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Migratory patterns of Ospreys (*Pandion haliaetus*) from central Norway

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Migratory behaviour is subject to intraspecific variation and may be determined by the age, sex and population origin of individuals. Here we equipped eight juvenile Ospreys (*Pandion haliaetus*) with GPS-based satellite-transmitters to investigate their migratory behaviour from a recently re-established breeding area in central Norway. Migration routes fanned out widely across Europe, and migratory behaviour differed between individuals. Five of the eight Ospreys completed their first southward migration to wintering areas in tropical Africa. They travelled a median distance of 7,482 km and spent from 21 to 92 days on their journeys. Median travel distance was 120% longer than a straight-line distance. Stopover sites were located just before or immediately after crossings of geographical barriers and the differences in the time spent on the migratory journeys was mainly a consequence of the number of stopover days. Only two individuals gave signals long enough to enable us to track their first northward migration in their third calendar year. By including repeated migratory journeys for these two individuals we tracked a total of 20 sea crossings lasting between 4 and 24 hours, and 14 trans-Saharan journeys. Four of the sea crossings included periods of nocturnal flight. The duration of the trans-Saharan journeys varied from 130 to 276 hours and the birds showed a strict diurnal rhythm, with movements only during daytime. Repeated migratory journeys showed that the Ospreys were faithful to wintering and stopover sites. Our results show that Ospreys from central Norway migrate on a broad front over Europe. However, the majority of the juvenile Ospreys followed flyways through central and eastern Europe and finally settled down in wintering areas in eastern parts of western tropical Africa.

1. Introduction

Strategies for migratory movements between breeding and wintering areas vary greatly among avian species (Newton 2007). Most long-distance migrants use a stopover strategy for refuelling, often using traditional sites (Newton 2007, Tombre *et al.* 2008, Alerstam 2011). Others use a fly-and-forage strategy (Strandberg & Alerstam 2007), while some, especially shorebirds, are capable of long and fast non-stop migration between breeding and wintering areas (Gill *et al.* 2009, Klaassen *et al.* 2011). The variability in bird migration strategies is a consequence of several factors i.e., food supply for refuelling, quality of stopover areas, fuel storage rates, traditions and predation risk (Newton 2007, Alerstam 2011). Knowledge of avian migration has greatly improved during recent decades by the introduction of new tracking technologies such as satellite transmitters and geolocators (Strandberg *et al*. 2010, Klaassen *et al.* 2011, Alves *et al*. 2016). In particular, the use of high-resolution GPS transmitters enables very precise determination of routes, speed and destination of migration (Crawford & Long 2017, Mackrill 2017), and improved insight into avian navigation ability and migratory behaviour (Horton *et al.* 2014, Duriez *et al*. 2018).

The Osprey (*Pandion haliaetus*) is a cosmopolitan species with a wide distribution range (Monti *et al.* 2015). Ospreys breeding in the northern hemisphere are long-distance migrants, generally moving to latitudes near the equator in the winter season (Hake *et al.* 2001, Martell *et al.* 2001). En route they use a fly-and-forage strategy combined with stopover periods for refuelling (Strandberg & Alerstam 2007, Klaassen *et al.* 2008).

Ospreys breeding in northern Europe spend the winter mainly in Africa south of the Sahara (Hake *et al.* 2001, Väli & Sellis 2015, Crawford & Long 2017). They migrate solitarily, normally during daytime, and use a combination of soaring and flapping flight (Kjellén *et al.* 2001, Alerstam *et al.* 2006, Klaassen *et al*. 2008). Juvenile Ospreys, with no previous experience, have to rely on an inherited programme to reach their wintering grounds (Newton 2007, Horton *et al.* 2014). Compared to adults they are more susceptible to wind drift and show higher range of variation in their migration routes (Thorup *et al.* 2003, Monti *et al.* 2018b).

Throughout Europe, the Osprey faced a considerable population decline during the 20th century (Saurola 1997, Schmidt-Rothmund *et al.* 2014). The huge population decline and the extirpation of many local populations in northern Europe have been attributed to persecution, exposure to organochlorine pesticides (especially DDT) and human disturbance (Saurola 1997). In central Norway all known nesting sites were abandoned in the 1980s. Since the late 1990s the population has re-established naturally and at present the breeding population in our study area, the northern part of Trøndelag county, has grown to about 20 pairs (own unpubl. data).

