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Autumn migration of Ospreys from two distinct populations in Poland reveals partial migratory divide

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Abstract:	Background Long-term ringing and telemetry studies show that the Osprey is a broad-front migrant following different migratory flyways, depending on the geographical location of their breeding populations. We have investigated two distinct and declining populations of Osprey in Poland, separated by only a few hundred kilometres, and hypothesised they may exhibit two different migration routes. We followed mortality causes, comparing them between migration and stationary phases of annual cycle, as well as between two distinct populations. Methods Nineteen Ospreys, both juveniles and adults, were equipped with GPS loggers in 2017-2020 in two populations in western and eastern Poland and followed on their autumn migration. We calculated the distance they covered on the migration, number of stopover days, migration duration, daily distances covered and departure dates to compare them between age and sex classes and between the eastern and western Populations. Results Ospreys from the western and eastern populations showed a partial migratory divide. While the first migrated through a western flyway, the second followed a central flyway, resulting in crossing the Mediterranean Sea in distant passes that affected the distance covered. Annual mortality reached 67-83% in juveniles and as much as 57-71% in adults. Mortality events were balanced between the migration and breeding/wintering periods in the western population, but its rate was higher during migration in the case of the eastern population. Conclusions We showed that two distinct osprey populations in Poland revealed a partial migratory divide, with one showing longer routes and covering greater distances over sea and deserts over the western flyway. This might affect individual survival rates and contribute to a steeper decline in one of the populations. In order for this to be confirmed, more individuals still have to be followed.
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Autumn migration of Ospreys from two distinct populations in Poland reveals partial migratory divide

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ABSTRACT

Background

Long-term ringing and telemetry studies show that the Osprey is a broad-front migrant following different migratory flyways, depending on the geographical location of their breeding populations. We have investigated two distinct and declining populations of Osprey in Poland, separated by only a few hundred kilometres, and hypothesised they may exhibit two different migration routes. We followed mortality causes, comparing them between migration and stationary phases of annual cycle, as well as between two distinct populations.

Methods

Nineteen Ospreys, both juveniles and adults, were equipped with GPS loggers in 2017-2020 in two populations in western and eastern Poland and followed on their autumn migration. We calculated the distance they covered on the migration, number of stopover days, migration duration, daily distances covered and departure dates to compare them between age and sex classes and between the eastern and western Populations.

Results

Ospreys from the western and eastern populations showed a partial migratory divide. While the first migrated through a western flyway, the second followed a central flyway, resulting in crossing the Mediterranean Sea in distant passes that affected the distance covered. Annual mortality reached 67-83% in juveniles and as much as 57-71% in adults. Mortality events were balanced between the migration and breeding/wintering periods in the western population, but its rate was higher during migration in the case of the eastern population.

Conclusions

We showed that two distinct osprey populations in Poland revealed a partial migratory divide, with one showing longer routes and covering greater distances over sea and deserts over the western flyway. This might affect individual survival rates and contribute to a steeper decline in one of the populations. In order for this to be confirmed, more individuals still have to be followed.

Keywords: *Pandion haliaetus*, stopover, GPS telemetry, mortality

BACKGROUND

Revealing bird migration patterns is crucial to understanding the factors limiting populations of long-distance migratory species. Migrations are considered the most dangerous part of the annual cycle and mortality at that time may exceed that of the breeding and wintering periods even six-fold (Klaassen et al. 2014). The differentiation of migration routes between populations is known to affect individuals' survival and, effectually, also whole population trends (Hewson et al. 2016). Therefore, it is justified to investigate migratory behaviour of selected, especially declining, populations of species, although they already seem sufficiently studied. One such extensively studied species is the Osprey *Pandion haliaetus* (see Bierregaard et al. 2014 for summary of migration studies). It is a true cosmopolitan species, considered a long-distance migrant in most of the Northern Hemisphere (Martell et al. 2011, MacKrill 2017), but also a sedentary or partial-migratory species in lower latitudes (Monti et al. 2018a). A great body of studies have shown that Ospreys can migrate in broad-front. A study by Østnes et al. (2019) can serve as a good example of such a flexible migration pattern, where juveniles dispersed in different directions and crossed the Mediterranean Sea at known bottlenecks but also through open sea. On the other hand, depending on the geographical location of populations, Ospreys tend to show some general 'highways' and minor paths (Fig. 1). Individuals from Western Europe (United Kingdom, Germany, Norway and Sweden) were shown to most frequently use (but not exclusively) the western-most

Mediterranean passage through the Iberian Peninsula (Alerstam et al. 2006, Klaassen et al. 2011, Mackrill 2017, Meyburg et al. 2018). This seems logical and, consequently, the Ospreys from eastern Europe (Russia, Baltic countries and some from Finland) passed the Mediterranean Sea along its eastern shore or the Balkan Peninsula (Väli and Sellis 2016, Babushkin et al. 2019, LUOMUS 2020). The central Mediterranean passage through Corsica and Italian Peninsula were used by the Ospreys from central (e.g. Germany) and both, eastern and western Europe, but to a lesser degree. Finally, crossing the sea at its full width without any insurance of peninsulas and islands is also a common phenomenon in the case of this species. However, taking into account that migratory behaviour of soaring raptors, such as the Osprey, is most likely governed by innate mechanism (Väli et al. 2018), resembling the one called 'clock and compass' known from Passerines (Helbig 1996), we can expect that migration direction differs between populations. This assumption is supported by the philopatry phenomenon known to occur in Ospreys (Monti et al. 2018b). In this context, it might be interesting to investigate migration routes of populations in the middle of the range to check if the migration direction exhibits a continuous range or a migratory divide between the eastern and western populations of the species.

The central part of the Osprey's European range shows a break that is further prolonged by the Baltic Sea (Fig. 1). In the eastern part, species range is continuous, while in the western part, the range is fragmented but the population is increasing thanks to conservation efforts (Dennis 2016). However, between the continuous eastern and growing German population, there are small "islands" in this species' range, located in Poland. Both are in decline. Therefore, conservation actions and studies were recently carried out in order to protect this species in its last Polish populations (Anderwald 2017). We have carried out a GPS telemetry study to follow spatial ecology and mortality rates, but also to reveal if those two populations will show contrasting migratory patterns that might affect the more isolated and faster declining eastern population in particular. Taking into account the migration studies conducted so far (Fig. 1) we predict that the eastern and western populations may show a migratory divide and, therefore, might also be subjected to different selective pressure. Thus, our aim was to check whether migration paths and migration patterns differ between the eastern and western populations as well as between different age and sex classes. Also, we followed mortality rates and reasons to reveal the crucial threats for those declining populations and to check if potentially different migratory behaviour might affect it.

METHODS

Study area and bird tagging

The study was carried out in two small, spatially distinct Polish populations, separated by about 235 km (between closest nests). The eastern population forms a small island (only 8-9 pairs in 2020) in the species range, about 200 kilometres from the nearest breeding sites in Lithuania. It is located in the vast Masuria Lakeland area, where Ospreys mostly nest in the interior of large forest complexes. The western population contains about 16 pairs (in 2020) scattered in forests, but some also nesting on electric pylons on farmland. This population is slowly increasing and some exchange of individuals with Ospreys from eastern Germany was observed to occur in both directions.

