	364.7	28.60	0.000
	5	Population	5	-177.085	365.7	29.57	0.000
Number of stopovers (48)	1	Population	5	-61.521	134.500	0.00	0.716
	2	Population + Age	6	-61.464	137.0	2.51	0.205
	3	Population + Age + Population \times Age	7	-61.054	138.9	4.44	0.078
	4	Null	4	-69.435	147.8	13.33	0.001
	5	Age	5	-69.369	150.2	15.70	0.000
Mean distance BS_STP1 (31)	1	Age	5	-232.579	477.6	0.00	0.394
	2	Population	5	-233.238	478.9	1.32	0.204
	3	Null	4	-234.765	479.1	1.51	0.185
	4	Population + Age	6	-231.793	479.1	1.53	0.183
	5	Population + Age + Population \times Age	7	-231.790	482.4	4.89	0.034
Mean distance STPlast_WG (26)	1	Population	5	-217.687	448.4	0.00	0.536
	2	Population + Age	6	-216.677	449.8	1.40	0.266
	3	Age	5	-219.199	451.4	3.02	0.118
	4	Population + Age + Population \times Age	7	-216.643	453.5	5.13	0.041
	5	Null	4	-221.854	453.6	5.24	0.039

Though Swedish LDM ospreys travelled distances five times larger than their SDM Mediterranean counterparts, their total migration speed was 2.4 times slower compared to SDMs. The main difference in total migration speed was due to a greater use of stopovers (both in number of stopovers and duration of stay at stopover) by LDMs compared to SDMs. Further, although both populations largely benefitted from wind assistance across their journey, experienced adults

performed better than juveniles at selecting favourable winds, as expected.

Migratory strategies and the use of stopovers

Although sharing the same east-Atlantic flyway, LDM and SDM osprey populations used different migratory strategies. Similarly in North America, LDM ospreys tracked from