Little is known about the migration habits and wintering-grounds of Ospreys breeding in Norway. To gain such information, we used GPS-based satellite tracking of Ospreys from this recently re-established population. Migratory behaviour and flyways of Ospreys breeding in northern parts of Europe have previously been studied in southern Sweden (Hake *et al.* 2001, Monti *et al.* 2018b), Scotland (Crawford & Long 2017, Mackrill 2017), Finland (LUOMUS 2018), Estonia (Väli & Sellis 2015) and north-western Russia (Babushkin *et al.* 2019). The aim of this study was to investigate whether Ospreys from our northerly study area use the same flyways as those previously tracked from southern Sweden (i.e., an area situated about 500 km southeast of our study area), or if they choose different migration routes and wintering areas. In addition, we document stopover sites, crossings of geographical barriers, wintering sites and repeated migratory journeys.

2. Material and methods

2.1. Tagging of nestlings

The Osprey nesting sites included in this study were all located within a radius of 50 km, in the north-eastern parts of central Norway (about 64°N, 13°E), close to the Swedish border. All nests were located at the top of Scots Pines (*Pinus silvestris*). In our study area Ospreys normally start breeding in the second half of May. When the nestlings (n = 8) were approximately 40 days of age, they were weighed to the nearest 50 g using a spring scale (Pesola 42500 Medio-Line, Switzerland), while wing and tail length were measured with a ruler to the nearest mm (Table 1).

The eight nestlings included in the study were from different broods that comprised two or three nestlings, and in each case the most developed nestling was selected for satellite tracking as we assumed they had greatest chance of fledging successfully. They were equipped with GPS-enabled solar-powered satellite transmitters (30-g Solar Argos/GPS PTT-100, Microwave Telemetry Inc. Columbia, Maryland, USA), programmed to take two GPS positions per day (the three 2007-birds)

Table 1. Sex, biometric measurements and date of last transmitter signal for eight juvenile Ospreys fitted with satellite transmitters in central Norway in 2007–2009.

Id.	Date of tagging	Sex	Body mass (g)	Wing (mm)	Tail (mm)	Date of last signal
49664	24 Jul 2007	Female*	1,850	315	120	20 Oct 2007
49665	27 Jul 2007	Male	1,600	285	125	12 Sep 2007
49667	01 Aug 2007	Male*	1,300	270	105	23 Dec 2007
81113	25 Jul 2008	Female	1,750	310	135	12 Dec 2008
81114	24 Jul 2008	Male	1,600	308	138	27 Sep 2013
81115	22 Jul 2008	Male*	1,350	245	95	28 Sep 2008
93559	27 Jul 2009	Female	1,700	340	145	25 Feb 2010
93560	21 Jul 2009	Female	1,550	285	110	25 Apr 2012

* Sexed based on biometric measurements according to Poole (1982, 1989).

or one position per hour between 05:00 and 22:00 (the other five birds). Transmitters were attached as backpacks using a harness made of 6 mm wide Teflon ribbon (Buehler *et al.* 1995). We used a loose fit to avoid wear on the skin during growth. The Teflon ribbon ends were secured across the upper part of the sternum with cotton thread, intended to degrade over time, so that the transmitter would eventually fall off. The weight of the transmitters was < 2% of the body mass of a fully grown nestling. All nestlings in the broods were ringed with a EURING (The Norwegian Bird Ringing Centre, Stavanger Museum) and a colour ring (year code) on the left leg, plus two colour rings on the right leg for individual recognition in the field. Total handling time was normally less than one hour.

2.2. Sex determination

A single feather was plucked from five of the eight nestlings for molecular sex determination. The tip of the calamus of each plucked feather was placed in a 2 ml Eppendorf tube, which contained 470 µl lysis buffer ATL (Qiagen, Hilden, Germany) and 30 µl Proteinase K (Qiagen). Feathers were digested overnight in an incubator at 56°C and pulse-vortexed twice during that period. Genomic DNA was extracted using the Maxwell® 16 Research System (Promega, Madison, WI, USA) and the Maxwell 16 tissue DNA Purification Kit following the manufacturer's protocol. Sex was determined using the Z-002D mark (Dawson 2007) that has recently been applied to sex Ospreys (Dawson *et al.* 2015).

Polymerase chain reaction (PCR) was performed with Qiagen's Multiplex PCR Kit following the manufacturer's protocol, but using 8.4 µl reaction volume. PCR products (1 µl) were mixed with 0.14 µl GeneScan 500 LIZ (Applied Biosystems, Foster City, CA, USA) size standard and 6.16 µl Hi-Di formamide following capillary electrophoresis on an ABI 3130xl Genetic Analyzer (Applied Biosystems). Allele sizes were assigned using GeneMapper v5.0 software (Applied Biosystems). A single band (127 base-pairs) was amplified in males and two bands (118 and 127 base-pairs) in females. For three of the nestlings we lacked feather samples to perform molecular sex determination. These were sexed based on biometric measurements (Table 1) according to Poole (1982, 1989).