Tagging was carried out in 2017-2020 and covered both chicks in nests and adults. In the first year, only a single juvenile was equipped with a 30g 'Ornitrack E30' GPS GPRS logger (manufactured by Ornitela Lithuania), while later on 4 individuals were tagged annually in 2018 and 2020 and 10 individuals in 2019, all with 35-40g 'Kite-M' GPS GPRS loggers (manufactured by Ecotone Poland). Well-developed chicks (body mass > 1420 g) were caught in the nests. Adults were caught with large mist nets, provoked by a stuffed white-tailed eagle close to their nests. Devices were mounted on the birds' backs with Teflon ribbon sewn at the sternum with the "Y" method described by Buehler et al. (1995). Data were acquired with a 15-minute interval, on average. Sex was identified according to body mass and biometrics (Poole 1982), although in the case of juveniles, they were treated as possible male and possible female as biometry measurements can sometimes overlap between sexes. In the case of adults, direct observations of behaviour at the nesting site and the extent of the breeding patch were found to be reliable criteria in identifying sex.

Analysis

The onset of autumn migration was determined as a long (over 30 km), directional (straight-line) movement in the southern or south-western direction undertaken over at least two consecutive days. A threshold of a daily distance of 30 km was chosen upon a histogram of daily distance covered during the expected time of migration (August-November). Distance up to 30 km formed a visibly more frequent class, while distances over 30 km were represented with a similar frequency range (Fig. S1). A stopover site was defined as an area where a bird spent more than two consecutive nights in a radius of less than 10 km. The end of autumn migration and beginning of wintering was considered to be the last day of the long, directional movement southwards. Migration direction was measured (in QGIS) as azimuth between location at start of migration and reaching the Mediterranean Sea. At the sea-crossing point, the innate migratory direction might already be distorted by choosing the most convenient site and trying to bypass this barrier, and therefore we measured it at the early migration stage. Mortality was, in most cases, confirmed in the field, while in some cases also assumed if tag of the adult bird showed no movement (further than 150m) for at least 3 weeks or suddenly stopped transmitting and the individual was not recorded (by trail camera / web camera) at its nest in the following breeding season.

Total and daily distance covered by the followed individuals were calculated using the *moveHMM* package (Michelot 2016) in R 4.0.3 and two-point equidistant projection. Straight-line distance was calculated with the same projection in QGIS 3.16. In order to check if sex, age and population had any impact on movement speed, they were used as fixed factors in linear mixed effects models with random effect of individual built into the *lme4* package (Bates 2015) to explain the logarithm of daily distance covered during migration. Stopover days were excluded by limiting the dataset to days with movement over 50 km. Models were built in additive pattern. The best supported model was chosen according to the Akaike Information Criterion (AIC). Models with ΔAIC < 2 were averaged in the *MuMIn* package (Bartoń 2020). In order to check whether migration patterns differed between individuals from the two distinct populations or individuals of different sex and age, departure date, migration duration, migration direction, number of stopover days and distance covered on migration were compared in above-mentioned pairs using the Mann-Whitney test.

RESULTS

Migration routes

Out of nineteen Ospreys tagged with GPS tags, we recorded the autumn migration of twelve: five adults (one for two seasons) and seven juveniles (Tab. 1). The remaining seven died before the onset of migration, juveniles mostly due to Goshawk predation or fell due to unknown reasons still at the nest or in its vicinity. Two adult males died due to poaching and electrocution at the breeding grounds. Unfortunately, three of migrating individuals recorded incomplete tracks, but came far enough to judge their general migration paths (Fig. 2a). The Ospreys showed broad-front migration and crossed th Mediterranean Sea in a vast belt from Gibraltar to the Balkan Peninsula to winter in the central part of Western Africa (Fig. 2a). The only exception was the juvenile that wintered in the Iberian Peninsula (Tab. 1). Some juveniles travelled long distances over open sea, while adults tended to use less hazardous paths along the eastern shore of the Iberian Peninsula, Corsica and Italian Peninsula (Fig. 2b). Ospreys from the eastern and western populations in Poland exhibited a partial migratory divide, with most of the individuals (86%, incl. all juveniles) from the eastern population heading south (azimuth 205.5 ± 16.8) and crossing the Mediterranean Sea at the middle to reach wintering sites in Ghana, Burkina Faso, Nigeria, Angola. On the contrary, most of the individuals (83%) from the western population headed south-west (azimuth 221.0 ± 20.3) to cross the Mediterranean Sea at its western narrowing and winter in

Senegal, Sierra Leone and Spain (Fig. 2c). Differences in azimuth were, however, not significant (U= 12, p= 0.23). At later stages, migration direction was similar between the eastern and western population.

Mortality

We observed high mortality in juveniles in their first year, reaching 67% in the case of certain deaths, but possibly even 83% together with cases of suspicious signal losses. Some cases even occurred before the onset of migration. Five died at fledgling stage: one in the nest of unknown reasons, three were killed by a Goshawk and another one was killed by a wind turbine. Two juveniles probably perished on migration: one on the Apennine Peninsula, the other in Morocco. Another two died at wintering sites: one was poached in Nigeria, the other died of unknown reasons in Senegal. The last death was confirmed at the start of spring migration in Spain, probably due to Goshawk predation. Only two juveniles certainly survived the first year and transmitted in the next season.

Surprisingly, the mortality of adults was also high and reached 57% (confirmed deaths) - 71% (assumed deaths) already in the first year of tracking. In this case, the reasons were highly anthropogenic in three known cases: two adults died because of electrocution (one in Senegal and one in Poland), one was poached (still in Poland). The reason for the two other death cases is unknown: one individual went missing while migrating in autumn through the Sahara (and did not appear the next season in its nests with the web camera) and one was simply found dead in Burkina Faso. In the second year of tracking, another adult female stopped transmitting on autumn migration and was assumed dead, because she did not came back to her territory and was replaced by another female.

The proportion of deaths in the breeding/wintering vs migration period were similar in adults (83 vs 17%) and juveniles (70% vs. 30%). In case of the eastern population, relatively more individuals died on migration (Tab. 2).

Factors affecting autumn migration

Models explaining daily distance covered on migration were poorly distinguishable between the base model with a random effect of individual only, comparing to models involving individual sex, age and source population (Tab. 3). Eventually, the averaged model involved all the factors, but all were insignificant (Tab. 4). The variance explained by the base model was low (conditional R^2 = 0.151) and barely increased when other predictors were added (conditional R^2 increased to 0.165 – 0.167, depending on the model).

The departure for autumn migration did not differ significantly between individuals of different age or sex, although in the last case, surprisingly, females left breeding grounds later than males (Fig. S2). Similarly, we found an effect of age or sex on migration distance, duration and number of stopover days (Table S1). However, when individuals from different source populations were compared, the distance covered on migration was almost significantly higher in the eastern than in the western population (Fig. 3) although straight-line distance was almost the same (U= 15, p= 0.286). When migration was divided into sections, juveniles covered some surplus kilometres across land in Europe, compared to adults (Fig 4). Individuals from the eastern population covered shorter distances over land in Europe, but longer over sea and the Sahara Desert. Unfortunately, the samples sizes were two small to perform reliable statistical comparisons.

In general, the dynamics of migration was rather even in adults, but showed longer stopovers and more pronounced stopover behaviour in some juveniles (Fig. S3). Individuals of both age groups were capable of covering a distance of around 800 km in 24 hours.