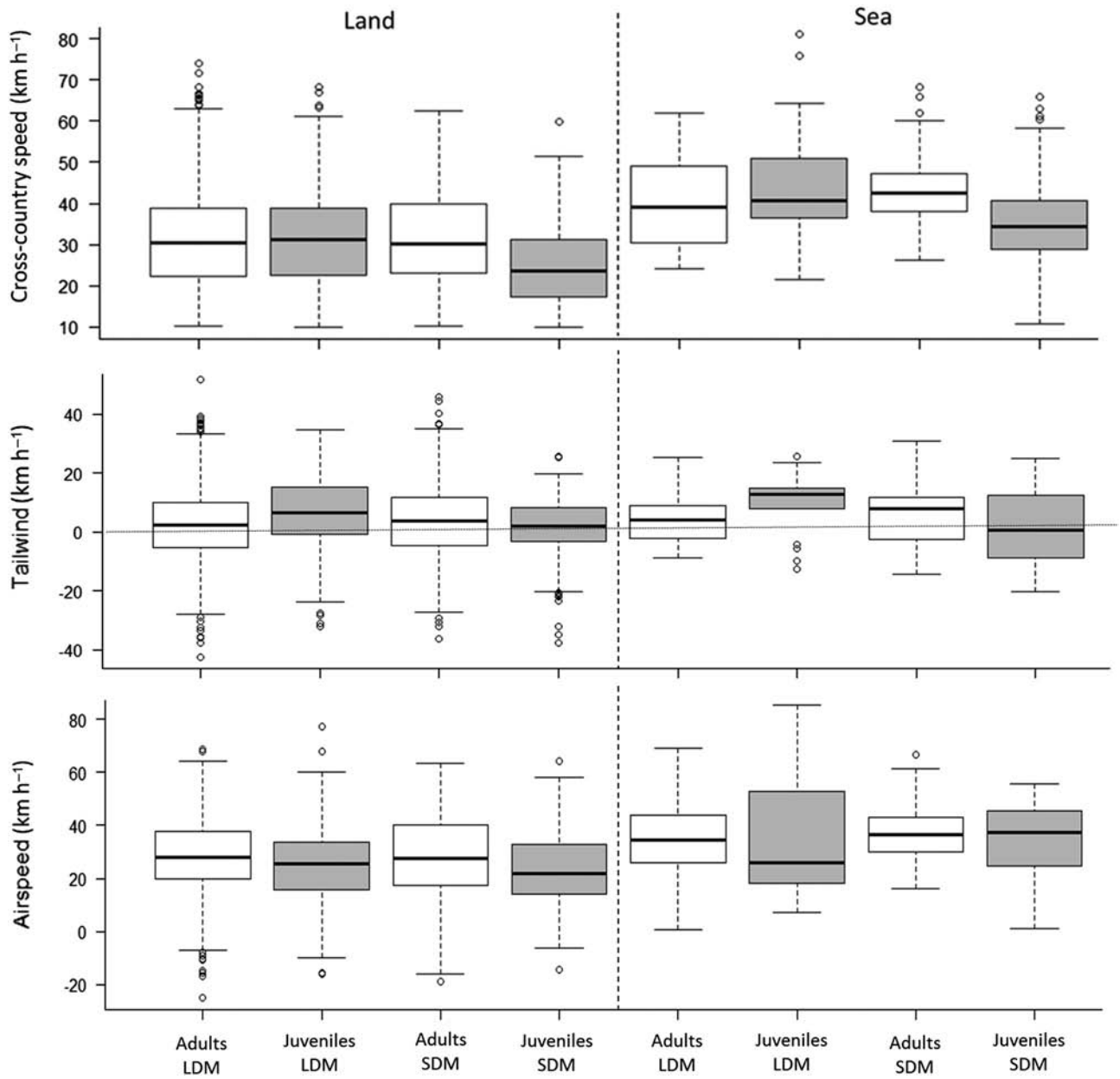


Figure 3. Flight parameters: cross-country speed, tailwind and airspeed for adults (white) and juveniles (grey) of both LDM and SDM ospreys. Values have been computed for both tracks over land and over sea.

three populations across a longitudinal gradient displayed population-specific migration strategies, in terms of both the flyways that were used and the amount of stop-overs and total

time spent at stop-overs (Martell et al. 2014). However, the latter study mostly compared the timing of migration rather than migration speed and/or use of stopovers; also, it did

Table 2. Summaries of selected models of GLMM on the effects of population, habitat and age on flight performances (cross-country speed, tailwind and airspeed, all units are in km h^{-1}) of migrating ospreys crossing the Mediterranean region. The complete model selection is reported in Supplementary material Appendix 1–4.

Response variable	Model	Model retained	K	logLik	AICc	ΔAICc	Weight
Cross-country speed (1906)	Best	Population+Habitat+Age, Population \times Age	8	-7276.12	14568.31	0.00	0.51
Tailwind (1642)	Best	Population+Habitat+Age, Population \times Age, Habitat \times Age	9	-6346.16	12710.44	0.00	0.33
	Second	Population+Habitat+Age, Population \times Age	8	-6347.97	12712.02	1.58	0.15
Airspeed (1642)	Best	Population+Habitat+Age, Habitat \times Age	8	-6562.54	13141.17	0.00	0.29
	Second	Habitat+Age, Habitat \times Age	7	-6564.48	13143.02	1.85	0.12

not include a population of SDM osprey, as those nesting in Florida (Washburn et al. 2014), that would have allowed direct comparison with our study. Most relevant is the study on migration of turkey vultures *Cathartes aura* comparing four populations of SDM and LDM (Dodge et al. 2014). The population of SDM vultures (breeding and wintering at the east coast of USA) spent almost the same duration in migration as LDM vultures, but their total migration speed was significantly slower, due to slower cross-country speed and reduced time in active movement per day (Dodge et al. 2014). Thus, it seems that SDM turkey vultures reduced their total migration speed compared to LDMs, by reducing flight speed rather than staying longer at stopovers, similar to passerines (La Sorte et al. 2013), but opposite to west-European ospreys.

Interestingly, the mean distance between stopovers recorded for LDM ospreys while crossing Europe, is similar to the whole migration distance covered by SDM ospreys. This suggests that: a) osprey from both populations can travel approximately 1000 km with limited need to refuel or rest at a stopover; and/or that b) Mediterranean osprey may choose their destination (wintering site) in order to stay within the physiological limit of 1000 flown km, in order to reduce the need of using stopovers which are scarce along their route (e.g. large open sea tracts between islands). Testing these premises would require more detailed behavioural studies during stopovers and at night-time roost, to understand whether osprey feed, or only rest, during overnight stops.

Routes chosen and barrier crossing

Crossing geographical barriers generally requires prolonged effort and high energy expenditure, due to the use of continuous flapping flight or absence of feeding and resting opportunities over long distances. Therefore, birds need to build physiological adaptations and refuel at stopover sites before departure (e.g. red knot *Calidris canutus*; Alerstam and Lindström 1990, Piersma and van Gils 2010). Flapping flight is the most energy demanding activity for large raptors, which prefer to use the more economic soaring-gliding flight using thermal ascending currents (Duriez et al. 2014). For these species, crossing the sea certainly represents a greater challenge than crossing a desert because thermal ascending currents are mostly generated over land during daylight at temperate latitudes (Kerlinger 1989, Strandberg et al. 2008, Chevallier et al. 2010). Thus, some large raptors avoid crossing large water bodies and tend to concentrate at narrow straits (e.g. short-toed eagle *Circaetus gallicus*; Mellone et al. 2011, 2015, Panuccio et al. 2012; oriental honey-buzzard *Pernis ptilorhyncus*; Yamaguchi et al. 2008; lesser spotted eagle *Clanga pomarina*; Meyburg et al. 2017). When long sea-crossing cannot be avoided, raptors need to rely on large fuel stores and/or on favorable tailwind (Nourani et al. 2018). The migratory strategy of osprey appears less rigid than in most raptors. The journeys of Swedish LDM ospreys were mainly performed over land, and water-crossing was reduced by travelling along the Spanish coast (Klaassen et al. 2008; but see

Strandberg et al. 2009b). Mediterranean SDM ospreys were able to cover long distances over open sea, as already observed in other osprey populations (DeCandido et al. 2006). The duration of flights over sea recorded for Mediterranean ospreys suggests that these birds build fat stores before departure. This hypothesis is supported by the observation that most SDM Mediterranean individuals performed pre-migratory movements to a secondary feeding site, several dozen of km from their nest (Monti et al. 2018). The function of such movements might be related to the necessity of building fat stores before crossing the barrier and/or to wait for favourable weather conditions.