2.3. Data analyses and mapping

Tracking data were provided by CLS Service Argos (Toulouse, France) once a month from August 2007 to September 2013, delivered on CD-roms (and were also available online on their webpage). The data were parsed using software delivered by the transmitter manufacturer into tab-delimited text-files and kml-files. Tracks were visually inspected using the kml-files in Google Earth, while the final maps were drawn using QGIS software v. 2.18.3TM (open source GIS).

The text files were imported into IBM SPSS v. 22 (IBM Corporation, Armonk, New York, USA) for statistical analyses. A SAS algorithm developed by D.C. Douglas, U.S. Geological Survey,

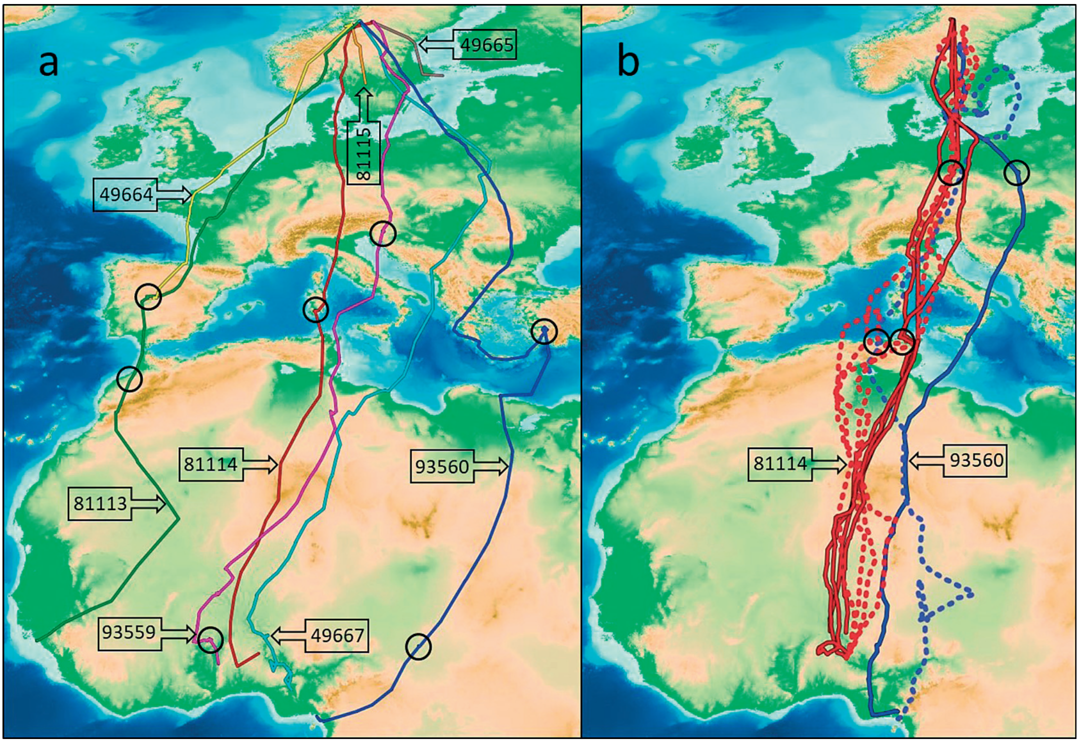

Fig. 1. Migration routes of Ospreys from central Norway. a) Southward migration routes of eight juvenile Ospreys. The routes of the different individuals are denoted with their individual codes, and circles denote stopover areas. Five of the Ospreys completed their migration to wintering sites in tropical Africa. b) Repeated migratory journeys of two of the Ospreys. Southward migration routes are indicated by solid lines and northward migration routes by broken lines.

AK, (http://www.movable-type.co.uk/scripts/latlong-vincenty.html) was rewritten into the SPSS command language to calculate distance between positions. In two cases, for males 49665 and 81115 during their initial migration, we used the less accurate Argos Doppler-based positions to determine their last positions and possible fates, since GPS positions were lacking for the last part of their tracks. Kernel density estimations (50% and 90%) of wintering home ranges were produced using the Spatial Analyst tool in ArcGIS 10.6.