DISCUSSION

Overall, the ospreys from the two distinct populations differed in their migration routes. With single exceptions, individuals from the eastern and western populations headed south and south-west, respectively. This applied in particular to juveniles from the eastern population, which are supposed to follow their innate migratory mechanism (Väli et al. 2018), who tended to cross the Mediterranean Sea at a similar longitude, further east than adults. Juveniles from the western population acted similar with one exception; they headed south. Taking into account that migratory direction is inherited, this case may show that the two populations are not entirely isolated. Osprey males are highly philopatric and breed in the radius of about 30 km from their natal sites (Kinkead 1985). On the contrary, females can show quite long dispersal and may breed hundreds of kilometers from their birth site. In the mentioned population of the Osprey in eastern Poland, alien females (but not males), ringed in Germany and Latvia (>500 km), were recorded to breed. Thus, gene flow with populations of different migration paths certainly occurs, although with low frequency, as shown for other European populations by Monti et al. (2018b). The authors of the above-mentioned paper reveal that gene flow and migratory behaviour are linked in Europe and the central location of Polish populations might attract dispersing females from three different migratory pathways. However, looking at the rather distinct migratory pathways of Ospreys belonging to the western and central populations studied, gene flow rates are rather low. Preliminary genetic analysis done on Polish Ospreys showed relatively high heterozygosity in the small sample set dominated by the western population. All individuals from this population represented one haplotype (Rutkowski 2019), common for ospreys in Northern and Western Europe (Monti et al. 2018b). On the other hand, unique alleles were found in a single individual examined from the eastern population (Rutkowski 2019). This fact may indicate relatively high genetic distance between the two mentioned populations, but needs further confirmation in a greater sample size.

Migration patterns, at least for tested traits, did not differ between age and sex classes. This was quite surprising, since many studies have shown females depart much earlier than males (Bai and Schmidt 2012, Väli and Sellis 2016, Meyburg et al. 2018), adult females and juveniles cover longer distances than adult males (Bai and Schmidt 2012), and males used fewer days for stopovers than females (Alerstam et al. 2006, Meyburg et al. 2018). In terms of the departure date, the difference should be sharp, but not only was this not observed in adult females, but we found them departing later than adult males. This might be an artefact caused by the low sample size, but also it may indicate that foraging conditions were optimal and inter-species competition is low in those small populations. Therefore, instead of moving to other foraging sites, the breeding grounds were suitable for ‘filling their tanks’ before migration. In contrary to other mentioned studies, we did not find age or sex to affect migration dynamics, but also showed that it is a variable, especially in the case of juveniles (Fig. S3).

Individuals from different source populations, although located along similar latitudes, exhibited close-to-significant differences in migration distance (Fig. 3), with individuals from the eastern population covering, on average, over 2,000 km more to reach wintering sites. When migration was divided into stages, we found that the main difference in migration length lies in the most risky parts: crossing the Mediterranean Sea and Sahara desert (Fig. S2). This fact may be a factor in differing survival rates and the opposite population trend patterns in the two populations across the migratory divide. Such a pattern was shown for the Common Cuckoo in Great Britain, which uses two different paths on its way to wintering sites in Africa (Hewson et al. 2016). Those that followed the central Mediterranean passage and later headed through the central part of the Sahara Desert exhibited higher mortality and, in consequence, declined.

We found mortality rates in Polish Ospreys to be high in juveniles, which was expected, but also high in adults. It seems odd that mature and experienced Ospreys do not demonstrate a significant increase in survival, but in fact, De Pascalis et al. (2020) showed that the Osprey, as the only out of six bird of prey species they investigated, even presented increasing mortality with age. However, other studies rather support the expected increase in survival with age (i.e. Wahl and Barbraud 2014). Monti et al. (2014) showed survival of translocated juveniles reaching only 26% in their first autumn/winter season, while in the second calendar year it reached 69%, and later increased in adults to 93%. In France, the survival of individuals reached 49% in their first year and as much as 87% in the second year and in older birds (Wahl and Barbraud 2014). Even higher rates were noted in Swedish Ospreys; 65% of year-old birds survived the first year and 81% thereafter (Ryttman 1994). In North America, survival in the first year was estimated to be as much as 47%, while in adults to ca. 81% (Henny and Wight 1967). All of these data reported above were based on ringing recoveries and are much higher than the ones reported in our telemetry study. Certainly, GPS devices are more precise in showing where and when mortality exactly occurred and probably less biased than survival estimates from capture-recapture methods.

In the case of adults, a huge part of mortality was attributed to anthropogenic reasons. Comparing the number of deaths in migration vs stationary (breeding and wintering) periods, we found it greater in the eastern population (Tab. 2). High mortality on migration is expected, given the results of Klaassen et al. (2014) on a few migratory birds of prey species, including the osprey, which also displayed considerably high mortality in adults (61%). However, relatively higher mortality during migration in the eastern population corresponds to greater distance covered, especially at the most hazardous points on the migration route (sea and desert, Fig. 4). Greater distance covered during migration is associated with a higher risk of mortality in Ospreys, but also in other migratory birds of prey (De Pascalis et al. 2020). The mortality reasons are not necessarily linked to longer and more hazardous paths, but may impact the birds' condition by weakening them and making them more susceptible to predation, poaching and starvation, i.e. "disappearing" in the deserts or dying of unknown causes. Certainly the high mortality of Ospreys from declining Polish population requires further investigation to reveal the most important threats and subsequently counteract them.

CONCLUSIONS

Two small and distinct Osprey populations showed a clear but incomplete migratory divide, despite being separated by only a few hundred kilometres, a distance that did not completely limit gene flow through female dispersal. We found high mortality rates in juvenile and adult Ospreys, which were relatively higher while on migration in the case of the eastern population. There may be a link between migration route and mortality rates that led to the steeper decline of the eastern population; however, the sample size of tagged individuals is too low at the moment to make any definite conclusions.

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DECLARATIONS

Availability of data and materials

The dataset supporting the conclusions of this article is stored in the Movebank repository, ID 365184781 and available on request.

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Ethics approval

Catching and tagging of Ospreys were carried out under the license of General Inspectorate for Environmental Protection – DZP.WG.6401.03.109.2017.dł.

Competing interests

The authors declare that they have no competing interests.

Contributions

DA designed the study and obtained funding. PM led data analysis and manuscript writing. DA, MZ, ŁC, SR participated in data analysis and writing. All co-authors were involved in the fieldwork.

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Table 1. Characteristics of autumn migration of twelve GPS-followed Ospreys from Poland. Column 'Mort.' reports mortality reasons on migration: elec. – electrocution, assu. – mortality assumed, but individual not found, unkn. – reason unknown., pred. – predation.