To face sea crossing in absence of thermals, Mediterranean ospreys probably adopted an active flapping flight, as suggested by higher airspeeds over sea than on land, and partially benefited from the use of tailwinds. The lower flight airspeeds recorded over land may be explained by the time spent in thermals, when birds gain height at the expense of horizontal distance, and the zig-zag track generated by the drift often observed when birds are soaring in thermal when wind direction is different than track direction, resulting in a reduced hourly distance travelled over land (e.g. flexibility of flight behaviour; Horvitz et al. 2014, Vansteelant et al. 2017b).

Our results showed that the migratory behaviour of Mediterranean ospreys is highly flexible and can be adapted to local circumstances. Since distances to wintering sites are short and relatively little time is required for migration, individuals can choose to cross the sea in case of favourable winds, otherwise selecting a safer but longer route over land. Similar strategies have been observed in North American ospreys in spring migration from South America, which may choose to cross the Gulf of Mexico or detour along the coast of Mexico and Texas (Martell et al. 2014).

As they only have a short migration ahead, SDM ospreys can probably decide to invest their energy stores in active flight over sea for a reduced time. On the contrary, LDM birds that must engage in a longer migration and have little leeway in their schedules, rather choose a risk-averse option of saving energy by using thermals over land instead of crossing the sea by active flapping flight. However, LDM ospreys tracked from more eastern populations (e.g. Germany, Finland, Estonia: Väli and Sellis 2016) can migrate over the Mediterranean Sea in autumn: in this sense they would differ from LDM ospreys from Sweden. So, these results may not necessarily be generalized for all LDM ospreys.

To better understand the costs and benefits of each migratory strategies, future studies should also use accelerometry and magnetometry to record behaviour, to help distinguish time spent in flapping flight versus soaring-gliding flight during each migratory bout (Williams et al. 2015, 2017), and estimate an energy budget for each migratory strategy (Duriez et al. 2014, Rotics et al. 2017).

Age variation in migratory performances

The development of migratory behaviour is a process being promoted by individual improvements related to age and

experience (Sergio et al. 2014). Previous studies highlighted how differences in age classes and experience play an important role in shaping migratory decisions and flight performances (Hake et al. 2003, Péron and Grémillet 2013, Thorup et al. 2013, Sergio et al. 2014, Harel et al. 2016b). Accordingly, we found that adults travelled faster and showed straighter migratory paths than juveniles, which conversely displayed a greater variance in the major axis of migration. As we hypothesized, this suggests that adults can rely on their experience from previous years to reach a precise goal, while strong divergence of juveniles suggests strong influence of sidewinds on migratory route of naïve juveniles. Similarly, Vansteelant et al. (2017a) showed how wind conditions alone account for more than half of the longitudinal spread in juvenile honey buzzards migrating for the first time. Similar differences between adults and juveniles were also observed in flight performances when crossing the sea: juveniles showing reduced speeds compared to adults and experiencing reduced tailwinds. Mediterranean SDM juveniles in particular were probably affected by the fact that their first long movements after fledging immediately entail a sea-crossing (compared with LDM juveniles who started migration over land). In general, lower flight performances in juveniles appeared to be related to a limited experience in using thermals (on land) or in choosing favourable wind currents (Klaassen et al. 2011, Vansteelant et al. 2017b).

Conclusion

All Swedish ospreys were LDMs, wintering in tropical west Africa. In contrast, the Mediterranean population showed a heterogeneous migratory behaviour, with high levels of variability in migratory routes (and direction of movements) and wintering grounds. The two populations clearly differed with respect to both temporal (total migration speed and use of stopover) and spatial (propensity to sea-crossing) components of migration strategy, based on average migration performances for the two populations.

How did such differences evolve during the evolutionary history of the species/populations? It is challenging to understand to what degree population differences are based on genetic influences on reaction norms and/or on individual adaptive flexibility/learning (i.e. ontogenetic perspective), respectively. In this case, these differences seem not to be 'hard-wired' by population-specific genetic constraints in behaviour, since individual flexibility is large enough to include e.g. high migration speed/little stopover use and wide sea-crossing among individuals of both populations (as recorded also in previous studies: Hake et al. 2001, Alerstam et al. 2006). Probably, it is a matter of genetic modification of reaction norms between the two populations, whereby the repertoires of reactions are similarly variable but responses to environmental situations differ across populations. Some of the population differences may also arise through adaptive flexibility and learning that exist among individuals of both populations.

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Supplementary material (Appendix JAV-01839 at <www.avianbiology.org/appendix/jav-01839>). Appendix 1–4.