3. Results

3.1. Pre-migratory movements

The median date of first flight (first position > 100 m from the nest) for the eight juvenile Ospreys (four males and four females) was 13 August (range: 8–22 August). Afterwards they stayed in the breeding area for a median of 33 days (range: 27–42 days). During this period, they only made short exploratory flights with subsequent returns to the nest sites. Median maximum exploratory distance recorded was 1.9 km (range: 0.3–5.6 km). Male 49665 had the lowest exploratory distance. His nest was located on a small islet, and he stayed close to the nest except for one excursion to the surrounding mainland. Median date of permanent dispersal (a movement from the nest of more than 1 km without subsequent return) for the eight Ospreys was 14 September (range: 5–26 September). From then onwards the flight was directed southwards.

3.2. First autumn migration

Three of the eight individuals either died or lost their signals during their first migratory journey

Table 2. Characteristics of first autumn migration of five juvenile Ospreys that completed the migration from nesting sites in central Norway to wintering sites in Africa.

Id.	Departure date	Arrival date	Wintering sites	Travelling days	Stopover days	Duration (days)	Distance (km)
49667	13 Sep	04 Oct	Nigeria	21	0	21	6,818
81113	17 Sep	12 Dec	Guinea Bissau	29	57	86	7,677
81114	12 Sep	19 Nov	Nigeria	23	45	68	6,950
93559	05 Sep	02 Dec	Togo	25	63	88	7,482
93560	15 Sep	16 Dec	Cameroon	35	57	92	9,543
Median				25	57	86	7,482

Table 3. Main stopover sites and durations of the stopover periods of juvenile Ospreys during their first autumn migration from breeding grounds in central Norway.

Id.	Stopover site in Europe/Asia	Arrival	Stopover days	Stopover site in Africa	Arrival	Stopover days
81113	Spain (40°N, 5°W)	28 Sep	45	Morocco (33°N, 7°W)	15 Nov	12
81114	Sardinia (39°N, 8°E)	21 Sep	45	–	–	–
93559	Slovenia (46°N, 14°E)	15 Sep	27	Ghana (11°N, 0°E)	26 Oct	36
93560	Turkey (37°N, 28°E)	02 Oct	37	Chad (10°N, 18°E)	07 Nov	20

(Id. 49664, 49665 and 81115), while five completed their migration to wintering sites in tropical Africa (Fig. 1, Table 2). Although they grew up near to one another, their migration routes differed (Fig. 1). Two individuals followed a westerly migration route, crossing the North Sea before they reached land in the UK and France, respectively. Afterwards they both headed for a stopover site in Spain where one individual (49664) disappeared shortly after arrival, having left a cluster of locations close to what appears to be a fish-farm near San Martin del Pimpollar in central Spain (Table 3). The other one (81113) crossed the Mediterranean Sea close to the Strait of Gibraltar and made a new stopover in Morocco. It then crossed the Sahara and finally reached a potential wintering site at the coast of Guinea Bissau. However, the terminal cluster of six locations from 12 December 2008 on a beach site could mean death.

Six individuals headed off for migration routes through central and eastern Europe (Fig. 1). Two of these lost their signals within three days after onset of migration, one in southern Sweden and one while crossing the Baltic Sea. The four remaining birds continued their migration through central and eastern Europe. Three crossed the Mediterranean Sea through or close to Italy. Then they moved across the Sahara and finally arrived at wintering areas in eastern parts of western tropical Africa (Fig. 1, Table 2). Female 93560 followed a more easterly migration route through the Greek islands to Turkey where she stayed for 37 days (Table 3). After crossing the Mediterranean Sea and the Sahara through Egypt and Chad, she arrived at her wintering site at the coast of Cameroon close to the Nigerian border (Fig. 1).

The five Ospreys that completed their first autumn migration travelled a median total distance (the cumulative sum of distances between GPS points) of 7,482 km (range: 6,818–9,542 km) and spent a median of 86 days on their journeys (range: 21–92 days, Table 2). The median travel distance was 120% longer than that of a straight-line between the start and end points (range: 112–143%). The journeys were composed of a median of 25 travelling days and 57 stopover days, and daily median distance covered for each individual during travelling days ranged from 264 to 324 km/day.

Different migratory strategies were evident for the five individuals. Four made use of a stopover period of 27 to 45 days before crossing the Mediterranean Sea (Table 3). Three of these individuals also spent a stopover period of 12 to 36 days in Africa, one before crossing of the Sahara and two right after (Table 3). Male 49667 travelled through Europa and crossed both the Mediterranean Sea and the Sahara without any stopover days and reached Nigeria only 21 days after departure from the natal area.