ID	Year	Sex	Pop.	Age	Tag. date	Depart.	Arrival	Stop-over days	Total duration (days)	Dist. (km)	Straight dist. (km)	Wintering destination	Mort.
Complete migration tracks													
17988	2017	F	West	juv	06.07	18.09	01.10	0	13	4381	3940	Nigeria	Elec.
LPP11	2020	F	East	juv	03.07	11.09	29.09	0	18	5135	4628	Niger	
LPP14	2020	M	West	ad	10.07	10.09	12.10	9	32	6069	5013	Senegal	Elec.
LPP15	2019	M	East	ad	22.06	27.08	11.10	18	45	6855	4921	Burkina Faso	Assu.
LPP01a	2018	F	West	juv	03.07	01.09	24.09	1	23	4242	3899	Senegal	
LPP02	2019	F	East	ad	15.06	14.09	13.10	1	29	6837	5237	Ghana	
LPP05	2020	F	East	juv	26.06	24.08	30.10	35	68	9066	6724	Angola	
LPP09a	2019	F	West	juv	22.07	21.08	02.11	47	73	3971	2512	Spain	Pred.
LPP09b	2020	F	West	ad	10.07	01.09	23.09	0	22	6468	5504	Sierra Leone	
Incomplete migration tracks													
LPP1b	2019	M	East	ad	10.08	8.09				4193	3731	lost in Algeria	Assu.
LPP04	2018	M	West	juv	03.07	31.08				2972	2623	lost in Morocco	Unkn.
LPP10	2019	F	East	juv	23.06	21.08				2229	1430	lost in Italy	Assu.
LPP02	2020	F	East	ad	2019	16.09				2905	2253	lost in Tunisia	Assu.

Table 2. Mortality numbers (incl. assumed deaths) of nineteen GPS-tagged Ospreys from Poland in 2017-2020

	Number of deaths		Mortality ratio	
Season	**Juveniles**	**Adults**	**Eastern Pop.**	**Western Pop.**
breeding	5	2	38%	55%
wintering	2	3		
autumn migration	2	1	38%	36%
spring migration	1	0		

Table 3. Components of linear mixed effects models of daily distance covered by GPS-tagged Ospreys from Poland on autumn migration in 2018-2020. Akaike Information Criterion (AIC) showed models #1-4 were barely distinguishable, therefore were averaged and their contribution to the best supported model is given in the 'weight' field.

#	Model components	df	logLik	AIC	ΔAIC	weight
1	Random effect of individual (1|ID)	3	-261.78	529.54	0	0.62
2	Age + (1|ID)	4	-261.71	531.42	1.88	0.13
3	Sex + (1|ID)	4	-261.76	531.52	1.98	0.13
4	Population + (1|ID)	4	-261.76	531.53	1.99	0.12
5	Age + Sex + Population + (1|ID)	6	-261.74	535.28	5.74	-

Table 4. The best supported model of daily distance (logarithm) covered by GPS-tagged Ospreys from Poland on their autumn migration in 2018-2020. Intercept includes adult females from the eastern population.

	log(daily distance)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	5.24	4.99 – 5.48	<0.001
Sex [male]	-0.03	-0.50 – 0.43	0.884

Population [west]	0.03	-0.42 – 0.48	0.904
Age [juvenile]	-0.06	-0.50 – 0.37	0.773
N ID	13		
Observations	232		

Figure 1. Main migration paths of Ospreys from Northern Europe and predicted migratory division (dashed line) between Osprey populations in eastern (red) and western (blue) Poland. Thin and thick lines show relative importance of migration paths and refer to studies by: (1) Mackrill 2017, (2) Østnes et al. 2019, (3) Alerstam et al. 2006, Klaassen et al. 2011, (4) Väli and Sellis 2016, (5) LUOMUS 2020, (6) Babushkin et al. 2019, (7) Meyburg et al. 2018.

Figure 2. Autumn migration paths of GPS-tagged Ospreys from Poland shown by individual (a), age (b) and source population (c).

Figure 3. Departure date (a), total distance (b), duration of migration (c) and number of stopover days (d) shown by GPS-tagged Ospreys from eastern (red) and western (blue) Poland on their autumn migration. *P* value of the Mann-Whitney test between populations is given for close-to-significant differences.

Figure 4. Distance covered on autumn migration by GPS-tagged Ospreys from Poland, depending on migration stage and divided by individual age (a) and source population (b). Yellow boxes represent juveniles, green – adults, red – eastern population, blue – western population.

Additional File 1

Table S1. Results of Mann-Whitney test comparing autumn migration traits between individuals of different sex, age and source population (eastern vs western) among nine Ospreys from Poland followed with GPS telemetry in 2017-2020.

Figure S1. Histogram of daily distance covered on migration by GPS-tracked Ospreys from Poland in 2017-2020.

Figure S2. Differences in departure dates between age and sex classes in GPS-tracked Ospreys from Poland on their autumn migration.

Figure S3. Distance covered daily on migration by juvenile (a) and adult (b) Ospreys from Poland followed with GPS loggers in 2017-2020.

Figure 1

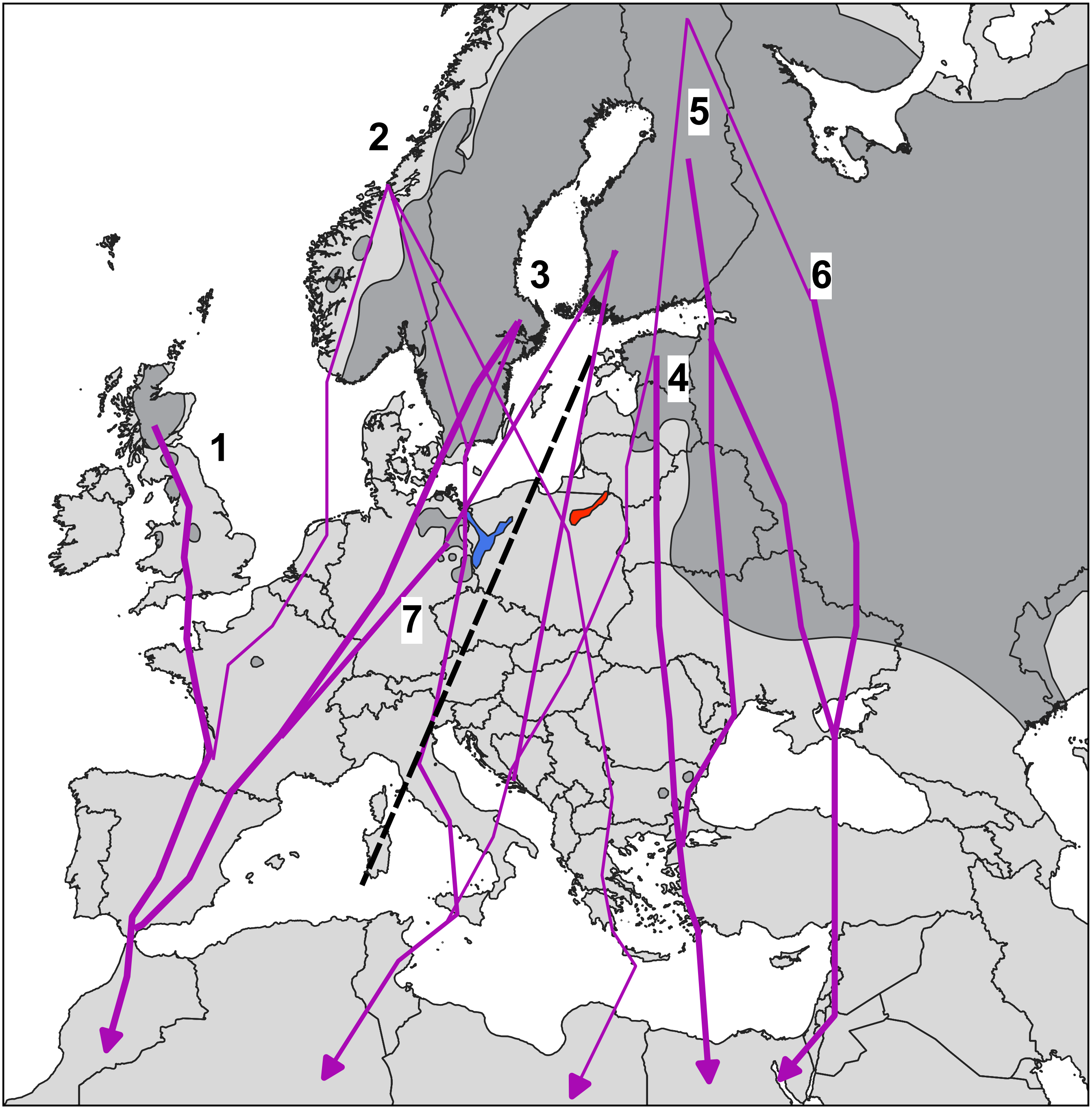


Figure 2

Click here to access/download;Figure;fig2.pdf

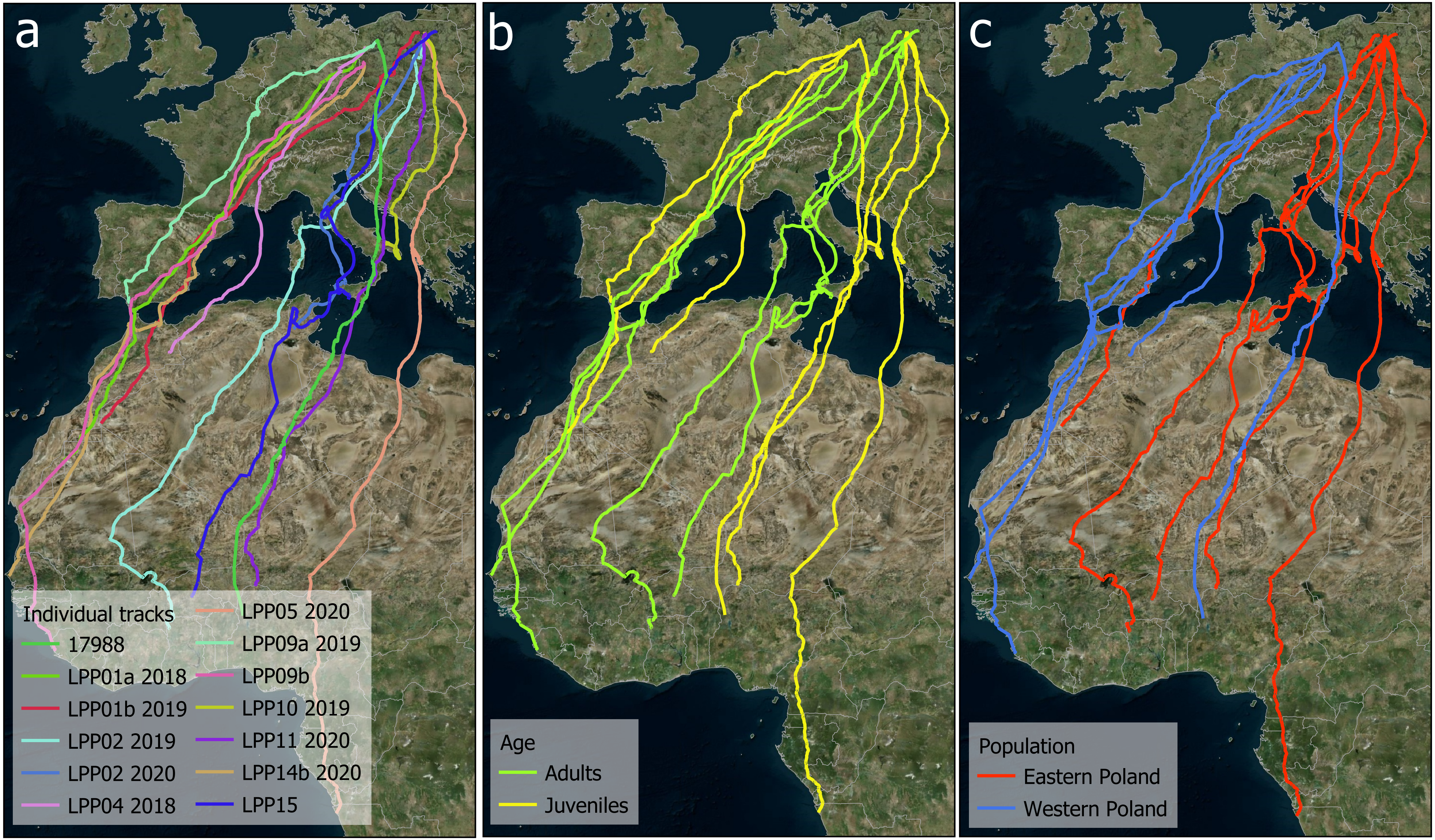


Figure 3

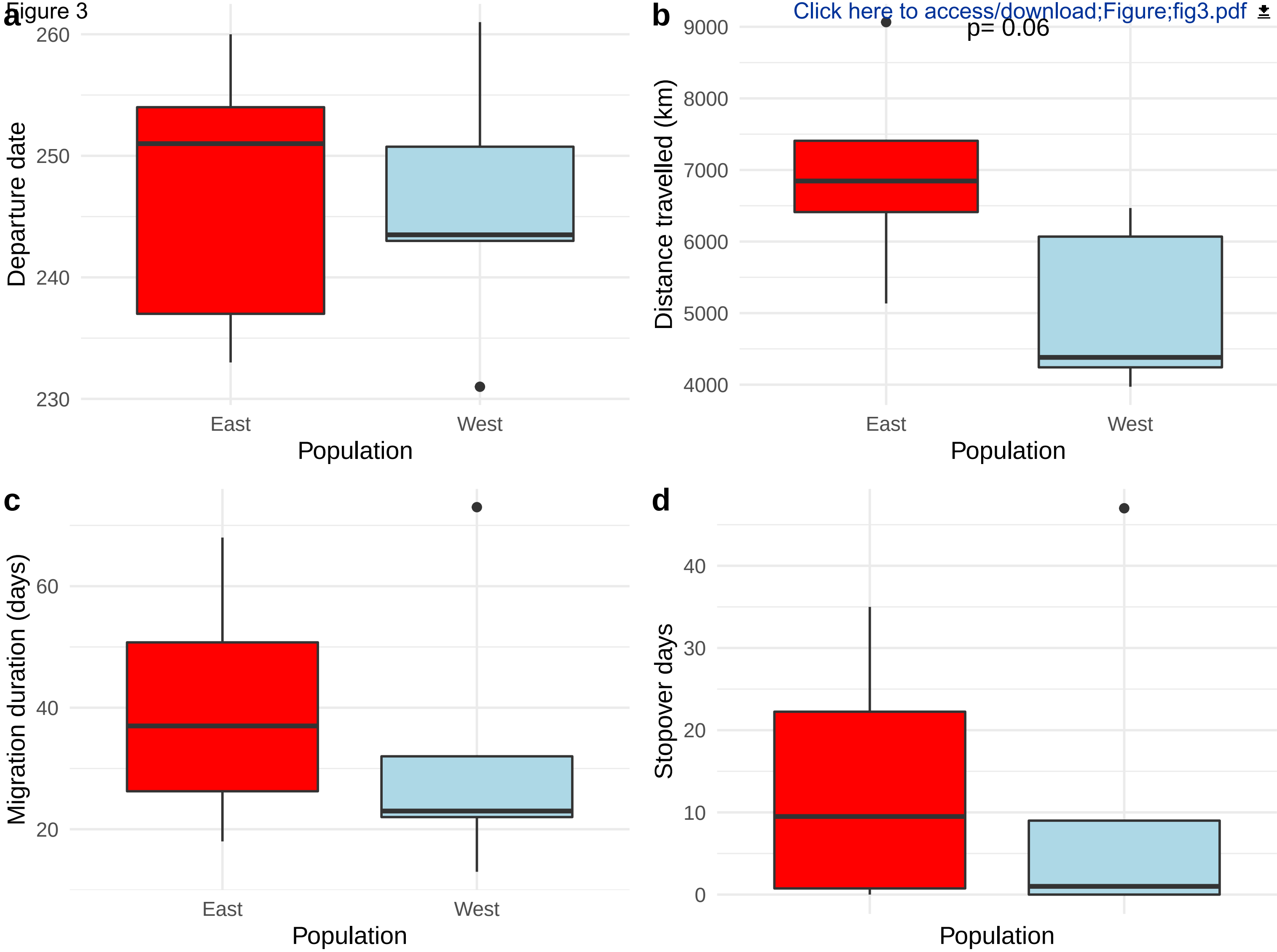
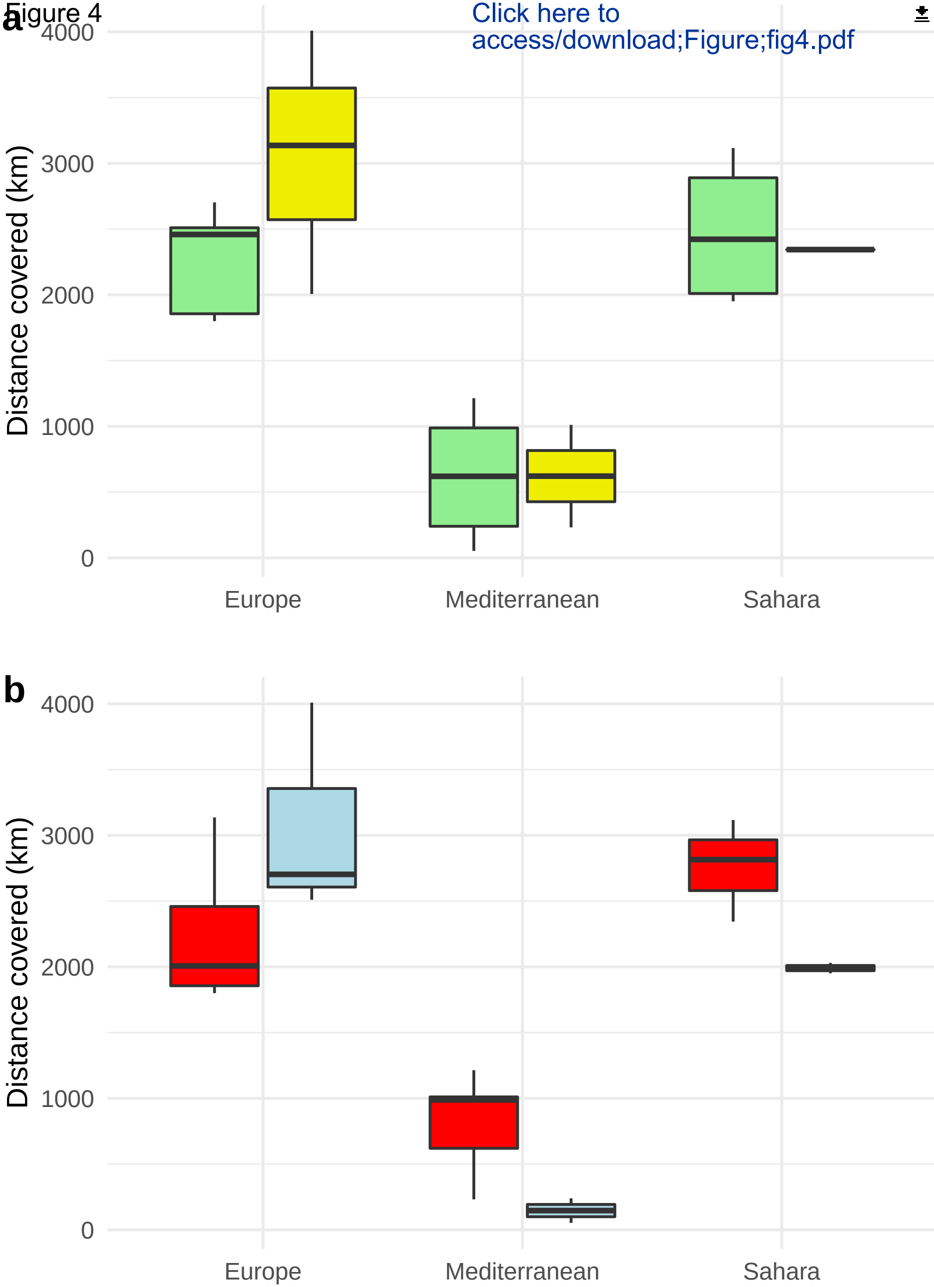

a
Departure date
260
250
240
230
East
West
Population
b
p= 0.06
Distance travelled (km)
9000
8000
7000
6000
5000
4000
East
West
Population
c
Migration duration (days)
60
40
20
East
West
Population
d
Stopover days
40
30
20
10
0
Population

Figure 4

Click here to access/download;Figure;fig4.pdf



Reviewer #1: This study well described the Autumn migration of Ospreys from two distinct populations in Poland and make sufficient analysis to try to reveal partial migratory divide. It lays important basis for this population's further research in the future. There are several issues need author's attention.

Thank You for Your help in improving our manuscript. Below we respond to each of the comments.

1) In Line 26 of page 2, for the Abstract part, "Mortality reached 83% in juveniles and as much as 71% in adults". It's really shocking high death rate. Maybe lose contact does not actually stand for death, otherwise it reveals the GPS loggers affected the normal life of the bird in a large great deal on the bad aspect, such as limiting the individual at the emerge situation.