3.3. Wintering sites and repeated migratory journeys

We lost the signals from three individuals (Id. 49667, 81113 and 93559) within three months after arriving at the wintering site, while two individuals were tracked for a total period of 33 and 62 months respectively (Table 1). These two individuals enabled analyses of the size of the winter home range, and of repeated migratory journeys. After arriving at their wintering sites in Cameroon and Nigeria, respectively, they stayed for a period of 16 (female 93560, Cameroon) or 18 (male 81114, Nigeria) months. During this period, they spent their time in rather limited areas. The 100% minimum convex polygon area (MCP home-range) in the second year of life of female 93560, was approximately 200 km^2 and located about 20 km NW of Mount Cameroon, but the core area (50% kernel) was very restricted, only 2.13 km^2, while the 90% kernel area was 5.84 km^2.

Male 81114, the most successful bird in our sample, had his main wintering-ground at the Kainji reservoir on the Niger River. During the stay in his second year of life he moved up and down the shores somewhat and the total 100% MCP home-range was 15,290 km^2, but he spent most of his time in three core areas, with a total 50% kernel area of 52.3 km^2 and a 90% kernel area of 146.7 km^2. The same wintering area was used by male 81114 in five consecutive winters after repeated migratory journeys and also by female 93560 during her second and third winter in Cameroon. Although they were both feeding in rivers, they behaved quite differently during their stays in Africa. While the female (93560) showed very restricted movements in Cameroon, the male (81114) staying by the Niger River moved distances of more than 100 km along the river shore. A similar pattern was also evident after repeated migratory journeys. In May of the third calendar year both individuals initiated their first northward migration.

Female 93560 departed from Cameroon on 1 May, crossing the Sahara using three weeks, moving further north via Sardinia and central Europe to central Sweden for a summer stay about 250 km away from her natal area (Fig. 1). Due to several changes of direction she travelled a total distance of 11,400 km and spent 74 days on her journey. After a three-week stay in Sweden she returned to her wintering area in Cameroon, crossing central Europe, the southern tip of Italy and the Sahara from Tripoli to Cameroon, travelling a total of 7,660 km along her route.

Male 81114 departed from Nigeria on 20 May. After crossing the Sahara, he continued across the Mediterranean Sea and nearly reached Sardinia, before he abruptly returned to Africa and stayed at the Gulf of Tunisia for four months (Fig. 1). Not until the fourth calendar year (his second migration northwards) did he complete a migration back to the natal area, which he also did the following two years. The travelling distances were nearly identical (about 6,700 km) during the three northward migrations and he spent 28 to 32 days on these journeys.

During three successive southwards migrations he followed a route quite similar to the first autumn migration, using from 44 to 56 days. The travel distances of the repeated north- and southward migrations varied between 109% and 114% compared with a straight-line distance. He used the same general stopover area at the Gulf of Tunisia both during spring and autumn migration in the fourth and fifth calendar year, while in the sixth calendar year he migrated without stopovers. During repeated migratory journeys both individuals crossed the Mediterranean Sea between Africa and Italy, but not necessarily using island stepping-stones or the shortest water-gaps.

We lost the signals from male 81114 in Togo in late September 2013 on the journey back to the wintering area, after some months with signs of radio failure (Table 1). There was no sign of a breeding attempt on any of his returns to Scandinavia in summer. The signals from female 93560 disappeared abruptly in Cameroon in late April 2012, close to her wintering area, at the time when we expected her to start the second northward migration.

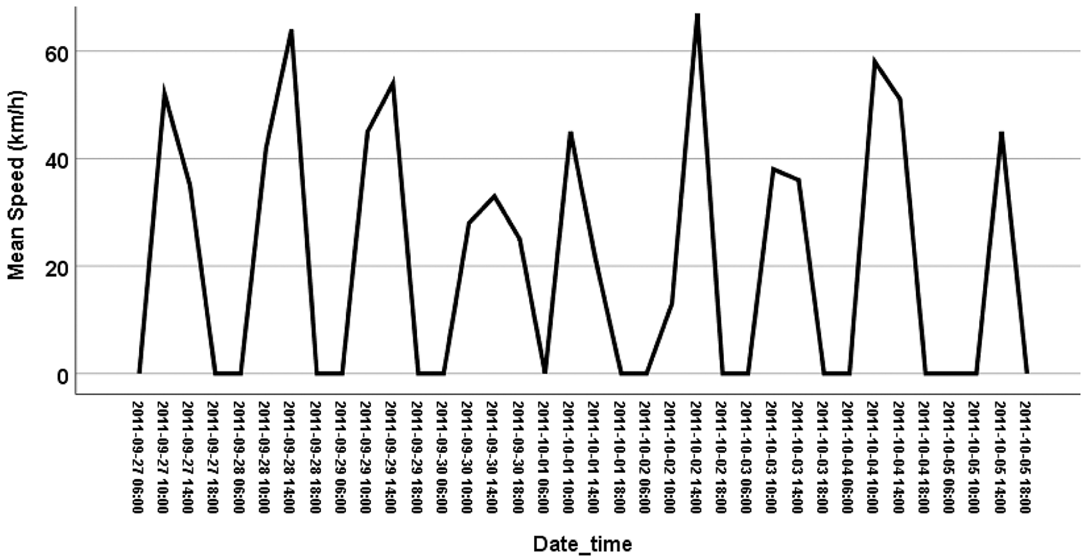

Fig. 2. During crossing of the Sahara the Ospreys showed a strict diurnal rhythm with movements during daytime and resting at night. This is exemplified by a nine-day trans-Saharan crossing of male 81114 during his southward journey in the autumn of 2011. The male was then in his 4th calendar year. Data are based on one position per hour between 05:00 and 22:00.

3.4. Crossings of geographical barriers

A total of 12 sea crossings lasting more than four hours were recorded for the juvenile Ospreys during their first autumn migration. Four of the sea crossings lasted between 14 and 24 hours and included a period of nocturnal flight. The longest distance of open sea crossing (1,025 km) was recorded for the male 49667 when crossing the Mediterranean Sea between Montenegro and Libya. The average speed during the 12 sea crossings, calculated as the distance travelled / time elapsed between GPS positions, varied from 28 to 58 km/h (median = 43 km/h). Distances travelled through the Sahara varied from 2,180 to 2,910 km (median = 2,635 km). These trans-Saharan journeys lasted from 130 to 229 hours and included a median of seven nightly stopovers. The average calculated speed (based on daily actual travel time) during crossings of the Sahara varied from 24 to 34 km/h.

Including repeated migratory journeys, we tracked a total of 20 sea crossings with a duration of 4 to 24 hours and 14 trans-Saharan journeys with a duration of 130 to 276 hours. During the trans-Saharan journeys, the Ospreys showed a strict diurnal rhythm with movements only during daytime (Fig. 2). Except for one individual that disappeared close to the shore of the Baltic Sea only two days after the onset of migration, none of the other Ospreys disappeared during crossings of geographical barriers.

4. Discussion

It has long been known that Ospreys breeding in northern Europe migrate on a broad front to wintering areas in tropical Africa (Österlöf 1977). During the last two decades, however, three main flyways have become apparent (Monti *et al.* 2018a). British Ospreys and the majority of Ospreys migrating from southern Sweden use a western flyway (Crawford & Long 2017, Mackrill 2017, Monti *et al.* 2018b). Most of the Ospreys from Finland migrate along a central European flyway (LUOMUS 2018), while those breeding in Estonia and north-western Russia use an eastern flyway (Väli & Sellis 2015, Babushkin *et al.* 2019).

Our results show that Ospreys from central Norway migrate along the western, central and eastern flyways through Europe, but point out the central one with crossing of the Mediterranean Sea via or close to Italy as the most important. Note that female 93560, which crossed the Mediterranean Sea from Turkey on her first southward migration, corrected the course to a more direct one during her second southward migration. A more direct route during the second southward migration indicates that she was able to correct her course with acquired experience. Surprisingly, only one of our birds crossed the Strait of Gibraltar. This would have been the shortest water-crossing on route to Africa, and is the path used by most Ospreys migrating from UK and Sweden (Crawford & Long 2017, Mackrill 2017, Monti *et al.* 2018b). The Ospreys in central Norway are breeding at a longitude east of those tracked from the UK and slightly west of those tagged in Sweden. A limitation of our study is the relatively low number of individuals tracked, so confirmation of the central flyway as the main route for Ospreys from central Norway requires further investigation.

Our study revealed considerable variation in the flyways and migratory pattern of juvenile Ospreys. A larger variability in orientation of juveniles compared with adults is a general pattern found in many species of migratory birds and experience seems to play an important role in shaping migratory decisions (Thorup *et al.* 2003, Newton 2007, Monti *et al.* 2018). Of the five individuals that performed a complete first autumn migration, the time spent on the entire migratory journey varied from 21 to 92 days, mainly due to the variance in the number of stopover days. One individual apparently just used a fly-and-forage strategy, while the others made one or two long stopover periods, probably for refuelling or to wait out bad weather. The distances travelled, use of stopover areas, and speed during traveling days were very similar to the results previously reported for Swedish Ospreys (Hake *et al*. 2001, Kjellén *et al.* 2001).