Yes, in fact those numbers are striking, especially for adults, because in juveniles high mortality was expected. We have now reported mortality as a range between certain deaths and certain+assumed deaths. We have also added a statement what we meant as assumed deaths in methods.

2) In line 93 of page 5, 35-40g loggers for birds with 1420g of body mass, taking 2.5% to 3.5% of the body mass. Can you provide some live experiments to show the proper result that the bird is sensitive for the mass of loggers? Maybe 1% is the top level they can afford?

There are papers that show the similar tag to bodyweight ratio did not affect survival:

https://www.tandfonline.com/doi/full/10.1080/00063657.2016.1271395. Also, we have documented direct reason of mortality in many cases: goshawk predation, death by collision with wind rotor, poaching, electrocution. Therefore we don't suspect the tag weight is one of the main reasons of mortality in this case, but also can't rule it out in some cases.

3) In line 146 of page 7, what's the meaning of " …one was gone", does it mean lost contract? Can you explain more about Osprey's normal life span, and the loggers affected their life activity?

Yes, we meant it stopped transmitting in this case.

We have followed this advice and discuss more on Osprey mortality and life span.

4) In line 223 of page 10, what's the meaning of "their weakening"? Can you estimate the mean life span to try to explain their activity and motility? If not, please leave this questions here for the authors.