However, while British and Swedish Ospreys mainly use wintering areas from Gambia to the Ivory Coast (Crawford & Long 2017, Mackrill 2017, Monti *et al.* 2018b), Ospreys from central Norway seem to end up in more eastern parts of western tropical Africa i.e., from Togo to Cameroon (Fig. 1). Compared with juvenile Ospreys from southern Sweden, the onset of migration was delayed by about two weeks. This is likely due to the later breeding season in the more northerly breeding area where the lakes are generally covered with ice until late May or early June. Though our Ospreys grew up within a very restricted area, it is not surprising that their migratory routes fanned out widely across Europe.

A similar pattern has been reported in earlier studies (Hake *et al*. 2001, Vardanis *et al*. 2016), and even siblings from the same brood may show large variations in their flyways (Österlöf 1977). The stopover areas used by the juvenile Ospreys were mainly situated just before or immediately after crossings of geographical barriers (open sea, deserts or mountain chains). Stopover sites adjacent to geographical barriers are probably important to prepare the Ospreys for energy-demanding crossings (Dennis 2008). Interestingly, however, Hake *et al*. (2001) reported that most adult Ospreys tracked during their migration from Sweden had stopovers north of 45ºN. Whether this represent a distinction between adult and juvenile Ospreys migrating from Scandinavia remains to be shown.

Unfortunately, only two of the Ospreys in our study were tracked until their first northward migration. In accordance with previous knowledge they stayed in the rich tropics near equator until the spring of their third calendar year (Österlöf 1977, Dennis 2008). It has previously been assumed that Ospreys defend their territory at the wintering sites (Hake *et al*. 2001, Alerstam *et al*. 2006). Male 81114, in particular, conducted such extensive movements that it would be impossible for him to defend such a large territory. The fact that both individuals returned to the same wintering site after repeated migratory journeys suggests that Ospreys are faithful to the wintering site they establish during their first autumn migration. This is interesting because Ospreys tracked from Sweden have shown more variable flyways and scattered destination of juveniles compared to adults (Hake *et al*. 2001, Monti *et al*. 2018b).

Previous studies have tracked the migration of Ospreys from northern Europe but information about repeated migratory journeys of individuals tracked during their first autumn migration is very scarce. Although we only were able to track repeated journeys for two individuals, they contributed valuable information. Our results suggest that their migratory capabilities improve with experience, but the two individuals behaved quite differently. Male 81114 succeeded in finding a favorable course during the first southward journey and continued to use this flyway during his subsequent migrations.

Compared with the first autumn migration, however, he reduced the travelling time mainly by reducing the number of stopover days. Female 93560, which corrected her course during the subsequent migratory journeys, showed some erratic movements during her first northward migration. In particular, when passing through the Sahara and when reaching the Baltic Sea, she made several changes in direction and thus made a total journey of more than 11,000 km. Whether this was caused by navigational problems remains unknown. While the female returned to Scandinavia during her first northward migration, the male made a four months summer stay at the Gulf of Tunisia. We expect that the male also intended to return to Scandinavia. However, he apparently encountered problems during crossing of the Mediterranean Sea because just before arriving at Sardinia he suddenly turned and returned to the Gulf of Tunisia. This area was later used as a stopover site during several subsequent spring and autumn migrations, indicating that some of the patterns shown by migrating Osprey are shaped by random events.

The high fidelity of Ospreys to wintering and stopover sites is probably related to their strictly piscivorous feeding behavior; areas rich in available fish are crucial to refuelling and survival. Other groups of Palearctic-Afrotropical avian migrants, relaying on food resources that are more variable in time and space, show less fidelity to the wintering and stopover areas (van Wijk *et al.* 2016, Vardanis *et al*. 2016).

Most large raptors avoid long sea crossings because they get easily exhausted when they have to sustain flapping flight for a prolonged period (Newton 2007, Bildstein *et al*. 2009). Several of our Ospreys performed long distance sea crossings that also included periods of nocturnal flight. Numerous studies during the last two decades have shown that this is a normal behavior for migrating Ospreys, which distinguishes them from most other raptors (DeCandido *et al.* 2006, Horton *et al*. 2014, Väli & Sellis 2015, Duriez *et al*. 2018). Recently, it has been demonstrated that Ospreys are able to use thermal uplift to accomplish periods of soaring-gliding flight during such sea crossings (Duriez *et al*. 2018).