Individuals using the paths with longer crossing through the desert, might get weakened, because there are no suitable stop-over sites to feed on their way. We have now referred to life span and mortality rates in other studies

5) For Table 1 and Table 2 of page 16, can you put the main information of Table 2 into the

Take 1, so that we can get detailed information for each tracked individual. For example, we should get Tracking ID, deployment time, departure time, age, dead or alive, death time, to have a better understanding and comparing analysis for each bird, especially for the dead ones.

Table 1 is now extended.

6) Please note death and lost contact, as they are different situation for birds.
Yes, we are aware of that. But, especially in adults we would expect to see those individuals back in their territories / nests next season. Even if they would lost tags, we would see their rings. Great part of the nests is registered with trail or web cameras. Instead we saw new partners in their nests.

Reviewer #2: MANUSCRIPT: AVRS-D-20-00211

Comments to author:

In this study, the authors investigate and confront migratory strategies of two Polish osprey populations. Authors were able to rely on a acceptable dataset, with sufficient temporal and spatial resolution, though few individuals have been tracked and provided full migratory data. The high mortality recorded for these individuals is an important aspect to be considered. In general, the study is well conducted and the working hypotheses are clearly stated at the end of the introduction. Results are supported by figures and tables in a proper way. Statistical analyses, despite thier low power owing to reduced sample size, are fine (except few details to be specified). Discussion is pertinent and refers to the most recent literature (few exceptions, please find them below), except for some missing information that would merit more attention and that would help to strengthen authors' conclusions.
Even if I am not a native speaker and the content of the text is still understandable, I think it is advisable to review the text by a native speaker to make the reading more fluent. There are unsuitable terms that should be replaced by more appropriate ones and somewhat complicated sentence structures.

Thank You for Your time spent on reading and commenting our manuscript. Those are all very valuable and helpful suggestions. We revised the manuscript according to them and asked a native speaker to edit the language. Below You will find our detailed responses.

General remarks:

Authors describe the presence of a migratory divide at this latitude, which is correct but would need more attention and discussion. In fact, in Europe it follows a longitudinal gradient and can be observed over a broad range. Previous published papers and tracking studies have already revealed this. For example, in 2001, a satellite project started in Finland for gathering information about the migration ecology of ospreys within the country, from Lapland to the southern regions of Satakunta, Kainuu and Häme. Looking at the GPS tracks of 25 ospreys from these regions (Saurola, 2014; https://www.luomus.fi/en/finnish-satellite-ospreys), Finland seems to be at the middle of a migratory divide: 12% (3 ind.) of these ospreys took a western flyway, a 44% (11

ind.) a central one and the remaining 44% (11 ind.) an eastern flyway.
A similar situation is evident for Swedish ospreys, commonly migrating via western and central flyways, with some that can choose to migrate eastward. German ospreys showed similar patterns. This variability, is particularly evident among juveniles which do not rely on previous experience and are more affected by wind strength and direction.

It's a pity that extensive data from Finland was not summarized and published. We have already viewed their data at this website to draw the main migration paths in Fig. 1. Now, we have also added the minor western pathway to this figure.

ABSTRACT
L11-13: the first sentence should be reorganised since it contains two information at the same time. I would rather say: Long-term ringing and telemetry studies showed Osprey is a broad front migrant following different migratory flyways depending on geographic location of their breeding populations.

Of course, sentence changed according to suggestion.
L13-14: being only few hundred kilometers apart, why (and how) authors consider them as completely separated populations? Are they connected or not? I suppose they are not entirely isolated, and that you can find the two preferred direction of migration in both populations (despite with different percentages between east and west). I think the limited sample size here would hide a higher variability, especially among juveniles. Are eastern populations connected with those from Lituania and Belarus?

In this particular sentence, we call those populations "distinct" and "separated by few hundred kilometers", but we don't call them isolated. Indeed, later on we advocate that the gene flow between them is limited. We discuss this issue in the first paragraph of the discussion. Gene flow between other populations is possible through females, that may breed away from their natal sites. Belarussian population is rather small, more distant than Lithuanian and probably moving more eastwards on migration but also during dispersal. Since a single female from Latvia was breeding in NE Poland, therefore, genes of Lithuanian and Latvian ospreys might be involved in Polish eastern population of ospreys.

L21: please replace "it" with "to compare them between…" ☑
L22 and 24: populations in low letter ☑
L25: Mediterranean Sea (sea in capital) ☑
L25: In my opinion both populations migrated following a predominant NE-SW major axis of migration, as showed by tracks in the maps. They followed two different flyways because of a longitudinal span between breeding grounds, but the orientation was quite similar. Thus, I would say that "while the first migrated through a western flyway, the second followed a central flyway, resulting in crossing the Mediterranean Sea in distant passes that affected the distance covered". We have followed this advice. There is not enough place for additional explanations, but in results we still report that the beginning of the migration differed a bit. The western population headed SW, while eastern one, rather S.
L30-31: I would rather suggest to write: We showed that two distinct osprey populations in Poland revealed partial migratory divide, with one showing longer routes and covering greater distances over sea and deserts over the western flyway. Thank You for this suggestion, we have followed it.

MAIN TEXT

L40-44: yes, this is true and I agree with authors about the importance of investigating patterns of single populations as they can reveal particular (and important from a conservation poit of view) trends. To see where and how mortality causes of European ospreys occur and how they changed both in space and time, please check this recent paper.

* De Pascalis, F., Panuccio, M., Bacaro, G. & Monti, F. (2020). Shift in proximate causes of mortality for six large migratory raptors over a century. Biological Conservation 251:108793

Thank You for this fresh reference. We have now used it in whole new paragraph in the discussion, where we focus on mortality.

L52: Individuals from western Europe (e.g. UK, continental France, Germany, Norway, Sweden) Sure, we added most of those countries, but we don't have a reference for continental France, therefore we omitted this one.

L55: …Ospreys from eastern Europe (e.g. some from Finland, Russia and Baltic countries) countries added in parenthesis
L57 and L128: please replace Appennine peninsula with Italian peninsula. Appenine is a chain of mountains within Italy (which is a peninsula). ☑
L57: were used by ospreys from central (e.g. Germany) and both, Western and Esatern ospreys, but to a lesser degree. ☑
L63-66: Excellent! Exactly what I was referring before. Nice to hear that
L67: Please replace "a" with "the" Baltic Sea. ☑
L70: maybe here the term islands should be reported within brackets. Of course, it's a metaphor.
L70-71: This is a curiosity. The Western population is receiving floaters and breeders from neighbouring Germany as authors say. In contrast, the Eastern populations seems to be quite isoltaed despite both in Lituania and Belarus breeding population exist. Don't you have any record of birds from these neighbouring countries in East Poland? Please at least mention it. We mention it in first paragraph of the discussion. Single ringing recoveries showed females from Germany and Latvia contributed to the eastern population.
L91: please delete "large" ☑
L94: Please provide device model and manufacturer details (model, city, country). Details on model and manufacturer were added
L97-98: ok, but I think that it is not possible to be 100% sure of sex determination using this approach on juveniles. Sexual characters are highly overlapping between sexes and the most reliable method for sex determination is through genetic analyses (via blood or feather sampling). There are other methods to infer sex such as discriminant analysis (https://doi.org/10.1080/00063651003674953). Thus, I would be cautios with that, especially for juveniles at nest or, at least, I would invite authors to better explain the way they assessed it.