Nevertheless, the Sahara crossings are probably the most energy-demanding tasks Ospreys face during migration to tropical Africa. The Sahara crossings, lasting a median of 9 days, involve flying through the most arid and hot landscape on earth. The prospects of finding food, let alone water, is almost non-existent during these journeys. Obviously, as shown in Figure 2, active flying is done during the day, while they rest during night. This is probably a strategy to prevent energy-expensive flapping flight because conditions for thermal soaring and gliding should be ideal. The distances travelled and time spent during crossings of the Sahara are well within the energy expenditure capacity of Ospreys as calculated by a fasting migration model (Candler & Kennedy 1995).

From a conservation perspective, information on mortality in migratory birds is a principal question (Klaassen *et al*. 2014). Earlier studies have shown that crossing of the Sahara represents a substantial cause of death for juvenile Palearctic-Afrotropical migratory raptors (Strandberg *et al*. 2010). Six of the eight Ospreys included in this study disappeared within eight months of tracking. We were not able to exactly decide whether this was caused by transmitter failure or death of the birds. However, we believe the majority of these individuals died since we had no prior indications of transmitter failure for any of these birds. Interestingly, none of our birds disappeared during a total of 14 trans-Saharan journeys. We lost the signals from two of the individuals only three days after onset of migration and the fate of these birds are unknown. The individual that got lost in Spain might have been a victim of illegal killing since it apparently was staying at a fish farm at the time it disappeared. Three individuals disappeared shortly after reaching the wintering sites in Africa. This points to that period as a critical phase of life for juvenile Ospreys, maybe because they are not able to find a suitable wintering site. However, illegal hunting has also been pointed out as a possible danger in tropical Africa (Klaassen *et al*. 2014).

The flyways and final destinations of juvenile Ospreys during their first southward journey must be guided by their genes and an innate compass, but also seems to be affected by stochastic events such as the weather conditions they encounter (Thorup *et al.* 2003, Monti *et al.* 2018b). Their strong fidelity to stopover and wintering sites during subsequent migratory journeys shows that their migration also involves a good memory, which enables them to recognize areas visited in previous years. Due to their migration on a broad front and their flexibility in choices of stopover and wintering sites, we expect the Osprey to be among the species of Palearctic-Afrotropical avian migrants that will be relatively resilient to global climatic changes. Their capacity to cross geographical barriers also implies they could be able to cope with increased desertification in the Sahara-Sahel region.

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Norjalaisten kalasääksien muuttoreitit

Lintujen muuttokäyttäytymisessä on huomattavaa lajinsisäistä vaihtelua, johtuen muun muassa iästä, sukupuolesta ja lähtöpopulaatiosta. Me selvitimme nuorien Keski-Norjan kalasääksien (8 lintua) muuttokäyttäytymistä GPS-paikantimien avulla. Muuttoreitit levittäytyivät laajasti Euroopan halki, ja muuttokäyttäytyminen vaihteli yksilöiden välillä.

Viisi kahdeksasta kalasääksestä saavutti talvehtimisalueet Afrikassa ensimmäisenä vuotenaan. Ne taittoivat matkaa keskimäärin 7,482 km, 21–92 päivässä. Mediaani muuttomatka oli 120 % pidempi kuin suoraviivainen etäisyys. Levähdyspaikat sijaitsivat juuri ennen tai jälkeen maantieteellisten esteiden. Muuttomatkan pituuden vaihtelua selitti eniten levähdyspäivien määrä. Kahdelta yksilöltä saatiin kerättyä myös aineistoa niiden pohjoiseen suuntautuvalta muutolta (3. kalenterivuosi).

Yhteensä keräsimme aineistoa 20 merenylitykseltä (kesto 4–24h) ja 14 Saharan autiomaan ylitykseltä. Neljässä merenylityksessä havaittiin myös yöllistä muuttoa. Saharan ylitys kesti 130–276 tuntia, ja ylitys tapahtui aina päivällä. Keräämämme aineisto, joka sisälsi samalta yksilötä useita muuttomatkoja, osoitti että kukin kalasääksi käytti toistuvasti samoja talvehtimis- ja levähdyspaikkoja. Keski-Norjan kalasääkset siis muuttavat laajasti Euroopan halki, mutta pääosa muuttoreiteistä keskittyi Keski-ja Itä-Eurooppaan, ja talvehtimisaluueet länsi-Afrikan itäosien trooppisille alueille.

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