Of course, biometry assessment of sex is less certain, especially that the size dimorphism is not marked that significantly. We added a comment on that. Finally, we don't conclude on any sex-related migratory behavior.

L102 and L105: "long, directional movement southwards" please quantify numerically (what is the threshold used and why)? These definitions are missing basic information. The threshold was now justified with histogram cluster used to discriminate between stationary and migratory behavior.

L103: very strange to define a day as a stopover using a daily temporal indicator. Maybe it would be better to say: "A stopover site was defined as an area where a bird spent more than two following nights in radius of less than 10 km." Surprisingly, you have quite low stopover days (TAB. 1) for many individuals of such long-distance migratory populations.

This sentence was now changed according to suggestion.

True, it's quite surprising, although Ospreys are known to feed during migration (Strandberg & Alerstam 2007). We would rather expect adults to forage effectively on migration, while juveniles, that are less experienced in hunting, to make more and longer stopovers. However, it turned out that both adults and juveniles could migrate quickly without stopovers. The key difference between "quick" migration and "long" one with many days on stopover – is the migration onset date. Ospreys that departed in August had more time to make stopovers, while ones that departed in September almost did not make any stops, but probably prepared to migration, building fat reserves in the known foraging sites, close to their nest sites.

L107: "moving at all for many days"- This definition is missing basic information. Please specify and quantify both spatially and temporally.

This part is now developed.

L111: Has movement speed been used as the only response variable here? Are you referring to daily distance? Why authors did not use also all the others migratory parametrs in model selection? Please specify or adjust it accordingly. It is not clear to me, but maybe I wrong, if they used instant speed or a daily average here, or other parameters as well as what is the list of repsonse variables included in model selection. Please provide the entire list on Tab. 3.

Movement speed, which is in fact the distance covered daily on migration was the response variable we tested. Migration speed was calculated for each day of migration for each individual, therefore obtained sample size was sufficient for testing. In case of migration patterns per whole migration time, the sample size would reach only n=13, because incomplete migrations would have to be discarded. Tab. 3 was in fact the complete list of tested factors. Now according to the next comment we also added year as random effect.

L112: Please run again the same models including YEAR as random effect too, in order to account for annual variability. This is because you followed birds in 4 different years.

This is reasonable, we have added it to models, but it's ΔAIC value dropped down below the threshold (ΔAIC=2), and it was not included in the final, averaged model.

L113: movement over 50 km. - justify this choice from an ecological point of view

We have now changed this predefined value to the one based on histogram clustering. This made the sample size going a bit higher, numbers in the models changed a bit, but the results obtained were the same.

L114: Ok, thus interactions among fixed factors were not included. Due to low sample size (especially per group category), I think it was the best choice.

In fact, now the sample size is a bit bigger and few models with interactions were added, but no significant results and those added models performed worse in the light of AIC criterion.

L122: please add a line about the other 7 ospreys missing. What's happened to them? Of course, two sentences were added to report on the reasons of missing individuals.

L129: the term populations is used alternatively in capital and lower letters. Please be consistent throghout the text. This issue was now solved by using lowercase letters elsewhere.

L130: heading south. Maps clearly shows that the preferred axis of migration followed an NE-SW orientation for both population that, given the different location of breeding grounds, resulted in different migratory routes and wintering areas. I think authors, even in the introduction, should refer to the preferred axis of migration. See my comment above. We highlighted the migratory direction at early stage, when it's governed mostly by the innate mechanism, not bypassing the natural barriers. We have now even measured the migratory direction at this stage and compared it between populations. Additional description was added to methods and results description was elaborated.

L130 and 132: please show the % within brackets in both cases.☑

L161-167: these results would require better discussion after. For example, you can support these findings with information from literature showing that:

1) You can also Link to L205 ◊ adults ususally show straighter migratory paths than juveniles, which conversely display a greater variance in the major axis of migration. 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. This is also evident when crossing different ecological barriers (sea and deserts), in the different use of stopovers and/or in the speeds across geographical regions.

You may find useful to have a look to (not necessary to cite them):

-Monti, F., Grémillet, D. Sforzi, A. Dominici, J.M., Triay Bagur, R., Muñoz Navarro, A., Fusani, L., Klaassen, R.H.G., Alerstam, T. & Duriez, O. (2018). Migration distance affects stopover use but not travel speed: Contrasting patterns between long- and short-distance migrating ospreys. Journal of Avian Biology, doi 10.1111/jav.01839

- Mellone, U., Klaassen, R.H.G., García-Ripollés, C., Limiñana, R., López-López, P., Pavón, D., Strandberg, R., Urios, V., Vardakis, M. & Alerstam, T. (2012). Interspecific Comparison of the Performance of Soaring Migrants in Relation to Morphology, Meteorological Conditions and Migration Strategies. PLoS ONE 7, e39833.

Thank You. We are aware of the expected differences between adults and juveniles, but we haven't found significant differences in migration patterns between age classes, therefore we have not raised this topic in discussion.

2) another aspect to be considered is that, when crossing Europe, osprey can rely on a great variety of suitable foraging sites (compared to lower latitudes). Europe is full of rivers, wetlands and artificial water bodies promoting the use of a fly-and-forage migratory tactic in the osprey. This would lead to cover greater distances in Europe, especially in juveniles.
You may find useful to have a look to (not necessary to cite it):
- Strandberg, R. & Alerstam, T. (2007). The strategy of fly-and-forage migration, illustrated for the osprey (Pandion haliaetus). Behavioral Ecology and Sociobiology 61, 1865-1875.
Shorter distances over land in Europe covered by individuals from Eastern population may depend on geographical features of this particular flyway. Yes, we also think that way, but haven't accent it enough. That was however the reason we have divided the migration to easier, European part and hazardous Sea and desert crossings.

L213: are authors referring to polish osprey populations only ? This because, finnish and german ospreys commonly use this central flyway and are not declining.
This refers to the study mentioned in previous sentence – so it concerns common cuckoos from Great Britain. This part was not rephrased to make it clear.

L234: here a see two issues for the Eastern population. First, as reported above, the more risky migratory flyway used, especially for juveniles. Second, the fact that this populations is quite isoltaed at breeding grounds without receiving any inputs (apprently) from neighbouring populations. I think authors can comment further on these concurrent factors.

Last but not least, I am surprised by the high mortality percentage at breeding grounds (overall), that probably would merite few lines more and some proposed corrective measures to adopt locally to limit mortality.
We agree, the high mortality observed in our study calls for more attention in discussion, therefore we added one more paragraph to comment it.

Table 3: here only one response variable (daily distance) is reported. It would be worth to see a complete table with all repsonse variables included in model selection. In addition, it would preferable to report all parameters such as K, logLik, AICc, ΔAICc, Weight for each model.

The daily distance was the only response variable, because sample size for all the other variables (like ones in Tab. 1) would be very small. Weights and AIC are given for each model. Models were run on few hundred observations of daily distance, so we did not have to use AICc corrected for small sample size. Columns with logLIK, ΔAIC and df values are added now.

Fig. 2: maybe it would be useful to show location of main stopovers, to be reported on the first map.

Unfortunately maps are quite small and adding more content will make them less clear. Moreover, we don't refer to location of stopovers in our results, so maybe there is no need to add it to the map.

FigS2: in my opinion it would merit to be included in the main text, buti t is just a proposal.

We also find it interesting and important to show. We have moved it to the main text (now, it's Fig. 4).